

Secondary Tree Growth Increments: Ring Development & Forms

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Trees attempt to occupy more space and control available resources through cell divisions and cell expansion. From the end of a shoot tip to the end of a root tip, trees elongate. Along this axis of growth, trees also expand radially, which is termed "secondary growth." Tree growth is initiated in the shoot tips (growing points / buds), root tips, vascular cambium (i.e. or simply cambium), and phellogen which generates the periderm.

The first two meristems are primary generation systems and the second two are termed secondary meristems. Cambial activity and xylem formation, visible as increases in growth increment volume, is radial growth, and reviewed here. The secondary meristem phellogen, sometimes generically referred to as the cork cambium, will not be discussed here although it does increase tree diameter.

Cambium

The cambium is a cell generation zone which blends (within several cell thicknesses) inward into the xylem (wood) and outward into the phloem (inner bark). The cambium occupies the circumference of the wood cylinder which comprises the bulk of a tree. The cambium is responsible for modifying cell divisions, cell forms, and cell wall materials in response to mechanical, biological and defensive stresses at each point along its surface. The cambium receives signals from sensors both internally (from dividing and expanding cells in the cambial zone) and externally (located locally farther inside and outside the cambium, and from shoot tips and root tips.)

A tree radially expands tissues as shoots and roots elongate. Every growth period (caused by rain/dry, warm/cold, or dormant/active timing) initiates coordinated longitudinal and radial expansion of woody tissues. This sheath of newly produced and expanded tissue acts as a base for all subsequent growth. Trees grow upward and outward in a layer-upon-layer pattern. From shoot tip to root tip, this sheath of living tissue is expanded, made functional, and used for transport of resources, structural support, storage of resources, and defense. Cones

The growth layers within a tree can be visualized in a simple form by use of conical shapes for growth increments. As trees elongate and expand (grow), a new layer of xylem (a three dimensional elongated hollow cone) is build upon the immediate past layer of xylem. This process over many growth periods generate "nested" or "stacked" cones of growth. These sacked cones of growth found running from one end of a tree to the other end, are of different radial thicknesses due to differing amounts of resources available and surface area of the last growth cone.



Especially in the temperate zone, growth cones in trees can be visually separated from one-another by various changes in cell form from one growth increment to the next. The last cells produced in one growth increment may be significantly different than the first cells produced in the next growth increment. The changing appearance across one, and between two adjacent, growth increments throughout a tree give rise to unique anatomical traits used for wood identification as well as providing a variety of patterns and grains in the wood when cut.

Rings

If you stack and nest a series of hollow cones on top of one-another, the whole collection becomes taller and wider with each new conical layer deposited. Figure 1. If you then use a saw to expose a complete cross-section, cutting through a stack of cones, the cross-section will possess separate rings (increments) where each cone was severed. The thickness of each ring is dependent upon the amount of resources used for its construction at that location. Ring thickness can vary from cross-section to crosssection.

Growth rings are two dimensional forms representing a three dimensional growth increment, sheath, or cone. Living trees construct periodic growth cones over twigs, branches, stems, and roots. Cutting a cross-section through these woody parts would present a series of growth increments visible as woody growth. These growth rings symbolize a system of progressive growth processes occurring over many growth periods or seasons.

Parts and Forms

The concentric growth rings visible in a cross-section of a stem is a common view of the inside of a tree. The visible components include, beginning from the outside and moving radially inward on a cross-section are: Figure 2.

- *periderm* -- a multiple layer tissue responsible for tree protection and water conservation generated over the outside of a tree from shoot to root, and produced by the phellogen (cork cambium); .
- *secondary cortex* -- an assorted layer cake of living, dead, and crushed phloem cells, terminal ray remnants, and periderm cells just beneath the latest periderm.
- *phloem* actively transporting raw and processed resources primarily from the photosynthetically active regions to storage areas and respiration sinks;
- *cambium* a zone of cell generation through division and expansion which adds tissue volume to the circumference of a tree with xylem generation to the inside and phloem generation to the outside;
- *sapwood xylem* an area of wood containing living cells and dead resource transport tissues with active vertical (longitudinal) transport confined to the youngest growth increments;
- *sapwood rays* radially oriented, living cells used for resource storage, for system maintenance and defense, and for radial transport into and out of growth increments;
- *heartwood* a central core of internally shed dead xylem and rays which can have their cell volumes or walls filled with defensive or waste materials;
- *pith* a residual core of tissue generated in the shoot over which all other cell layers were deposited (not found in roots); and,





tree growth increments shown in a longitudinal cross-section. The dark bar across the stem represents location of radial cross-section view showing growth increments or "rings."





Figure 2: An idealized radial tree cross-section with more than 13 growing season increments represented. Key componets include:

1) pith (in stems only); 2) heartwood; 3) sapwood; 4) a growth increment (one growth ring); 5) early-wood (Spring-wood within one growth increment); 6) late-wood (Summer-wood within one growth increment); 7) rays; 8) cambium with xylem generated to the inside and phloem generated to the outside; 9) periderm.



growth increment – xylem tissues developed over one growth period and separated in time from more internal adjacent tissues by generation after a non-growing or dormant period (i.e. a growth ring).

The two primary forms of growth increments are differentiated by within-growth-increment (within-ring) diameter differences of longitudinal cells called vessels. Growth increments where initial growth is composed of large diameter vessels quickly changing to small vessel diameters produce distinct ring beginnings and ends and are termed "ring porous." This term is reserved for Angiosperms although some Gymnosperms with determinant growth may generate distinct earlywood and latewood. Growth increments where little or no differential in vessel cell diameter size occurs throughout the growing season are termed "diffuse porous." Names of the forms come from the visible "pores" or vessels seen in cut cross-sections. Growth increment forms are directly related to shoot growth patterns.

Xylem Components

Xylem within growth increments is composed of axial (longitudinal) components and radial components. The axial elements include: transport and structural cell types called tracheids and vessels (angiosperms only); structural cell types generically called fibers; and, storage and defensive cell types classified as parenchyma. These cells types have cell wall structures which differ according to function. Generally, the thicker a cell wall, the more structural impact each cell has -- while thinner walls suggest active physiological processes. Axial components can be seen on-end (in cross-section) when looking at a cross-section of xylem growth increments.

The radial components of xylem, seen as radial lines of cells in a growth increment cross-section, are comprised almost entirely of parenchyma. These cells in the sapwood are living and conduct resources between actively transporting xylem and phloem, and more interior growth increments. These radial parenchyma (rays) store resources and react quickly in defense. All parenchyma, upon decline and death, may concentrate or generate a number of materials compartmentalized away from living cells which provide a passive defense for internally shed growth increments (heartwood).

Interconnections

To appreciate interconnections between living cells and actively transporting dead space, a textile model can be used. Figure 3. Textiles have threads crossing at right angles to each other – some threads run up-and-down and some run horizontally. These threads represent the axial and radial components in the xylem within one growth increment. Everywhere two living cells cross, they can form both a living and structural connection. These connections are indentations or pits in each cell wall which allows close connections between cells. The pits contain minute cytoplasm bridges which connect the inside of one cell with the inside of the other cell (i.e. continuous cell membrane between cells). If the crossing point includes one living and one dead cell, connections will be structurally different than if both cells are living.

The axial components and radial components form an interconnected system of living cells surrounding and interacting with dead cells and cellular spaces. The three-dimensional interconnections within a growth increment assures cell health, resource efficiency, and an effective defense. The physical structures of these cells and interconnections generate small defensible spaces which can be sealed-off biologically and physically from the rest of a tree in case of dysfunction, damage, or attack. Tree structure, although primarily composed of dead tissues, supports biological health.



Figure 3: Two dimensional textile model of axial and radial conductors and their connections with in a tree. Axial connectors (i.e. vertical lines) act as conductors (tracheids & vessels), support (fibers), and storage / defense (parenchyma). Radial connectors (i.e. horizontal lines) act as conductors, storage, and defense (parenchyma). Axial and radial systems can be interconnected where the elements cross each other.







Cell Walls

Cell wall characters facilitate cell function. The outermost (exterior) portion of a single tree cell is composed of soft materials with low concentrations of net-like cellulose fibrils. This primary wall, the surrounding deposited materials, and the neighboring cell's primary wall are called the middle lamella. Immediately inside the primary wall can be the first of three secondary walls. Figure 4

The first secondary wall is thick with individual sheets of high angle cellulose fibrils impregnated and encrusted with lignin, which binds the fibrils in position. In cell wall formation, high energy resource periods allow cellulose strands to be welded together and deposited on the inner side of the current wall. During intervening low energy resource periods, lignin deposits are made over the wall surfaces. These layers can represent day to night changes (i.e. laminations).

The second secondary wall is laid to the inside of the first secondary wall. The difference between these two secondary walls is in orientation of cellulose fibrils. The second secondary wall can become very thick with low-angle (longitudinal / axial) cellulose strands in sheets with lignin filling the gaps in-between. Mechanically, the addition of secondary cell walls provide strength against bending, shear, twisting, expansive and contractive forces.

A third secondary wall is thinner than the second secondary wall and has cellulose fibrils oriented similar to the first secondary wall (high angle). The inside of the third wall may appear to be textured or bumpy (warty layer) where living contents of the cell finally biologically evaporated away. Tension wood cells (the reaction wood of Angiosperms) may contain a densely concentrated cellulosic cell wall called by early anatomists a gelatinous layer because it looked wet and shiny under the microscope.

Layered Growth

The secondary growth of trees, derived from the cambium, provide the circumferential expansion of woody tree parts. This cambial zone, responsible for secondary growth, is a reaction center responding to changing internal and external growth constraints. Xylem accumulation rates, as seen in growth increments, can help estimate vitality and understand differential tree growth due to mechanical loads, as well as glean information regarding the passage of time, climatic changes, and disturbance events.

Trees sense and respond to a host of environmental events and changes. Trees integrate these separate responses to individual conditions into a general whole-tree reaction. A growth increment represents hundreds of internal and external variables put into an equation with only one answer – tree survival and growth. One growth increment mirrors the annual biological status of a tree within the local cambial neighborhood. Understanding information which is available in accumulated xylem growth increments is critical to tree health.

Counting Time

Cells generated by the cambium divide, grow, and mature. The thickness of growth increments are dependent upon both whole-tree and local resources and conditions. Externally, meteorology constraints on essential resources play a dominant role for growth increment volume development. This highly correlated climatic component of growth increment thickness has been utilized for time and climate measures stretching over centuries and millennium. The use of variations in tree growth increments to plot climatic changes is called "dendrochronology." Dendrochronology can provide reasonably accurate and precise estimates of climatic variation because of how growth increments in trees are developed and laid-down.







Environmental Constraints

Growth increments integrate many site, pest, climate, health, and resource availability problems. The size (radial thickness of growth increments in cross-section) for each growth ring can be summarized as dependent upon a few dominant features. Figure 5. The four dominant environmental features accounting for most of the variation in growth increment radial width are precipitation, light (quality and quantity), temperature (as it moves away from 70 - 85°F optimum), and relative humidity (micro-site and boundary layer). These features influence a tree instantaneously, but a tree's response will include biological adjustments which occur over various lengths of time. The lag time between sense and final response activities can lead to incomplete or inappropriate reactions to major changes.

The single dominant biological feature influencing growth increment radial width is the photosynthetic (Ps) and respiration (Rs) balance in a tree. This balance is impacted by water availability, temperature and light values. Root and leaf array effectiveness both synthesize a multitude of site features into an integrated Ps / Rs balance. The Ps / Rs balance within a tree helps generate various levels and types of growth regulators, and symbolize the amount of carbohydrate (CHO) and other processed materials available for cambial growth. These biological growth materials are a direct result of shoot elongation growth and productivity.

Biological Constraints

The processed materials and growth regulators responsible for cambial growth must also be made available throughout a tree. Cell division, cell expansion, and cell maturation processes are all dependent upon different resource mixes for initiating and sustaining activities. All these processes are required for increasing growth increment width. Transport and storage allocation problems can cause disruption of radial growth.

Throughout all the interacting processes, resource availabilities, and environmental changes, there are many steps and levels where growth increment radial width can be modified by small changes. Different stress (abiotic and biotic) processes or organisms can influence one or many steps, processes, or resources affecting growth increment width. The ultimate input to growth increment width remains tree productivity and health, while maintaining structural integrity to withstand average mechanical load conditions.

Productivity

Each growth increment has an associated energy production cost. Wider growth rings represent a much larger energy investment derived from tree productivity than narrow increments. Because of geometric features of cambial growth in a tree, similar increment widths across a cross-section each represent a different energy production investment. A given amount of xylem tissue spread over the circumference of a three-inch diameter tree will generate a much larger growth increment than if the same amount of xylem tissue is spread around the circumference of a 30-inch diameter tree. With identical annual tree productivity, increment widths would be expected to decline each year. Table 1 demonstrates the annual diameter growth rate percent in trees of various diameters and various growth increment widths.

Beginnings & Ends

The process of differentiating between growth increments is dependent upon visual differences within each growth increment and uniqueness of each terminal boundary between growth increments. The

Secondary Tree Growth Increments -- Dr. Kim D. Coder







Table 1: Estimate of annual tree diameter growth rate in percent based upon last year's growth increment radius in inches.

Tree Diameter (in)	Last Growth Increment Radius (in)			
	1"	1/2"	1/4"	1/8"
4	333%	86	35	18
6	115	42	18	8
8 10	79 58	30 24	13 11	6 6
12	43	19	9	4
14	36	16	8	4
16	31	14	7	3
18	27	12	6	3
20	23	11	5	3
22	21	10	5	2
24	19	9	4	2
26	18	8	4	2
28	16	8	4	2
30	15	1	3	2
32	14	7	3	2
34	13	6	3	2
36	12	6	3	1
38	11	6	3	1
40	11	5	3	1
42	10	5	2	1
44	10	5	2	1
46	9	5	2	1
48	9	4	2	1
50	9	4	Z	1
52	8	4	2	1
54	8	4	2	1
56	8	4	2	1
58	/ 7	4	2	1
UG	/	3	2	1%



terminal increment boundary in some species can be composed of high concentrations of axial parenchyma or thick-walled fibers. Many species have "squashed" elliptical-shaped (radially flattened) cells composing the last row of cells in a growth increment. Still other species generate thicker than normal cell walls in the last layer of an increment. The interconnections between cells are also altered at the growth increment boundary, both because of increasing fiber concentrations through the growth increment, and changing pit-field locations and numbers.

The boundary between growth increments may not be visible without significant magnification. For annual increment delineation and wood identification, within-growth-ring anatomy can provide information to the unaided eye (or under low magnification). Within angiosperms (hardwoods) anatomists have provided four general classifications for describing growth increment structure and form. These structural forms can be used to delineate growth increments and provide clues to other tree processes.

Early & Late

Growth increments are divided into two anatomical time periods mirroring shoot and leaf activities. The first time period is from just before bud changes in Spring until just after full leaf expansion of bud-held or pre-formed leaves. Because of growth regulator levels and carbohydrate (CHO) availability, the cambium generates cellular structures jointly termed "Springwood" (occurring primarily in dormancy requiring temperate areas) or "earlywood." Earlywood cells in some species tend to be larger in diameter and have thinner cell walls, with associated lower density xylem, than latewood.

The second time period seen in growth increments begins just after full leaf expansion and continues until whole-tree growth cessation, dormancy, or a major environmentally initiated pause in activities. Generically this period is considered the remainder of the growing season after full leaf expansion of bud-held or pre-formed leaves. The changing CHO production and allocation patterns, as well as shifting growth regulation signals, compel the cambium to generate cellular structures jointly termed "Summerwood" (in dormancy-requiring temperate areas) or "latewood."

Anti-Tropical

Because of the academic bias of location, much of the language surrounding growth increment delineation and anatomical typing of trees are Northern hemisphere, temperate zone specific. Latewood is invoked immediately after the first shoot elongation period and bud-resident or preformed leaves have been fully expanded. This biological station-point is critical to assure a new photosynthetic array is functional and effectively displayed. In continuously growing species, little environmental periodicity may exist. Where multiple shoot expansion periods exist (multiple flushing), the biological uniqueness of the first expansion period can be lost among internal allocation patterns and external environmental constraints. Many anatomical concepts and terms lose meaning in tropical / subtropical trees.

Porosity

The greater the distinction between shoot elongation patterns, growth period length in a tree, and total available growing season length -- the greater the distinction between earlywood and latewood within a growth increment. The primary cell type which provides most of the visible changes across a growth increment are vessel cross-sections in Angiosperms. Large vessel earlywood and small vessel latewood generate a cross-sectional growth increment pattern (and wood grain) termed "ring porous." Figure 6. This term was coined due to the abrupt vessel porosity changes appearing on the face of cross-





Figure 6: An example of two growth increments in a tree with ring-porous xylem.



sections. The growth increments can be delineated by a dense latewood "ring" ending one growing season and a "pore-filled" low density earlywood "ring" at the beginning of the next adjacent growth increment. Examples include <u>Castanea</u>, <u>Catalpa</u>, <u>Celtis</u>. <u>Fraxinus</u>, <u>Gleditsia</u>, <u>Morus</u>, <u>Quercus</u>, <u>Robinia</u>, and <u>Ulmus</u>. See Appendix 1.

Growth increments of species with few major cell cross-section shapes, slow shifts in growth regulators, and relatively constant carbohydrate allocation patterns across a growing season tend to generate little vessel size differences between earlywood and latewood. Because vessel size does not vary, delineation of earlywood and latewood within one growth increment cross-section and between neighboring growth increment cross-sections is difficult to impossible. Species with constant vessel size across growth increments are termed "diffuse porous." Figure 7. This term is used to describe constant vessel diameters diffused across a growth increment. Actual vessel numbers can change significantly over the growth increment but they remain similar in size relative to each other. Examples include <u>Acer, Betula, Carpinus, Fagus, Liriodendron, Platanus, Populus, and Pyrus</u>.

Intergradations

There are two commonly identified gradation steps between ring-porous and diffuse-porous classifications. One form is called "semi-ring porous." Semi-ring porous species have few large early-wood vessels gradually declining in diameter into latewood (Juglans, Sassafras, Diospyros). The other intermediate classification is "semi-diffuse porous." Semi-diffuse porous species have many small diameter earlywood vessels which decline gradually into even smaller diameter vessels into the latewood (Populus, Salix). Because of positional variation within trees (like inside to outside; height; juvenile / mature; or shoot / root) gradations between growth increment forms can have many subjective variations. These intermediates still have value in wood identification, in expectation of shoot activity, and in understanding tree growth.

The type of growth increment porosity and associated shoot growth form, carries some adaptive advantages and have been genetically selected for over time. Porosity type is not necessarily the same throughout a tree. Because growth ring width is highly correlated with water availability, and a ring-porous growth form is associated with survivability under summer droughts and cold winter temperatures, (i.e. water transport is up to ten times faster in ring porous trees versus diffuse porous trees) ring-porous growth increments can be found in above ground portions of some trees. These same ring-porous trees may have variously porous roots. Cellular types and proportion may stay relatively stable from shoot tip to root tip, but ring-porous architecture of shoots may grade into diffuse porous architecture of roots near root ends.

Non-Porous Wood

Gymnosperms are considered to have no vessels (or pores) in their cross-section. This wood form is termed "non-porous" as opposed to the porous wood forms of the angiosperms (hardwoods). All the axial components are tracheid elements (fiber tracheids in latewood), or parenchyma associated with resin canals. The rays can be thin (1-2 cells wide) with occasional ray tracheids along the sides. Earlywood tracheids are thinner-walled with circular interconnections between cells. Latewood tracheids have thicker walls and oval interconnections. Anyone having viewed a Southern yellow pine would declare (inaccurately) they are ring porous given their abrupt transition between earlywood and latewood.

Thin-walled axial parenchyma can be found in the podocarps, *Cupressaceae* (<u>Thuja</u>, <u>Cupressus</u>, <u>Chamaecyparis</u>, <u>Juniper</u>), and *Taxodiaceae* (<u>Sequoia</u>, <u>Taxodium</u>). Little or no axial parenchyma is found in





Figure 7: An example of two growth increments in a tree with diffuse-porous xylem.



araucaria, *Pinaceae* (<u>Pinus</u>, <u>Larix</u>, <u>Picea</u>, <u>Pseudotsuga</u>, <u>Tsuga</u>, <u>Abies</u>), and *Taxaceae* (<u>Taxus</u>, <u>Torreya</u>). Resin ducts or canals can be associated with both axial and radial parenchyma, but are not to be confused with vessels. Some resin ducts are common vascular features, while some are initiated by injury. <u>Pinus</u> (pines), <u>Larix</u> (larch) and <u>Pseudotsuga</u> (Douglas-fir) all have normal resin ducts. <u>Picea</u> (spruce) have less abundant but noticeable resin canals. Abies (fir), <u>Sequoia</u>, and <u>Taxodium</u> (baldcypress) generate resin canals only upon injury.

False Rings

Growth increments usually represent one organized cycle of cambial activity. Whether due to precipitation, temperature, dormancy factors, or photoperiod, there are start and stop mechanisms within a tree controlling initiation and duration of cambial activities. Sometimes multiple growth increments occur. These multiple or "false" growth increments represent a multiple shoot growth period and associated multiple cambial growth period.

Pest defoliation, major wet and dry soil fluctuations, multiple flushing of preset shoots, periods of major sprout release and growth, fire or wind-damaged foliage regeneration, juvenile trees, and short term but severe crown disturbance / stress impacts all can lead to an early near cessation of cambial growth with a later renewal of growth within the same growing season.

False ringing is most prevalent in branch-wood down to the base of the living crown, only occasionally in the stem. Simple growth increment counts can be highly inaccurate because of visual misidentification of single growth increments with multiple growing season characteristics. Careful crosssectioning and the use of significant magnification is essential in identifying true growth cessation points.

Mini-Rings

There are conditions where a truncated growth increment or no growth increment is produced. Marginal branches, rapidly declining trees, cambial damaged areas, or growth regulation disruption / destruction zones may not activate or sustain cambial activity. Truncated growth rings occur when only the first set of cells divide and expand. These cells were setup for growth at the close of last year and these cells complete division and growth as a first activity of the new growing season. Lack of any growth ring denotes a loss of meristematic tissue altogether, a major disruption of physiological functions, or simple starvation. Cambial activity can be reinitiated by living parenchyma (redifferentiation).

Conclusions

Tree growth increments contain many forms of information -- some about the tree, some about resources changes on-site, and some about large-scale climate. By understanding tree growth increment formation and appearance, information can be extracted regarding tree biology which can help a tree health care provider make better decisions.



Appendix 1: Tree Increment Porosity Forms In Selected Angiosperms

In any cross-section, the largest conducting vessels can be either clearly visible to the unaided eye or can be minutely small. Due to shoot growth rates and timing, and leaf expansion periods, different growth conditions affect vessel size and xylem composition. Xylem formed under the influence of rapid shoot growth and leaf expansion tends to have larger-sized components.

The first xylem developed in a growth period is considered "earlywood" or "Springwood." As growth slows and environmental constraints initiate changes within a tree, later xylem components may rapidly decrease in size, gradually decrease in size, or stay roughly the same throughout the growing season. This later xylem is considered "latewood" or "Summerwood." Visible features differentiating earlywood from latewood within a single growth increment cross-section is the basis for xylem porosity classifications.

Tree increment porosity patterns are summarized into four primary forms below: 1) ring-porous; 2) semi-ring-porous; 3) semi-diffuse-porous; and, 4) diffuse-porous. The classic species examples of these within-increment xylem forms are: A) <u>Quercus alba</u> (white oak), a determinant shoot growth form with distinct growth increments visible due to a clear earlywood to latewood transition -- a ring-porous structure; and, B) <u>Platanus occidentalis</u> (sycamore), an indeterminate shoot growth form which shows little xylem diameter size differences between earlywood and latewood – a diffuse-porous structure.

Ring-Porous Trees (Many large vessels quickly declining to small vessels)

7)

Semi-Ring-Porous Trees (Few large vessels declining to small vessels)

- <u>Carya</u> spp. <u>Catalpa</u> spp. <u>Cladrastis</u> <u>Diospyros</u> <u>Juglans</u> spp. <u>Morus</u> spp. <u>Prunus</u> spp. <u>Quercus</u> spp. <u>Sassafras</u> <u>Ulmus</u> spp.
- (hickory)
 (catalpa)
 (yellowwood)
 (persimmon)
 (walnut)
 (temperate mulberry)
 (cherry)
 (live oak group)
 (sassafras)
 (elm)

Secondary Tree Growth Increments -- Dr. Kim D. Coder

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(Appendix 1 continued)



Diffuse-Porous Trees

(Many small vessels across growth increment)

<u>Acer</u> spp.	(hard / soft maple)
Aesculus spp.	(buckeye)
<u>Afzelia</u> spp.	(lingue)*
<u>Alnus</u> spp.	(alder)
<u>Antiaria</u> spp.	(ako)*
<u>Arbutus</u> spp.	(madrone)
<u>Aucoumea</u> spp.	(okoume')*
<u>Betula</u> spp.	(birch)
<u>Canarium</u> spp.	(aiele')*
<u>Carpinus</u> spp.	(hornbeam)
Ceratonia spp.	(carobtree)
Chlorophora spp.	(odoum / iroko)*
<u>Cornus</u> spp.	(dogwood)
<u>Corylus</u> spp.	(hazel)
Dalbergia spp.	(rosewood)*
<u>Dumoria</u> spp.	(makore')*
Entandrophragma	spp.
(kosipo / sape	le / sipo / tiama)*
Fagus spp.	(beech)
<u>Gonystylus</u> spp.	(ramin)*
<u>Guibourtia</u> spp.	(amazakoue')*
<u>Ilex</u> spp.	(holly)
<u>Khaya</u> spp.	(acajou)*
Liquidambar spp.	(sweetgum)
Liriodendron	(yellow-poplar)
Lithocarpus	(tanoak)
<u>Lovoa</u> spp.	(dibetou)*

Diffuse-Porous Trees

(Many small vessels across growth increment)

Magnolia spp. (magnolia) Mansonia spp. (bete')* Microberlinia spp. (zebrano / zingana)* (tropical mulberry)* Morus spp. Nauclea spp. (opepe)* (gum / tupelo) Nyssa spp. (balsa)* Ochroma spp. (olive-tree) Olea spp. (hophornbeam) Ostrya spp. Oxydendrum (sourwood) (white lauan)* Parashorea spp. <u>Platanus</u> spp. (sycamore) <u>Populus</u> spp. (poplar / aspen / cottonwood) (padauk)* <u>Pterocarpus</u> spp. Rhamnus spp. (buckthorn) (willow) Salix spp. Shorea spp. (red lauan)* (mountain ash) Sorbus spp. (mahogany)* Swietenia spp. (niangon)* Tarrietia spp. Terminalia spp. (afara / idigbo)* Tilia spp. (basswood / linden) Triplochiton spp. (obeche)* Umbellularia spp. (laurel)

Semi-Diffuse

(Many small vessels declining slightly to smaller vessels)

<u>Lithocarpus</u>	(tanoak)
<u>Populus</u> spp.	(poplar / aspen / cottonwood)
Quercus spp.	(evergreen oak group)
<u>Salix</u> spp.	(willow)



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