UNIVERSITY OF GEORGIA
Warnell School of Forestry & Natural Resources

Publication WSFNR-22-76C

October 2022

Tree Anatomy: Stem Components

Dr. Kim D. Coder, Professor of Tree Biology & Health Care / University Hill Fellow
University of Georgia Warnell School of Forestry & Natural Resources

---

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 periderm. The first two meristems are primary generation systems and the second two are termed secondary meristems. Cambial activity and xylem formation, as seen as visible increases in growth increment volume are radial growth, and reviewed here.

Cross-Section

Tree stem anatomy is usually visualized in cross-section. In this form, two-demensional "layers" or "rings," and tissue types can be identified. More difficult is to visualize these two-dimensional cross-sections and incorporate them into a three dimensional object which changes and grows over time.

Moving from outside to inside a stem, tissues encountered include those associated with periderm, secondary cortex, phloem, xylem, and pith. A traditional means of describing a mature tree stem cross-section defines which tissue type is cut first, second and third using a handsaw. A list of generic tissues in stems from outside to inside could include: Figure 1.

epidermis and primary cortex = exterior primary protective tissues quickly rent, torn, and discarded with secondary growth (expansion of girth by lateral meristems – vascular cambium and phellogen).

periderm = a multiple layer tissue responsible for tree protection and water conservation generated over the exterior of a tree from shoot to root, and produced by the phellogen (cork cambium – lateral meristem). Included in periderm is phellem (cork) with lenticels to the exterior, phellogen, and phelloderm generated to the interior of the phellogen.

secondary cortex = assorted layers and lines of living, dead, and crushed phloem cells, terminal ray remnants (dialated phloem rays), and phelloderm cells just beneath the latest phellogen.

phloem = living cells actively transporting raw and processed resources primarily from photosynthetically active regions to storage areas (i.e rays) and respiration sinks (i.e. roots). Included in phloem is older non-conducting phloem, dialated phloem rays, and a thin layer of conducting phloem.

vascular cambium = a zone of cell generation through division and expansion (a lateral meristem zone – not always a continuous layer) which adds tissue volume around the circumference of a tree with xylem generation to the inside and phloem generation to the outside.

sapwood = an area of xylem (wood) containing living cells and dead tissues in both radial and longitudinal directions. Active vertical (longitudinal) transport is confined to the youngest growth increments (cells are dead when actively transporting vessel segments). Xylem includes sapwood rays which are vertical ribbons in various sizes of radially oriented living cells used for resource storage, for system maintenance and defense, and for radial transport of phloem materials into and out of recent growth increments. Sapwood xylem also includes older non-conducting xylem, axil living cells, and fiber cells.

sapwood / heartwood transition = area of older xylem (not necessarily associated with annual increment boundary) where vessel segments begin to become plugged with tyloses, gums, and suberin. Tyloses are balloon-like enlargements and expansions of non-conducting sapwood axial and radial parenchyma cell membranes surrounding vessel elements. They push out into vessel elements causing blockage of the vessel and provide a framework for other sealant materials to be deposited, like suberin. Local ray cells use remaining stored energy to begin shedding cells in more interior locations.

heartwood = a central core of internally shed dead xylem and rays (wood) which can have their cell volumes or walls filled with defensive or waste materials. Heartwood can be darker, lighter, or the same color as sapwood. Some forms of defensive compartmentalization processes can generate chemically modified xylem which is not true heartwood but can be mistaken for heartwood.

pith = a residual small central core of primary tissue generated in an initial growing point before any secondary growth. Between the exterior epidermis / primary cortex and interior central pith, all other cell layers visible are generated by secondary growth from lateral meristems. Pith is surrounded with a sheath of special parenchyma cells called the medullary sheath or layer. Ray cells do not penetrate or breach the medullary sheath into the pith. Pith is not found in true tree roots, but is found in horizontal stem tissues in soil like rhizomes.

Cambium

The cambium is a cell generation zone which blends (within several cell thicknesses) inward into the xylem (wood) and outward into the phloem. Cambium occupies the circumference of the wood cylinder which comprises the bulk of a tree. 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, and/or dormant/active timing) initiates coordinated longitudinal and radial expansion of woody tissues in trees. This sheath of newly produced and expanded tissues act 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

Growth layers within a tree can be visualized in a simple form by use of conical shapes for growth increments. Figure 2. As trees elongate and expand (grow) a new layer of xylem (a three dimensional elongated hollow cone) is build upon and over the immediate past layer of xylem. Over many years, growth increments produce a "nested" or "stacked" set of growth increment cones. Stacking or nesting a series of hollow increment cones on top of one-another allows the whole series to become taller and wider with each new conical layer generated.

A cross-section of these cone stacks in a stem or branch will show a series of growing season increments visible as rings. The thickness of each increment is dependent upon the amount of resources available and used for its construction at each specific location within a tree.

Temperance

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 wood when cut.

Growth Variables

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. 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.

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 changes because of how growth increments in trees are developed and laid-down.

Environmental Constraints

Growth increments ("rings") integrate many site, pest, climate, health, and resource availability problems. The size (radial thickness of growth increments in cross-section) for each growth ring is dependent upon a few dominant features. Figure 3. The four dominant environmental features accounting for most of the variation in growth increment 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.

Biological Constraints

The single dominant biological feature influencing growth increment 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 a Ps / Rs balance. The Ps / Rs balance within a tree helps generate various levels and types of growth regulators, and symbolizes the amount of carbohydrate (CHO) and other processed materials available for cambial growth. These biological growth materials are a direct result of elongation growth and leaf productivity.

Trees have evolved great biological potential to be successful in their environment. The environment generates a host of resistances (ecological and biological friction) to constraint tree growth. Environmental constrainsts limit tree success. Tree biological potential uses and manages environmental constraints to survive and thrive. Figure 4.

Transport Health

Processed materials and growth regulators responsible for cambial growth must also be made available throughout the tree. Cell division processes, cell expansion processes, 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 where growth increment 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.

For example, 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. Figure 5 demonstrates the annual diameter growth rate percent in trees of various diameters and various growth increment widths.

To appreciate interconnections between living cells and actively transporting dead space, a textile model can be used. Figure 6. 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 xylem within one growth increment. Figure 7.

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 living cell with the inside of the other living cell (i.e. continuous cell membrane between cells).

Basket-Weaving

Tree tissues are an interlaced or interwoven basket of axial and radial cells, approximately 90% of which are dead. The axial component is a transporter of resources across long distances (between leaves and root tips). Axial elements include transport and structural cells like tracheids and vessels, structural cells generically called fibers, and storage and defensive cells classified as axial parenchyma.

The radial component is a transporter across short distances as between active phloem and more exterior phellogen or more interior live cells in xylem sapwood, and a materials storehouse. Radial elements include storage and defensive cells classified as ray parenchyma. Living parenchyma cells (both axial and radial) are responsible for storing food (CHO) shipped through phloem.

Dead Health

The axial and radial components form an interconnected system of living cells surrounding and interacting with dead cellular spaces. The three-dimensional interconnections within a growth increment assures cell health, resource use 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. Treestructure is from what living tissues are draped.

Gymno Axial Xylem

The axial component of generic gymnosperm xylem is usually composed of three primary cell types: tracheids which comprise around 90% of axial cells; a few axial parenchyma; and epithelial cells (parenchyma around a cavity secreting resin / gum). Tracheid walls vary in thickness and strength. Earlywood tracheids tend to have thinner walls and latewood tracheids tend to have thicker cell walls. Note, in latewood within one growth increment, a structural cell form with thick walls called a fiber tracheid is found.

Axial parenchyma is a cell form found in older genera. Trees with thin-walled axial parenchyma include podocarps, *Cupressaceae* (<u>Thuja</u>, <u>Cupressus</u>, <u>Chamaecyparis</u>, <u>Juniper</u>), and *Taxodiaceae* (<u>Sequoia</u>, <u>Taxodium</u>). Trees with little or no axial parenchyma include araucaria, *Pinaceae* (<u>Larix</u>, <u>Picea</u>, <u>Pseudotsuga</u>, <u>Tsuga</u>, <u>Abies</u>), and *Taxaceae* (<u>Taxus</u>, <u>Torreya</u>). No axial parenchyma is found in pines (<u>Pinus</u>).

Gymno Radial Xylem

The radial component of generic gymnosperm xylem is usually composed of horizontal ray tracheids, ray parenchyma, and/or epithelial cells surrounding resin ducts. Ray parenchyma are usually found as a single (uniserate) or double (biserrate) form. Ray tracheids can occasionally be found along the sides of ray parenchyma.

Interconnected resin ducts or canals are associated with both axial and radial parenchyma. Resin ducts can be a normal feature of xylem in a species, or can be initiated by injury. For example, normal resin duct occurance is found in Pinus (pines), Larix (larch) and Pseudotsuga (Douglas-fir). Less abundant or rare resin ducts are found in Picea (spruce). Abies (fir), Sequoia, and Taxodium (baldcypress) generate resin canals only upon injury.

Localized and non-interconnected pitch pockets can occur naturally in conifers, or are associated with injuries. They are usually found terminating an annual growth increment. Pitch pockets are elliptical cavities in xylem containing solid or liquid resin.

Angio Xylem

Angiosperm xylem is a more modern evolved tissue than gymnosperm tissues. Axial components of angiosperm xylem is composed of vessel elements, tracheids, axial parenchyma, and structural fibers. Fibers comprise most of the xylem. In addition, there can be two types of parenchyma cell bands visible within an annual increment: apotracheal and paratracheal. The paratracheal parenchyma is associated with, and surrounding, pores. Apotracheal parenchyma is not associated with pores and can be found across and around annual growth increments.

The radial component of angiosperm xylem is composed of ray parenchyma. Ray parenchyma can be found in various forms, and described by how they are radially viewed. Rays can be narrow, wide, or aggregate. An aggregate ray is made of multiple narrow rays closely spaced together.

Phloem

Phloem is responsible for axial transport of growth materials to living cells between leaf and root tip. Phloem is composed of short-lived sieve tubes which collapse quickly as surrounding parenchyma and new sieve tubes continue to enlarge. Because of expansion of surrounding cells, phloem does not show clear annual increment boundaries or any associated early / late season phloem growth appearance changes. Active phloem which is conducting materials is only operating in a radial space outside the vascular cambium of less than a few millimeters wide. The sieve elements are surrounded by companion cells which help maintain transport and structural effectiveness.

As phloem becomes non-conductive, cells are modified to support and protect the actively conducting phloem. Non-conducting phloem begins to be: sclerified with thickened walls; locations for crystal development and deposition; deformed and collapsed; and, pushed aside by phloem ray cell dilation.

Carbo-Loading

Food (sugar) is shipped in active phloem. Food is accumulated in living axial and ray parenchyma as bound clumps of sugars called starch. Starch is a large, chemically and osmotically benign, low maintenance storage substance held within living cells. Starch (larger clumps are called starch granules) can be built or broken-down into component sugars depending upon the needs of a tree and surrounding tissues. Starch granules can be seen within cells and tissues by using iodine stains. Starch construction can only occur in living cells connected to other living cells. Figure 8.

Starch granules remaining in dead cells are unavailable to a tree, but can serve as a resource for other organisms. Living parenchyma cells age, decline and die as they are incrementally grown over each subsequent year. The farther inside a tree a cell lives, the greater chances it will be unable to attract enough resources to live.

Extracting

As interior cells begin to die, in the sapwood / heartwood transition area, they begin to convert any remaining starch and other growth resources into antibiotic and chemically reduced materials. These cells also concentrate materials in cell spaces which are partially modified or degraded.

These dying cell generated materials (extractives) provide less usable materials for any invading organism, and can provide a passive defense for a tree even though the tissue is dead. Some extractives are phenolics and alkaloids which can be toxic to living organisms such as fungi and bacteria. Extractives can cause color and scent changes in heartwood, compared with sapwood. Heartwood is internally shed cell wall materials and volume filled with unused and modified materials.

Miscellaneous Stems

Within woody plant growth there are three other types of stems recognized other than the large upright tree stem. These stem types, though associated with the soil surface, are not roots and have a pith in their center. A rhizome is a horizontal stem which elongates below the soil surface. A stolon is a horizontal stem elongating on the soil surface or in surface litter. A runner is a horizontal stem which elongates above the soil surface in bounds of growth. Figure 9.

Tree stems can generate other growth anomalies. A burl or woody stem / branch gall is comprised of abnormal wood development caused by tree reactions (both organized and unorganized) to insect, mite, thrips, nematodes, chemicals, and pathogens. Burls can range from immense to tiny. Some burl-like growths are caused by natural changes in vascular cambium and growing point generation (not through an exterior stimulant), like the aerial roots under large branches in *Ginkgo* (i.e. chichi), or round nodules of xylem found surrounded by secondary cortex (sphaeroblasts) as in *Zelkova*.

One common diagnostic gall in trees is witches broom. Like a number of other galls there are many causes generating the same type of witches broom. Witches broom is a proliferation of growing points, buds and shoots in one spot along a branch or stem initiated by pest, mechanical, or chemical damage. Witches broom is tree tissue, as opposed to mistletoe (parasitic flowering plant) brooms composed of parasite tissue.

Stem / Roots

The difference between stem tissues and root tissues are significant and represents different services provided to the whole tree by each part. Stems have a pith left from primary shoot tip development and elongation, while root tips develop differently and do not generate a pith. Stem tissue, due to its mechanical loading from gravity and wind are relatively high in lignin concentration while root tissue is intermediate in lignin content. Stem secondary cortex tissue can have chlorophyll, especially on young twigs, while root tissues seldom have a chlorophyll layer just beneath its exterior. Roots can generate pigments, including chlorophyll, when exposed to light, but do not maintain chlorophyl in tissues.

Tropical Apology

Because of the academic bias of location, much of the language surrounding growth increment delineation and anatomical typing of trees are Northern hemisphere and 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.

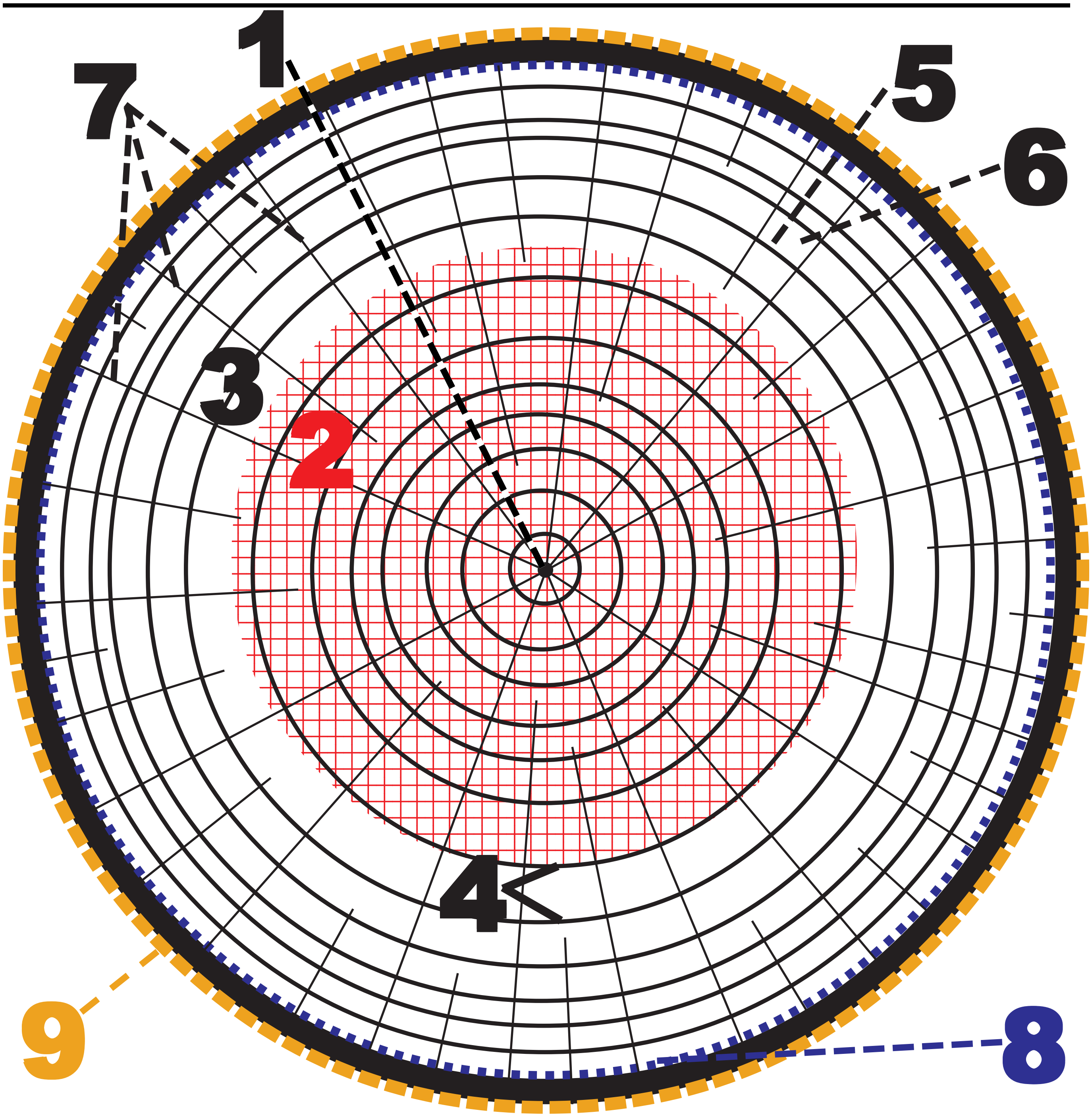

Figure 1: An idealized tree cross-section with more than 13 growing season increments represented.

Key componets: 1) pith (in stems only); 2) heartwood (shaded); 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.

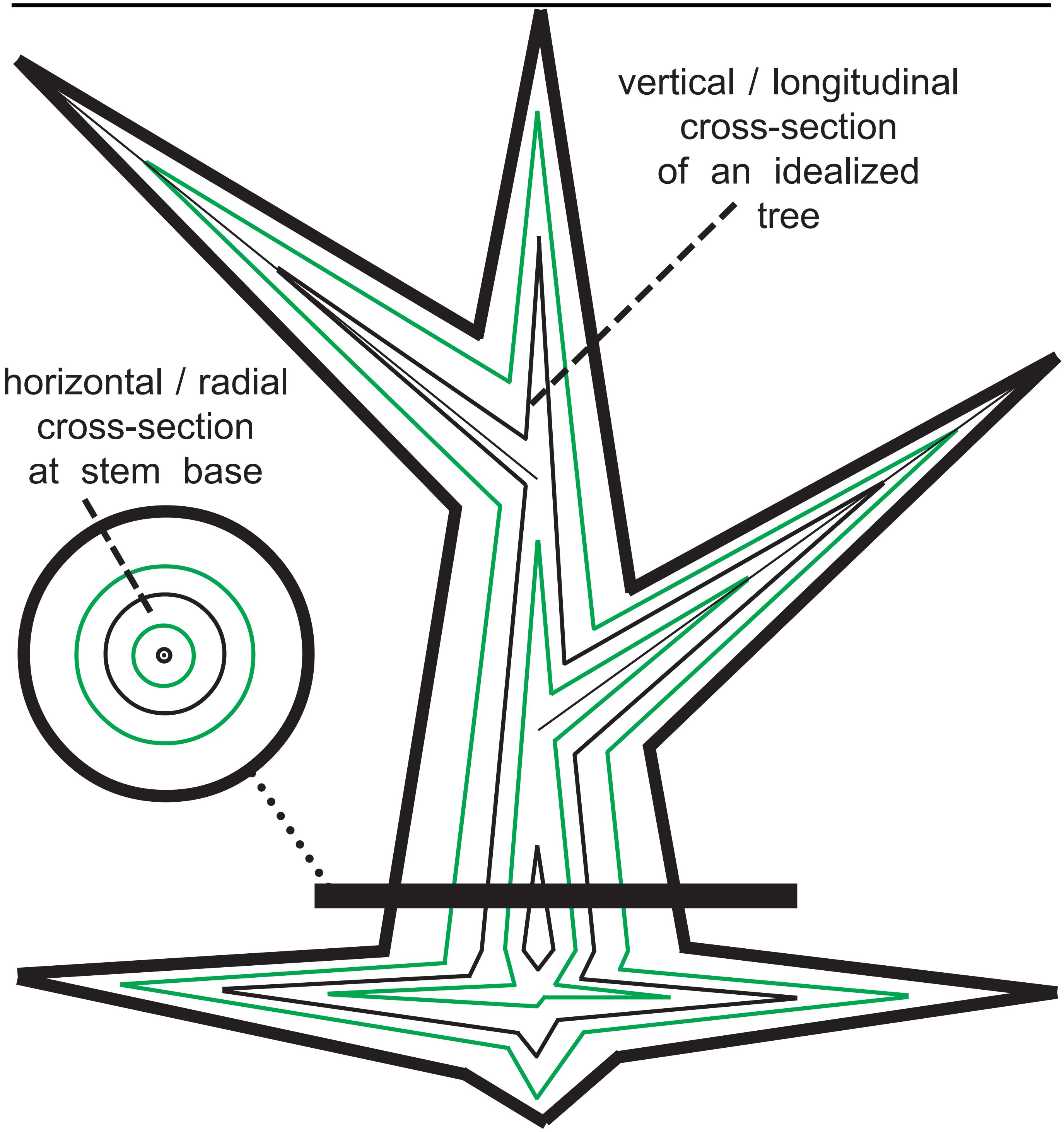

Figure 2: Simplified two dimensional representation of nested cones of tree growth increments shown in a longitudinal cross-section. The broad dark bar across the stem represents location of radial cross-section view of tree showing growth increments or "rings."

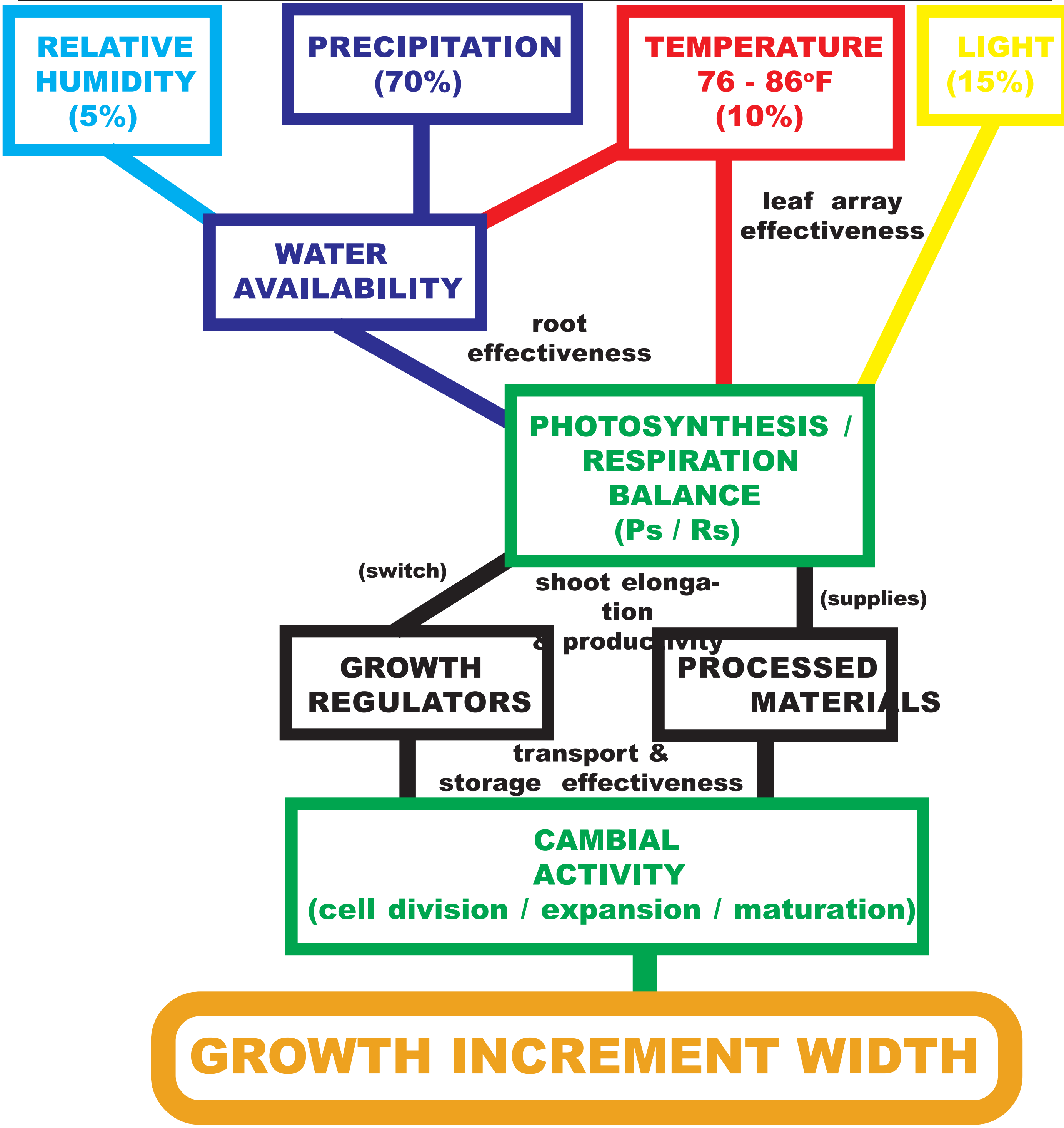

Figure 3: General factors identified as most responsible for tree growth increment (ring) width. Stress can modify any step. Percentages are relative importance values.

Tree Life Resistance

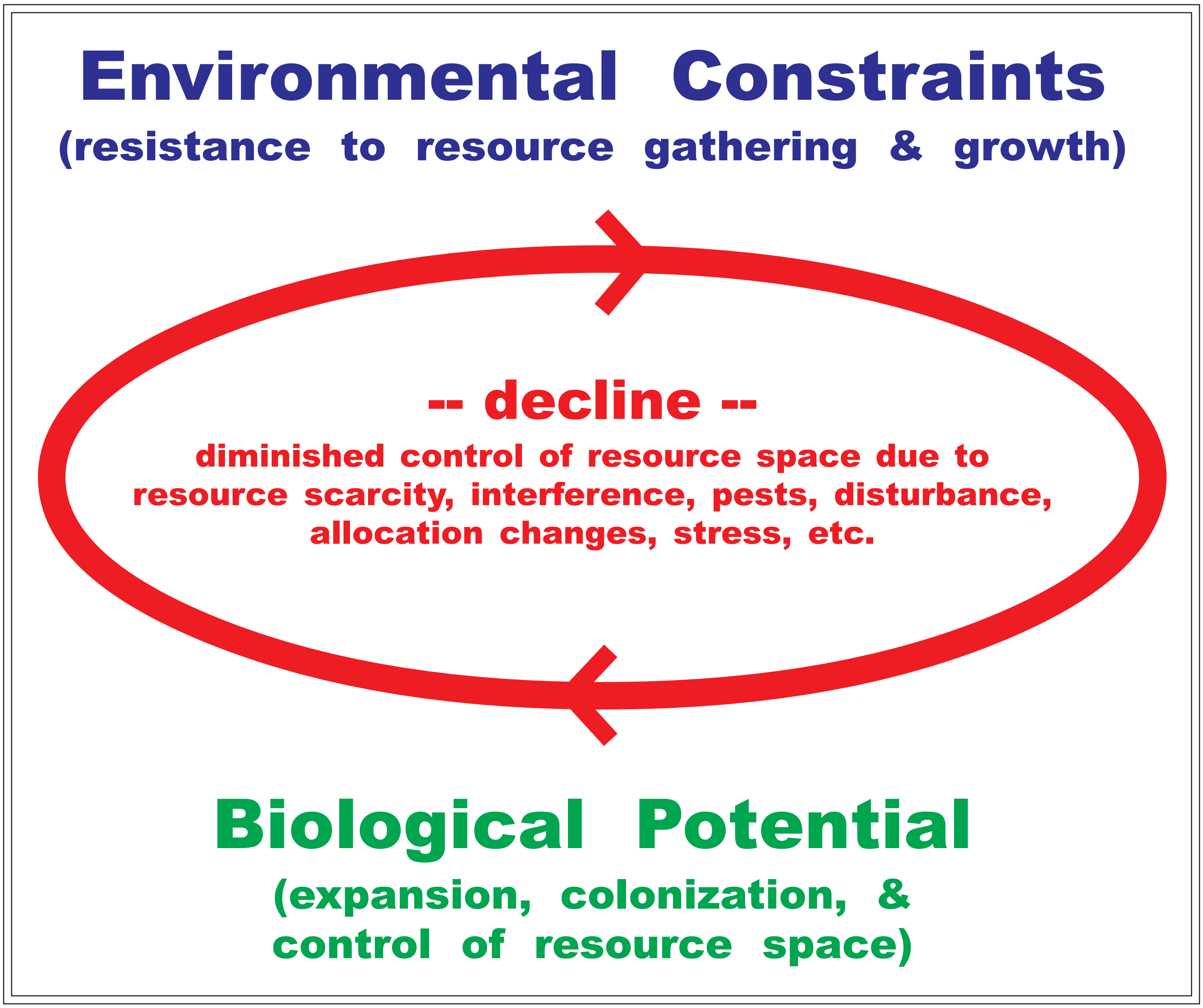

Figure 4: Life circle of a tree. Trees use capabilities to grow while the environment resists.

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	79	30	13	6
10	58	24	11	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	7	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	2	1
52	8	4	2	1
54	8	4	2	1
56	8	4	2	1
58	7	4	2	1

Figure 5: Estimate of annual tree diameter growth rate in percent based upon last year's growth increment (radius inches). For example, a 40 inch diameter tree generating 1/4 inch of radial increment per year is growing at 3% per year.

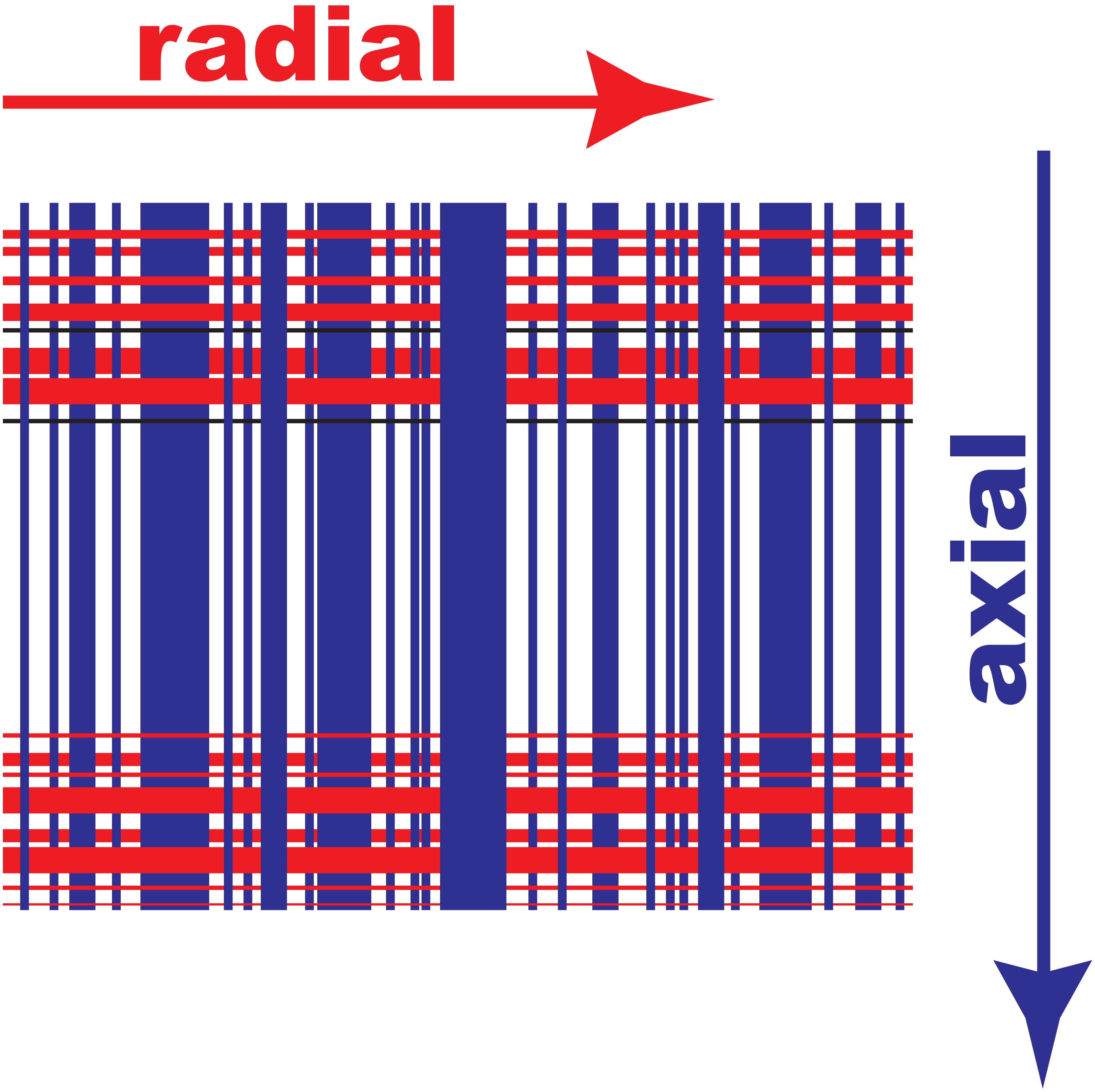

Figure 6: A two dimensional textile model of axial and radial conductors and their connections in a tree. Axial and radial systems can be interconnected where elements cross each other. In a tree, this system is a three-dimensional set of elements.

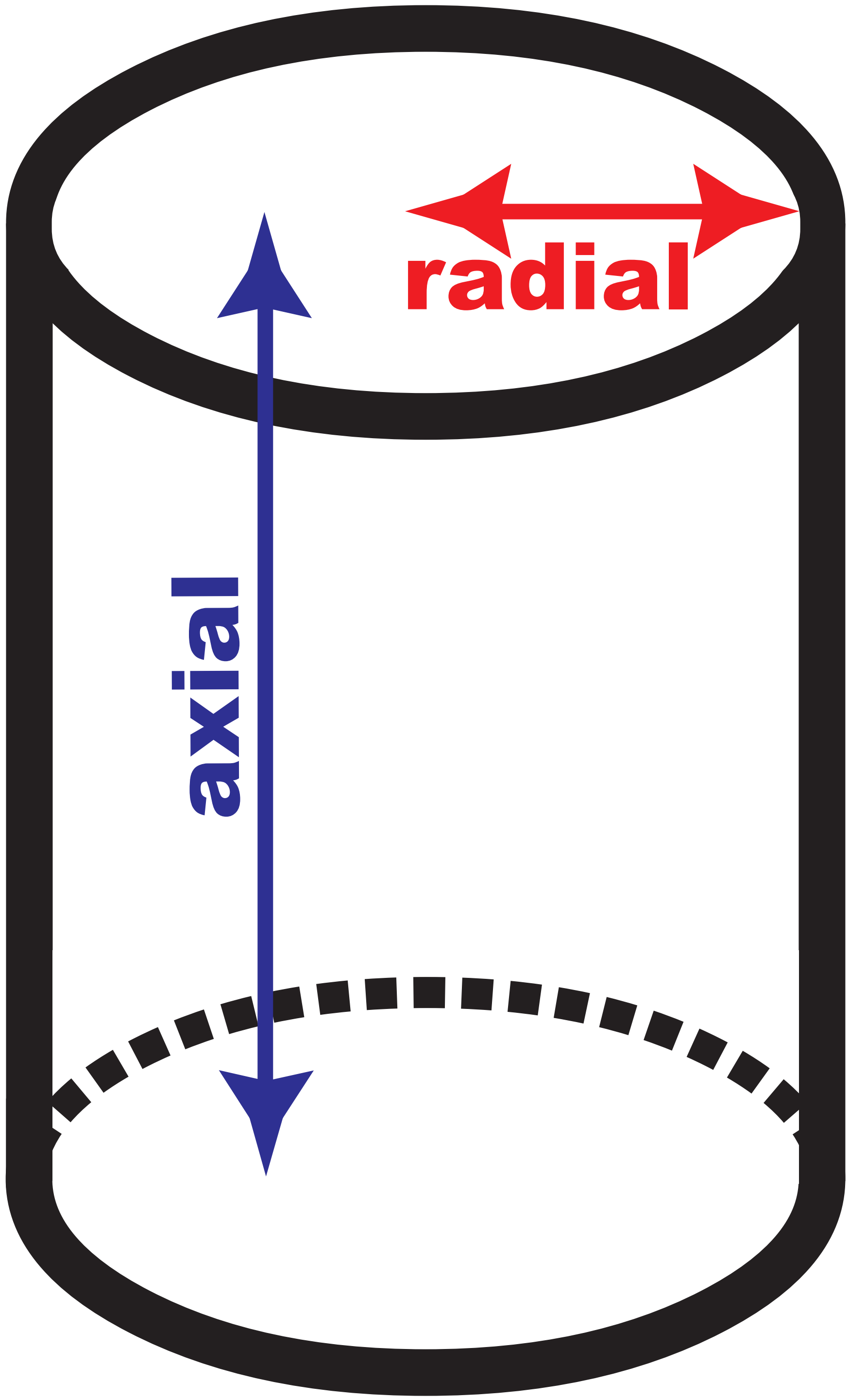

Figure 7: Axial connectors act: as conductors (tracheids & vessels); in mechanical support (fibers); and, for storage and defense (parenchyma). Radial connectors act as conductors, storage, and defense (parenchyma).

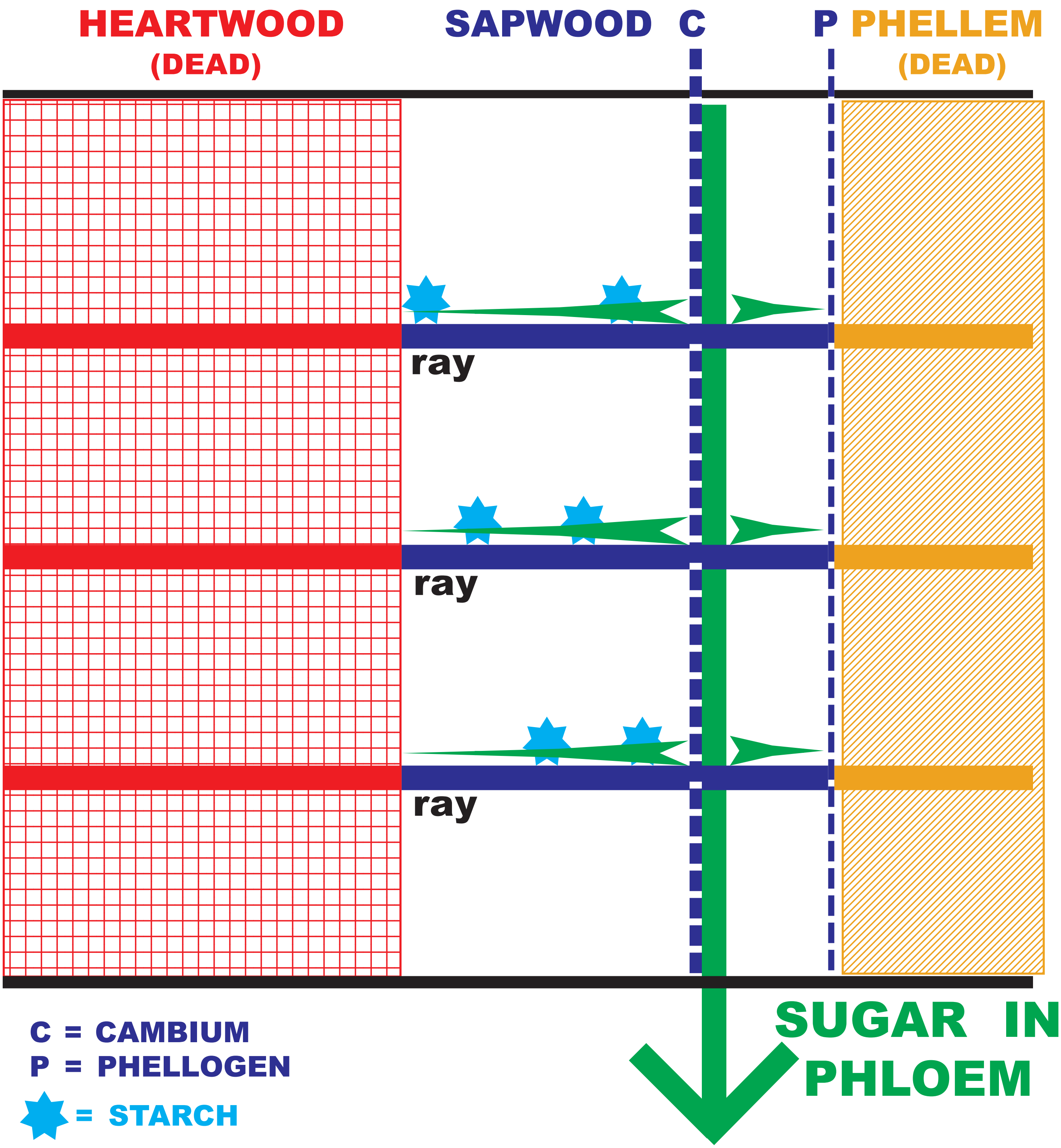

Figure 8: Sugar transport (green arrows) in phloem and rays, and starch storage in ray cells. All sugar transport and storage cells must be living.

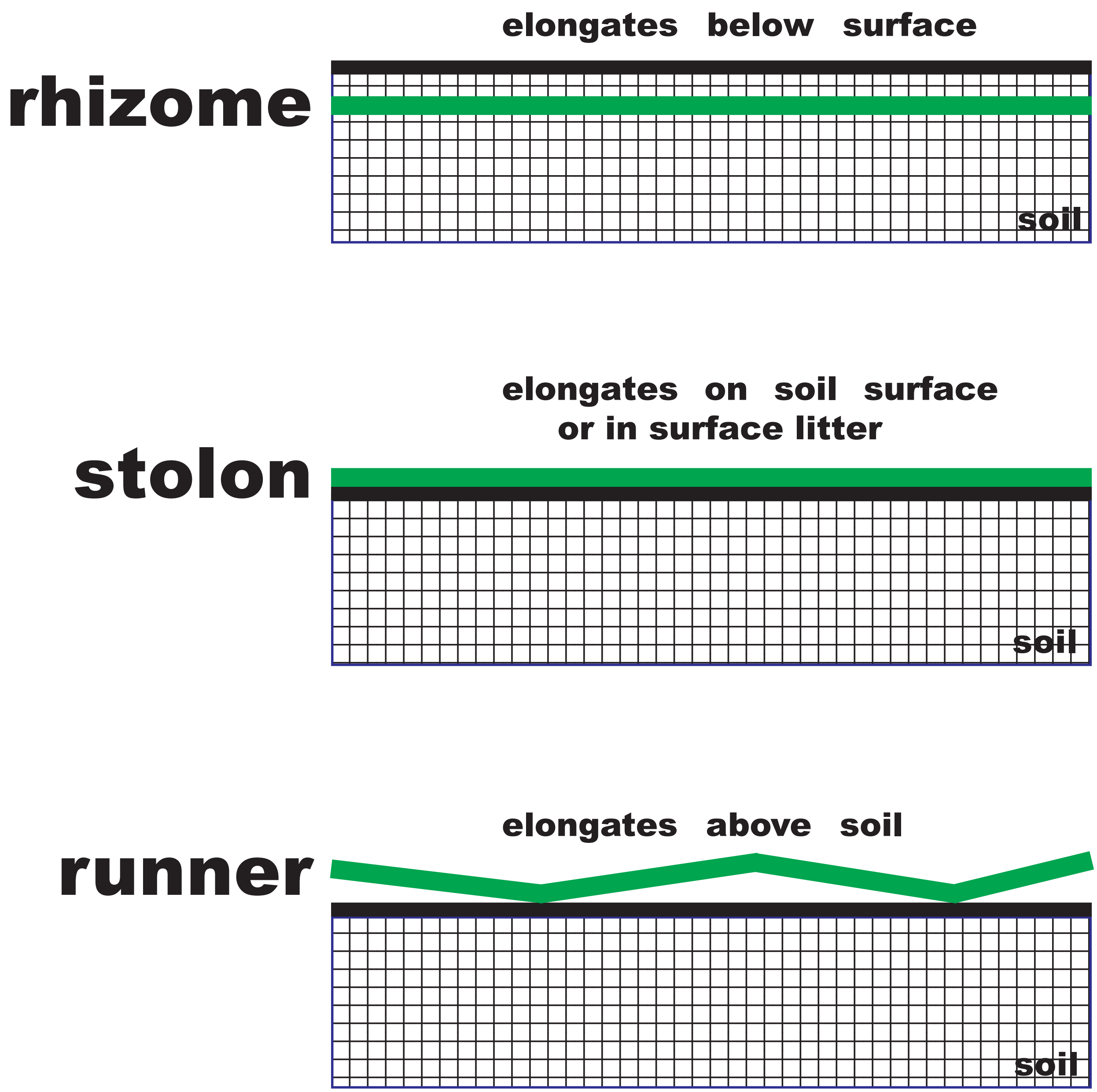

Figure 9: Horizontal stem forms confused with roots, usually not generated by trees.

Citation:

Coder, Kim D. 2022. Tree Anatomy: Stem Components. Warnell School of Forestry & Natural Resources, University of Georgia, Outreach Publication WSFNR-22-76C. Pp.17.