Outreach
Warnell School of Forestry & Natural Resources
UNIVERSITY OF GEORGIA

Tree Anatomy:
SHOOTS & GROWTH PATTERNS

Dr. Kim D. Coder, Professor of Tree Biology & Health Care, Warnell School, UGA

Tree shoots, or the terminal elongating portions of above ground vegetative components, generate and hold leaves, buds, and growing points all integrated into vascular and live cell-to-cell connections. Unfortunately, there are many meanings for the word "shoot."

Shooting

The word "shoot" has three general meanings in trees:

1) a shoot is a modular twig section comprised of one node with an associated leaf (leaves) and axillary meristem(s), associated with an elongated internode section below (and an apical meristem above if a shoot is in a terminal position). Other terms for this type of shoot is a module, phytomer, or metamer. This shoot concept is a technical construct allowing for multiple shoot stacking and growth. Figure 1.

2) a shoot is any above ground portion of a tree directly bearing leaves, as contrasted with roots and branches. This definition is most used as a generic term for any leaf bearing portion of a tree whether big / small, old / young, original developed / newly elongated origin, or less than one year (growing season) old / several years old.

3) a shoot is any above ground elongated portion of a tree comprised of twigs or branchlets.

Branching Position

Three different generic shoot types are usually recognized based upon the point of origin on a tree. A terminal leader is a shoot (twig / branchlet) growing from a terminal or near-terminal position. Lateral shoots (twig / branchlets) grow from side, lateral, or axillary positions. Basal shoots can be divided into coppice shoots generated at the stem base, or root suckers (root derived shoots). Figure 2.

Another type of subdivision / branching form in trees occurs where three or more branches and branchlets are generated from a single nodal torus (circumferential node area). This growth form is termed a whorl. Branches and branchlets generated from a whorl can be clearly visualized in some conifers, like Eastern white pine *Pinus strobus*. Other terms used regarding whorled branching forms include a verticel or one whorl, and verticillate which simply means whorled. Figure 3.

More Shooting

Epicormic growth is new elongating shoots from adventitious or preventitious growing points on a trunk or branches. These new shoots can be categorized by their location on a tree.

-- Coppice is a new shoot from adventitious or preventitious growing points developing at the ground line or on a short stump.

-- Pollard is a tree cultural term for concentrating new shoots generated from adventitious or preventitious growing points anywhere from two feet above the ground on up to

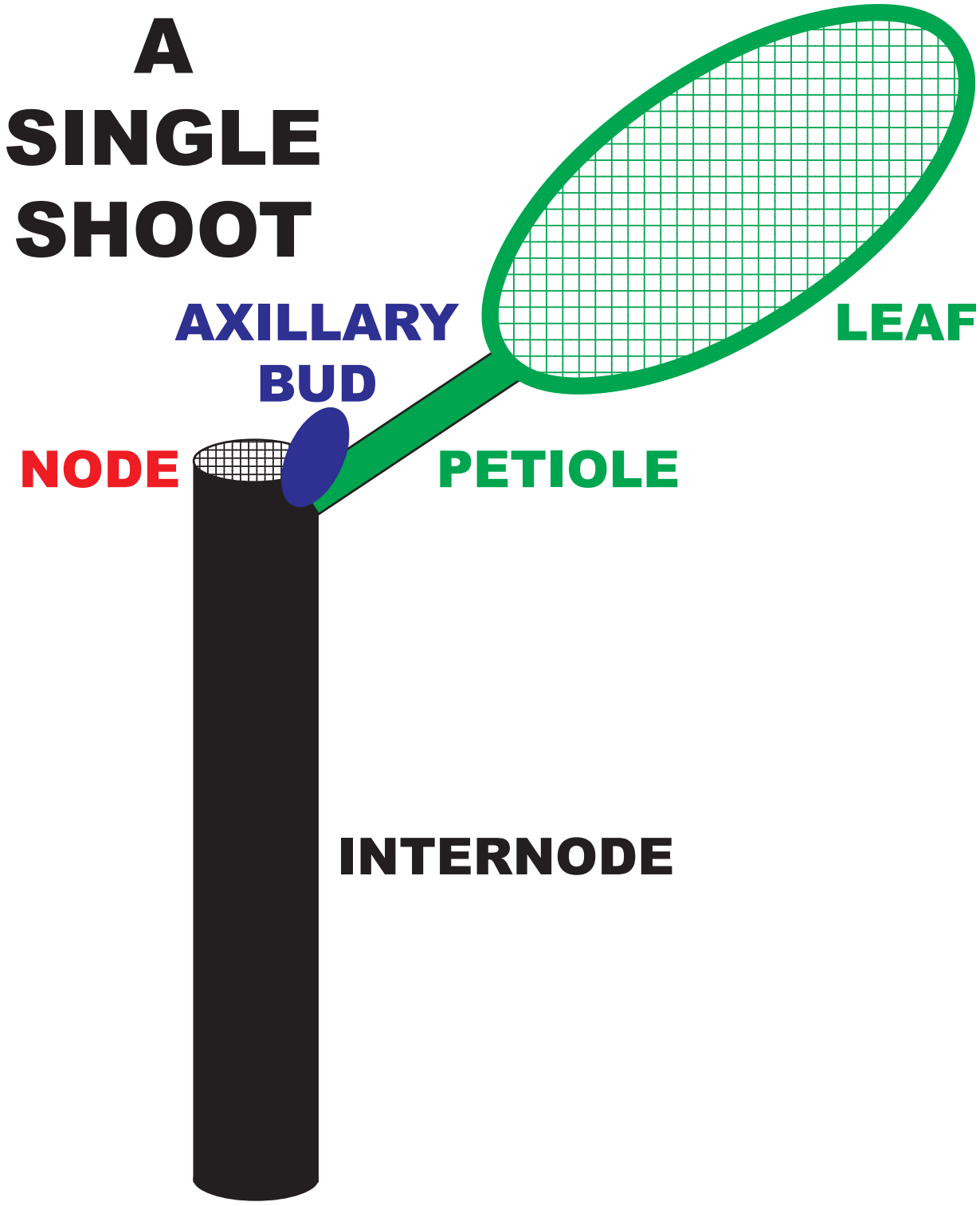

Figure 1: Defining a non-terminal shoot, module, phytomer, or metamer (one modular twig segement). A terminal shoot would also contain an apical growing point.

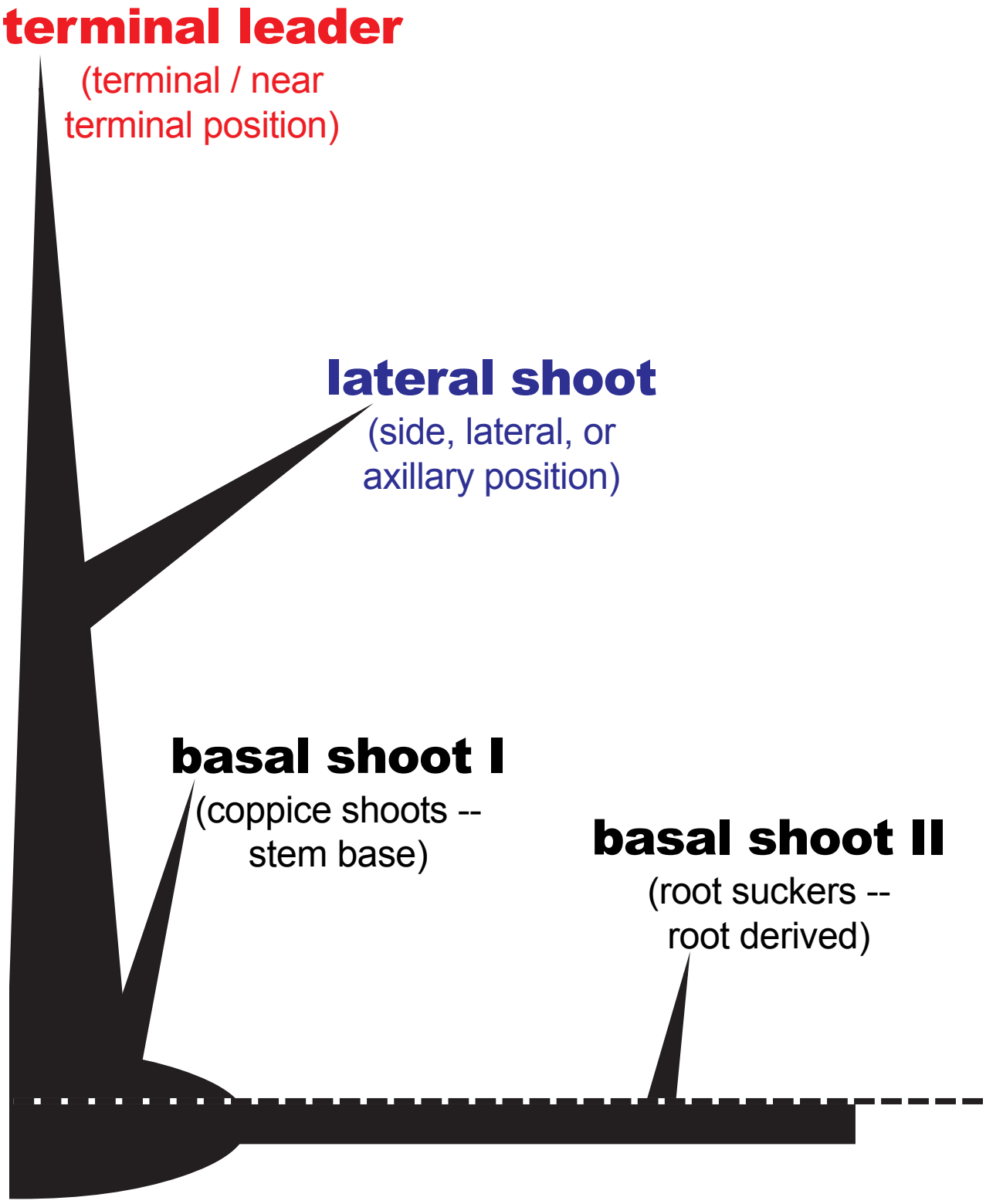

Figure 2: Generic shoot types by point of origin on tree.

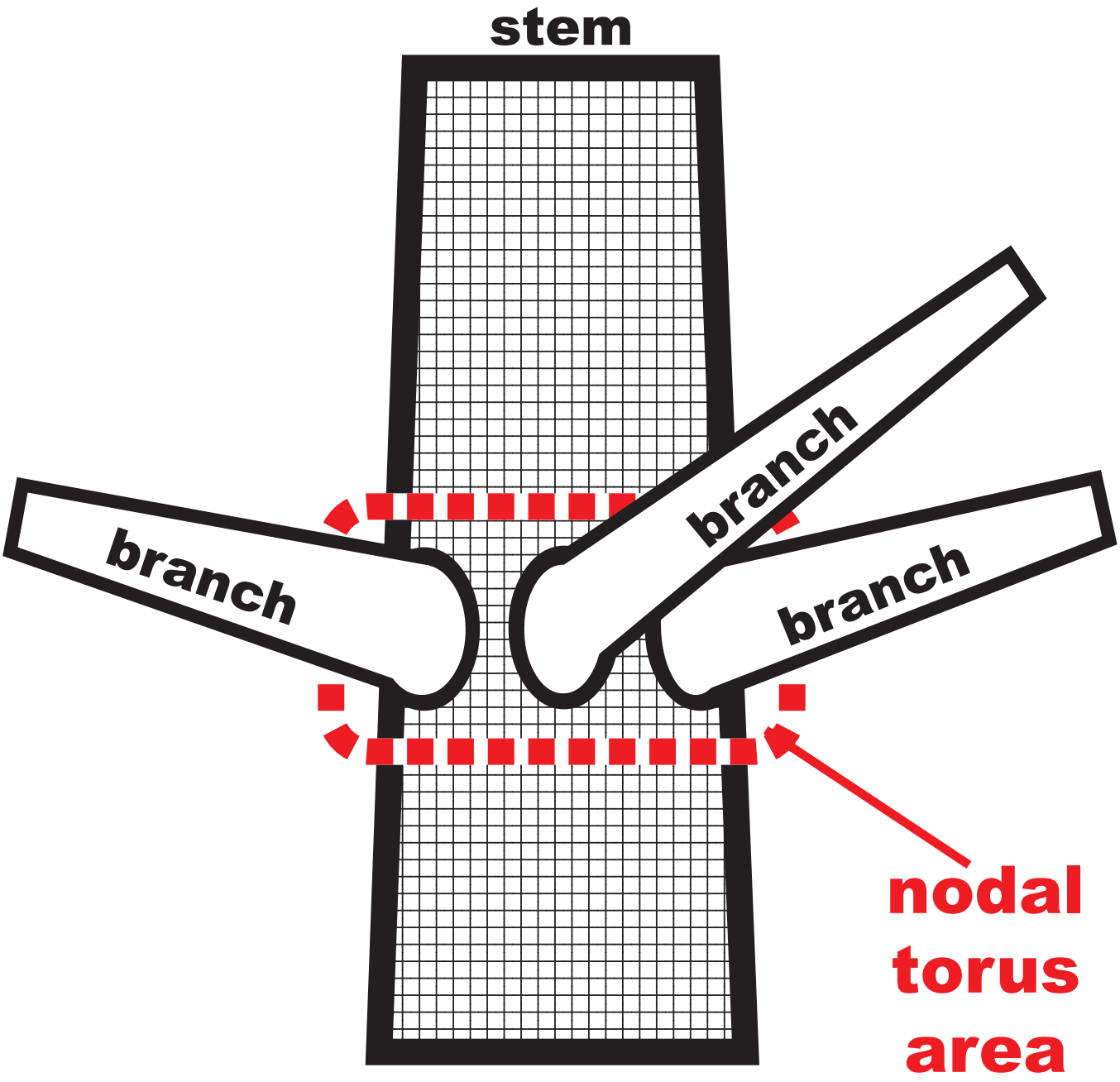

Figure 3: A whorl of branches generated in the same nodal torus area.

somewhere less than the normal height of a tree on branches or on the main stem. This type of foliage concentration in specific places is also called low pollarding, styving, high coppicing, or naving.

-- High pollarding is an old tree cultural practice to develop multiple height canopies along a length of stem without necessarily lessening tree height. Adventitious or preventitious growing points are allowed to elongate in clumps or in multiple layers. This type of foliage concentration technique is also called shredding or rising.

As Ordered

Branch order in trees (the time sequence of individual branch formation – 1st, 2nd, 3rd, ...) is usually evident. Figure 4. A tree crown is composed of twigs, branchlets, and branches holding leaves. On a new seedling, a lateral twig may elongate and survive. The next year, a lateral twig may form, elongate and survive on last year's twig (now a branchlet). The third year out, a lateral twig may elongate on the second year branchlet. The first branching away from the main axis is termed a primary or first order branch. Any branching from the first order branch would be a second order branch. A third order branch grows from a second order branch.

A tree which is one-hundred years old could have 100 branch orders if all twigs, branchlets, and branches survive. Most trees only carry between 4-9 branch orders with the rest sealed off or self-pruned. Only the most efficient branches at making food are conserved by a tree. Any branch tissue visible has been successful and provided great benefits to the whole tree. Old, mature, shaded crown trees may carry only 3-5 branch orders while young, pioneer species in full sun may carry 7-15 branch orders. In an old tree, almost all of the twigs elongated over time have been sealed off and died.

Growing Points

Trees elongate and expand in girth over time (increase in size), termed accrescent. Expansion in size (growth) is due to growing zones called meristems. A meristems is a point, layer or area of cells capable of generating new cells and tissues. Primary meristems (apical meristems) generate elongation of shoot tips and root tips. Secondary meristems (lateral meristems) generate radial expansion in diameter. Figure 5. Primary meristems generate primary tissues and secondary tissues generate secondary tissues. A tree grows using both primary and secondary meristems.

Primary meristems generate new cells which then expand to elongate shoot and root ends. Primary meristems, also called apical meristems, sets-up nodes, leaves, axillary growing points and other tissues in the stem. Figure 6. Axillary growing points are primary growing points established in the nodal torus area in the confluence (axis) of a leaf.

Seconds

Secondary meristems generate new cells which grow generating radial expansion and protection. The two secondary meristems include the inner vascular cambium and the more exterior phellogen. Vascular cambium is layer or area generating xylem, rays, phloem, and other cell types to the outside and over previous growing season tissues. The vascular cambium is a thin lateral meristem zone which initiates, generates, and sheathes secondary vascular growth. Figure 7.

The phellogen (cork cambium) is a layer or area generating phelloderm and phellem (cork). Phellogen provides tissue for environmental protection of vascular tissues, storage tissues, and symplast. It defends a tree while allowing for gas exchange and minimizing water loss. Phellem layers can continue to build up over the exterior circumference of a tree providing both thermal and mechanical

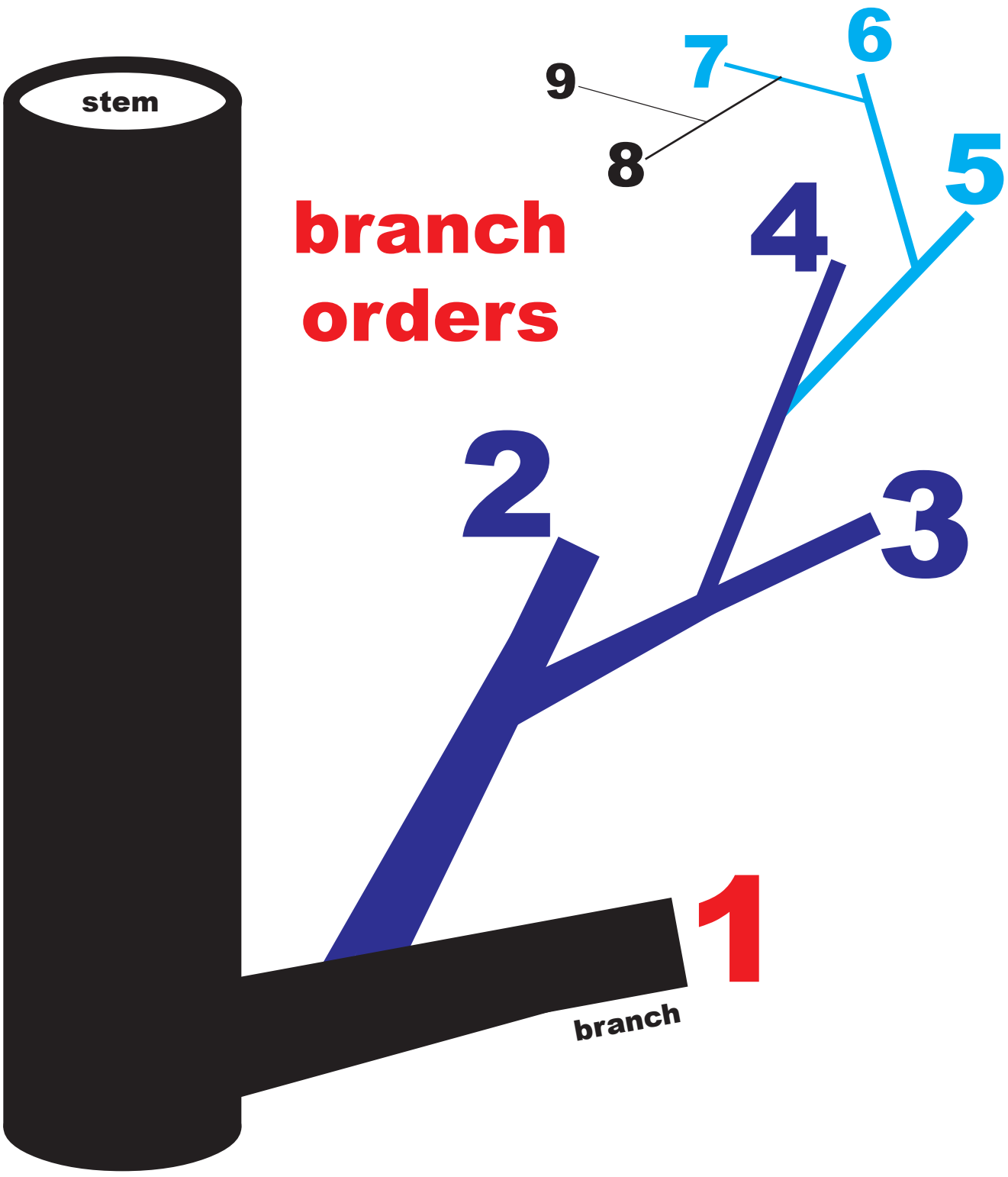

Figure 4: Diagram demonstrating how branch orders are counted. This set of branches and twigs have 9 (nine) branch orders. More branch orders signify more transport resistance and resource stress.

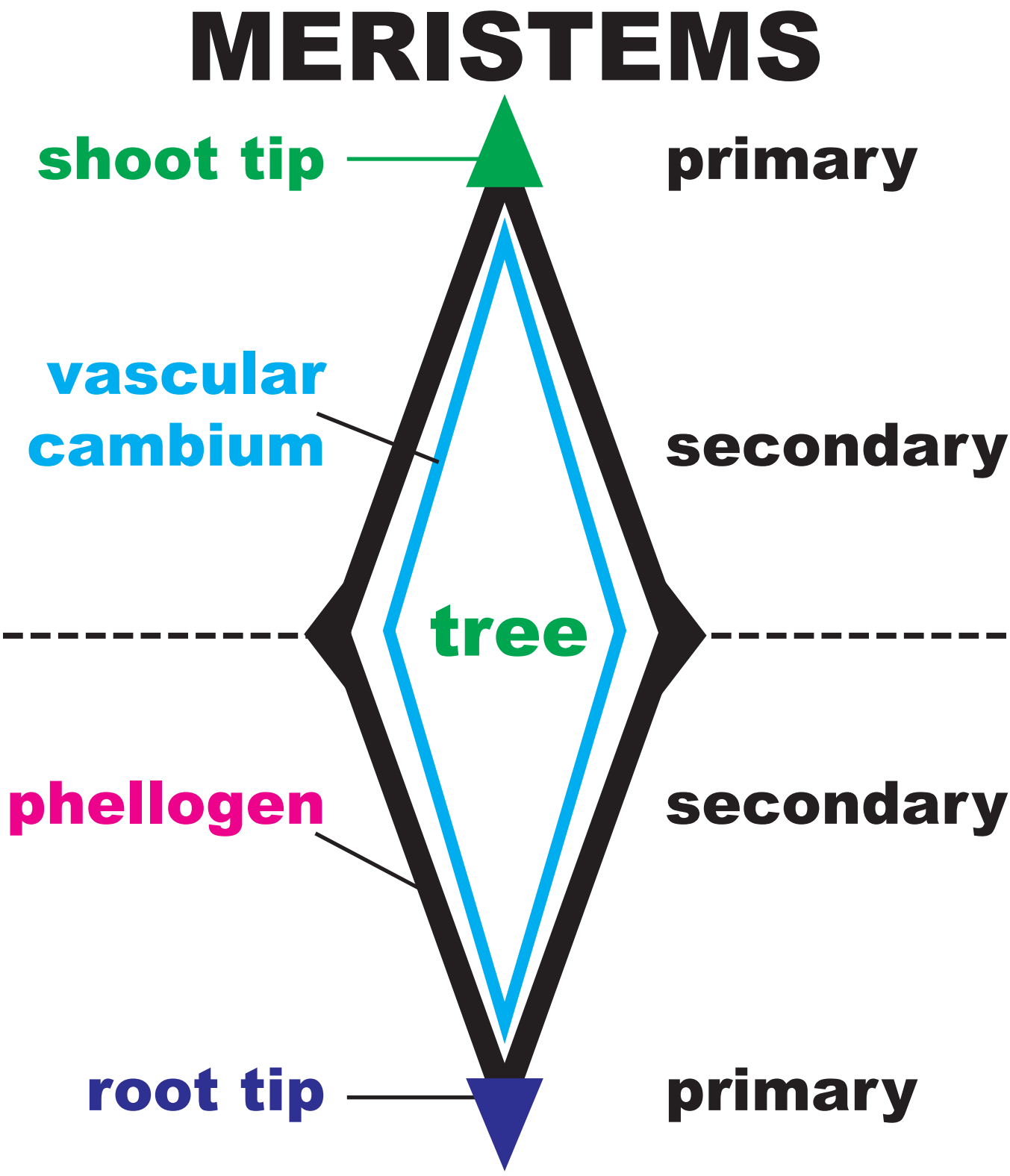

Figure 5: The four main tree meristems.
Axillary growing points are not shown.

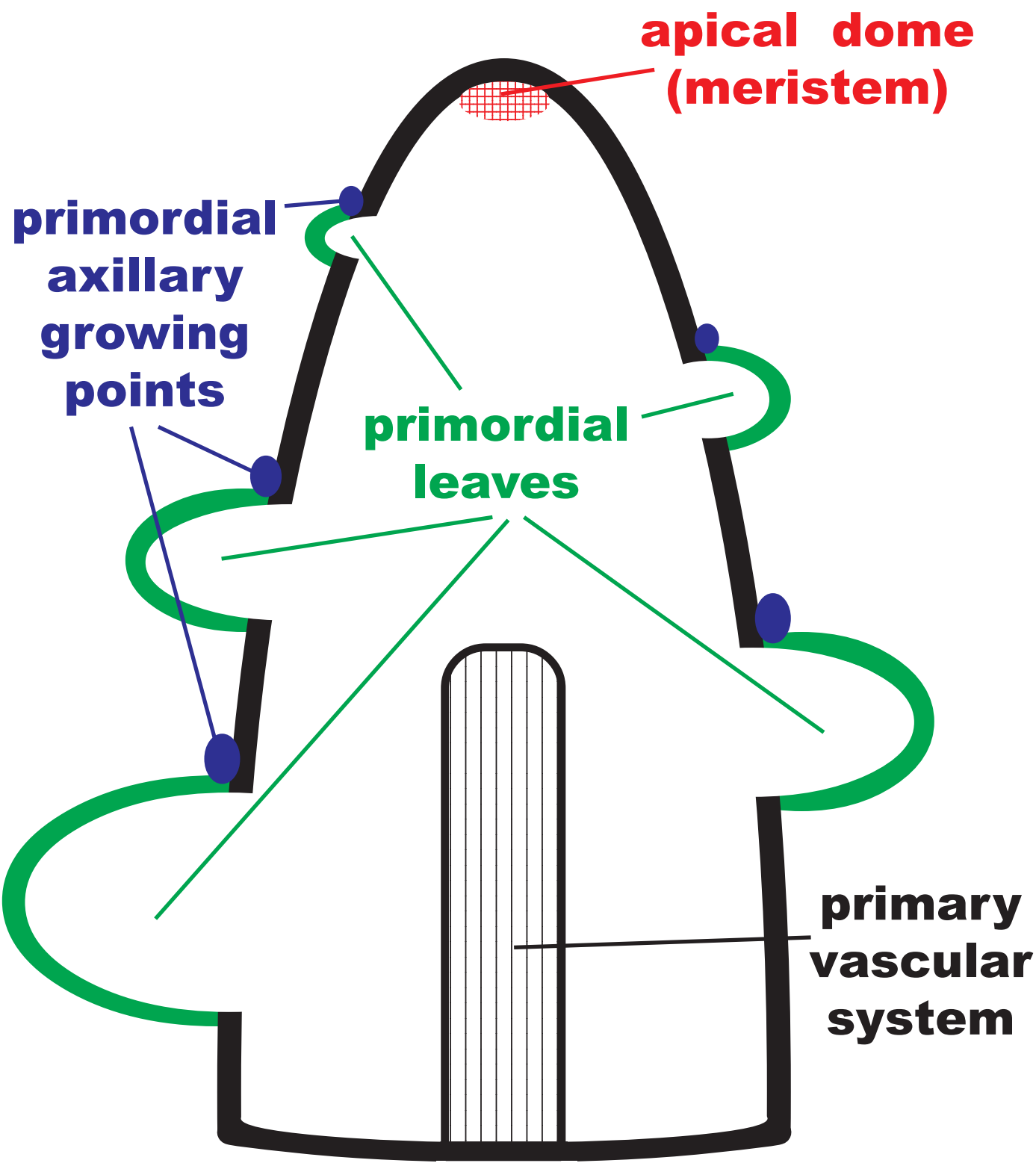

Figure 6: Primary apical vegetative growing point with primordial tissues forming and developing.

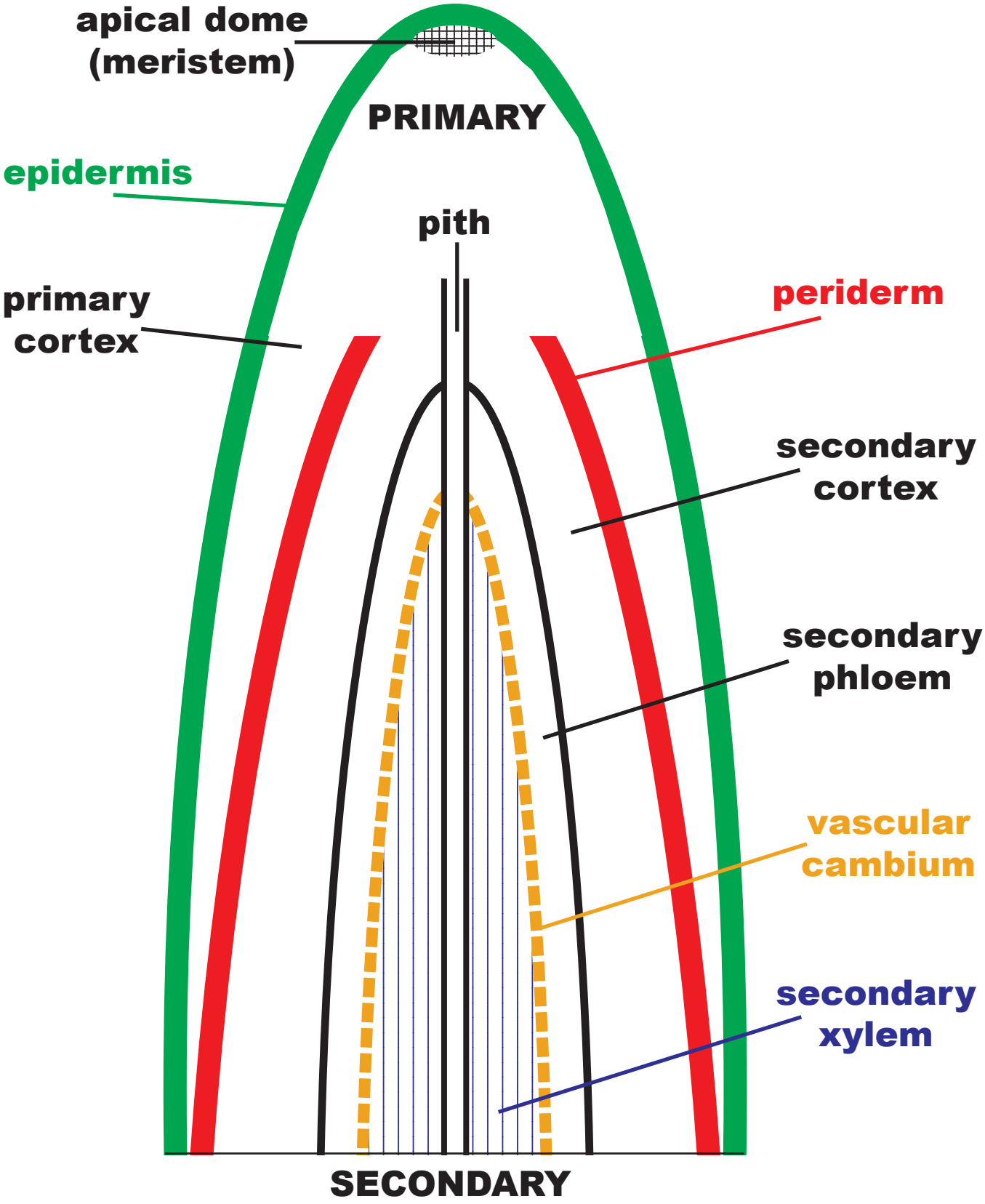

Figure 7: Growing tip transitioning from primary growth to secondary growth.

injury protection. Phellogen and vascular cambium generate between them a combination tissue layer called a secondary cortex which acts as an environmental sensor for the symplast of a tree. Figure 8.

Points of Growing -- Pre

There are two ways to differentiate non-terminal growing points – preventitious and adventitious. Figure 9. Preventitious growing points are formed in axillary positions and grow a little each year, but are suppressed. These growing points may be clustered together due to other preventitious growing points formed inside old lateral buds. Preventitious growing points form from differentiated tissues which did not grow in the first season formed.

Preventitious growing points remain suppressed, slowly growing at the distal radial end of a bud trace through the xylem. When released from suppression, these growing points generate epicormic shoots. These growing points are not dormant but are suppressed, slowly elongating to keep from being over-grown by xylem and killed. Common names used for these types of growing points include dormant, latent, or preformed buds or growing points.

Points of Growing -- Ad

Adventitious growing points are formed from secondary tissues like small islands of parenchyma cells in the secondary cortex over dilated phloem rays, or next to preventitious buds. Adventitious growing points develop from undifferentiated callus tissues and elongate as soon as formed. These growing points are generated outside axillary or terminal positions with no historic bud trace.

Usually adventitious growing points are generated in injury / wound areas from callus tissue, from an exposed cambial zone, or without injury from secondary cortex. Adventitious growing points form in the current year and grow on if not suppressed.

Not A Trace?

Preventitious and adventitious growing points are maintained by a growing point trace. These traces are collections of radially aligned cells supplying essential resources to a growing point and acting as a conduit for growth regulators produced in a growing point to flow out. A growing point trace is a visible vascular connection behind the growing point within xylem which looks similar to a large xylem ray. The older a growing point, the longer and older its connecting trace. Preventitious growing points have traces which were laid down when the growing point was first started in a twig. Adventitious growing point traces are only as long as the age of the growing point.

Meristem Homes

Growing points or meristematic points in a tree are primary tissues with no protective coverings. Buds are primary meristems inside protective coverings (scales, leaves, and/or tricombes) containing unexpanded or undeveloped leaves, flowers, and axillary growing points on compacted nodes and unelongated internodes. Figure 10. A bud is a resting phase or protective phase of a growing point and associated tissues.

Buds can be categorized in a number of ways. Bud types are divided among five (5) categories:

A) active / dormant / suppressed – (growth activity);

B) terminal / lateral, axillary / extra-axillary – (position on shoot);

C) preventitious / adventitious -- (age of formation);

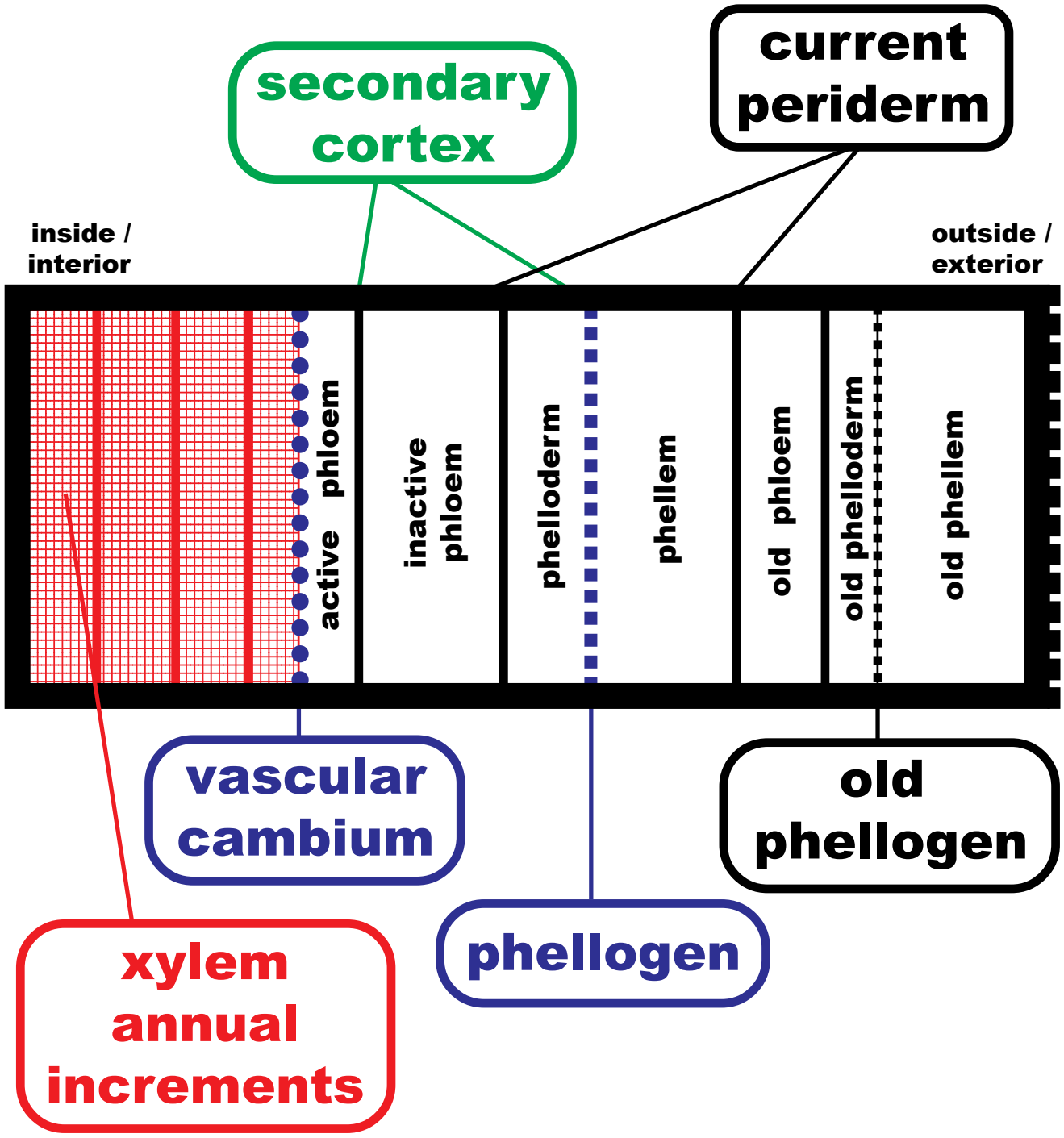

Figure 8: Diagram of last few annual increments of xylem, vascular cambium, phloem, secondary cortex, current phellogen generating current periderm, and one older shed phellogen with generated periderm around outside of a stem, root or large branch.

Preventitious growing points

-formed in axillary / terminal positions
-may be clustered due to formation inside old lateral buds

-generated from differentiated tissues which did not grow in first season formed

names = dormant, latent, or preformed buds or growing points

Adventitious growing points

-formed in secondary cortex over dilated phloem rays or next to preventitious buds

-generated from undifferentiated tissues of current year & immediately elongate if not suppressed
-can be generated in injury / wound areas from callus tissue or exposed cambial zone

name = adventitious buds or growing points

Figure 9: Definitions and genesis of preventitious & adventitious growing points.

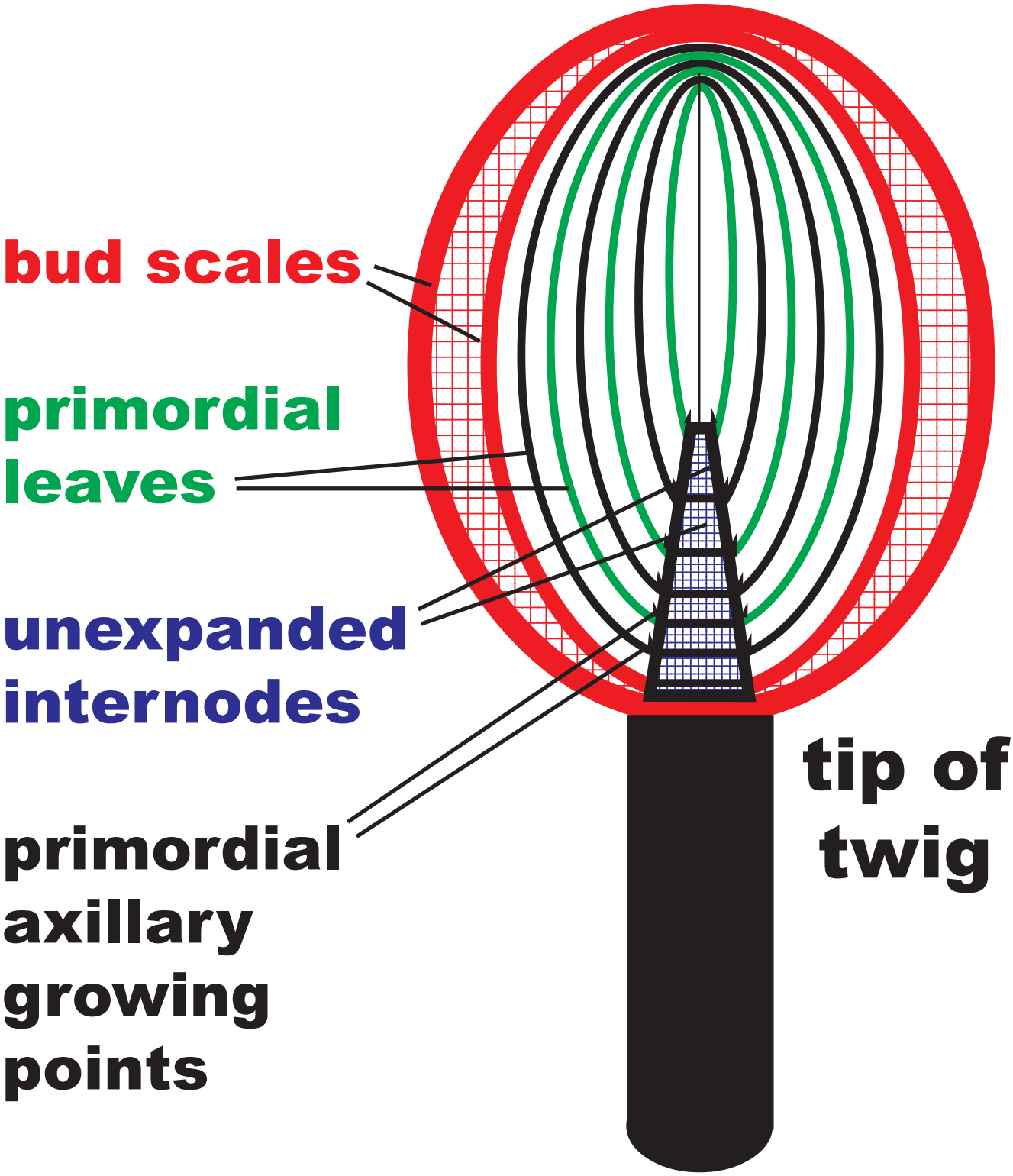

Figure 10: An idealized cross-sectional view of a terminal vegetative bud. Note bud scales, unexpanded leaves and internodes, and axillary growing points.

D) vegetative, flowering, mixed – (content); and,

E) live / shed & dead.

Axils

An axillary bud is a primary meristem located at base of leaf (in a leaf axil) containing unexpanded and undeveloped leaves with associated primordial axil growing points, and/or flower primordia, within a protective covering. A resting axillary bud is also called a suppressed or lateral bud. An axillary bud is called a suppressed bud because it is a protected axillary growing point constrained from growth by more apically positioned buds. A dormant bud is kept quiescent by dormancy factors between growth periods, where as a suppressed bud is kept from expanding due to apical bud control.

An axillary bud position on a twig could be sunken or subpetiolate. A sunken bud is a suppressed axillary bud partially or completely hidden within a twig. A subpetiolate bud is a suppressed axillary bud concealed by the base of a leaf petiole. An extra-axillary bud is a generic term for a bud formed anywhere else but in a leaf axil.

Bud Contents

Buds can contain vegetative parts, flower parts, or both. A vegetative bud contains unexpanded or undeveloped leaves with axillary growing points. The distinct packing of leaves in a vegetative bud is called prefoliation. How the embryonic leaves are folded in a vegetative bud is called ptyxis.

Flower buds contain embryonic and unexpanded flower parts. An antiquated term used to describe a flower bud is albastrum. When growing points develop in the axils of sepals and petals of a flower bud it is called prolification. An ambiparous bud contains a mix of both embryonic / unexpanded leaves, axillary growing points, and embryonic / unexpanded flowers.

Strange Happens

Rarely growing points and buds generate unexpected growths. A sphaeroblast is a growth anomaly where localized radial growth of the growing point outward is disrupted. Radial growth of secondary tissues and cell wall thickening push growing points sideways off the trace end. The growing point survives and generates a ball of tissue within the secondary cortex.

Proliferation (growing point proliferation) is multiple abnormal growing point development which has non-elongating internodes, nodes generated on nodes, and buds on buds caused by pest or chemical problems. This “witches’ broom” growth implies a disruption of normal growing point development and maintenance.

Live or Dead

Trees are large and complex structures derived from living cells. All living cells in a tree are connected, in essence sharing one membrane folded and expanded into a myriad of cellular spaces. This network of interconnected living cells in a tree are called symplast. Components within a tree’s external limit or extent, outside the living cell network, is called apoplast. Apoplast is the dead and non-living volume within a tree. Sometimes the apoplast is further divided into two transport componenets:

A) apoplast = short distance transport within dead cell walls and intercellular gas exchange channels / spaces; and

B) lumina = long distance transport cavities inside cell walls of non-living cells (tracheids & vessels).

The symplast generates apoplast volume as part of tree structure, and when symplast portions are shed and die, they become apoplast. Of the tree which is visible, symplast represents the living mass and apoplast the dead volume. The symplast and apoplast are an intermeshed and woven together set of tissues forming a tree.

All cells, cell walls, and intercellular spaces are either part of symplast or apoplast. In a middle aged tree with good structure and health, the proportion of living and dead components are roughly 10% symplast and 90% apoplast. In other words, most of a sound and functioning tree is made of dead materials and spaces.

Determinant Shooting

There are two primary terminal growth patterns in trees (i.e. determinant and indeterminant), and several atypical or abnormal terminal growth types. Determinant terminals, also called fixed or monopodial growth pattern, elongate for a period of time which is followed by a period of inactivity when a new terminal bud is formed. Elongation begins again after the bud is released from dormancy controls and expands. In this terminal growth pattern, all twig parts are set-up one growing season for expansion in the next.

In determinant growth, the apical meristem terminates its elongation periodically. If only one "flush" of growth is generated per growing season, it is termed a single flush. If several growth flushes are generated per growing season, it is termed a multi-flush. Multiple growth waves or flushes keep forming a fixed bud, but then immediately release and grow without a dormancy period.

Indeterminant Shooting

Indeterminant terminal growth, also called a free or sympodial growth pattern, does not expand from a terminal bud. Indeterminant terminal growth is generated from axillary buds behind the twig terminal. The terminal growing point is aborted / shed, or it represents a live flowering terminal bud. Indeterminant terminals show continuous new production of nodes and internodes with no resting phase inbetween. Example genera with an indeterminant terminal growth pattern include*: Betula, Carpinus, Catalpa, Corylus, Diospyros, Gleditsia, Platanus, Robinia, Salix, Tilia,* and *Ulmus.*

The apical meristem area of a twig continues to elongate until the environment ends this growing season's growth. At the end of the growing season, a tree generates a resting bud to survive environmental constraints, like harsh cold or dry periods. The following growing season as near terminal buds elongate and leaves expand, all the leaves for an entire growing season may appear the same or leaves may have two distinct forms. The first or early leaves were preformed in a resting bud and subject to various forms of damage. Later leaves are newly formed and expand during the current growing season.

Abnormal Terminals

There are a number of atypical terminal growth patterns in trees. One set of terminal elongation patterns considered abnormal include unexpected growth during the growing season. Unexpected terminal elongation patterns within the growing season include:

1) late Summer / early Fall lammas shoots (Lammas Day = Aug. 1) from terminal buds;

2) Summer proleptic or Summer shoots from lateral buds close to terminal; and,

3) Spring sylleptic or Spring shoots released from axillary buds on a twig before the determinant resting bud is generated.

All these patterns of terminal growth are noticeable because they are free and fast growing when compared to normal / mature terminal growth patterns in the same individual or species.

Another atypical terminal growth pattern seen on a few species is generation of spur twigs. Spur twigs are short and can be hardened at the tip. They can be mistaken for a thorn. Spur twigs (spur branches or spines) are formed when an apical meristem shuts down, is sealed-off and the surrounding area is lignified / suberized. A spur twig may bear leaves, axillary buds, and/or flowers / fruit. A spur twig can show leaf and bud scars (cicatrices).

Summary Layers

The major tissue layers or zones around a tree branch, beginning on the outside (exterior) include: (Figure 11.) phellem, phellogen, phelloderm, secondary cortex, non-conducting phloem, mature conducting phloem, dividing phloem / phloem mother cells, vascular cambium initials, xylem mother cells / dividing xylem, mature xylem, dead actively transporting xylem, dead inactive xylem, and pith. Radial lines of cells (rays) are generated by secondary meristems for transport, storage, and defense.

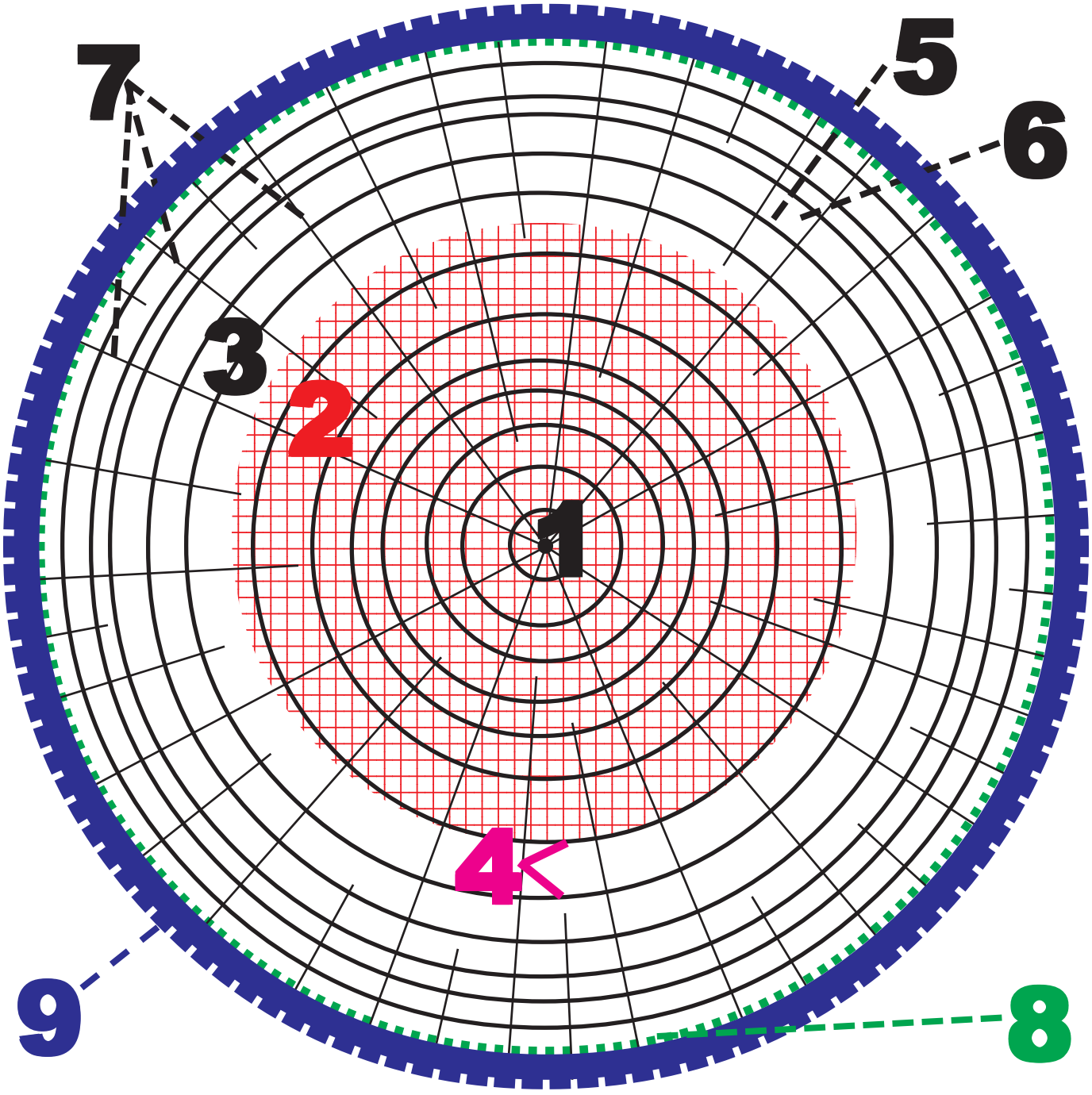

Figure 11: Idealized tree cross-section with more than 13 growing season increments represented.

Key componets include:

1) pith (in stems only); 2) heartwood; 3) sapwood; 4) 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 inside and phloem generated to outside; 9) periderm layers.

Outreach

Warnell School of Forestry & Natural Resources

UNIVERSITY OF GEORGIA

Citation:

Coder, Kim D. 2018. Tree anatomy: Shoots and growth patterns. Warnell School of Forestry & Natural Resources, University of Georgia, Outreach Publication WSFNR-19-36. Pp.18.

Publication WSFNR-19-36 **September 2019**