UNIVERSITY OF GEORGIA
Warnell School of Forestry
& Natural Resources

Publication WSFNR-22-67C

Sept. 2022

Tree Anatomy: Leaf Structure & Function

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One of the primary visual keys to tree life and identification are leaves. Leaves provide clues to species, health, and history. Leaves are the workhouses of trees, turning an invisible gas in the air and soil water into carbohydrates using a few essential elements and a sunlight energy source. The term photosynthesis, making life-stuff powered by light, represents the power for 98% of all life on Earth, and demonstrates how tree forms have been sustained over 420 million years. Leaves are the wet cauldrons within which photosynthesis and its associated sustaining processes are contained.

Tree leaves provide visual texture, structure and color. Leaves generate white noise from their movement showing the passage of wind and precipitation. Leaves provide an electron source for ecological parasites in the neighborhood. Leaves are one of two active interfaces between a tree's internal life, and a dry and dangerous environment filled with other living things interfering with each other.

Life Energy

Tree leaves hold and sustain dense pigment nets for capturing light energy. Leaves generate shade by physically blocking and reflecting light. Leaves act as selective light filters using specific energy wavelengths and passing on the rest of the energy spectrum. A leaf reflects, transmits, absorbs, utilizes, and retransmits light energy. The modified light energy environment or shadow behind / below a leaf opposite the sun, is composed of direct shade (umbra) and indirect shade (penumbra) for a distance based upon leaf size (i.e. shade effect distance).

Leaves are the visible and tangible act of seasonal survival for a tree, as well as the host of other gene sets which depend upon trees. Leaves are a factory, transporter, warehouse, and communicator for a tree. Leaves are short-lived organs placed to assure tree life is long and healthy. The life of leaves are the life of trees, even though ephemeral. Flower components and stipules are sometimes confused with leaves, especially if they precede leaf development in Spring. The term hysteranthous denotes leaves developing after flowering.

Function vs. Anatomy

To understand and appreciate the complexity of tree leaf anatomy, all life processes performed must be placed within physical structures to occur. Leaf anatomy is designed for, and symbolizes, leaf function – the function of a leaf is determined by its anatomy. Limited resources within the environment make sure all living things must follow similar rules of conduct in order to survive and successfully reproduce. Anatomy of tree leaves is a study of positions, shapes, surfaces, and volumes sustaining tree life.

Categorized Leaves

To identify native trees using their leaves, several observation points are used which can quickly eliminate many families, genera, and species. The observation order is usually deciding whether leaves are: 1. evergreen or deciduous; 2. simple or compound; and, 3. attached in an opposite or alternate fashion. Figure 1 summarizes the first step in looking critically at native tree leaves -- evergreen or deciduous. Most trees (73%) have deciduous leaves, with 21% having evergreen leaves.

Figure 2 summarizes additional native tree leaf attributes. Simple, compound, needles / scales, and palm-like / fan-like leaves comprise the photosynthetic arrays in our native trees. Most tree leaves are simple (72%), and most of these (86%) are attached to their twig axis alternating from node to node (one leaf per nodal torus).

Leaf Life-Spans

Tree leaves do not last long compared to the rest of a tree. Leaf life-spans can have a number of terms applied. Figure 3 lists the usual terms applied to leaf life-spans, ranging from deciduous to perennial. Leaves are considered perennial if they are functional for three or more years. An evergreen leaf habit (also called sempervirent) mean all leaves are not lost at any one time, but are compartmentalized off over at least one and one-half growing seasons. Figure 4 lists native trees with evergreen leaves.

Persistent leaves remain attached to a tree beyond one year / one growing season. Subevergreen trees have some leaves persisting through winter, most falling with spring shoot and leaf expansion. Figure 5 lists native trees with sub-evergreen or persistent leaves.

Late-deciduous leaves describe leaves which fall in Winter before Spring bud expansion. Deciduous leaves are shed at the end of growing season, also called therophyllous or fugacious (i.e. not permanent and soon-fading). Figure 6 lists native trees with deciduous leaves. Note a large majority (73%) of native trees utilize the deciduous leaf habit. Marcescence leaves die and brown-out attached to the tree in Winter, but fail to fall.

Leaf Position

Leaves are held upon an axis. An axis is the supporting structure for a leaf or place of its attachment, like a twig or shoot. How and where a leaf is connected to its supporting axis can help in identification. Where a leaf begins, and its supporting axis ends, is determined by the position of an axillary bud. This lateral bud is generated in the node / nodal torus at the confluence of the leaf petiole or rachis, and the twig. On the top side of a leaf blade, petiole, or rachis where the leaf and twig join, is the leaf axil. A leaf axil can contain one or several buds, and they can be vegetative, flowering, or both.

The axillary bud is not part of a leaf, but is part of the twig node. All tissues holding the photsynthetic array beyond or more distal from the axillary bud is a leaf. A leaf may have a number of supporting structures and multiple areas of leaf lamina (leaf blade). Figure 7 shows the defining position of an axillary bud in a simple and compound leaf. The axillary bud position defines the leaf beyond.

Up & Down

When looking at a leaf, the apical end is toward the apex or tip of a leaf, sometimes called the distal end. The distal end means the point farthest from its axis of attachment. The basal end of a leaf is toward the base or proximal end where the leaf is attached. A number of terms have been developed to describe parts of a leaf and its areas.

Native Tree Species
Leaf Life-Span

DECIDUOUS	73%
SUB-EVERGREEN / PERSISTENT	6%
EVERGREEN	21%

Figure 1: Native tree species (for 225 tree species) leaf life-spans divided into three categories. Note sub-evergreen / persistent leaves remain on a tree until new leaves expand.

LEAF TYPES

1. SIMPLE LEAVES		**72%**
A. ALTERNATE ATTACHMENT	**86%**	
B. OPPOSITE / WHORLED ATTACHMENT	**14%**	
2. COMPOUND LEAVES		**17%**
A. ALTERNATE ATTACHMENT	**64%**	
B. OPPOSITE ATTACHMENT	**33%**	
3. NEEDLE / SCALE LEAVES		**10%**
4. PALM-LIKE LEAVES		**0.8%**

Figure 2: Statistical breakdown of native tree (225 species) leaf types and attachment forms among native trees.

LEAF LIFE-SPANS

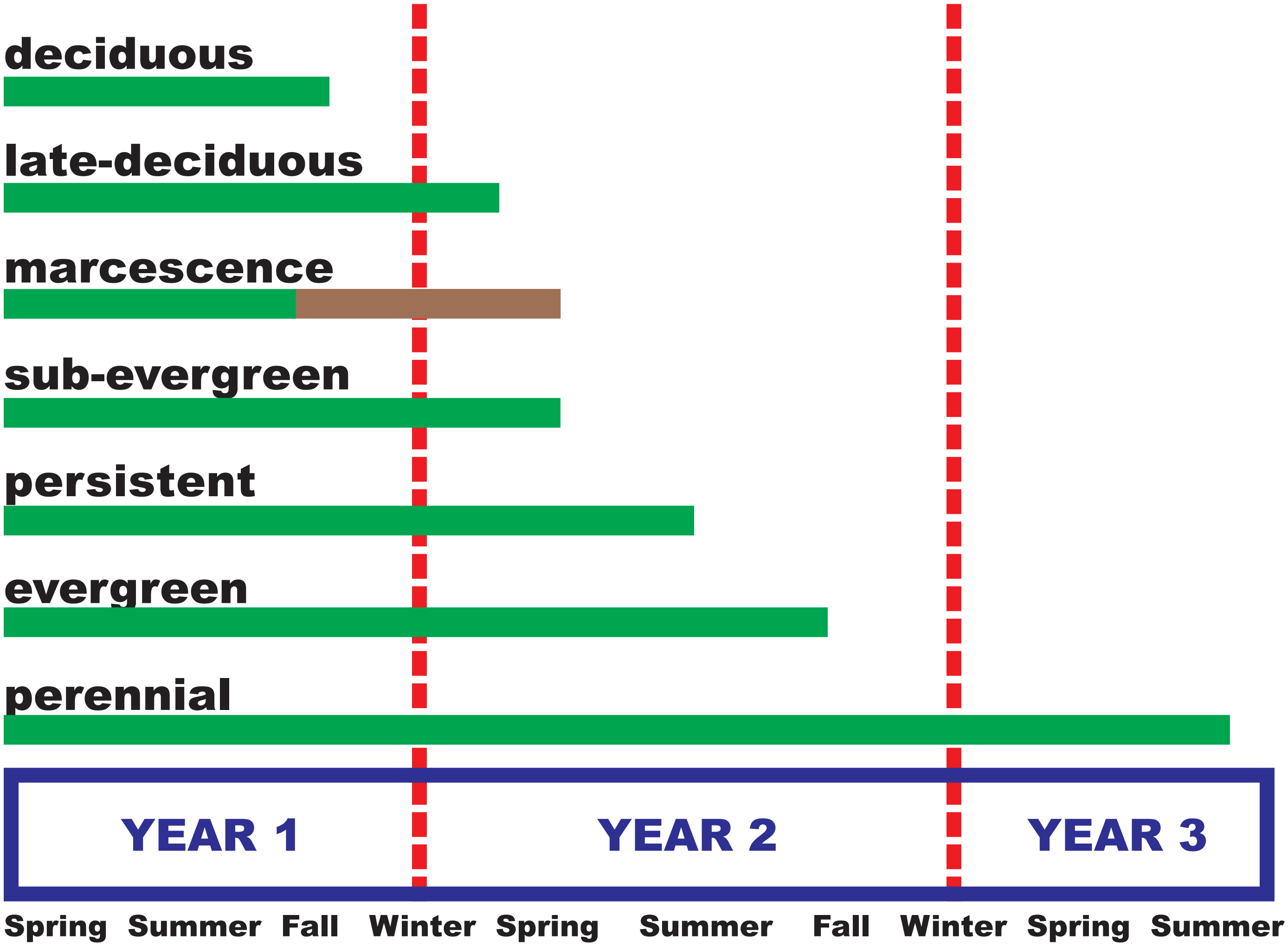


Figure 3: Leaf life-span terms used for length of time leaves are functional and held on tree.
(marcescence leaves are held onto a tree, but are not functional for the entire period.)

Figure 4: Native trees with evergreen leaves.

Abies fraseri	Fraser fir	*Pinus rigida*	pitch pine
Chamaecyparis thyoides	Atlantic whitecedar	*Pinus serotina*	pond pine
Cliftonia monophylla	buckwheat tree	*Pinus strobus*	Eastern white pine
Forestiera segregata	Florida-privet	*Pinus taeda*	loblolly pine
Gordonia lasianthus	loblolly bay	*Pinus virginiana*	Virginia pine
Ilex cassine	dahoon	*Prunus caroliniana*	laurelcherry
Ilex coriacea	large gallberry	*Quercus geminata*	sand live oak
Ilex myrtifolia	myrtle dahoon	*Quercus myrtifolia*	myrtle oak
Ilex opaca	American holly	*Quercus virginiana*	live oak
Ilex vomitoria	yaupon	*Rhododendron catawbiense*	purple-laurel
Illicium floridanum	Florida anisetree	*Rhododendron maximum*	rosebay-laurel
Illicium parviflorum	yellow anisetree	*Sabal palmetto*	cabbage palmetto
Juniperus communis	common juniper	*Serenoa repens*	saw palmetto
Juniperus silicicola	Southern redcedar	*Sideroxylon lanuginosa*	gum bumelia
Juniperus virginiana	Eastern redcedar	*Sideroxylon tenax*	tough bumelia
Kalmia latifolia	mountain-laurel	*Torreya taxifolia*	torreya
Leitneria floridana	corkwood	*Tsuga canadensis*	Eastern hemlock
Lyonia ferruginea	staggerbush	*Tsuga caroliniana*	Carolina hemlock
Magnolia grandiflora	Southern magnolia	*Viburnum cassinoides*	Northern possumhaw
Myrica cerifera	wax-myrtle	*Viburnum dentatum*	Southern arrowwood
Myrica heterophylla	evergreen bayberry	*Viburnum lentago*	nannyberry
Myrica inodora	odorless bayberry	*Viburnum obovatum*	small-leaf arrowwood
Osmanthus americanus	devilwood	*Yucca aloifolia*	Spanish-bayonet
Persea borbonia	red-bay	*Yucca gloriosa*	moundlilly yucca
Persea palustris	swamp-bay		
Pinus echinata	shortleaf pine		
Pinus elliottii	slash pine		
Pinus glabra	spruce pine		
Pinus palustris	longleaf pine		
Pinus pungens	table mountain pine		

Figure 5: Native trees with sub-evergreen or persistent leaves.

Cephalanthus occidentalis	buttonbush
Cyrilla parvifolia	littleleaf titi
Cyrilla racemiflora	swamp titi
Magnolia virginiana	sweetbay
Quercus chapmanii	Chapman oak
Quercus hemisphaerica	laurel oak
Quercus imbricaria	shingle oak
Quercus laurifolia	swamp laurel oak
Quercus nigra	water oak
Quercus palustris	pin oak
Sapindus marginatus	Florida soapberry
Sideroxylon lycioides	buckthorn bumelia
Symplocos tinctoria	sweetleaf
Vaccinium arboreum	farkleberry
Zanthoxylum clava-herculis	Hercules’ club

Figure 6: Native trees with deciduous leaves.

Acer barbatum	Southern sugar maple
Acer leucoderme	chalk maple
Acer negundo	boxelder
Acer nigrum	black maple
Acer pensylvanicum	striped maple
Acer rubrum	red maple
Acer saccharinum	silver maple
Acer saccharum	sugar maple
Acer spicatum	mountain maple
Aesculus flava	yellow buckeye
Aesculus glabra	Ohio buckeye
Aesculus parviflora	bottlebrush buckeye
Aesculus pavia	red buckeye
Aesculus sylvatica	Georgia buckeye
Alnus serrulata	hazel alder
Amelanchier arborea	serviceberry
Aralia spinosa	devil's walkingstick
Asimina parviflora	dwarf pawpaw
Asimina triloba	pawpaw
Baccharis halimifolia	Eastern baccharis
Betula alleghaniensis	yellow birch
Betula lenta	sweet birch
Betula nigra	river birch
Carpinus caroliniana	American hornbeam
Carya aquatica	water hickory
Carya australis	Southern shagbark hickory
Carya cordiformis	bitternut hickory
Carya glabra	pignut hickory
Carya laciniosa	shellbark hickory
Carya myristiciformis	nutmeg hickory
Carya ovalis	red hickory
Carya ovata	shagbark hickory
Carya pallida	sand hickory
Carya tomentosa	mockernut hickory
Castanea dentata	American chestnut
Castanea pumila	chinquapin
Catalpa bignonioides	Southern catalpa
Celtis laevigata	sugarberry
Celtis occidentalis	hackberry
Celtis tenuifolia	Georgia hackberry
Cercis canadensis	redbud
Chionanthus virginicus	fringetree
Cladrastis kentukea	yellowwood
Clethra acuminata	sweet pepperbush
Cornus alternifolia	alternate-leaf dogwood
Cornus florida	flowering dogwood
Cornus foemina	stiff dogwood
Cornus stricta	swamp dogwood
Cotinus obovatus	smoketree
Crataegus aestivalis	mayhaw
Crataegus aprica	sunny hawthorn
Crataegus brachyacantha	blueberry hawthorn
Crataegus calpodendron	pear hawthorn
Crataegus crus-galli	cockspur hawthorn
Crataegus flabellata	fanleaf hawthorn
Crataegus flava	yellow hawthorn
Crataegus intricata	Biltmore hawthorn
Crataegus marshallii	parsley hawthorn
Crataegus phaenopyrum	Washington hawthorn
Crataegus pruinosa	waxy-fruit hawthorn
Crataegus pulcherrima	beautiful hawthorn
Crataegus punctata	dotted hawthorn
Crataegus spathulata	littlehip hawthorn
Crataegus succulenta	succulent hawthorn
Crataegus triflora	three-flower hawthorn
Crataegus uniflora	dwarf hawthorn
Crataegus viridis	green hawthorn
Diospyros virginiana	persimmon
Elliottia racemosa	Georgia plume
Euonymus atropurpureus	burningbush
Fagus grandifolia	American beech
Forestiera acuminata	swamp-privet
Franklinia alatamaha	Franklin tree
Fraxinus americana	white ash
Fraxinus caroliniana	Carolina ash
Fraxinus pennsylvanica	green ash
Fraxinus profunda	pumpkin ash
Fraxinus quadrangulata	blue ash
Gleditsia aquatica	water locust
Gleditsia triacanthos	honeylocust
Halesia carolina	little silverbell
Halesia diptera	two-wing silverbell
Halesia tetraptera	mountain silverbell
Hamamelis virginiana	American witch-hazel
Ilex ambigua	Carolina holly
Ilex amelanchier	sarvis holly
Ilex decidua	possumhaw
Ilex longipes	Georgia holly
Ilex montana	mountain holly
Ilex verticillata	winterberry
Juglans cinerea	butternut
Juglans nigra	black walnut
Liquidambar styraciflua	sweetgum

Figure 6: Native trees with deciduous leaves. (CONTINUED)

Liriodendron tulipifera	yellow-poplar
Magnolia acuminata	mountain cucumber-tree
Magnolia cordata	Piedmont cucumber-tree
Magnolia fraseri	mountain magnolia
Magnolia macrophylla	bigleaf magnolia
Magnolia pyramidata	pyramid magnolia
Magnolia tripetala	umbrella-tree
Malus angustifolia	Southern crabapple
Malus coronaria	sweet crabapple
Morus rubra	red mulberry
Nyssa aquatica	water tupelo
Nyssa biflora	swamp tupelo
Nyssa ogeche	Ogeeche-lime
Nyssa sylvatica	blackgum
Ostrya virginiana	Eastern hophornbeam
Oxydendrum arboreum	sourwood
Pinckneya bracteata	fevertree
Planera aquatica	planertree
Platanus occidentalis	American sycamore
Populus deltoides	Eastern cottonwood
Populus heterophylla	swamp cottonwood
Prunus alabamensis	Alabama cherry
Prunus americana	American plum
Prunus angustifolia	Chickasaw plum
Prunus mexicana	Mexican plum
Prunus pensylvanica	fire cherry
Prunus serotina	black cherry
Prunus umbellata	flatwoods plum
Ptelea trifoliata	hoptree
Quercus alba	white oak
Quercus arkansana	Arkansas oak
Quercus austrina	bluff oak
Quercus breviloba	Gulf oak
Quercus coccinea	scarlet oak
Quercus falcata	Southern red oak
Quercus georgiana	Georgia oak
Quercus incana	bluejack oak
Quercus laevis	turkey oak
Quercus lyrata	overcup oak
Quercus margaretta	sand post oak
Quercus marilandica	blackjack oak
Quercus michauxii	swamp chestnut oak
Quercus minima	dwarf live oak
Quercus montana	chestnut oak
Quercus muehlenbergii	chinquapin oak
Quercus oglethorpensis	Oglethorpe oak
Quercus pagoda	cherrybark oak
Quercus phellos	willow oak
Quercus prinoides	dwarf chinquapin oak
Quercus rubra	Northern red oak
Quercus shumardii	Shumard's oak
Quercus similis	swamp post oak
Quercus sinuata	bastard (Durand) oak
Quercus stellata	post oak
Quercus velutina	black oak
Rhamnus caroliniana	buckthorn
Rhus copallinum	winged sumac
Rhus glabra	smooth sumac
Rhus typhina	staghorn sumac
Robinia hispida	pink locust
Robinia pseudoacacia	black locust
Robinia viscosa	clammy locust
Salix caroliniana	Coastal Plain willow
Salix floridana	Florida willow
Salix nigra	black willow
Salix sericea	silky willow
Sambucus canadensis	American elder
Sambucus simpsonii	Southern elder
Sassafras albidum	sassafras
Sorbus americana	American mountain-ash
Staphylea trifolia	bladdernut
Stewartia malacodendron	silky camellia
Stewartia ovata	mountain camellia
Styrax americanus	American snowbell
Styrax grandifolius	bigleaf snowbell
Taxodium ascendens	pond-cypress
Taxodium distichum	bald-cypress
Tilia americana	American basswood
Tilia caroliniana	Carolina basswood
Tilia floridana	Florida basswood
Tilia heterophylla	white basswood
Toxicodendron vernix	poison sumac
Ulmus alata	winged elm
Ulmus americana	American elm
Ulmus rubra	slippery elm
Ulmus serotina	September elm
Viburnum nudum	Southern possumhaw
Viburnum prunifolium	blackhaw
Viburnum rufidulum	rusty blackhaw
Zanthoxylum americanum	prickly-ash

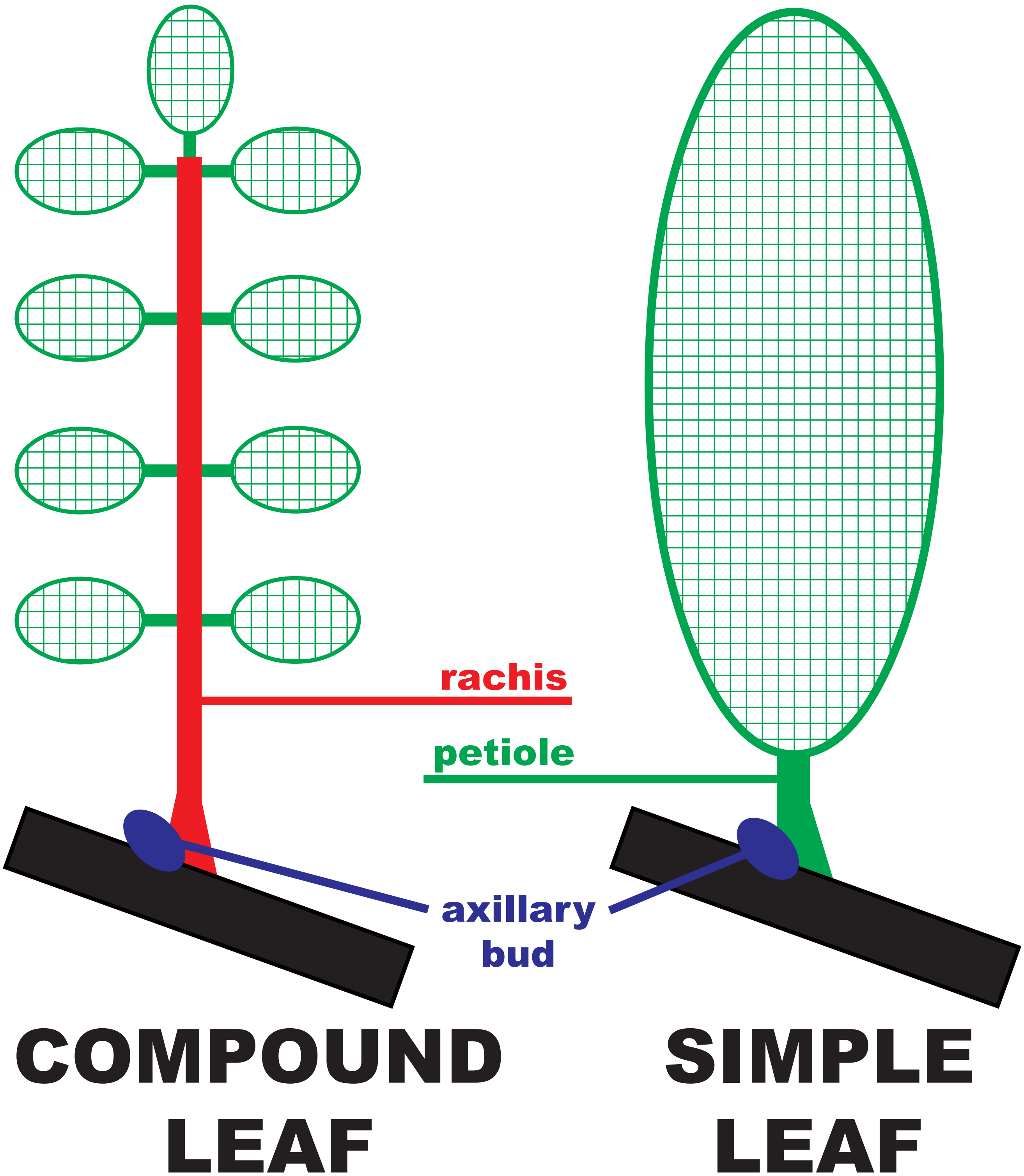


Figure 7: Simple and compound tree leaves.
The axillary bud is not part of a leaf, but grows from the twig at the base of a leaf and shows where a leaf begins.

The apex is at the apical end of a leaf, representing the farthest 25-33% of leaf length (plus any extensions) away from the attachment point. The base of a leaf is the basal end of a leaf, representing the nearest 25-33% of leaf length (plus any extensions) to the attachment point. Figure 8 shows a leaf divided into its apical, middle, and basal thirds lengthwise. Note the presence and position of the axillary bud at the base of the leaf.

A leaf's surfaces can be described as: abaxial for the leaf surface underside or bottom (meaning away from the axis); or, adaxial (antical) for the leaf surface upperside or leaf top (meaning adjacent to or facing the axis). The prefix ab- (away from), and ad- (toward or facing) is used for many situations in tree anatomy. Figure 9 shows the adaxial side of the leaf with the axillary bud at its base. The abaxial surface faces away from the axis and is the underside of a leaf. On the same leaf, the adaxial and abaxial surfaces can be similar or vary greatly, and this trait can help in tree identification.

Midvein.

On many broad leaves, the relative location of the main or primary vascular vein is used as a marker for determining position. An admedial location is toward the midvein from the leaf margin. An exmedial position is away from the midvein toward the leaf margin. The term mediolateral axis of a leaf is from the midvein to leaf margin across the middle (widest point) of the leaf (i.e. leaf radius distance). Figure 10.

Leaves occur in a myriad of shapes and sizes. The symmetry of a leaf blade on either side of the midvien can be used to help identify tree genera and species. A medial symmetrical leaf has a leaf radius which is roughly equal on both sides of the midvein at its widest point (Figure 11 -- A = B). A medial asymmetrical leaf has a leaf radius which is noticeably unequal on either side of the midvein at its widest point (leaf radius A is not equal to leaf radius B).

Leaf base symmetry can be especially useful in identification. A leaf base which is symmetrical means the basal third of the leaf lacks any width differences on either side of the midvein. A leaf base which is asymmetrical shows the basal third of a leaf with distinct blade width differences on either side of the midvein. Figure 12.

Leaf Maps

Phyllotaxy is the mapping of leaf axils (and the leaves they support) as arranged along a twig. Phyllotaxic rank describes how leaves, axils, and buds are arranged in a helical pattern, or how their attachment points spiral along twig length. For example, a bilateral phyllotaxy describes leaves arranged on two opposite sides of an axis.

The position with which leaves are held on their axis can represent identification attributes. A leaf which is accumbent lays against the twig axis. An applanate, appressed, complanate, or compressed leaf is noticeably flattened against the twig axis. All these terms can have subtle differences in how tightly positioned leaves are held to twigs.

Needle, Scale & Palm-Like

For trees with needle-form leaves, there are several unique anatomical components. Needle leaves can be quite broad and feather-like, and still be termed needles. If multiple needles are held together, the dense bundle or tuft of needles is called a fascicle, or the leaf is said to be fasciculate (bundled together). A fascicle sheath is the basal scales enclosing needle bases. Figure 13 lists needle, scale, and awl-shaped leaves, giving the number of needles per fascicle.

Native tree forms with fan-like or palm-like leaves are listed in Figure 14.

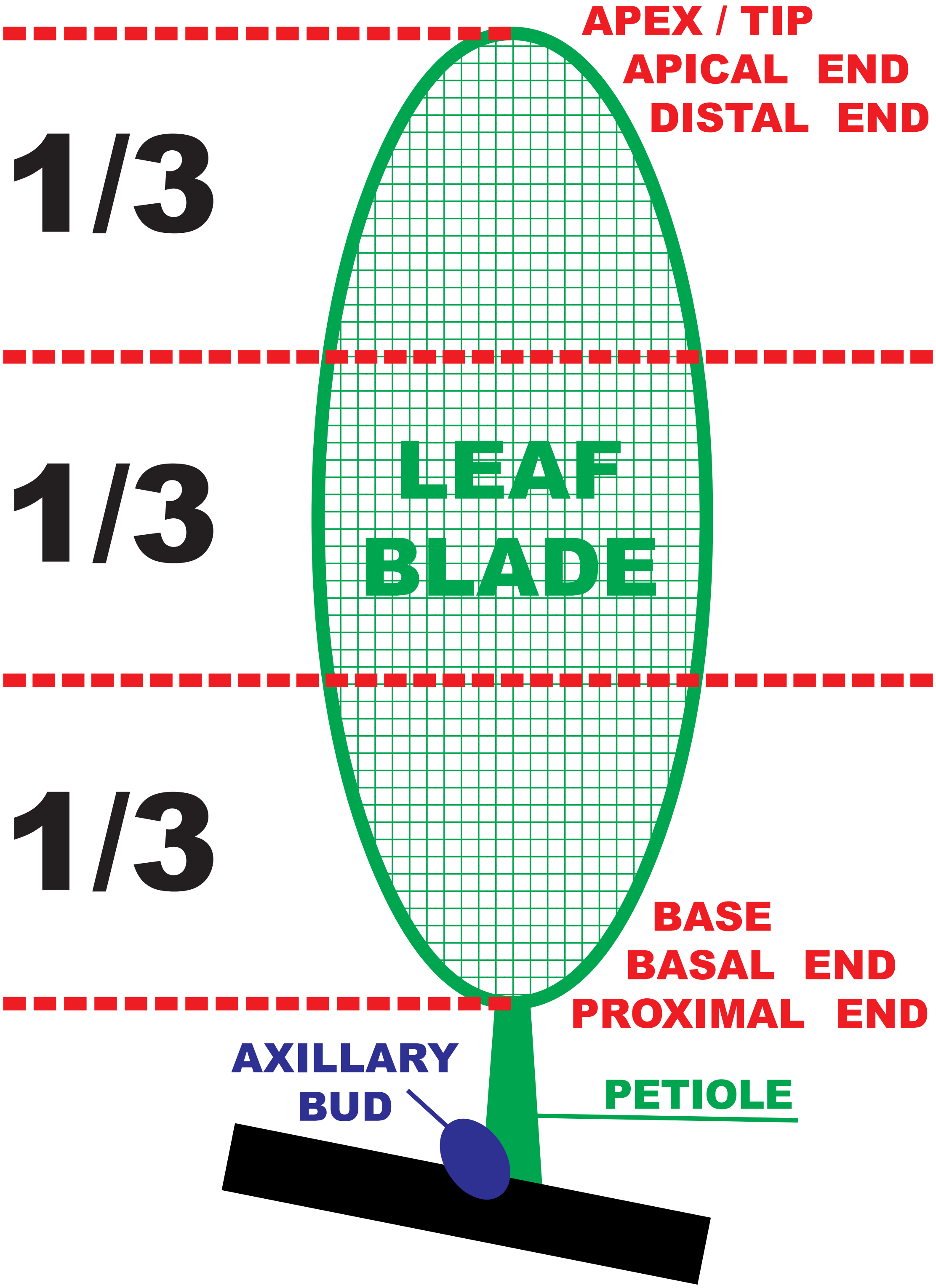


Figure 8: Simple leaf attached to a twig showing three areas of a leaf blade -- tip, middle, and base thirds.
The axillary bud is not part of a leaf, but grows from the twig at the base of a leaf and shows where a leaf begins.

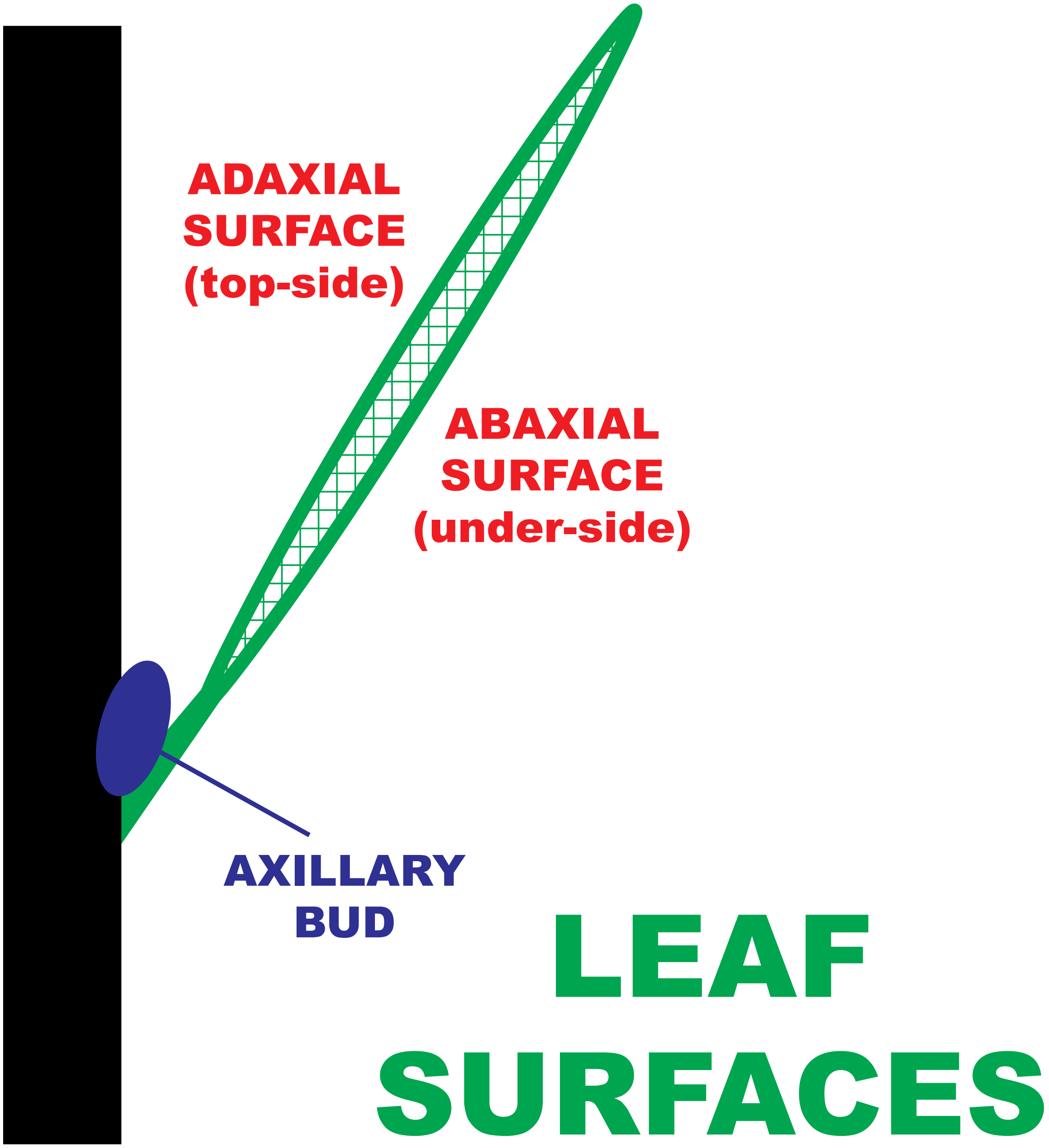


Figure 9: Simple leaf attached to a twig axis showing upper / top surface toward axis (adaxial surface), and lower / botton surface away from axis (abaxial surface).

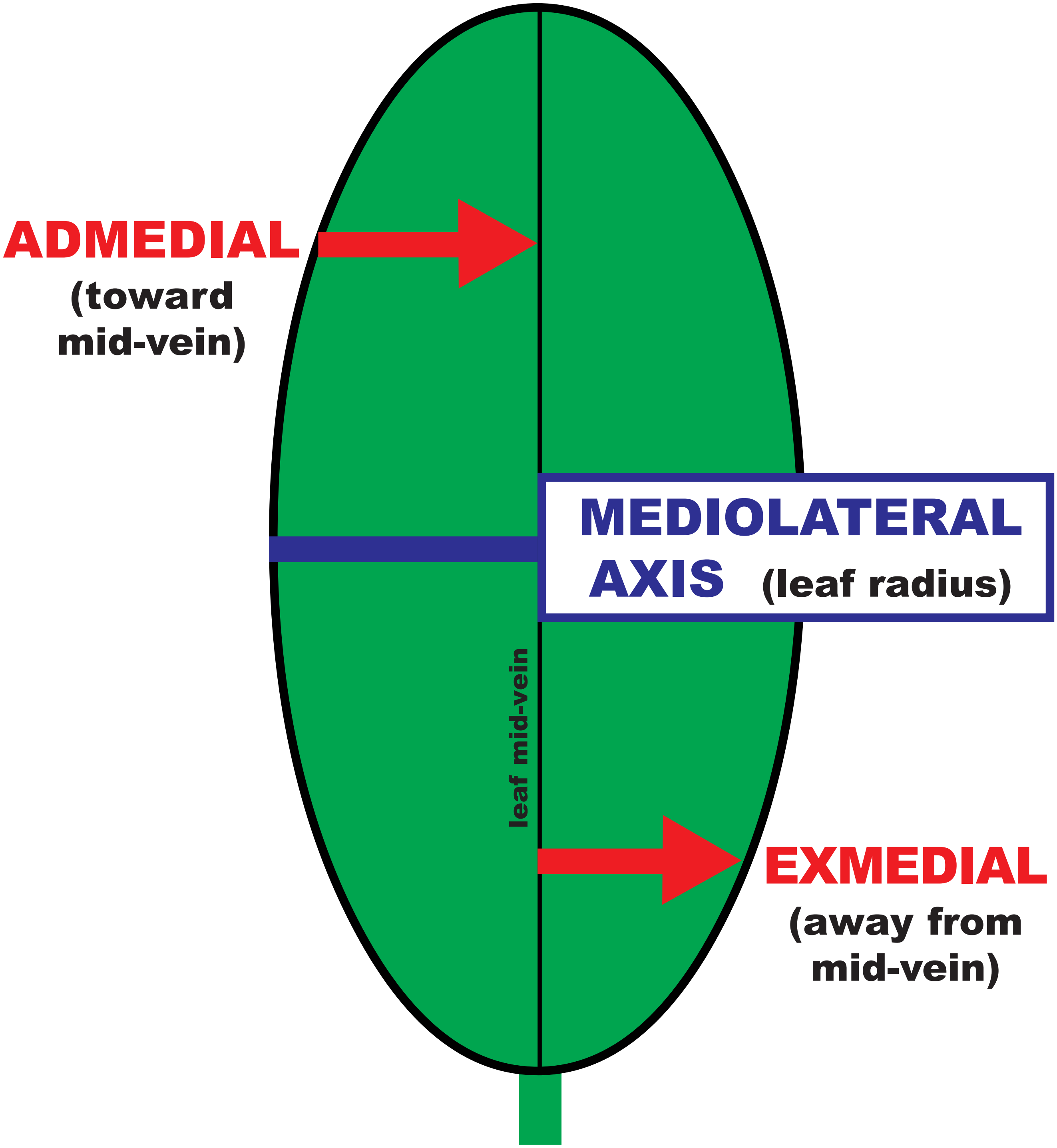
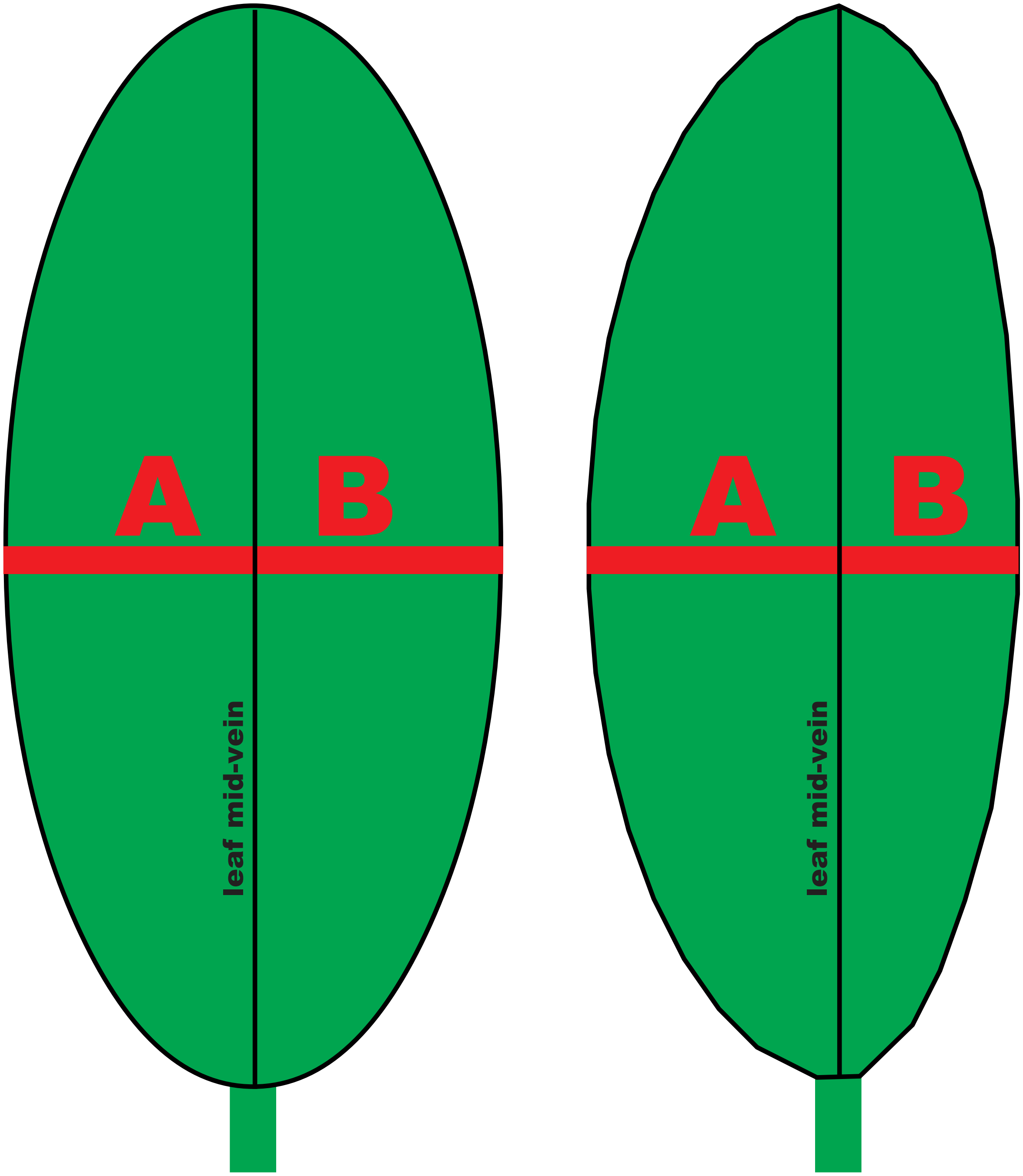


Figure 10: Leaf mid-vein is used for determining relative locations. The leaf radius is the widest point from mid-vein to leaf margin.

LEAF RADIUS

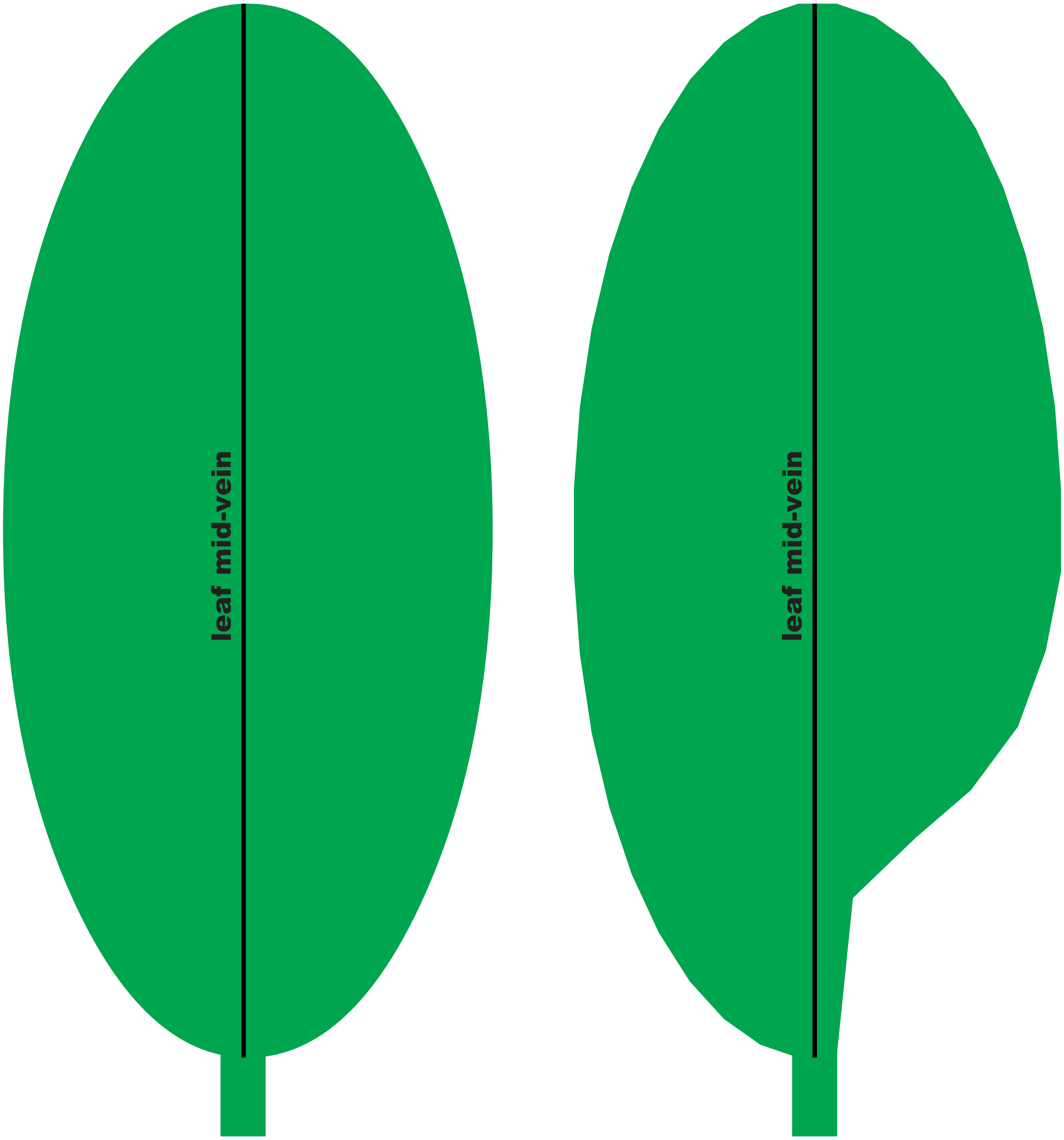


medial symmetrical

medial asymmetrical

Figure 11: Leaf radius is the distance from the mid-vein (medial line) to the leaf margin at its widest point.

LEAF BASE



symmetrical **asymmetrical**

Figure 12: Leaf / leaflet base symmetry across mid-vein.

Figure 13: Native trees with needle, scale, or awl-like leaves, listing scientific name, common name, and number of leaves / needles per bundle on twig.

NEEDLE / SCALE / AWL – SINGLE LEAF		
Abies fraseri	Fraser fir	1
Chamaecyparis thyoides	Atlantic whitecedar	1
Juniperus communis	common juniper	1
Juniperus silicicola	Southern redcedar	1
Juniperus virginiana	Eastern redcedar	1
Taxodium ascendens	pond-cypress	1 FA
Taxodium distichum	bald-cypress	1 FO
Torreya taxifolia	torreya	1
Tsuga canadensis	Eastern hemlock	1
Tsuga caroliniana	Carolina hemlock	1
NEEDLES IN TWOS		
Pinus echinata	shortleaf pine	2-3
Pinus elliottii	slash pine	2-3
Pinus glabra	spruce pine	2
Pinus pungens	table mountain pine	2-3
Pinus rigida	pitch pine	2-3-5
Pinus virginiana	Virginia pine	2
NEEDLES IN THREES		
Pinus echinata	shortleaf pine	2-3
Pinus elliottii	slash pine	2-3
Pinus palustris	longleaf pine	3
Pinus pungens	table mountain pine	2-3
Pinus rigida	pitch pine	2-3-5
Pinus serotina	pond pine	3-5
Pinus taeda	loblolly pine	3
NEEDLES IN FIVES		
Pinus rigida	pitch pine	2-3-5
Pinus serotina	pond pine	3-5
Pinus strobus	Eastern white pine	5

NUMBER OF NEEDLES PER FASICLE / BUNDLE: FO = FEATHER-LIKE OPEN; FA = FEATHER-LIKE APPRESSED. UNDERLINED NUMBER IS MOST COMMON

Figure 14: Native tree species with palm-like or fan-like leaves, listing scientific name and common name.

Sabal palmetto	cabbage palmetto
Serenoa repens	saw palmetto

There are two types of broadleaf forms identified based upon location of the axil bud on its supporting axis: simple leaves and compound leaves. Here simple leaves will be reviewed first. A simple leaf is a primary photosynthetic organ of a tree with a single broad / flat lamina (leaf blade) of mesophyll cells enclosed within an epidermis, usually held on a supporting petiole in association with an axillary bud at its base on the adaxial side. For a tree to be simple leaved is termed integrifolius.

A simple leaf has five generic parts or locations: lamina (blade); midvein; margin; trichomes; and, a connection point to its axis. Figure 15. The lamina or leaf blade is a broad and flattened photosynthetic area expanded in two opposite directions around a primary supporting vein. The midvien is the dominant, primary vascular connections containing tissue running through, and supporting the lamina.

A leaf margin represents the extent and reach of the lamina, or its outer edge. Trichomes (plant hairs) are components of the leaf epidermis which support and protect leaf functions. The leaf connection point is where a leaf is attached to the twig (axis). Figure 16 lists native trees which have simple leaves.

Knowing Differences

Juvenile tissues can generate leaves which are distinctly different from leaves generated by mature or older tissues. A leaf form difference occurring from juvenile to mature generated tissue is considered heteroblastic, if the difference or change is significant, abrupt, and distinct. A leaf form difference is termed homoblastic when there is only a small or gradual change from juvenile to mature tissue generated leaves. A tree can have several forms of leaves. A tree is heterophyllous if there are two or more different leaf forms on the same tree, and homophyllous if all leaves have the same form on the same tree.

There are other types of leaves or leaf forms. These are unusual and rare forms, being more prevalent is specialized environments like deserts and beaches. A phyllode is a green organ which is a modified petiole flattened like a leaf and which photosynthesizes. A cladode is a modified stem flattened like a leaf and which photosynthesizes.

A cladophyll or phylloclade are two terms for a modified stem form (usually not flattened) acting as a functional leaf. Other descriptive forms for specialized leaves include: a cataphyll which is a reduced form of leaf resembling scale-like leaves or appearing like bud scales; pachyphyllous is term for having thick leaves; and, sclerophyll is a hard, stiff leaf form which is heavily cutinized.

As leaves show stress from pests or resource issues, their shapes and functions can change. For example as the normal high maintenance chlorophyll pigment begins to fade due to stress, more yellow and beige colors of carotenoid pigments are exposed. One term defining a yellowing problem is etiolation. Etiolation is the abnormal yellowing or bleaching of a leaf, along with leaf stunting and long internode production caused by low light levels (little PAR or little intensity). Chlorosis is leaf tissue yellowing or bleaching caused by essential element problems, flood / drought issues, toxins, pesticides, or poor light quality.

Axis Positions

There are four primary ways to describe the position of a leaf on a twig (it's axis): alternate; opposite; sub-opposite; and, whorled. The attachment of leaves on twigs help with identification and can help with understanding normal structural development in a tree crown, as well as places where faults could be generated. Figure 17. shows each of these four leaf attachment positions on a twig. Each leaf is generated at a node or nodal torus.

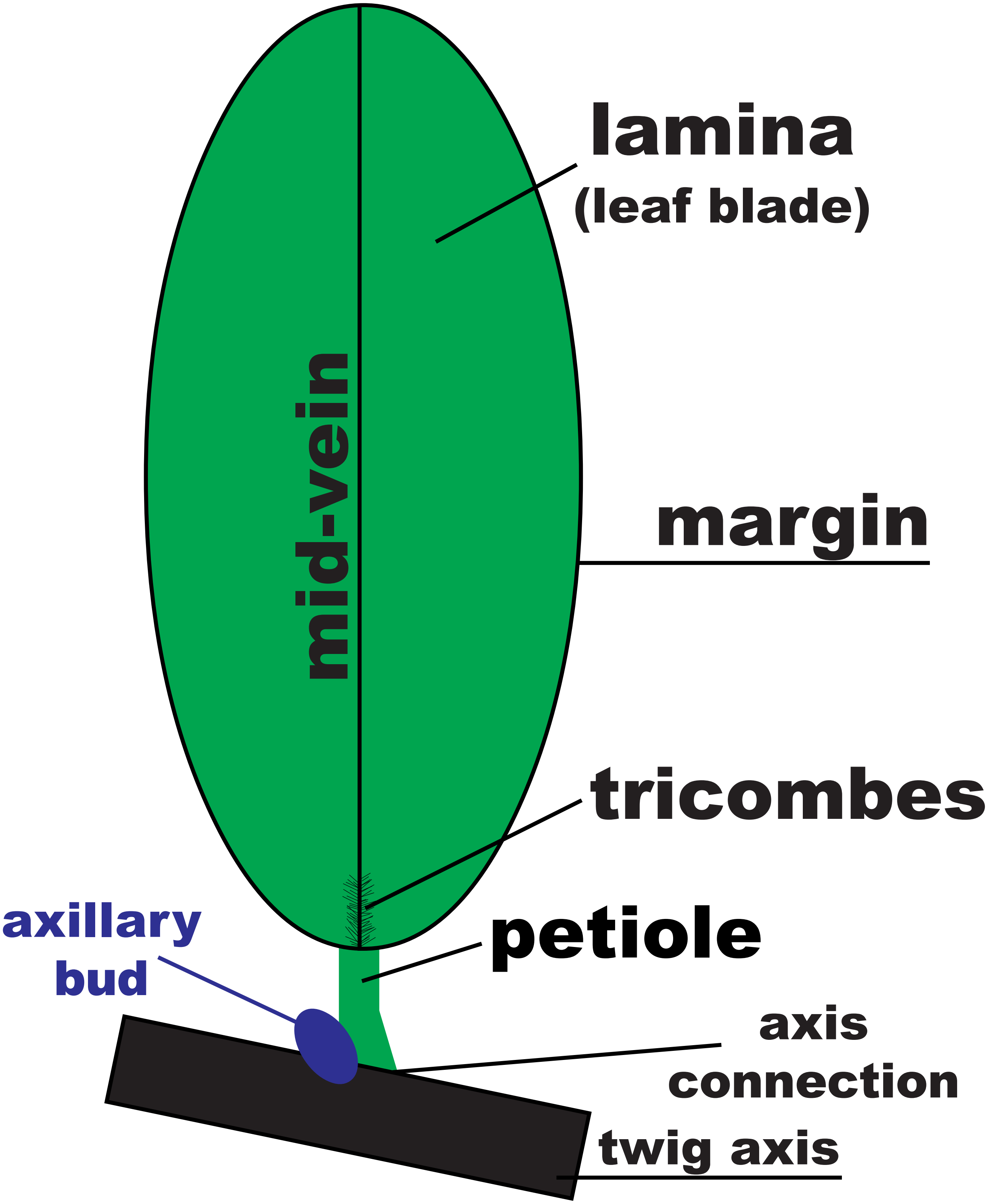


Figure 15: Simple leaf generic part locations.

Figure 16: Native trees with simple leaves.

Acer barbatum	Southern sugar maple
Acer leucoderme	chalk maple
Acer nigrum	black maple
Acer pensylvanicum	striped maple
Acer rubrum	red maple
Acer saccharinum	silver maple
Acer saccharum	sugar maple
Acer spicatum	mountain maple
Alnus serrulata	hazel alder
Amelanchier arborea	serviceberry
Asimina parviflora	dwarf pawpaw
Asimina triloba	pawpaw
Baccharis halimifolia	Eastern baccharis
Betula alleghaniensis	yellow birch
Betula lenta	sweet birch
Betula nigra	river birch
Carpinus caroliniana	American hornbeam
Castanea dentata	American chestnut
Castanea pumila	chinquapin
Catalpa bignonioides	Southern catalpa
Celtis laevigata	sugarberry
Celtis occidentalis	hackberry
Celtis tenuifolia	Georgia hackberry
Cephalanthus occidentalis	buttonbush
Cercis canadensis	redbud
Chionanthus virginicus	fringetree
Clethra acuminata	sweet pepperbush
Cliftonia monophylla	buckwheat tree
Cornus alternifolia	alternate-leaf dogwood
Cornus florida	flowering dogwood
Cornus foemina	stiff dogwood
Cornus stricta	swamp dogwood
Cotinus obovatus	smoketree
Crataegus aestivalis	mayhaw
Crataegus aprica	sunny hawthorn
Crataegus brachyacantha	blueberry hawthorn
Crataegus calpodendron	pear hawthorn
Crataegus crus-galli	cockspur hawthorn
Crataegus flabellata	fanleaf hawthorn
Crataegus flava	yellow hawthorn
Crataegus intricata	Biltmore hawthorn
Crataegus marshallii	parsley hawthorn
Crataegus phaenopyrum	Washington hawthorn
Crataegus pruinosa	waxy-fruit hawthorn
Crataegus pulcherrima	beautiful hawthorn
Crataegus punctata	dotted hawthorn
Crataegus spathulata	littlehip hawthorn
Crataegus succulenta	succulent hawthorn
Crataegus triflora	three-flower hawthorn
Crataegus uniflora	dwarf hawthorn
Crataegus viridis	green hawthorn
Cyrilla parvifolia	littleleaf titi
Cyrilla racemiflora	swamp titi
Diospyros virginiana	persimmon
Elliottia racemosa	Georgia plume
Euonymus atropurpureus	burningbush
Fagus grandifolia	American beech
Forestiera acuminata	swamp-privet
Forestiera segregata	Florida-privet
Franklinia alatamaha	Franklin tree
Gordonia lasianthus	loblolly bay
Halesia carolina	little silverbell
Halesia diptera	two-wing silverbell
Halesia tetraptera	mountain silverbell
Hamamelis virginiana	American witch-hazel
Ilex ambigua	Carolina holly
Ilex amelanchier	sarvis holly
Ilex cassine	dahoon
Ilex coriacea	large gallberry
Ilex decidua	possumhaw
Ilex longipes	Georgia holly
Ilex montana	mountain holly
Ilex myrtifolia	myrtle dahoon
Ilex opaca	American holly
Ilex verticillata	winterberry
Ilex vomitoria	yaupon
Illicium floridanum	Florida anisetree
Illicium parviflorum	yellow anisetree
Kalmia latifolia	mountain-laurel
Leitneria floridana	corkwood
Liquidambar styraciflua	sweetgum
Liriodendron tulipifera	yellow-poplar
Lyonia ferruginea	staggerbush
Magnolia acuminata	mountain cucumber-tree
Magnolia cordata	Piedmont cucumber-tree
Magnolia fraseri	mountain magnolia
Magnolia grandiflora	Southern magnolia
Magnolia macrophylla	bigleaf magnolia
Magnolia pyramidata	pyramid magnolia
Magnolia tripetala	umbrella-tree
Magnolia virginiana	sweetbay
Malus angustifolia	Southern crabapple
Malus coronaria	sweet crabapple
Morus rubra	red mulberry
Myrica cerifera	wax-myrtle
Myrica heterophylla	evergreen bayberry

Figure 16: Native trees with simple leaves. (continued)

Myrica inodora	odorless bayberry
Nyssa aquatica	water tupelo
Nyssa biflora	swamp tupelo
Nyssa ogeche	Ogeeche-lime
Nyssa sylvatica	blackgum
Osmanthus americanus	devilwood
Ostrya virginiana	Eastern hophornbeam
Oxydendrum arboreum	sourwood
Persea borbonia	red-bay
Persea palustris	swamp-bay
Pinckneya bracteata	fevertree
Planera aquatica	planertree
Platanus occidentalis	American sycamore
Populus deltoides	Eastern cottonwood
Populus heterophylla	swamp cottonwood
Prunus alabamensis	Alabama cherry
Prunus americana	American plum
Prunus angustifolia	Chickasaw plum
Prunus caroliniana	laurelcherry
Prunus mexicana	Mexican plum
Prunus pensylvanica	fire cherry
Prunus serotina	black cherry
Prunus umbellata	flatwoods plum
Quercus alba	white oak
Quercus arkansana	Arkansas oak
Quercus austrina	bluff oak
Quercus breviloba	Gulf oak
Quercus chapmanii	Chapman oak
Quercus coccinea	scarlet oak
Quercus falcata	Southern red oak
Quercus geminata	sand live oak
Quercus georgiana	Georgia oak
Quercus hemisphaerica	laurel oak
Quercus imbricaria	shingle oak
Quercus incana	bluejack oak
Quercus laevis	turkey oak
Quercus laurifolia	swamp laurel oak
Quercus lyrata	overcup oak
Quercus margaretta	sand post oak
Quercus marilandica	blackjack oak
Quercus michauxii	swamp chestnut oak
Quercus minima	dwarf live oak
Quercus montana	chestnut oak
Quercus muehlenbergii	chinquapin oak
Quercus myrtifolia	myrtle oak
Quercus nigra	water oak
Quercus oglethorpensis	Oglethorpe oak
Quercus pagoda	cherrybark oak
Quercus palustris	pin oak
Quercus phellos	willow oak
Quercus prinoides	dwarf chinquapin oak
Quercus rubra	Northern red oak
Quercus shumardii	Shumard's oak
Quercus similis	swamp post oak
Quercus sinuata	bastard (Durand) oak
Quercus stellata	post oak
Quercus velutina	black oak
Quercus virginiana	live oak
Rhamnus caroliniana	buckthorn
Rhododendron catawbiense	purple-laurel
Rhododendron maximum	rosebay-laurel
Salix caroliniana	Coastal Plain willow
Salix floridana	Florida willow
Salix nigra	black willow
Salix sericea	silky willow
Sassafras albidum	sassafras
Sideroxylon lanuginosa	gum bumelia
Sideroxylon lycioides	buckthorn bumelia
Sideroxylon tenax	tough bumelia
Stewartia malacodendron	silky camellia
Stewartia ovata	mountain camellia
Styrax americanus	American snowbell
Styrax grandifolius	bigleaf snowbell
Symplocos tinctoria	sweetleaf
Tilia americana	American basswood
Tilia caroliniana	Carolina basswood
Tilia floridana	Florida basswood
Tilia heterophylla	white basswood
Ulmus alata	winged elm
Ulmus americana	American elm
Ulmus rubra	slippery elm
Ulmus serotina	September elm
Vaccinium arboreum	farkleberry
Viburnum cassinoides	Northern possumhaw
Viburnum dentatum	Southern arrowwood
Viburnum lentago	nannyberry
Viburnum nudum	Southern possumhaw
Viburnum obovatum	small-leaf arrowwood
Viburnum prunifolium	blackhaw
Viburnum rufidulum	rusty blackhaw
Yucca aloifolia	Spanish-bayonet
Yucca gloriosa	moundlilly yucca

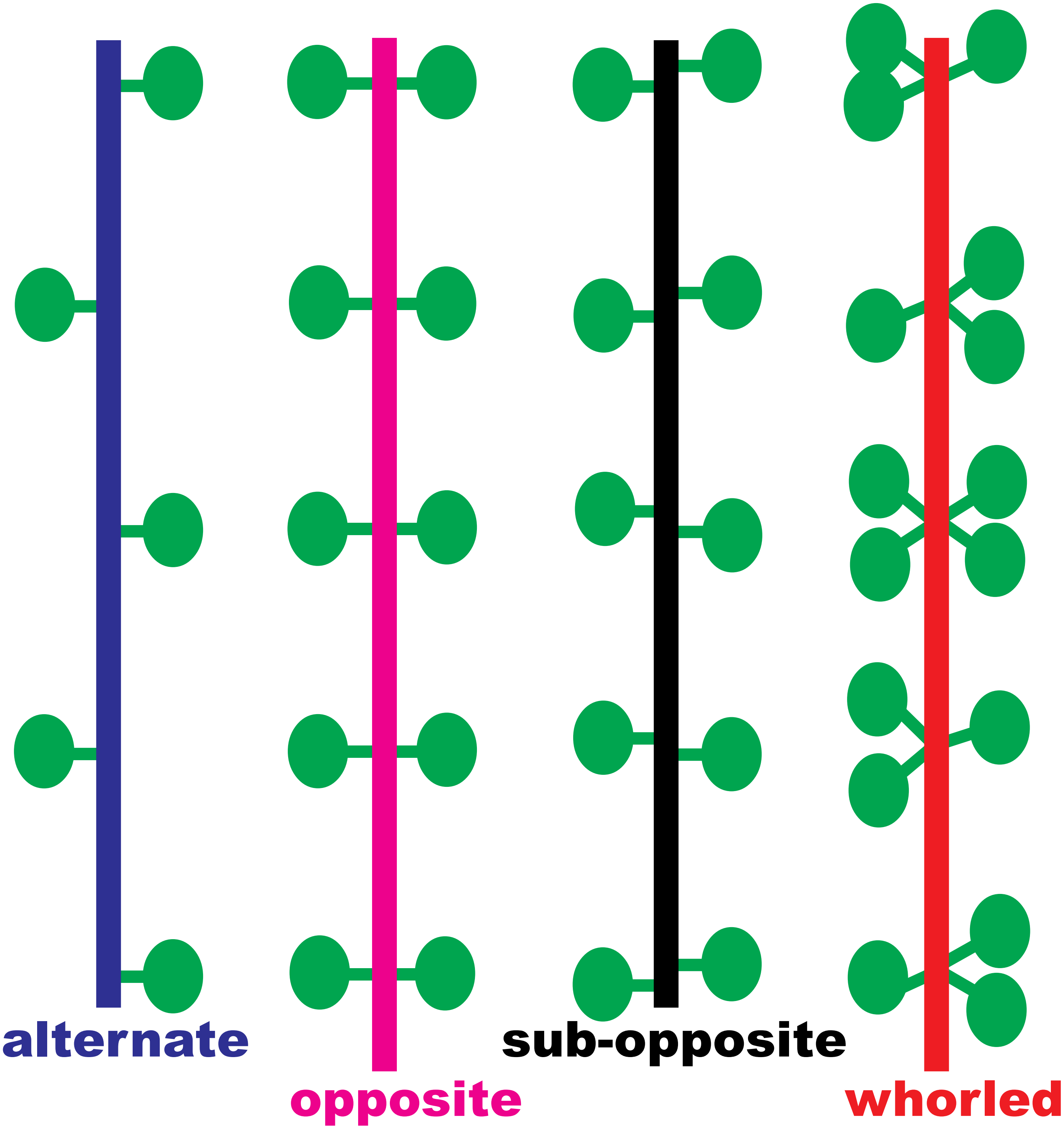


Figure 17: Four primary leaf attachment types. Leaves are generated from nodal torus positions on twigs seperated by internodes.

Alternate

Alternate leaf attachments along a twig are defined as having one leaf attachment point per nodal torus, each separated by an internode. Alternate leaf attachments come is several forms. A distichous alternate attachment form for leaves is when each leaf attachment per nodal torus separated by an internode and generates a two ranked appearance with every other leaf attachment on the same side of the twig. This appearance is of a row of leaves growing along each side of a twig in ordered rows.

A helical alternate leaf attachment form comes from one leaf attachment per nodal torus separated by an internode, which spirals along the twig. This leaf attachment arrangement shows either a dextrose helix from twig base to tip (right-handed spiral), or a sinistrose helix form which spirals along and around the twig, to its tip in a left handed spiral. Figure 18 lists native trees with simple leaves alternately attached to their axis.

Opposite

Opposite leaf attachments along a twig are defined as two leaf attachments points per nodal torus with each pair of leaves separated by an internode. A jugum is a term used for a pair of opposite leaves on the same nodal torus. Opposite leaf attachments come in three general forms: decussate, distichous, and spirodecussate. Figure 19 lists native trees with opposite simple leaf attachment.

Leaf attachments are decussate opposite if the two leaf attachments per nodal torus each separated by an internode, have every other leaf pair on the same sides of the twig and the next nodal torus has attachment points which are perpendicular to the previous or next nodal torus. Each leaf attachment pair is always 90^o (perpendicular) to the next pair.

Leaf attachments which are distichous opposite have two leaf attachments per nodal torus each pair separated by an internode, where the leaf pairs are aligned (two-ranked) with leaf pairs above and below. The twig leaf array can appear flat.

Leaf attachments which are spirodecussate opposite have two leaf attachments per nodal torus each pair separated by an internode, which have leaf pairs in various positions or angles (not at the same or 90^o angle) compared to leaf pairs above and below along the twig.

Sub-Opposite

The third primary leaf attachment form is termed subopposite. Subopposite attachments are when two leaf attachments nearly, but not perfectly align across from each other arising from the same nodal torus on the twig with each pair separated by an internode. The subopposite sub-forms are similar to opposite leaf attachment forms: decussate; distichous; and, spirodecussate.

Decussate subopposite has two leaf attachments nearly but not perfectly across from each other along a twig each pair separated by an internode, with leaf pairs at each node perpendicular to leaf pairs above and below. Distichous subopposite has two leaf attachments nearly but not perfectly across from each other on the same nodal torus along a twig, each pair separated by an internode, with leaf pairs at each nodal torus in alignment (two-ranked) with leaf pairs above and below.

The third sub-form of subopposite is spirodecussate subopposite which has two leaf attachments nearly but not perfectly across from each other on the same nodal torus along a twig, each pair separated by an internode, with leaf pairs at each nodal torus at various angles (not at the same or 90^o angle) to leaf pairs above and below.

Figure 18: Native tree species with simple alternate attached leaves, listing scientific name and common name.

Alnus serrulata	hazel alder
Amelanchier arborea	serviceberry
Asimina parviflora	dwarf pawpaw
Asimina triloba	pawpaw
Baccharis halimifolia	Eastern baccharis
Betula alleghaniensis	yellow birch
Betula lenta	sweet birch
Betula nigra	river birch
Carpinus caroliniana	American hornbeam
Castanea dentata	American chestnut
Castanea pumila	chinquapin
Celtis laevigata	sugarberry
Celtis occidentalis	hackberry
Celtis tenuifolia	Georgia hackberry
Cercis canadensis	redbud
Clethra acuminata	sweet pepperbush
Cliftonia monophylla	buckwheat tree
Cornus alternifolia	alternate-leaf dogwood
Cotinus obovatus	smoketree
Crataegus aestivalis	mayhaw
Crataegus aprica	sunny hawthorn
Crataegus brachyacantha	blueberry hawthorn
Crataegus calpodendron	pear hawthorn
Crataegus crus-galli	cockspur hawthorn
Crataegus flabellata	fanleaf hawthorn
Crataegus flava	yellow hawthorn
Crataegus intricata	Biltmore hawthorn
Crataegus marshallii	parsley hawthorn
Crataegus phaenopyrum	Washington hawthorn
Crataegus pruinosa	waxy-fruit hawthorn
Crataegus pulcherrima	beautiful hawthorn
Crataegus punctata	dotted hawthorn
Crataegus spathulata	littlehip hawthorn
Crataegus succulenta	succulent hawthorn
Crataegus triflora	three-flower hawthorn
Crataegus uniflora	dwarf hawthorn
Crataegus viridis	green hawthorn
Cyrilla parvifolia	littleleaf titi
Cyrilla racemiflora	swamp titi
Diospyros virginiana	persimmon
Elliottia racemosa	Georgia plume
Fagus grandifolia	American beech
Franklinia alatamaha	Franklin tree
Gordonia lasianthus	loblolly bay
Halesia carolina	little silverbell
Halesia diptera	two-wing silverbell
Halesia tetraptera	mountain silverbell
Hamamelis virginiana	American witch-hazel
Ilex ambigua	Carolina holly
Ilex amelanchier	sarvis holly
Ilex cassine	dahoon
Ilex coriacea	large gallberry
Ilex decidua	possumhaw
Ilex longipes	Georgia holly
Ilex montana	mountain holly
Ilex myrtifolia	myrtle dahoon
Ilex opaca	American holly
Ilex verticillata	winterberry
Ilex vomitoria	yaupon
Illicium floridanum	Florida anisetree
Illicium parviflorum	yellow anisetree
Kalmia latifolia	mountain-laurel
Leitneria floridana	corkwood
Liquidambar styraciflua	sweetgum
Liriodendron tulipifera	yellow-poplar
Lyonia ferruginea	staggerbush
Magnolia acuminata	mountain cucumber-tree
Magnolia cordata	Piedmont cucumber-tree
Magnolia fraseri	mountain magnolia
Magnolia grandiflora	Southern magnolia
Magnolia macrophylla	bigleaf magnolia
Magnolia pyramidata	pyramid magnolia
Magnolia tripetala	umbrella-tree
Magnolia virginiana	sweetbay
Malus angustifolia	Southern crabapple
Malus coronaria	sweet crabapple
Morus rubra	red mulberry
Myrica cerifera	wax-myrtle
Myrica heterophylla	evergreen bayberry
Myrica inodora	odorless bayberry
Nyssa aquatica	water tupelo
Nyssa biflora	swamp tupelo
Nyssa ogeche	Ogeeche-lime
Nyssa sylvatica	blackgum
Ostrya virginiana	Eastern hophornbeam
Oxydendrum arboreum	sourwood
Persea borbonia	red-bay

Figure 18: Native tree species with simple alternate attached leaves, listing scientific name and common name. (continued)

Persea palustris	swamp-bay
Planera aquatica	planertree
Platanus occidentalis	American sycamore
Populus deltoides	Eastern cottonwood
Populus heterophylla	swamp cottonwood
Prunus alabamensis	Alabama cherry
Prunus americana	American plum
Prunus angustifolia	Chickasaw plum
Prunus caroliniana	laurelcherry
Prunus mexicana	Mexican plum
Prunus pensylvanica	fire cherry
Prunus serotina	black cherry
Prunus umbellata	flatwoods plum
Quercus alba	white oak
Quercus arkansana	Arkansas oak
Quercus austrina	bluff oak
Quercus breviloba	Gulf oak
Quercus chapmanii	Chapman oak
Quercus coccinea	scarlet oak
Quercus falcata	Southern red oak
Quercus geminata	sand live oak
Quercus georgiana	Georgia oak
Quercus hemisphaerica	laurel oak
Quercus imbricaria	shingle oak
Quercus incana	bluejack oak
Quercus laevis	turkey oak
Quercus laurifolia	swamp laurel oak
Quercus lyrata	overcup oak
Quercus margaretta	sand post oak
Quercus marilandica	blackjack oak
Quercus michauxii	swamp chestnut oak
Quercus minima	dwarf live oak
Quercus montana	chestnut oak
Quercus muehlenbergii	chinquapin oak
Quercus myrtifolia	myrtle oak
Quercus nigra	water oak
Quercus oglethorpensis	Oglethorpe oak
Quercus pagoda	cherrybark oak

Quercus palustris	pin oak
Quercus phellos	willow oak
Quercus prinoides	dwarf chinquapin oak
Quercus rubra	Northern red oak
Quercus shumardii	Shumard's oak
Quercus similis	swamp post oak
Quercus sinuata	bastard (Durand) oak
Quercus stellata	post oak
Quercus velutina	black oak
Quercus virginiana	live oak
Rhamnus caroliniana	buckthorn
Rhododendron catawbiense	purple-laurel
Rhododendron maximum	rosebay-laurel
Salix caroliniana	Coastal Plain willow
Salix floridana	Florida willow
Salix nigra	black willow
Salix sericea	silky willow
Sassafras albidum	sassafras
Sideroxylon lanuginosa	gum bumelia
Sideroxylon lycioides	buckthorn bumelia
Sideroxylon tenax	tough bumelia
Stewartia malacodendron	silky camellia
Stewartia ovata	mountain camellia
Styrax americanus	American snowbell
Styrax grandifolius	bigleaf snowbell
Symplocos tinctoria	sweetleaf
Tilia americana	American basswood
Tilia caroliniana	Carolina basswood
Tilia floridana	Florida basswood
Tilia heterophylla	white basswood
Ulmus alata	winged elm
Ulmus americana	American elm
Ulmus rubra	slippery elm
Ulmus serotina	September elm
Vaccinium arboreum	farkleberry
Yucca aloifolia	Spanish-bayonet
Yucca gloriosa	moundlilly yucca

Figure 19: Native tree species with simple opposite or whorled attached leaves, listing scientific name and common name.

Acer barbatum	Southern sugar maple
Acer leucoderme	chalk maple
Acer nigrum	black maple
Acer pensylvanicum	striped maple
Acer rubrum	red maple
Acer saccharinum	silver maple
Acer saccharum	sugar maple
Acer spicatum	mountain maple
Catalpa bignonioides	Southern catalpa
Cephalanthus occidentalis	buttonbush
Chionanthus virginicus	fringetree
Cornus florida	flowering dogwood
Cornus foemina	stiff dogwood
Cornus stricta	swamp dogwood
Euonymus atropurpureus	burningbush
Forestiera acuminata	swamp-privet
Forestiera segregata	Florida-privet
Osmanthus americanus	devilwood
Pinckneya bracteata	fevertree
Rhamnus caroliniana	buckthorn
Viburnum cassinoides	Northern possumhaw
Viburnum dentatum	Southern arrowwood
Viburnum lentago	nannyberry
Viburnum nudum	Southern possumhaw
Viburnum obovatum	small-leaf arrowwood
Viburnum prunifolium	blackhaw
Viburnum rufidulum	rusty blackhaw

Whorled

The fourth primary leaf attachment form is called whorled (verticillate). Whorled leaf attachments have three or more leaves attached at each nodal torus. A eucyclic whorled form is when the same number of leaves are generated on each nodal torus.

Figure 20 provides an outline of leaf attachment forms / sub-forms on a twig.

Compound Leaves

Some trees have compound leaves, or a single leaf composed of a number of individual leaflets. A leaf's inception point is determined by where the axillary bud is located. All leaf tissues, including all leaflets and their supporting tissues beyond the axillary bud is considered to be one leaf. If multiple separate leaflet blades exist, then the leaf is considered a compound leaf.

A compound leaf is a primary photosynthetic organ of tree with two or more separate, non-contiguous areas of lamina (multiple leaflets), on a supporting rachis with an axillary bud at its base on adaxial side. A leaflet is a distinct, separate unit of leaf lamina, without an axillary bud, attached to a rachis or rachilla within a compound leaf. A decompound leaf has multiple compounding, or multiple orders of divided leaflets. A leaf with many leaflets is termed multifoliate.

Compound leaf leaflets are held on a rachis, not a petiole. A rachis (sometimes historically written as rhachis) is an extended supporting stalk to which leaflets are attached, and the primary axis of a compound leaf. Rachilla is a term for a second order branch from the primary rachis to which leaflets are attached. The leaflet stalk (without an axillary bud) which attaches a leaflet blade to a rachis or rachilla is called a petiolule. Leaflets attached directly to a rachis or rachilla, with no supporting stalk, are termed a sessile leaflet.

Compound Species

Figure 21 lists native trees with compound leaves, and provides the usual number of leaflets on each compound leaf. There are four main types of how leaflets are held in native tree compound leaves: pinnate, bipinnate, trifoliate, and palmate. Compound leaves are attached to their twig axis in alternate and opposite rachis connections. Figure 22 lists native trees which have compound leaves attached alternately along the twig axis. Figure 23 lists compound native tree leaves which are attached to the twg axis in an opposite pattern.

Compound Shapes

Compound leaf forms are generated in three primary forms depending upon how the leaflets are attached: pinnate, palmate, and trifoliate. Two additional unusual compound leaf forms are bifoliate and unifoliate. Compound leaf forms are defined by how and where leaflets are attached to the rachis.

Pinnate compound leaves have leaflets attached along the length of the rachis, and appearance varies by leaflet distribution, presence of a terminal leaflet, and where each leaflet is attached relative to neighboring leaflets. Leaflet distribution across a compound leaf structure is described by the number of sub-divisions or order of compounding seen: Figure 24.

1. Once-pinnate compounding is where leaflets are attached in a pinnate pattern connected to the rachis, or primary pinnately compound.
2. Bipinnate compound leaves have leaflets arranged in pinnate pattern, each on rachilla which are then attached to a rachis, or twice pinnately compound.

LEAF POSITIONS ON AXIS

ALTERNATE

= one leaf attachment per node.

distichous alternate = two ranked, alternating nodes, opposite sides along axis.

helical alternate = spiraling along axis from base to tip.

OPPOSITE

= two leaf attachments per node / nodal torus.

decussate opposite = leaf pairs at each node perpendicular to leaf pairs above & below.

distichous opposite = leaf pairs at each node aligned (two-ranked) with leaf pairs above & below.

spirodecussate opposite = leaf pairs at each node at various angles (not at the same or 90° angle) to leaf pairs above & below .

SUBOPPOSITE

= two leaf attachments per node, nearly but not perfectly across from each other.

decussate subopposite = leaf pairs at each node perpendicular to leaf pairs above & below.

distichous subopposite = leaf pairs at each node in alignment (two-ranked) with leaf pairs above & below.

spirodecussate subopposite = leaf pairs at each node at various angles (not at the same or 90° angle) to leaf pairs above & below.

WHORLED

= three or more leaves attached at each nodal torus.

Figure 20: Outline of leaf attachment forms / sub-forms.

Figure 21: Native trees with compound leaves, listing scientific name, common name, and number of leaflets per leaf.

COMPOUND PINNATE LEAF

Carya aquatica	water hickory	9-17
Carya australis	Southern shagbark hickory	5-7
Carya cordiformis	bitternut hickory	7-11
Carya glabra	pignut hickory	3-5-7
Carya laciniosa	shellbark hickory	7
Carya myristiciformis	nutmeg hickory	5-9
Carya ovalis	red hickory	5-7
Carya ovata	shagbark hickory	5-7
Carya pallida	sand hickory	5-7-9
Carya tomentosa	mockernut hickory	5-9
Cladrastis kentukea	yellowwood	5-11
Fraxinus americana	white ash	5-7-9
Fraxinus caroliniana	Carolina ash	3-7
Fraxinus pennsylvanica	green ash	7-9
Fraxinus profunda	pumpkin ash	7-9
Fraxinus quadrangulata	blue ash	5-7-9
Gleditsia aquatica	water locust	12-24
Gleditsia triacanthos	honeylocust	12-126
Juglans cinerea	butternut	11-17
Juglans nigra	black walnut	15-23
Ptelea trifoliata	hoptree	3-5
Rhus copallinum	winged sumac	9-23
Rhus glabra	smooth sumac	11-27
Rhus typhina	staghorn sumac	11-31
Robinia hispida	pink locust	9-29
Robinia pseudoacacia	black locust	7-21
Robinia viscosa	clammy locust	7-23
Sambucus canadensis	American elder	5-7-9
Sambucus simpsonii	Southern elder	5-9
Sapindus marginatus	Florida soapberry	4-9
Sorbus americana	American mountain-ash	7-17
Toxicodendron vernix	poison sumac	11-31
Zanthoxylum americanum	prickly-ash	7-19
Zanthoxylum clava-herculis	Hercules' club	7-19

(CONTINUED)

Figure 21: Native trees with compound leaves, listing scientific name, common name, and number of leaflets per leaf.

(CONTINUED)

COMPOUND BIPINNATE LEAF

Acacia farnesiana	sweet acacia	8-30
Aralia spinosa	devil's walkingstick	45-54
Gleditsia triacanthos	honeylocust	12-126
Ptelea trifoliata	hoptree	3-5

COMPOUND TRIFOLIATE LEAF

Acer negundo	boxelder	3-7
Staphylea trifolia	bladdernut	3

COMPOUND PALMATE LEAF

Aesculus flava	yellow buckeye	5-7
Aesculus glabra	Ohio buckeye	5-7
Aesculus parviflora	bottlebrush buckeye	5
Aesculus pavia	red buckeye	5
Aesculus sylvatica	Georgia buckeye	5

NUMBER OF LEAFLETS PER COMPOUND LEAF
UNDERLINED VALUE MOST COMMON

Figure 22: Native tree species with compound alternate attached leaves, listing scientific name and common name.

Aralia spinosa	devil's walkingstick
Carya aquatica	water hickory
Carya australis	Southern shagbark hickory
Carya cordiformis	bitternut hickory
Carya glabra	pignut hickory
Carya laciniosa	shellbark hickory
Carya myristiciformis	nutmeg hickory
Carya ovalis	red hickory
Carya ovata	shagbark hickory
Carya pallida	sand hickory
Carya tomentosa	mockernut hickory
Cladrastis kentukea	yellowwood
Gleditsia aquatica	water locust
Gleditsia triacanthos	honeylocust
Juglans cinerea	butternut
Juglans nigra	black walnut
Ptelea trifoliata	hoptree
Rhus copallinum	winged sumac
Rhus glabra	smooth sumac
Rhus typhina	staghorn sumac
Robinia hispida	pink locust
Robinia pseudoacacia	black locust
Robinia viscosa	clammy locust
Sapindus marginatus	Florida soapberry
Sorbus americana	American mountain-ash
Toxicodendron vernix	poison sumac
Zanthoxylum americanum	prickly-ash
Zanthoxylum clava-herculis	Hercules' club

Figure 23: Native tree species with compound opposite attached leaves, listing scientific name and common name.

Acer negundo	boxelder
Aesculus flava	yellow buckeye
Aesculus glabra	Ohio buckeye
Aesculus parviflora	bottlebrush buckeye
Aesculus pavia	red buckeye
Aesculus sylvatica	Georgia buckeye
Fraxinus americana	white ash
Fraxinus caroliniana	Carolina ash
Fraxinus pennsylvanica	green ash
Fraxinus profunda	pumpkin ash
Fraxinus quadrangulata	blue ash
Ptelea trifoliata	hoptree
Sambucus canadensis	American elder
Sambucus simpsonii	Southern elder
Staphylea trifolia	bladdernut

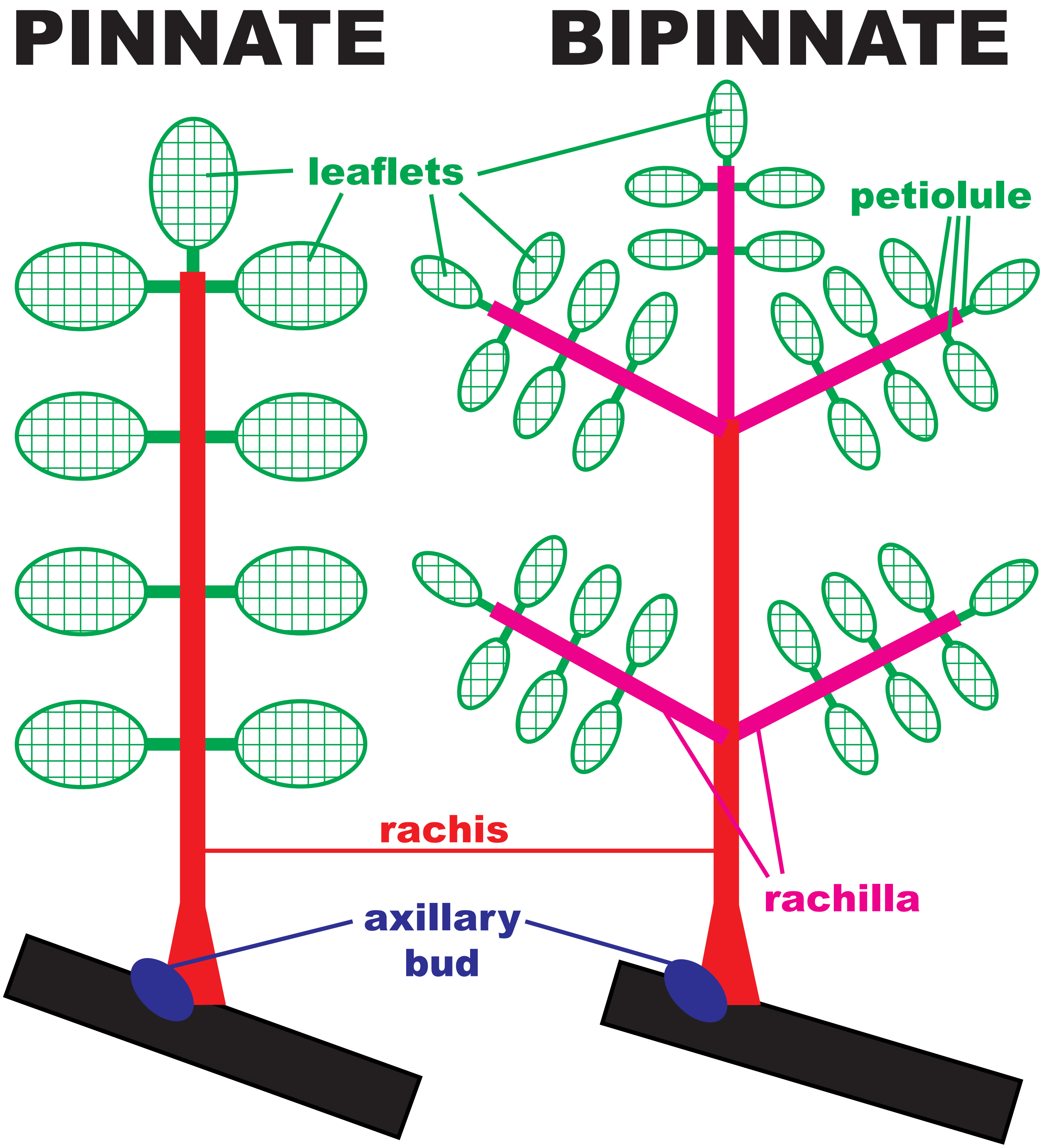


Figure 24: Representation of leaflet distributions in two types of compound leaves showing rachis (main axis), rachilla (secondary axis), and petiolule.

The axillary bud is not part of a leaf, but grows from the twig at the base of a leaf and shows where a leaf begins.

3. Tripinnate compound leaves have leaflets in three sub-levels of pinnate leaflet attachments on rachilla, attached to rachilla, attached to a rachis, or triple pinnately compound.
4. Quadrapinnate compound leaves continues the sub-division of leaflets across the leaf with four sub-levels of pinnate leaflet attachments.

Odd or Even Pinnate

The presence or absence of a terminal leaflet in a pinnately compound leaf can help determine genera and species. If a pinnately compound leaf has an even number of leaflets and no terminal leaflet, the compound leaf is termed an even-pinnate, abrupt pinnate, or a paripinnate compound leaf. If a pinnately compound leaf has an odd number of five or more leaflets with a terminal leaflet, the compound leaf is called odd-pinnate, unequally pinnate, or imparipinnate compound leaf. Figure 25.

Individual leaflet attachment positions along a rachis in a pinnately compound leaf can be opposite, subopposite, or alternate. An opposite pinnate leaflet form has leaflet attachments opposite each other across and along the rachis. Subopposite pinnate leaflet compound leaves have leaflet attachments nearly in pairs, but not perfectly aligned, across from each other on the rachis. Alternate pinnate leaflet compound leaves have leaflet attachments alternating along the length of the rachis.

Palmate

Palmate compound leaves have four or more leaflets attached to a common point at the apex of a rachis. Figure 26. A digitate compound leaf is an antiquated term for palmate compounding meaning diverging from central point. Leaflet attachment position is divided between: a peltate palmate compound leaf where leaflets are attached around the entire end point of rachis; and, a non-peltate palmate compound leaf where leaflets are attached only to a portion of rachis end point.

Trifoliate

Trifoliate compound leaves are generated in sets of three leaflets. Trifoliate compound leaves forms include:

1) pinnately ternate compound leaves with three leaflets separated in a odd-pinnate pattern (one leaflet is terminal) on a rachis;
2) biternate compound leaves with three, three-leaflet groups, each attached to three rachilla attached to the rachis (i.e. three groups of three leaflets, or a total of nine leaflets); or,
3) triternate compound leaves with a triple compound leaflet organization of three leaflets on each of three rachilla, each in-turn on three rachilla, held on a rachis (i.e. nine groups of three leaflets, or a total of 27 leaflets). Figure 27.

Trifoliate compound leaves can have two other forms of subtle leaflet attachment: pinnately trifoliate where three leaflets are separated in an odd-pinnate pattern attached directly to rachis; or, palmately trifoliate where three leaflets are attached at the rachis apex either as sessile leaflets or on petiolule.

Compounded

Figure 28 summarizes the compound leaf forms among native trees. The pinnate form is by far the most commom (76% of all compound leaf species). Trifoliate compound leaves are quite rare (4%). Even more rare

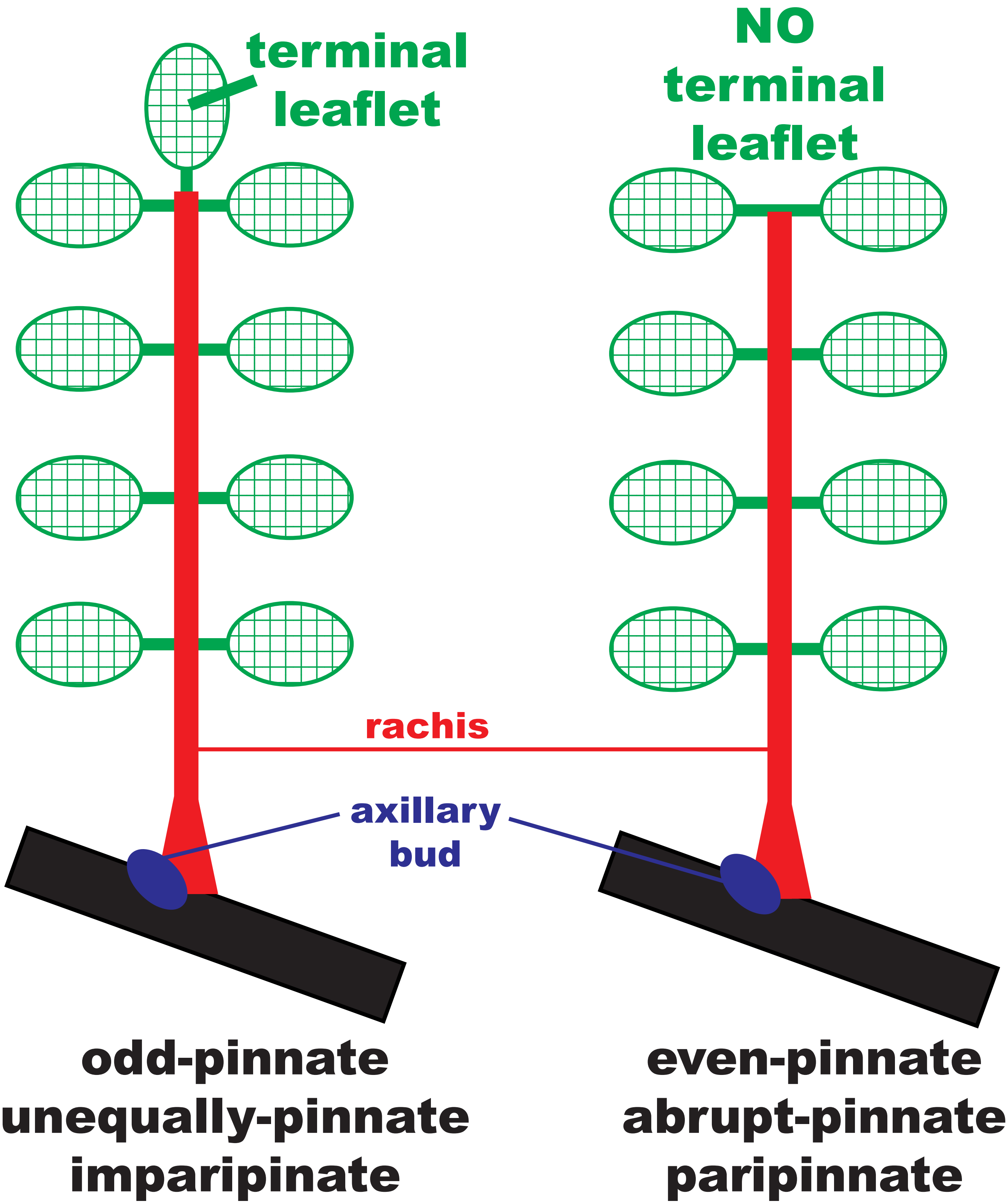


Figure 25: Pinnate compound leaf forms with five or more leaflets.

PALMATE

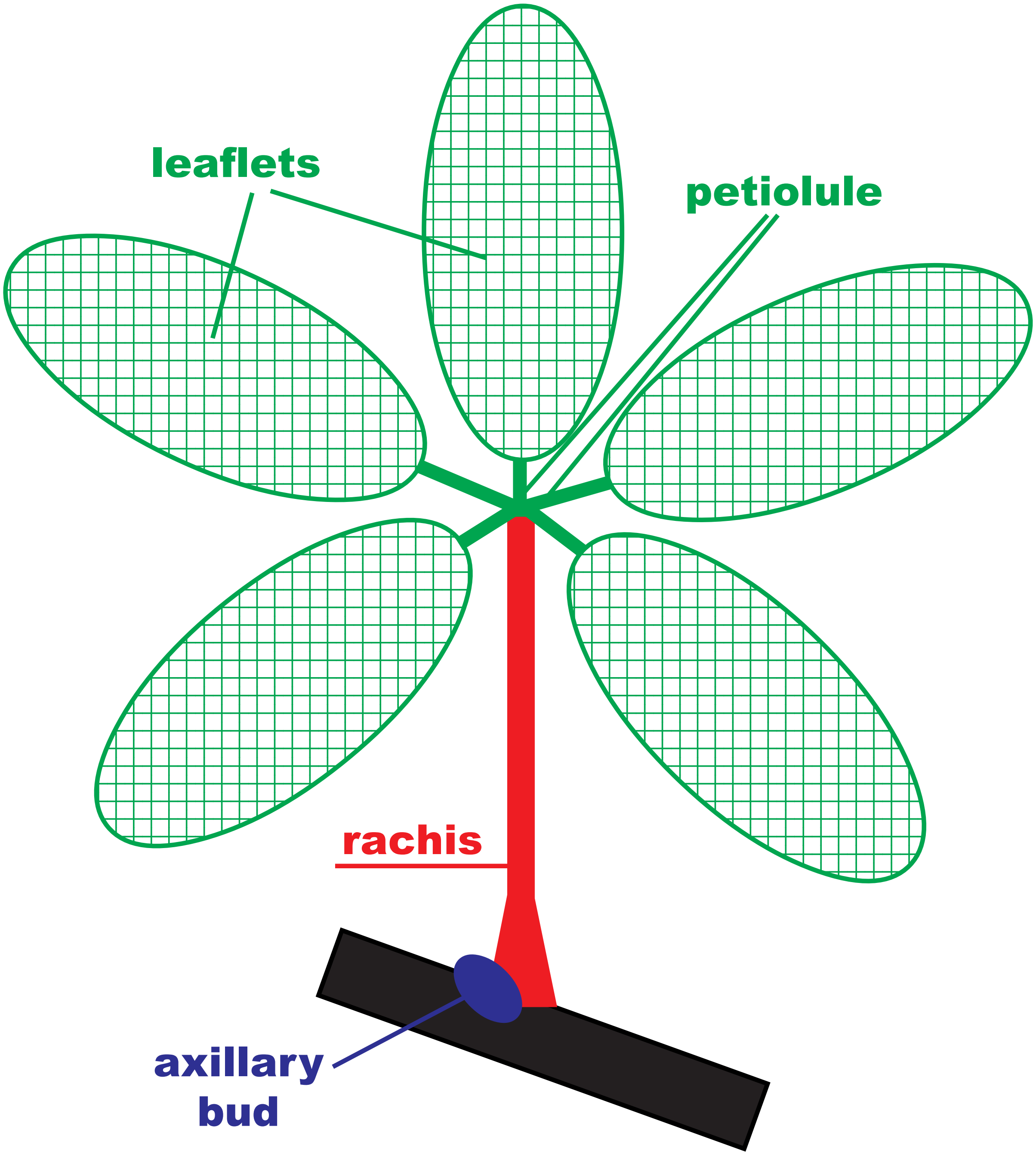


Figure 26: Representation of four or more leaflets (in this case five leaflets) distributed in a palmate compound leaf showing rachis (main axis) and petiolule.
The axillary bud is not part of a leaf, but grows from the twig at the base of a leaf and shows where a leaf begins.

TRIFOLIATE

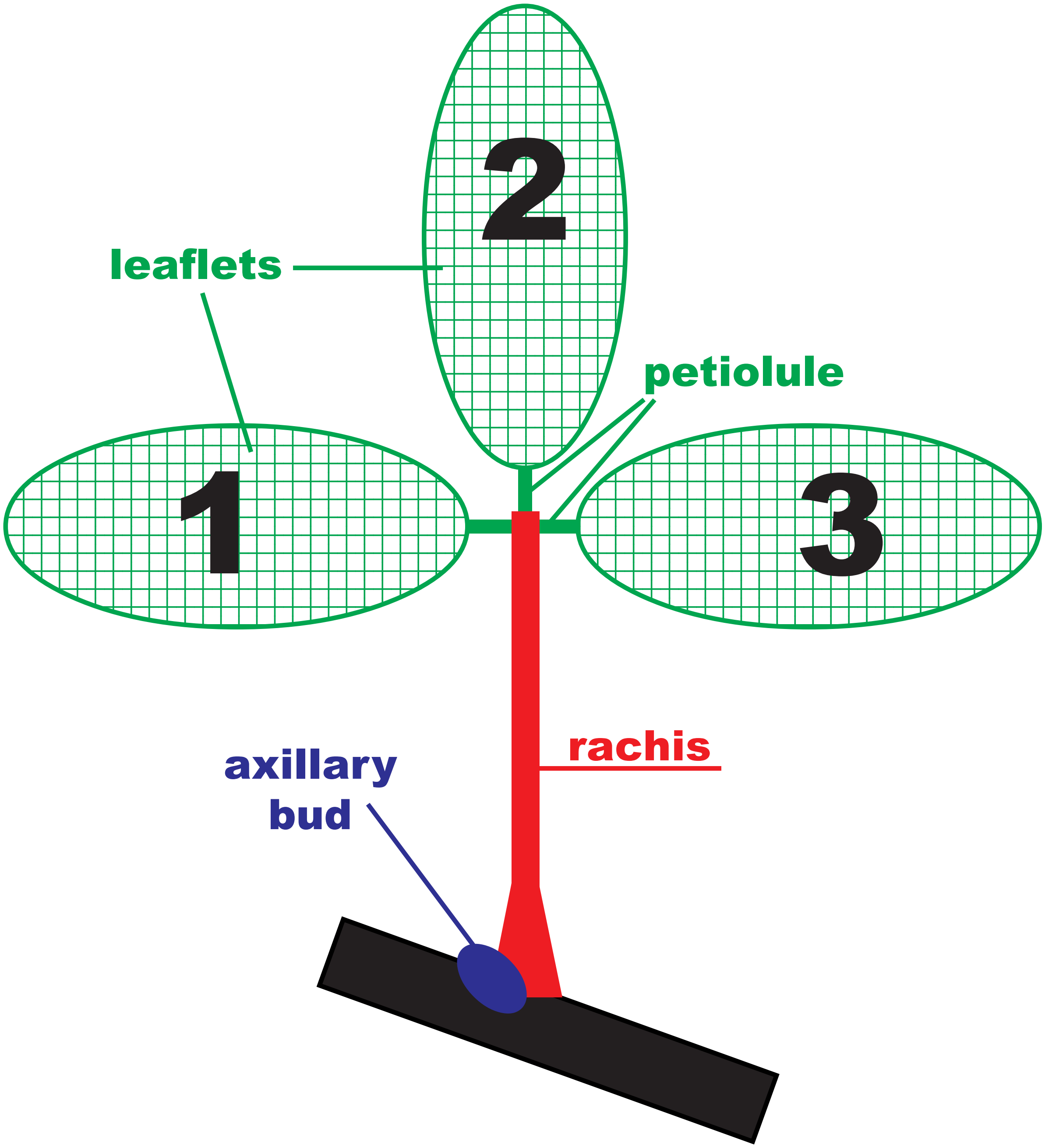


Figure 27: Representation of three leaflets distributed in a trifoliate compound leaf showing rachis (main axis) and petiolule.

The axillary bud is not part of a leaf, but grows from the twig at the base of a leaf and shows where a leaf begins.

COMPOUND LEAF FORMS

1. PINNATE	76%
2. BIPINNATE	9%
3. TRIFOLIATE	4%
4. PALMATE	11%

Figure 28: Statistical breakdown of compound leaf forms among 45 native trees with compound leaves.

are two unusual compound leaf types which can be quite confusing when examining tree leaves -- bifoliate and unifoliate compound leaves. Bifoliate compound leaves have two leaflets on a rachis. The most difficult to determine without knowing tree family and genera natural history is unifoliate compound leaves, where only one leaflet is held on the rachis, and appears as a simple leaf (i.e *Cercis* spp.).

Leaf / Leaflet Support

Most tree leaves are not sessile or growing directly from a twig, but they are held away from a twig on a petiole or a rachis. A leaf petiole is a stalk which attaches the leaf blade to the twig axis. A rachis (rhachis) is an extended supporting stalk upon which leaflets in compound leaves are attached, and the primary axis of a compound leaf which is attached to the twig axis. A rachis is not a petiole and a petiole is not a rachis – the two terms should never be used interchangeably.

A rachis is the primary axis of a compound leaf to which leaflets may be attached and is itself attached to the twig. A rachilla is a second order (or higher order) branch of a rachis to which leaflets are attached. The small stalk attaching a leaflet blade to a rachis or rachilla, without an axillary bud at its base, is a called a petiolule.

Petioles

Petioles or petiolules come in many forms including being absent (the leaf or leaflet is sessile - no supporting stalk). A normal petiole / petiolule is straight with no noticeable thickening. An inflated petiole / petiolule is thickened. A petiole / petiolule with a swollen base, or a leaflet petiolule base or apex in a compound leaf, which acts as a hinge allowing turgor driven movement of the leaf or leaflet, is termed pulvinulate or pulvinus.

Petioles or petiolules are termed sheathing due to their base expanding or flattening to grasp or enclose a twig. A leaf base or petiole base partially or completely surrounding a twig is termed clasping. Some petioles or petiolules can be winged with a narrow strip of leaf blade material on each side (i.e haft). Stipules and associated petioles can be fused along a twig, know as an adnate petiole.

Petioles or petiolules can also be glandular with localized swollen secretory tissue points or areas. Acropetiolar glands are swollen secretory tissue points or areas at the apex of a petiole or petiolule just before connection to the leaf blade, often seen as a pair of glands.

Shapes

Petiole and rachis cross-sectional shapes can include: round, oval, edged, star-shaped, crescent, lined, and winged. A terete petiole and rachis is round and a semiterete petiole and rachis is semicircular or oval. An angular petiole and rachis have sharp edges (i.e. triangular or square) cross-sections. A petiole and rachis can be star-shaped, fluted, or crescent shaped in cross-section. A canaliculate petiole and rachis has linear indentations from longitudinal channels, canals, or grooves. An allate petiole and rachis have tissue wings or lateral ridges, or bears leaf lamina tissue.

Figure 29 shows common native tree leaf petiole and rachis mid-point cross-sections. The leaf petiole scar which remains on a twig after leaf abscision can have a variety of shapes due to size and shape of the basal portion of the petiole and how it interacts with the axillary bud and stipules, if any.

Twig Features

Associated with a petiole or rachis, are several twig features. Stipules are paired or single fused outgrowths from the basal area of a petiole (or sessile leaf base) and its associated twig connection, forming a

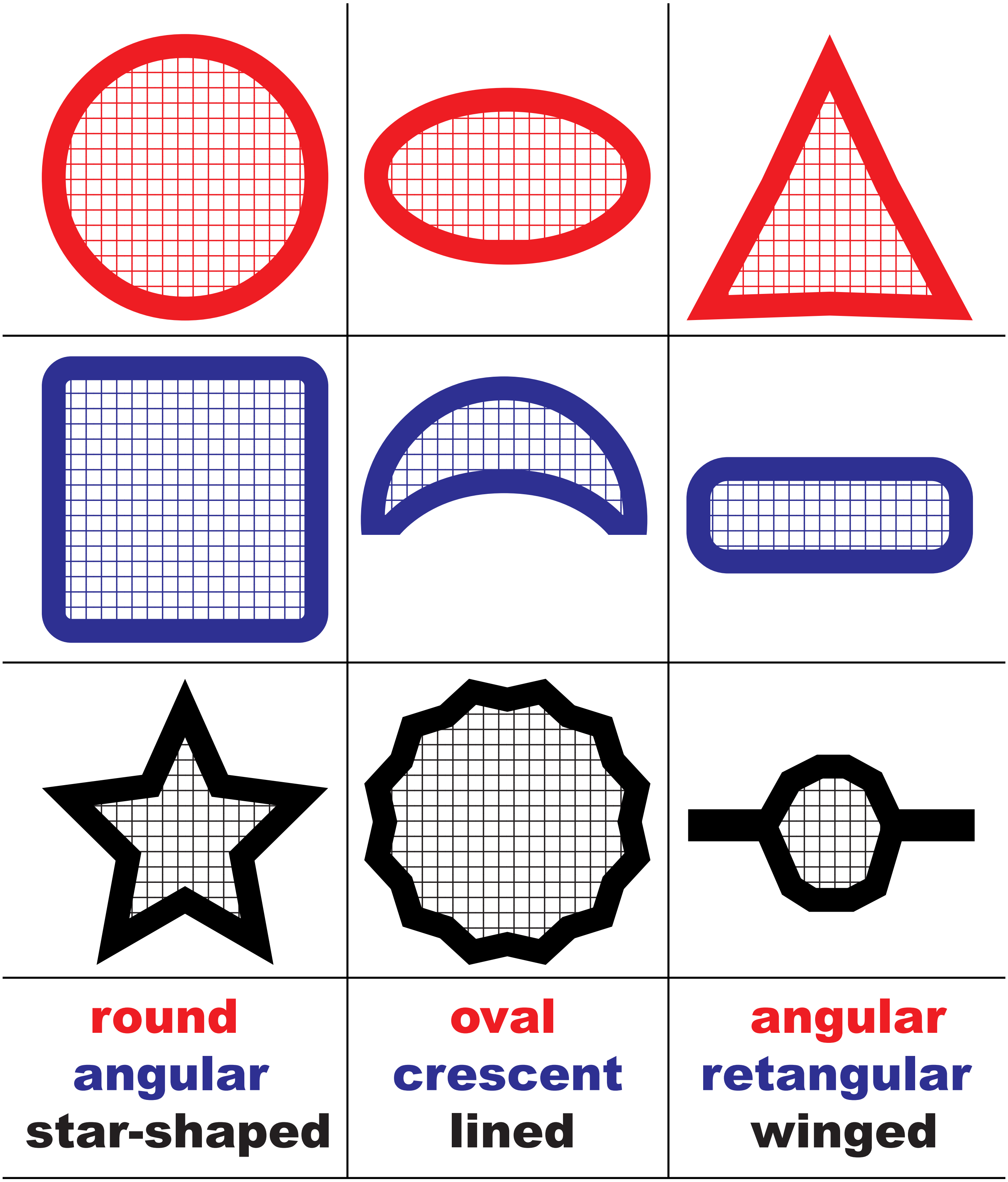


Figure 29: Petiole and rachis cross-sectional shapes.

reduced lamina, scale or spine. An abscission zone is a layer of cells in the base of a sessile leaf or leaflet, or within the base of a petiole or rachis, which allows for tissue weakening, separating, and shedding.

The area of the petiole or rachis base can generate armaments (sharp points). A prickle is a sharp thin elongated woody epidermal / subepidermal emergence on leaf. A spine, usually one or a pair, is a sharp point derived from leaf stipule origins at the petiole / rachis base. A thorn is derived from a twig axil growing point origin, which is composed of modified twig tissues with an internal vascular bundle and usually a sharp point. A thorn is a highly modified twig or shoot. In rare cases a thorn may bear a reduced or dwarf leaf.

Associated Things

A phyllode is a specialized type of leaf / petiole which is an expanded winged petiole or rachis without leaves or leaflets. A phyllode can resemble a leaf blade but is an expanded / flattened petiole.

In some gymnosperms, leaves / needles are held on a peg structure or sterigma, which is a short persistent stub holding a needle which is not abscised (i.e. *Picea* & *Tsuga*). This peg structure should not be called a petiole.

A petiole and rachis, associated with a leaf or leaflets, should not be confused with a stem holding flowers or fruit. Individual flowers or a multiple flower inflorescence are held on a peduncle. A pedicel is the stem holding an individual flower stalk within an inflorescence.

Leaf / Leaflet Tissues

Leaves have a number of anatomical characteristics, only some of which are clearly visible at a macro-scale. A major division in leaf anatomy is generally described as needle-leaved and broad-leaved, usually meaning gymnosperm and angiosperm species, respectfully. These whole leaf shape designations are not precise nor accurate, but can be used as a first pass in starting a leaf and tree identification process.

Angios-

Angiosperm leaves can be seen to have several layers or parts of internal tissue. Past the cuticle and epidermis, most of the leaf is internally mesophyll. Mesophyll tissues are composed of two parenchyma cell types: palisade parenchyma and spongy parenchyma. Palisade parenchyma is usually on the upper side or outside of the leaf. Spongy parenchyma are concentrated on the lower side or inside of the leaf, in a loosely attached matrix of cell walls. Figure 30 shows a broadleaf cross-section including a stomate.

There are many spaces between the elongated cell walls in palisade cells, exceeding the surface area of atmospheric contact over spongy parenchyma by greater than three times. Palisade cells are usually found in 1-3 layers, with each layer shorter in length the farther into leaf it is generated. The transition between palisade cells to spongy cells within a leaf is usually abrupt, with many more chloroplasts in palisade cells.

In and among these chlorophyll containing parenchyma cells are veins of vascular tissues. These vascular tissues permeate mesophyll with xylem closer to the top leaf surface and phloem closer to the bottom leaf surface. The larger veins are surrounded by non-photosynthetic rib cells. The role of the small veins is to deliver water and essential elements to cell wall spaces surrounding the photosynthetic cells, and load manufactured carbohydrates. The role of large veins is transport of materials to maintain photosynthetic rates and water supply.

Most angiosperm leaves have two general forms, sun leaves and shade leaves. These descriptions relate to the light environment the generating bud and associated leaves were formed under. These architecture forms as usually determined near the end of a growing season (i.e. late Summer / August) of the year before.

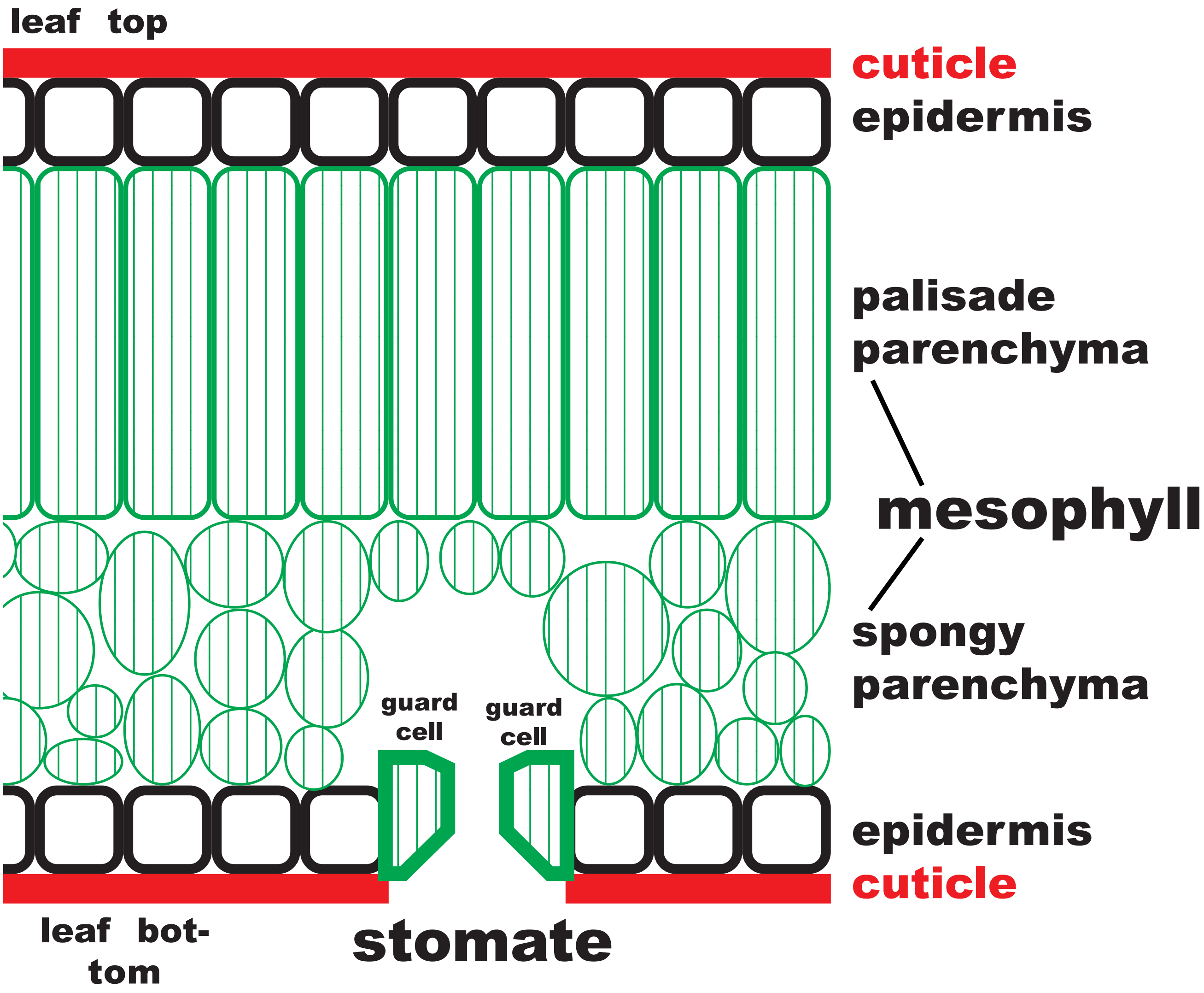


Figure 30: Idealized cross-sectional diagram of a tree leaf blade showing different non-vascular cell layers and a stomate. Cells with shading have chlorophyll.
The top and bottom leaf surfaces are covered with a wax cuticle, which may or may not have tricombes protruding.

Shade leaves are usually larger, thinner, less deeply lobed, with a thinner epidermis / cuticle, less palisade layers and cells, less transport tissues, and fewer stomates than sun leaves. Not all tree species generate these differing architectural leaf types.

Gymnos-

Gymnosperm leaves are usually scale, awl, or needle forms, but not always. For example, leaves are broad and flat in Araucaria, and scale-like in cypress and sequoia. Gymnosperm leaves are primarily evergreen. Most are linear (needle-like) and can be flattened, triangular, or quadrangular in cross-section.

Gymnosperm leaf structures vary by evolutionary age of the species / genera. Older gymnosperms tend to have some palisade and spongy mesophyll cells, like fir (*Abies* spp.) Newer gymnosperms tend to have no palisade cells, like pines (*Pinus* spp.). Gymnosperm leaves usually have stomates set deep below the general surface level and in rows. The stomatal guard cells have subsidiary cells which assist in opening and closing stomates. Needles can have resin ducts and many open spaces.

Gymnosperm leaves can be tough and stiff. For example, pines (*Pinus* spp.) have an epidermis carrying a heavy cuticle over a hypodermis of thick-walled, tough supporting sclerenchyma cells. Vascular tissues (stele) are surrounded by transfusing tissue made of intermingled living and dead cells, which act as a waiting room for solutes from the xylem water stream to be off-loaded and carbohydrate (food) to be loaded into phloem. There is usually an endodermis cell layer which surrounds the transfusion tissue with a water-tight casparium strip.

Senescence

Leaf senescence is an organized, planned, and essential part of tree life. Senescence is a process of closing down, reallocating resources, and sealing off a leaf. There are both environmental events and genetic switches which signal trees to commence senescence. Evolutionary time has selected for internal seasonal calenders and sensors which track day lengths and temperatures in native trees. Tree genetic materials have been crafted to minimize tree liability over the impending poor growth period of winter. Autumn coloration in tree leaves is a symptom of deciduous leaf senescence.

In senescence, a tree recalls valuable resources on-loan to leaves, and then enter a resting life stage. Tree roots continue at a slower pace to colonize and control space, and gather resources, waiting for better conditions. Frosts and freezing temperatures kill living cells in tree leaves. Dead cells cannot conserve and transport materials back into a tree. Cold temperature-killed leaves, which have not started to senesce, are a sign many tree resources were unable to be recalled and now lie outside a tree in falling leaves.

The final step in senescence is a leaf being sealed off from the rest of a tree. A weak zone at the leaf base is initiated when normal growth control messages and supply of food materials moving out of a leaf are reduced. Shorter days, longer cool nights, and changing light quality help throw internal genetic switches which change growth regulators and food allocation patterns. The tree begins to activate a physical and chemical seal across several layers of living cells near the leaf petiole base. On the leaf side of the seal, cell walls are weakened and become thinner. Figure 31.

Abscision

An abscission zone occurs at the bases of a leaf petiole / rachis, base of leaflets, and basal nodes of twigs. As leaf petiole base cells weaken, internal pressure causes them to swell more than surrounding cells. This mechanical strain causes one living cell to shear away from its neighbors. This zone of separation, or abscission zone, is a design feature of many mature tree leaves.

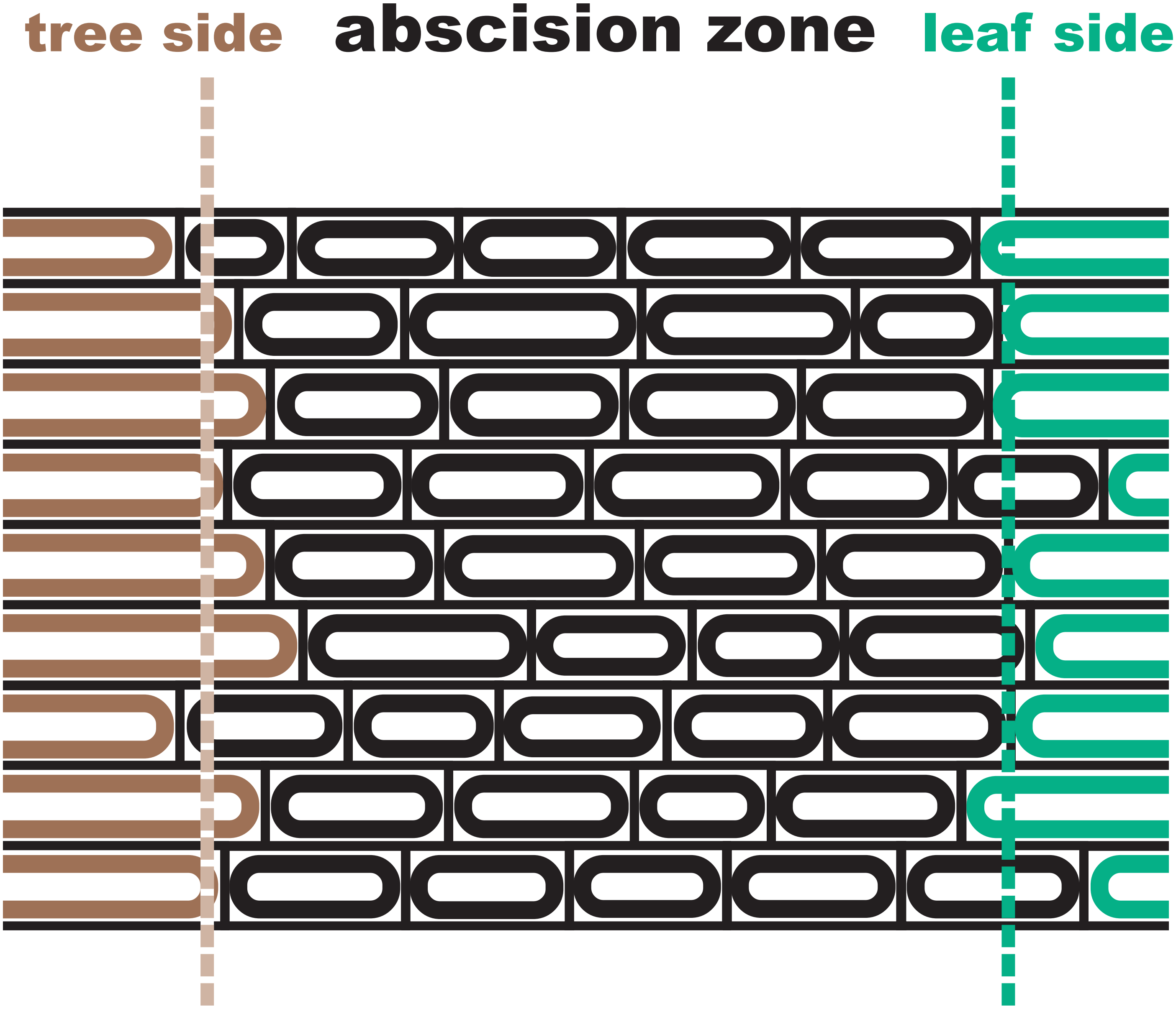


Figure 31: Diagram of cells in a leaf petiole base abscision zone pre-staged for later use.

The tree side of the abscission zone generates a protective layer of thick walled, suberized cells which seal-off a leaf from the rest of the tree. Most leaf abscission zones are pre-positioned to facilitate shedding, and may or may not be utilized by the tree. Abscission zones are set-up to act as a potential barrier and boundary. Figure 32.

Trees are always shedding parts and pieces which had a carbon cost to generate. For example, in one study a mature tree was found to shed / abscise more the 30,000 tissue fragments per year, not including leaves. Trees shed inefficient or dead tissues internally as heartwood. Trees also shed tissues to the outside as root turnover, leaf and twig abscission, periderm shedding, and through general compartmentalization. Leaves are the most visible of tree organs shed.

Shedding living and dead cell volumes allow trees to maintain the most effective and efficient tissues to assure survival. If internal allocation problems or external environmental damage occurs, trees can eliminate unsustainable living mass through shedding. Cladoptosis is the technical term for abscission or shedding of shoots (twigs and branches).

Juvenile trees may not establish effective abscission zones and hold dead leaves throughout winter. Understory trees may hold leaves because of juvenility or because they are protected from climatic events which could knock off leaves. Some trees may abscise all their leaves except on new late-season sprouts.

Summing-Up

In summary, tree leaves are valuable for tree life, and are designed to be disposable, passing through a senescence process which ends with abscission.

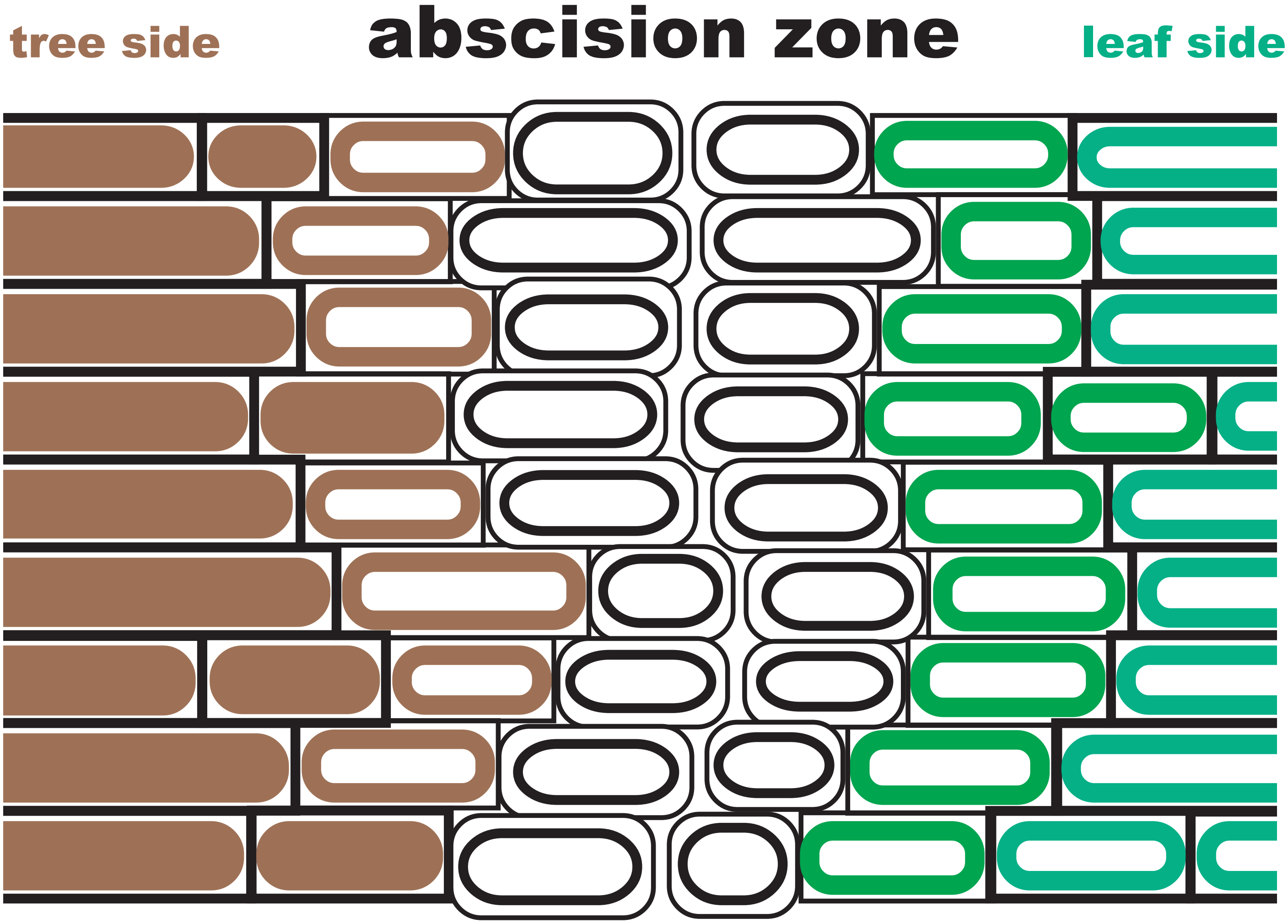


Figure 32: Diagram of cells in a leaf petiole base abscision zone with a fracture line between cells. Note tree protection zone on the tree side, wall degradation areas, and cell expansion zone all disrupting cell-to-cell connections.

Citation:

Coder, Kim D. 2022. Tree anatomy: Leaf structure & function. Warnell School of Forestry & Natural Resources, University of Georgia, Outreach Publication WSFNR-22-67C. Pp.48.