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THE PRODUCTION OF BORDERED PITS ON THE TANGENTIAL WALLS OF PICEA SITCHENSIS TRACHEIDS

by

M. P. Denne and N. Ledsham

In most coniferous woods, bordered pits usually occur on the radial walls of the tracheids. But in many species they are frequently found on the tangential walls of the last few rows of tracheids in the latewood (Greguss, 1955; Panshin, de Zeeuw, and Brown, 1964), the number of tangential pits increasing up to a maximum in the double wall between the last row of the latewood and the first row of the earlywood. More rarely, tangential pits also occur sporadically in the first few rows of the earlywood in Picea abies (Laming and ter Welle, 1971), Picea sitchensis (Greguss, 1955), and the southern pines (Howard and Manwiller, 1969). Laming and ter Welle (1971) suggested that these tangential pits developed in tracheids that had overwintered as xylem mother cells.

What determines the change in the position of the bordered pits from the radial to the tangential walls? Their position is not likely to be associated with the thickness of the secondary wall, since the microfibrillar structure characteristic of bordered pits has been recognized in the later stages of primary wall formation (Imamura and Harada, 1973, in Pinus densiflora). Possibly the change in position may be related to the decrease in radial tracheid diameter towards the end of the latewood, or it may be determined by chemical or physical changes associated with the approach of cambial dormancy.

These last two possibilities have been explored in wood from 7-year-old Picea sitchensis. Figure 1 compares the number of tangential pits in the last four rows of latewood with that of tracheids of similar radial diameter in drought rings. These data are means from eight trees, the number of pits in the tangential walls being shown as a percentage of the total number. In tracheids of the same radial diameter, tangential pits were far more frequent in latewood than in drought rings; thus in tracheids of 9-10 μm radial diameter, 90% of the bordered pits of the latewood tracheids were on the tangential walls, while in tracheids of the same radial diameter in drought rings only 10% were on the tangential walls.

This suggests that the position of the pit is not determined by radial tracheid diameter alone. Hence it seems likely that the change in pit position is associated with the onset of cambial dormancy. Possibly this may be used for the distinction of “false” growth rings from “true” growth rings. It should also be useful as an indicator of the approach of dormancy in cambial development work.

It would be interesting to know if there is a functional advantage in the change in pit position at the end of the latewood. Possibly this may be related to the ease of liquid flow between the latewood and the differentiating earlywood tracheids when the cambium is reactivated after dormancy.

References


Legend to Figure 1
Number of tangential bordered pits as a percentage of the total number in the latewood and in drought rings of Picea sitchensis. Arrows show limits of least significant difference at P=0.05.
THE DEVELOPMENT OF MICROSCOPIC SEPARATIONS IN RED PINE AND WHITE SPRUCE

by

G. Chauret and E. Perem1

Abstract

Differences were observed in the nature of microscopic separations caused by seasoning in red pine (Pinus resinosa Ait.) and white spruce (Picea glauca [Moench] Voss.) The parenchyma cells of the sapwood of red pine with their thin, incompletely lignified walls contract and shivel in seasoning, creating long radial separations throughout the sapwood. No such separations occur in white spruce, a fact that may explain certain differences in the way in which seasoning influences some wood properties of the two species.

Introduction

The principal direction of stresses which develop in wood across the grain during seasoning is determined by the difference in the shrinkage potential of wood in the tangential as compared with the radial directions. The approximately two-fold shrinkage capacity in the tangential direction of the ray parenchyma cells, with the cell, and radial direction causes the development of tensile stresses at right angles to the rays. These stresses are normally released through formation of separations in the plane of the rays. Radial checks are usually prominent in seasoned roundwood and in timbers containing the pith. In pieces of wood that do not contain the pith, the visible signs of release of seasoning stresses across the grain are usually limited to distortion of the shape of the cross-section of the piece without the presence of major checks. Nevertheless, such pieces of wood develop radial separations because of stresses which exist during the early stages of drying as a result of moisture gradients in the piece. These stresses are classified as transient (Schniwied 1960) because in slow, set-free, drying, they tend to become insignificant after a uniform moisture content has been reached in a piece of wood. Under such conditions the visible checks which formed earlier, close. The mechanisms involved in the development of different types of seasoning stresses and the associated formation of checks in wood have been discussed in detail by Schniwied (1960, 1963). He states that the checks are formed either in the prosenchyma next to rays or within the rays.

Microscopic separations between prosenchyma and rays were observed by Hale (1957) to be usually restricted to the dense summerwood portion of annual layers.

The selection of the two species—red pine and white spruce—as test material for the present study was prompted by evidence that changes induced by seasoning affect pine differently from spruce. For example, while both pine and spruce are readily treated with water-borne preservatives when the wood is freshly cut, their treatabilities with oil-borne preservatives vary, air dry differ. Sufficient penetration of preservative into air-dry spruce sapwood is easily achieved by pressure treatment, but air dry spruce sapwood is practically impervious to oil-borne preservatives.

Materials and Methods

Green (unseasoned) white spruce (Picea glauca [Moench] Voss.) and red pine (Pinus resinosa Ait.) were collected. Blocks, 25 mm long x 19 mm square in cross section were either air-dried under room conditions or overried overnight at 104°C. To observe the characteristics of the separations which developed in drying, specimens were split tangentially and radially. Two-stage replicas of the surfaces were examined in a Philips 100 electron microscope. Surface observations were also made in an incandescent lamp with a stereo microscope. Sections (1-2 m), both radial and tangential, embedded in Spurr's low viscosity embedding medium, were examined with a compound microscope.

Results and Discussion

Over four hundred microscopic separations that had formed in test blocks in storage or in seasoning, as a result of stresses due to moisture gradients, were examined. In both species all microscopic seasoning checks initiated in the latewood in the vicinity of the rays, mostly in the region between the rays and the longitudinal elements (Fig. 1). They developed mainly along uniseriate rays, although they were also seen fairly frequently in fusiform rays (Fig. 4). The majority of the separations observed were contained within the width of the summerwood band. Occasionally the separations extended into the springwood and progressed through several annual layers.

Examination of the surfaces of radial separations by the replication technique showed that the separations had initiated in the primary walls of the ray cells. Occasionally, however, the break deviated from the primary wall of the ray cell into the middle lamella between the ray and the adjacent prosenchyma cells (Fig. 2). In some instances, the break extended across the cell walls of the ray cells (Fig. 3).

Separations which developed at the ray/prosenchyma interface sometimes extended beyond the ray-contact area. Such separations between tracheids tended to be located in the primary wall (Fig. 5). The separations extended only occasionally into the S1-layer of the secondary wall. In red pine, the separations usually did not extend longitudinally a great distance beyond the ray-contact area, but stopped in the vicinity of another ray (Fig. 6).

A specific type of microscopic separation was found to occur in the sapwood of red pine, different from the microscopic seasons checks described above. In that it formed exclusively within the rays, both in earlywood and latwood. As a result, in pine sapwood, numerous fine separations having their long axes radially across the grain perforated the sample from one face to the other (or to the heartwood boundary). These separations formed when the thin-walled ray parenchyma cells of the sapwood of red pine shrank and collapsed in drying (Fig. 7 and 8). The anatomical characteristics believed to be responsible for these microscopic separations in red pine are the thinness of the walls of the ray parenchyma cells and the lack of lignification of these walls in the sapwood. Balatinecz and Kennedy (1967) demonstrated that, unlike other confers, lignification of the ray parenchyma of hard pines with window-like pits, such as red pine, is generally delayed until heartwood formation. Even then lignified ray parenchyma cells may still occur deep in the heartwood zone.

The foregoing observations on the development of separations in wood tissue were always associated with seasoning. To observe whether or not separations could develop in green wood kept wet, samples of unseasoned red pine and white spruce stored in water in gallon jars at 2°C for a year were examined for separations. It became apparent that the parenchyma cells in the sapwood of red pine were severely affected by bacteria during the prolonged water storage. A large proportion of the ray cells were either collapsed or completely disintegrated (Fig. 9). No such effects were seen in spruce. However, it has been reported (Unligl 1971) that water storage under conditions favorable to bacterial attack can result in the destruction of some ray parenchyma cells in the peripheral zones of spruce sapwood. It is apparent that the permeability of wood to liquids and gases can be significantly increased by the Oliver cells, and the creation of microscopic radial channels in wood, since every longitudinal tracheid is in contact with several rays. Widespread observations on the improved treatability of pine wood water-driven or stored in water date back several decades, the studies of Ellwood and Ecklund (1959) were probably the first to establish that the cause of this increased porosity originated from bacterial attack. Studies by Knuth and McCoy (1962), Lies and Korph (1968), and Greaves (1971) have subsequently provided more information on the effects of bacterial activity on wood structure.

Conclusions

During the early stages of seasoning, radial separations develop in wood due to stresses which result from moisture gradients. The majority of these checks are small and close when equilibrium moisture content is reached. Such checks, which remain recognizable under a microscope as fine separations, develop both in white spruce and red pine.

Another type of microscopic separation, observed to occur in red pine sapwood, develops in seasoning when the thin-walled un lignified ray parenchyma cells shrink and collapse. The presence of such radial checks in the wood of red pine air dried in white spruce, might explain some of the differences in the behavior of air-dry wood observed between the two species and particularly, the good permeability of air-dry red pine. Observations on the effect of certain storage conditions not involving seasoning indicated that similar microscopic separations in wood tissue may develop in green wood in water storage due to ray parenchyma collapse or disintegration as a result of bacterial action.

Literature Cited


Figure 1. Light micrograph of transverse section, showing a microscopic seasoning check between ray cells and tracheids. White spruce 160x

Figure 2. Electron micrograph showing a separation through the middle lamella and the primary wall of a ray parenchyma cell. (Arrow indicates ray cell direction.) White spruce, radial plane, 22,800x

Figure 3. Light micrograph of a tangential section, through a microscopic seasoning check, showing broken ray cells (Arrowheads). White spruce 780x

Figure 4. Similar to Figure 3, showing a separation through a fusiform ray. White spruce 400x

Figure 5. Electron micrograph showing a separation in the primary wall of two tracheids. White spruce, radial view 9900x. (Arrow indicates fiber direction.)

Figure 6. Similar to Figure 3, showing a microscopic seasoning check extending from the surface, (large arrow). Small arrows indicate seasoning checks that developed subsequently in response moisture gradients. Red pine incident light, 55x

Figure 7. Light micrograph showing voids (arrows), created by the contraction and collapse of parenchyma cells in seasoning. Red pine, tangential section 230x

Figure 8. Similar to Figure 7, showing severe shrinkage of the ray parenchyma cells after seasoning. Red pine tangential section 590x

Figure 9. Light micrograph showing a ray with destroyed parenchyma cells. Red pine 750x

R=ray P=primary wall ML=middle lamella
THE EXTERIOR MORPHOLOGY OF VESSEL ELEMENTS

by
W. N. Audenaert and F. W. Taylor

Introduction
The exterior surfaces of vessel elements are difficult to observe. Thin-walled vessels with their large lumens represent an area of weakness, hence split or cut longitudinal sections seldom expose exterior vessel walls. Maceration does expose exterior walls, but the limited depth of field of light microscopes and light interference by structures on inner walls make imaging of exterior wall sculpturing difficult.

Methods now available for drying vessels without large drying stresses that cause cell collapse, coupled with the scanning electron microscope's large depth of field allow views of exterior vessel morphology not previously possible (see photographs).

Procedure
Hardwood blocks may be macerated by numerous procedures (3). The method used to prepare samples for this study was a modification of Franklin's method (2). After saturation in water, small wood blocks were macerated in a 50-50 mixture of glacial acetic acid and 30 percent hydrogen peroxide for 48 hours at a temperature of 50°C. A slurry of macerated tissue about one-eighth inch deep was placed in a Stender dish and observed with a dissecting microscope. Fibers and other unwanted wood elements were teased away from vessel elements with dissecting needles. Vessel elements were then transferred by a pipet to a grid holder. Vessels (contained in the grid holder) were then carried through a graded series of ethanol and critical-point dried in a Bomar EX900 drier, with carbon dioxide used as the transitional fluid.

At the critical point no interface exists between the liquid and vapor phase, hence no surface tension forces are present. Critical-point drying is a process involving saturating a material with transitional fluid, placing it in a pressure cylinder, heating it until the critical point of the fluid is reached, and then bleeding the fluid off as a vapor. For a detailed review of the physics of critical-point drying see Barstyn (1).

After drying, vessel elements were mounted on double-stick tape coated stubs by three methods:
1. Transfer of a 200-mesh grid, upon which vessels were originally deposited in the grid holder, directly to the stub without disturbing the vessels.
2. Inverting the grid upon which vessels were dried and shaking dried vessels directly to the tape coated stub surface.
3. Transfer of lens paper (used as a grid during drying) bearing vessel elements directly from the grid holder to the stub surface.

Method 3 is the easiest to use. However, the fiber background is least desirable for viewing and photographing. Prepared stubs were coated by vacuum evaporation using an initial carbon coat with final coat of 60:40 Au/Pd. Sputter coating was also used. Both methods produced good results. Examination was with a Hitachi HHS-2R scanning electron microscope.

Results
The micrographs illustrate the usefulness of critical-point drying and scanning electron microscope viewing. The procedure shows much promise as a method for the examination of cellular wood elements. The exterior surface of wood elements is clearly visible. Interpretation of some features is enhanced since only one surface and one side of the cell wall is visible.

Literature Cited
A. Vessel element of Betula algephaisensis Britton, 300 X magnification. Note the impressions in the cell wall where the vessel segment was in contact with other cells.

B. A portion of photograph "A", 525X magnification, showing pitting in areas where the vessel element contacted ray cells.

C. Vessel element of Ulmus americana L., 300X magnification. Pitting of ray contact area and tyloses are distinct.

D. Vessel element of Ulmus americana L., 375X magnification.

E. Vessel element of Frazinus americana L., 340X magnification.

F. Vessel element of Quercus falcata Michx., 325X magnification. Areas of contact with ray parenchyma and vasicentric tracheids are identifiable.

G. Vessel segment of Juglans nigra L., 225X magnification. Zones of pitting between vessel elements and longitudinal elements (probably paratracheal parenchyma) are quite evident.

H. Vessel element of balsa (Ochroma sp.), 225X magnification. Contact with other longitudinal cells results in distinctive vessel wall markings.

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BOOK REVIEW


Ecological Strategies of Xylem Evolution is not a textbook or a standard work of reference; it is an essay by Dr. Carlquist reinterpreting the anatomy of xylem in terms of functional adaptation during its evolution in the different major groups of vascular plants. Functional and ecological wood anatomy have admittedly received more attention in recent years than previously, but we must credit Dr. Carlquist with being the first radical pioneer approaching wood anatomical diversity comprehensively from a Neo-Darwinistic angle.

In his introduction the author gives a clear outline of what is to come: "the keys to xylem evolution that have not been appreciated hitherto are primarily in the following areas: adaptation to degree of moisture availability and transpiration rate; fluctuation in moisture availability; and requirements for mechanical strength.

A lucid and critical survey of the morphological aspects of xylem evolution as established by the Bailey school followed by physiological and ecological considerations provides the reader with a good background understanding the next chapter, in which Carlquist reinterprets xylem evolution in ecological and functional terms for Pteridophytes (ferns and others; living and fossil), Cycads and Ginkgo, Conifers and Taxads, Monocotyledons, Gnetales and Dicotyledons. There are also chapters on stelar types and extrasympy tissue.

For the readers of this Bulletin, a discussion of the chapters on the wood of Conifers, Taxads and Dicots is perhaps the most interesting. For Conifers and Taxads Carlquist finds a very clear positive correlation between plant size and tracheid length. This, in his opinion, can be explained by the fact that longer tracheids provide greater strength, necessary for big trees and heavy branches. According to him this is supported with reports in the literature that ecological factors such as increased aridity, increased altitude, or the stunning effects of winds result in decreased tracheid length, since these factors also result in reduced plant size. However, I find it curious that the shorter tracheids in wind-swept stunted trees have not induced Carlquist to criticize his own mechanical explanation of the tree-size/tracheid-length correlation. According to this hypothesis one would expect these exposed plants to have very long tracheids in order to resist the external forces. In general, the tracheid characters are said to be governed by three major factors: resistance to negative pressures, which may result in narrow tracheids in xeric species like junipers; mechanical strength for self-support of large trunks and branches; and area of tracheid overlap and its pitting, which determines conductivity. A number of examples is presented to substantiate these claims. Carlquist rightly does not limit himself here (or elsewhere) to wood anatomical considerations only, but also includes some leaf anatomical and root physiological data in his discussion.

For the Dicotyledons there are separate chapters on vessels in genera, on dicots with primitive vessels (these are more or less compared with Gnetales), and on the more specialized majority. The vessels' condition in some broad-leaved dicots calls for conditions of moist soil and minimal transpiration, and according to Carlquist all vessels in dicots have an ecology complying with these requirements. The same is said to hold true for dicotyledons with primitive long vessel members with scalariform perforation plates. This claim is substantiated by examples from different floral regions and by a general survey of all dicots with scalariform perforations. All arguments together are rather convincing, but the attempts of Carlquist to explain the exceptions to the rule in terms of special adaptive significance (e.g., mangrove plants to the Rhizophoraceae) appear to me highly artificial and inspired by wishful thinking. The heavy bars to the vessel perforations of the mangrove Rhizophoraceae are thought to have stopped collapse at times of high negative pressure in the xylem due to high transpiration rates during periods of strong illumination. It is in this and other instances that Carlquist's approach of fantasy begins to show, because it is hard to believe that the thick-walled vessels would benefit more from the thick bars of a simple perforation than from a thick circular perforation rim of a simple perforation. Moreover, it seems most unlikely that in such elements extra constructional devices are at all necessary to prevent collapse. The same criticisms are valid for Carlquist's functional and mechanical interpretation of Magnoliaceae or Lauraceous heavy or vestigial bars in their perforation plates.

In referring to latitudinal trends in vessel characteristics, Carlquist displays some interesting inconsistencies in interpretation of data from the literature. The paucity of representatives in the tropical lowland species is interpreted by Carlquist as a consequence of rapid change in temperature and aridity and resistance to wind thrust and area of tracheid overlap and its pitting, which determines conductivity. A number of examples is presented to substantiate these claims. Carlquist rightly does not limit himself here (or elsewhere) to wood anatomical considerations only, but also includes some leaf anatomical and root physiological data in his discussion.

However, with the same ease, my findings in lix that temperate species have fewer bars per perforation plate than the tropical lowland species are interpreted by Carlquist as a consequence of rapid change in temperature and aridity and resistance to wind thrust and area of tracheid overlap and its pitting, which determines conductivity. A number of examples is presented to substantiate these claims. Carlquist rightly does not limit himself here (or elsewhere) to wood anatomical considerations only, but also includes some leaf anatomical and root physiological data in his discussion.

The shortening of cambial initials in the course of phylogeny is "explained" by the presumed adaptive value of short vessels to resist high negative pressures, and the increased intrusive growth of the imperforate cambial derivatives is said to safeguard the mechanical strength of the wood as a whole. The functions and adaptive significance of specialization in axial and ray parenchyma are also discussed. Most interesting is the application of the adaptive interpretation of mainly vessel characters to the wood anatomy of species of various ecological types and growth forms. Vines and lianas, stem succulents, desert shrubs, annuals, rosette trees, parasites are compared with mesophytes and shown to exhibit xylem characteristics most advantageous (according to Carlquist) for their specialized ecology, habit and physiology. The paedomorphosis theory is restated and now explained in terms of "release from mechanical strength" resulting in deviating length on age curves for the cambial derivatives.

After reading Dr. Carlquist's new book twice, I cannot help feeling confused and incapable of judging the scientific value of all individual suggestions. Some objections to the general approach should, however, be made. Carlquist's view of xylem evolution is based on the belief that natural selection has caused tissue and cell characteristics to be optimally suited to physiological and mechanical demands of the plant species involved. No structural feature escapes Carlquist's interpretative mind, and the wood anatomists of diverse groups are thus "explained" (using Carlquist's own word). However, in xylem evolution and plant evolution in general we must, I think, admit that a great diversity of structures is capable of functioning perfectly well under the same ecological conditions. In other words, numerous structural modifications arisen in the evolution through random mutations apparently pose no limiting factor on the physiology of the plant as a whole. As a logical consequence of this I would expect numerous wood anatomical features to escape all attempts of functional or adaptive interpretation. No wonder that several of Carlquist's suggestions seem artificial and strained. Part of this is, of course, also due to the paucity of physiological and of ecological, sometimes even of anatomical data, which Carlquist fully admits. Part of the artificiality (as subjectively experienced by me) on the other hand is due to the many ways in which it is possible to interpret a certain wood as either perfectly adapted to comply with water conduction demands or with mechanical demands. All elements of controversy are hidden in the wood itself in the most literal sense! The trouble is that with our present knowledge we have no means of telling which structural aspects of the plant's anatomy become limiting in determining the survival of a certain species.

In his chapter on axial and ray parenchyma, Carlquist notes that a functionally adaptive interpretation of evolutionary patterns "obviously requires a preposterously complex synthesis." I am convinced that the interpretation of vessel and fiber characteristics in combination with all other structures (roots, nodes, leaves) involved in water conduction and mechanical functions requires an equally preposterously complex synthesis—taking for granted that enough data for a compulsory complex analysis prior to this would be available. The confusion in the reader's mind will also be due to the fact that many of Carlquist's generalizations are based on small groups of genera or merely on individual examples. After some careful consideration it will probably be easy enough to find examples providing conflicting evidence and negating Carlquist's suggestions.

Instead of ending this review in the negative, I should stress that the book as a whole is most stimulating, thought provoking and inspiring for anyone interested in wood anatomy. Subsequent research may appear to support several of Carlquist's ideas. Carlquist has accepted the challenge of integrating physiological, ecological and anatomical data at this stage of scanty information. We must admire him for this heroic effort, but we must also realize that it is a preliminary progress report in a field which can also be approached from angles, other than the natural-selection-through-survival-of-the-fittest philosophy.

Pieter Baas
WOOD ANATOMY ACTIVITIES AROUND THE WORLD
Changes in the Identification of Herbarium Vouchers of Wood Samples of the Stahel Wood Collection (Suriname)

by Alberta M.W. Mennen

In 1948 Dr. C.J.H. Amshoff published an “Enumeration of the herbarium specimens of a Suriname wood collection made by Professor G. Stahel,” followed in 1950 by a 4-page supplement. In later years, many names in this enumeration have had to be changed largely as a result of taxonomical revisions of families or genera. No longer being able to keep track of the numerous institutions all over the world where the Stahel collection of woods is to be found at present, I much appreciated Professor Cfit’s approval of my suggestion to prepare a list of all changes to be published in the IAWA Bulletin in order to reach all curators of wood collections interested in having their specimens correctly labelled.

1. Apodytesa margaritaeformes Woods.
2. Neolunca angleri (Eyma) Aubrev. and Pellegrin
3. Liria cayanensis (Meisn.) Koster.
4. Anisocarpa guineensis (Aubl.) Huber
5. Herbarium in a mixture of Dikarya paniculata and Schizophyllum Compact Reuter
6. Schlottia guineensis Bentham var. guineensis
7. Neolochos robus Mart. and Eichl. Aubrev. and Pellegrin
8. Trebouxiella hirsutiflora Mart.
9. Cavaleria multiflora (Smith) Eyma
11. Schottia tetragona (DC.) Morley
13. Cavaleria multiflora (Smith) Eyma
14. Qualis isidii Ducru
15. Licinia atrodes (Hoffm. ex R. and S.) O. Ktze
16. Morentozae specified (Ducke) Kilip
17. Apodytesa albus (Vahl) R. Ben.
18. Hirtella hirtella (Mart. and Zucc.) var. pubescens Ducru
19. Helicteris leonensis (P. and E.) Roxby
21. Some wood samples Alchornea trinera Lam.
24. Sunfloweria aegyptia (Sandw.) Aubrev. and Pellegrin.
25. Braunea perisiotia Ducru ssp. perisiotii Ducru
27. Tapura capitulata Baill.
28. Nyctelis dava (Eyma) Aubrev. and Pellegrin
29. Nyctelis cauliflora (Sandw.) Aubrev. and Pellegrin
30. Licinia cayanensis (Meisn.) Koster.
31. Coixolliella acuta A.C. Smith
32. Marapintus poriferum (Amsh.) Knoeppen
33. Cavaleria guineensii Aubl.
34. Licinia hypoloma B.th.
35. Apodytesa albus (Vahl) R. Ben.
36. Pseudos robus Bent.
37. Neolochos robus Mart. and Eichl.
38. Myrtis perpusilla (Desv. ex Ham.) Nied.
39. Castelinae ingens Bentham
40. Tympanytum senescens Ducru
41. Guiera guineensis (L.) C. Rich.
42. Chrysobalanaceae. Without voucher.

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8Botanical Museum and Herbarium, State University of Utrecht, Wood Anatomy Section