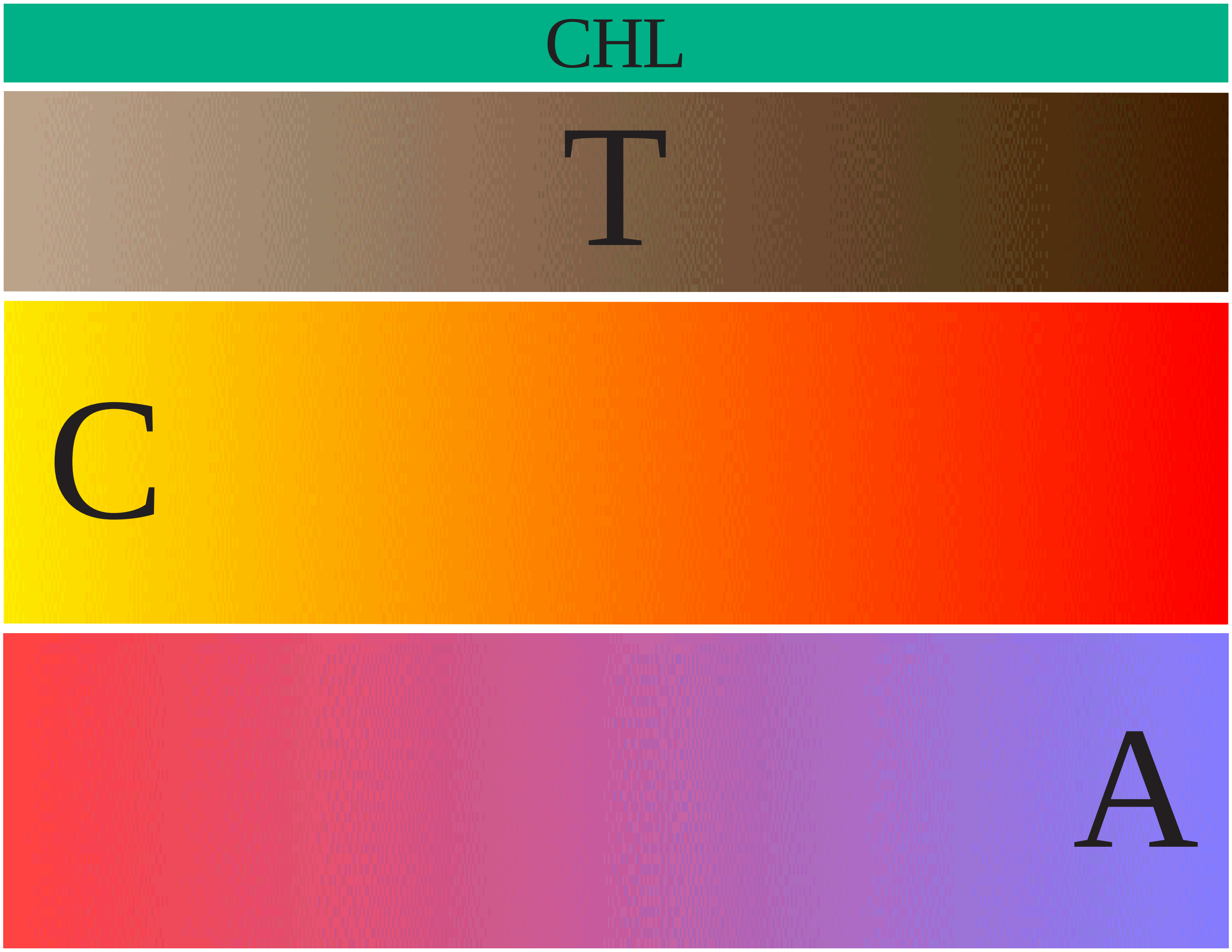
Primer On Autumn Tree Leaf Colors

by Dr. Kim D. Coder, Professor of Tree Biology & Health Care,
Warnell School of Forestry & Natural Resources
University of Georgia September 2008

WARNELL
School of Forestry and Natural Resources
The University of Georgia

Outreach Monograph WSFNR08-28



Primer On Autumn Tree Leaf Colors

□□ □□. □□□ □. □□□□□, □□□□□□□□□ □□ □□□□ □□□□□□□ & □□□□□□ □□□□,
□□□□□□□ □□□□□□ □□ □□□□□□□□ & □□□□□□□ □□□□□□□□□, □□□□□□□□□□ □□ □□□□□□□, □□□□□□□□□ 2008

Introduction

Trees have many strategies for life. Some grow fast and die young, others grow slow and live a long time. Some trees colonize new soils and new space, while other trees survive and thrive in the midst of old forests. A number of trees invest in leaves which survive several growing seasons, while other trees grow new leaves every growing season. One of the most intriguing and beautiful result of tree life strategies is autumn leaf coloration among deciduous trees.

An eco-centric human might imagine tree leaves change colors just for a visual feast. But, what we see as fall coloration is a planned passage to rest by temperate region trees avoiding the liabilities of Winter. In human terms, we are allowed to witness trees getting ready for bed to assure a Spring filled with opportunities for growth.

Why?

Why do trees express colors in Fall? Research has suggested many reasons over many years. The most enduring and tested reasons for Fall color include five groups of research citations. These cited reasons for autumn color are listed here in order of importance as assessed through the literature.

1) A by-product of the senescence process as trees prepare to enter a quiet phase of life over Winter.

2) A sunscreen and filter for both ultraviolet and visible wavelengths of light protecting the reabsorption process in a leaf.

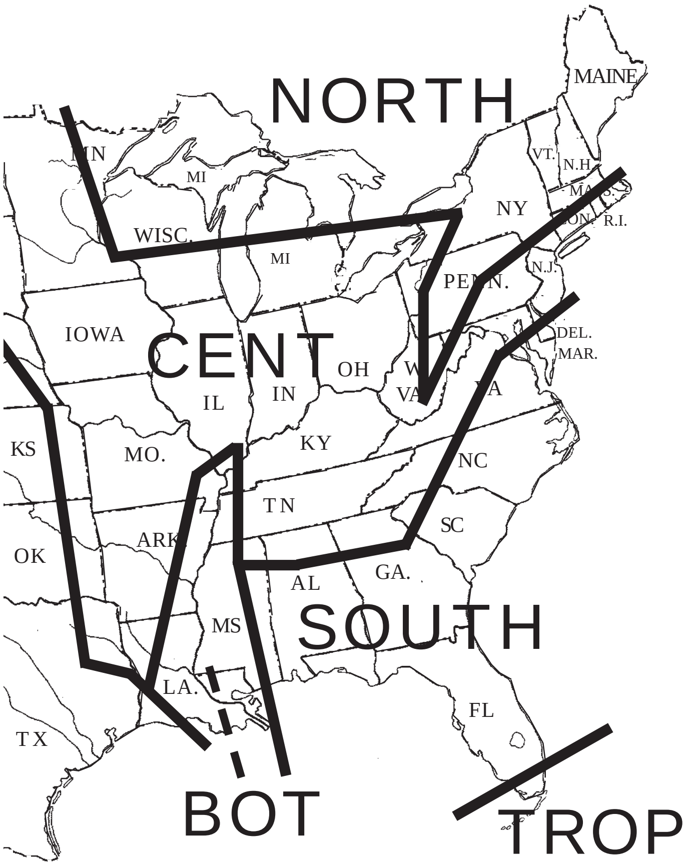
3) As antioxidant protection for the chlorophyll system as it is progressively closed down for the season.

4) Helping regulate osmotic changes in the senescing leaf minimizing damage from drought and frost.

5) An environmental signal (coevolution) to pests to minimize infestation.

Location!

Autumn coloration changes we see in temperate zone trees at the end of a growing season move from North to South in the Northern Hemisphere, and from South to North in the Southern Hemisphere. Earth's north-south mountain ranges in temperate zones with continental climates accentuate tree color potential. Different forest types have different sets of trees growing along altitudinal (high / low) and moisture (wet / dry) gradients. Some forest types are highly diverse over short distances while other are monotypic across large landscape areas. Figure 1. Color is expressed at the forest, stand, species and individual tree level, all differing from season to season.



BOT	= bottomland hardwoods	-- cottonwood, gums, baldcypress, oaks
CENT	= central hardwoods	-- oaks, maples, cherry, yellow poplar, walnut
NORTH	= Northern hardwoods	-- maples, beech, birches
SOUTH	= Southern oaks & pines	-- yellow pines, southern oaks, sweetgum
TROP	= tropical hardwoods	-- mangrove, mahogany

Figure 1: Simplified distribution of major forest types and inherent diversity in the Eastern United States.

Due to the diversity of deciduous tree species, density of multi-storied and multi-successional forests, and great topographical and climatic variation all across a long distance, Eastern North America is one of the places on Earth for a great tree color show. Fall sends tree color expression rolling down the Appalachians, and flowing southward until fading into South Florida and the maritime forests of the Gulf Coast.

Pioneering or Climax

The successional status of tree species impacts color expression. Early successional tree species, like willow and cottonwood, tend to begin leaf senescence within the crown in more inefficient leaves. Interior crown color expression is shaded and muted by outer leaves. Outer crown leaves can be quite colorful but with a limited pallet. Outer leaves on early successional species tend to generate few stress initiated pigments like anthocyanins, and stay green until killed by frosts, browning-out quickly. A notable exception to these trends is sweetgum (*Liquidambar styraciflua*).

Late successional species, like white oak, tend to begin senescence around the outer portions of their crowns. These species generate many more stress pigments and maintain colored pigments in leaves well into Fall and Winter even after abscission. Late successional species are considered to be more conserving of essential elements and more effective at reabsorbing nutrients, compared with early successional species.

Rest & Resurrection Signal

The colors of rest and impending death are celebrated by people in many parts of the world. There are only a few places where all the conditions and trees come together in a perfect combination to generate the shock and awe of fantastic autumn colors. In order to understand fall colors, or tree life in general, you must review senescence, colored pigments, abscision, and how color is expressed across the landscape. These will be the subject areas covered in the rest of this primer.

Color Symptoms

Autumn coloration in trees is a symptom of deciduous leaf senescence. Senescence is an organized, planned, and essential part of tree life. Senescence is the 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 minimum temperatures in native trees.

Tree genetic materials have been crafted to minimize tree liability over the impending bad growth period of Winter. Fall color expression is a sign of this process. Leaf senescence is initiated when shortened warm days, and decreasing but not freezing nighttime temperatures are recognized by the leaves and buds of a deciduous tree. Daylength and daily minimum average temperature are the most direct signals related to color expression. Atypical climatic events, and trees planted out of their native neighborhood, can lead to severe problems for tree survival and change color expression. Trees in better health tend to express colors more brightly, which could influence pest recognition of suitable hosts.

Save The Good Stuff!

A primary task of senescence is to remobilize and reabsorb valuable resources used for food production during the past growing season. Key among these valuable resources are essential elements nitrogen, phosphorus, potassium, magnesium, and sulfur. In order to remove these elements from the leaves for future use, they must have their physiological cages dismantled and be placed into a transport form. These elements are pulled back into buds and twigs behind and below senescing leaves. Any residual starch supplies in the leaf are broken down into constituent sugars and removed. The leaf is cleaned out of valuable materials before it is sealed-off for good. Generally, the brighter the colors, the more vigorous the tree and the better food production was this past growing season.

The central physiological purpose of a deciduous leaf is to support light energy capture and food production machinery in a disposable unit. Chief among this machinery, and accounting for a huge amount of production and maintenance resources, is chlorophyll. Chlorophyll is the antenna which receives and absorbs energy from specific wavelengths of sunlight. Chlorophyll absorbs select red and blue wavelengths of light and reflects green light. It is attached in dense arrays on specialized membranes within cells. Cells with a full supply of chlorophyll molecules are heavy with all of life’s resources and sport a deep green color.

De-Greening

As day length wains, chlorophyll becomes harder to maintain at peak efficiency. Sensor input from the leaf and basal bud signal for senescence process genes to be switched on. As autumn is approached, the expensive and high maintenance chlorophylls are not as rapidly repaired every day as in full summer. Cooling air temperatures slow many life processes within the leaf. Chlorophylls begin to be degraded, dismantled, and component parts shipped from the leaf. As chlorophylls begin to fade, other colored pigments are unmasked which have been present all season. Most noticeable are the carotenoids -- bright colored yellows and orange pigments. Figure 2.

The carotenoids act as small antennas capturing selected light wavelengths and blocking light intensities which would damage chlorophyll. The carotenoids also help dissipate energy unusable by the cellular machinery. These bright pigments act as antioxidants for the leaf. As the chlorophylls are decommissioned into colorless components, the carotenoids can finally be revealed. At the beginning of senescence leaves begin to appear yellowish-green.

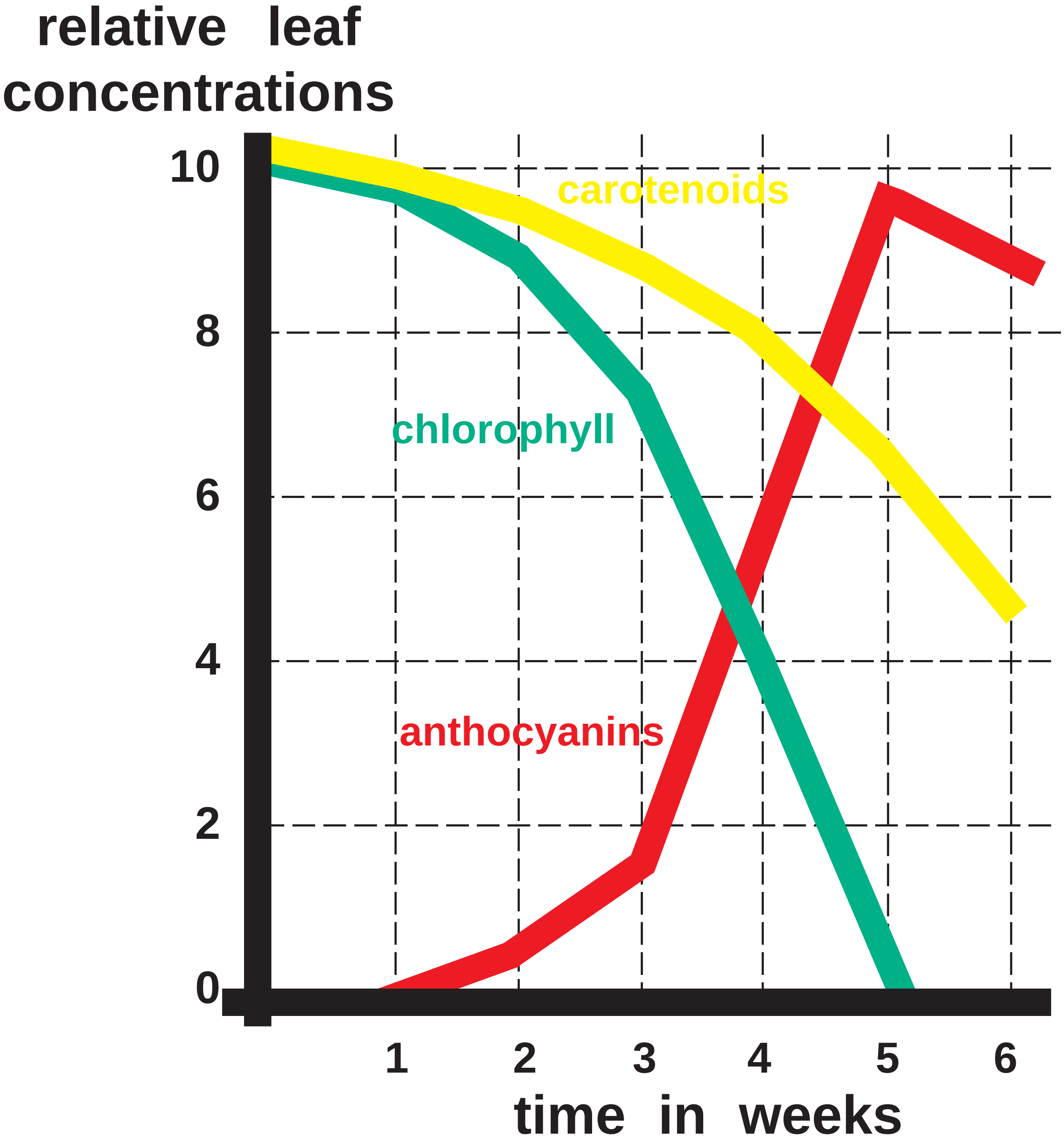


Figure 2: Relative change in primary tree leaf pigment concentrations over the fall senescence period.

(partially derived from Matile 2000)

Sun-Screen

With bright fall sunshine and low temperatures, the photosynthetic system becomes progressively more inhibited and inefficient. The lower the temperature, the more inhibited energy capture and food production become. But senescence requires energy to function, and photosynthesis and other cellular processes must continue. In order to protect the dwindling and sensitive machinery of the cell, new pigments are generated which function as sun-blocks and selective filters to prevent too much light of too short of wavelength from impacting living cells.

New carotenoids are produced to help in senescence. In addition, as chlorophyll contents fall to about half their normal Summer concentration, flavonoids are generated. The largest component of these new pigments are anthocyanins. Anthocyanin concentrations are controlled by environmental stress. Too much or too little light, low but not freezing temperatures, essential element shortages, and drought all help facilitate production of new anthocyanins. The anthocyanins are attached to sugars and dissolved in the water solution of the cell. Anthocyanins provide limited antifreeze protection for leaves.

Driven Into Winter

Fall color expression is controlled by the pace of chlorophyll decline, the degree of carotenoid retention past chlorophyll extinction, anthocyanin synthesis rate, and formation of dark oxidation products (phenolics). Environmental conditions which inhibit photosynthesis tend to accelerate chlorophyll decline, reveal and generate more carotenoids, and increase formation of anthocyanins. Bright sunlight, shorter daylengths, drought conditions and cooling daytime and nighttime temperatures tend to generate more color expression. Figure 3.

Eventually, freezing temperatures and decay organisms kill or isolate the remaining living cells in a leaf. Cells begin to self destruct, chemically burning the last remnants of cellular components into the “tars” of death. The final step in senescence is the leaf being sealed off from the rest of the tree. This final process severs all living connections between tree and leaf. Most leaves are designed to abscise, or fall off, separating along a special layer of cells at the base of the leaf petiole. Rain, wind, and animals may actually break the leaf off a tree at this abscission layer. Leaves may remain colored for weeks or months after abscission as the pigments fade to brown and the cells decay.

Color Descriptions

Although an almost infinite number of colors can be expressed by senescing trees and recognized by humans, it is convenient to classify these tree colors into discrete groups. Tree fall leaf colors can be categorized into 15 Coder Leaf Color Code values. These values are a numeric code defining general color expression in autumn tree leaves. The primary colors of autumn trees are green (1), yellow (3), orange (5), red (7), and purple (9). Each of these primary tree colors combine to yield the secondary colors of green-yellow (2), yellow-orange (4), orange-red (6), red-purple (8), and purple-blue (10). Each primary tree color category can also be modified by browning (B). All color descriptions / coding can also be further modified along the gradients of light (L) / dark (A), and by intense (I) / dull (U). See Figure 18 in Appendix 1 for a graphical color definition.

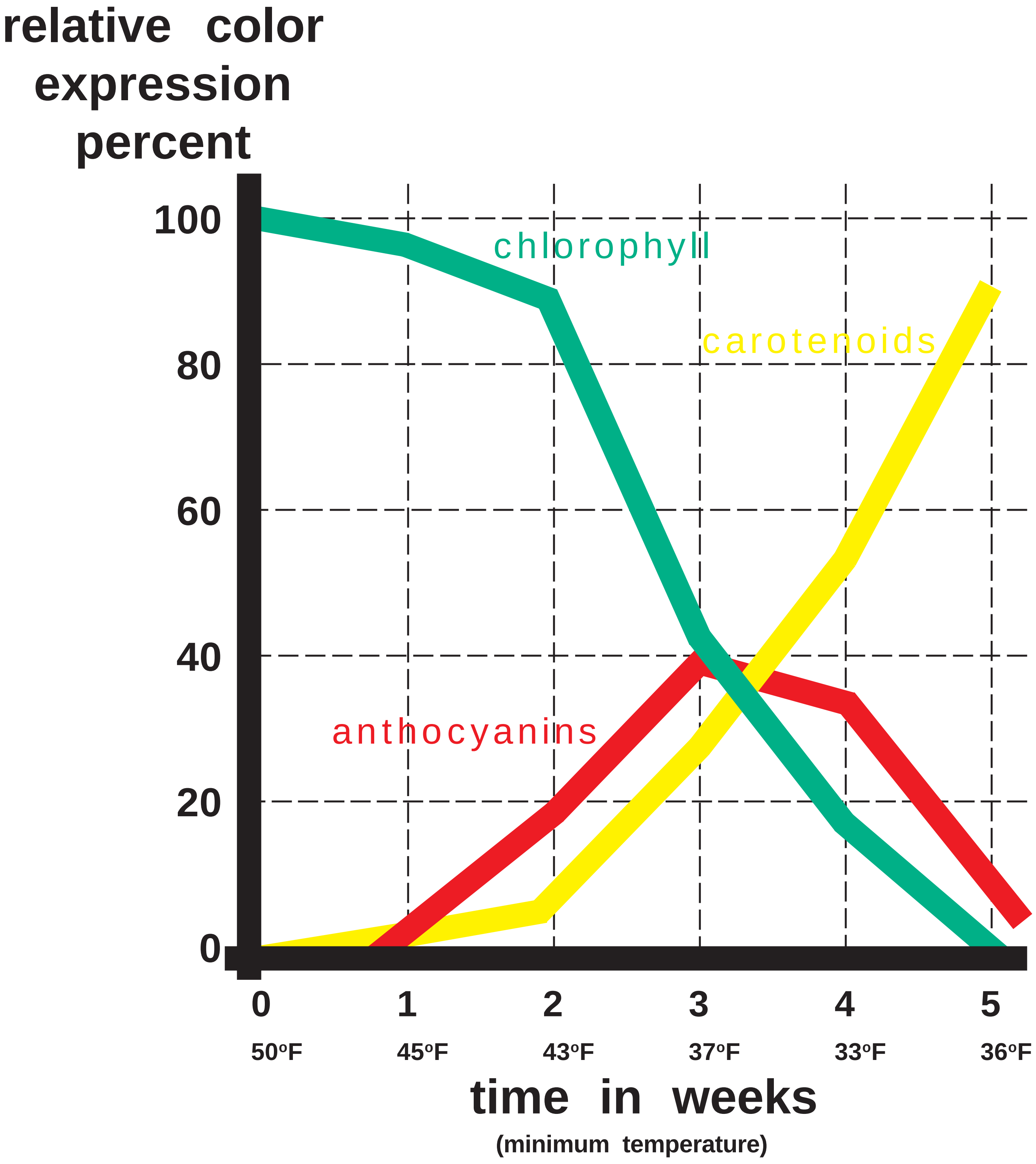


Figure 3: Relative color expression changes in a stand of sugar maple (*Acer saccharum*) trees in the Northeastern United States over one senescence period. (after Schaberg et.al. 2003)

Leaf Senscence

Spring flower colors are raised in fall to crown the trees. Many of the pigments are the same but the colored containers have changed from dainty petals to coarse, broad leaves. It is living leaves that reveal in their decline and fall last summer's results and next spring's promise. The living process in a tree generating autumn colors is called senescence.

Designer Colors

Senescence is the pre-planned and orderly dismantling of light gathering structures and machinery inside a leaf. Part of senescence is the development of a structurally weak zone at the base of a leaf stock or petiole. Live cells are needed in the leaf to unmask, manufacture, and maintain the tree pigments we appreciate as autumn colors. Fall coloration is a result of this positive life process in a tree. Freezing temperatures kill leaves and stop the senescence process with only decay remaining.

Endings & Beginnings

Senescence is a planned decommissioning process established with leaf formation. Inside the leaf, as photosynthesis began to generate food from carbon-dioxide, light, water and a few soil elements, a growth regulation timer was started that would end in Winter dormancy. The fullness of Summer production helps establish dormancy patterns as dormancy processes establish allocations for the next growing season.

In senescence, a tree recalls valuable resources on-loan to the leaves, and then enter a resting life stage. The 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 the tree, and so do not produce colored pigments as a by-product. Temperature-killed leaves, which have not started to senesce, are a sign that many tree resources were unable to be recalled and now lie outside the tree in falling leaves.

Green Is Life

To appreciate new and unmasked colors of fall, consider the color of tree life -- green. The green color comes from a large, hard-to-maintain and expensive to build molecule with a magnesium atom in its center called chlorophyll. Chlorophyll is the most precious of molecules. The tree conserves, protects, and maintains chlorophyll. With failing light, food, elements or energy, loss of the chlorophyll pigment is a first visible sign of problems. Yellowing or chlorosis in trees is a symptom of many different pests and environmental impacts because chlorophyll manufacture and maintenance is so sensitive to damage.

Trees do not manufacture chlorophyll until well illuminated. In healthy but unlighted tissues, a good supply of colorless chlorophyll components (requiring iron (Fe) to make) are kept in storage. Until there is light to capture, chlorophyll is not produced. After leaf tissues are exposed to light, the pale yellowish tissue colors are cloaked by the green of chlorophyll. Chlorophyll is clearly visible and concentrated in leaves. Chlorophylls are also found in most near-surface tissues in a tree exposed to light. The inner bark of twigs (cortex), light-exposed roots, and inner portions of buds all possess chlorophyll.

Last Effort

In fall, with changing resource availabilities (like light quantity and quality), chlorophyll production and maintenance begins to decline. The preliminary steps needed to make chlorophyll are slowed and stopped by low temperatures, regulation signals generated from the tree's light sensors, and a build-up of photosynthesis by-products. At the same time, longer dark periods, cool temperatures and bright sunlight, help initiate chlorophyll demolition. Drought conditions can accentuate chlorophyll loss. The green curtains in the leaf begins to withdraw.

Leaf starch or stored food, begins to be rapidly broken apart and shipped out of the leaf. What chlorophyll remains, continues to generate energy gradients used to power remaining living cells. The products being shipped from leaves are having a more difficult time escaping through the developing abscision zone in the leaf-stem base. More sugars and mobile elements are unbound in the transport and production cells. These conditions lead to chlorophyll loss when leaf energy concentrations are still relatively high.

Revealed Colors

Chlorophyll veils slowly drop away and reveal a great pallet of colors, some brand new to this autumn and some having lain hidden all season. One of the tough pigments that share chlorophyll's cellular containers, are the red, orange and yellow carotenoids. These pigments were made to shield and protect chlorophylls, but now can be clearly seen. Some color pigments are newly made using materials that cannot quickly leave the leaf. Rich sugar contents, slight drought stress, and developing element deficiencies in living cells help initiate anthocyanins, blue to red colored pigments used to protect light sensitive processes in leaves.

The artistic pallet of tree colors is diverse. Carotenoids are like bright oil paints. The always variable anthocyanins are like watercolors, blending across a tree covered landscape. Behind all these colors remain the deep browns of tannins (the color of tea) and the basic light browns of tree tissues. The number of different color combinations is almost infinite. See Appendix 1 for color expressed by species. In some forests, all the colors contrast with evergreen trees. The colors in deciduous leaves eventually fade to brown, the color of the earth.

Failing Connections

A weak zone at the leaf base is initiated when normal growth control messages and supply of food materials moving out of the 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 build a physical and chemical seal across several layers of living cells near the leaf stem base. On the leaf side of the seal, cell walls are weakened and become thinner. Across this basal zone of change, the living connections between food transport cells (phloem) become more tenuous.

Water connection (xylem) cells continue to supply water to replace evaporative losses in the leaf. These water supply cells are part of strong but dead connective strands within the leaf stem. As the leaf blows in the wind and is loaded by rain, the leaf stem starts to tear at its weakest point, the leaf-stem-base. As leaf-stem-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.

Falling Leaves

A point is reached when all living cell connections are broken at the leaf-stem-base and only the dead water connections hold the leaf onto the tree. Only a little bit of force is needed to snap these connections and the leaf will fall to the ground. A single fall wind storm can sweep the colors from the trees. The wound left on the tree (a leaf scar), sometimes highly characteristic of a given species, is the outward face of a constructed barrier wall established to keep the environment outside. The tree is now fortified against the Winter.

Tree Pigment Palette

Autumn tree colors grace our landscapes. The palette of potential colors is as diverse as the natural world. The climate-induced senescence process that trees use to pass into their Winter rest period can present many colors to the eye. The colored pigments produced by trees can be generally divided into the green drapes of tree life, bright oil paints, subtle water colors, and sullen earth tones. See Appendix 1 for tree fall leaf color descriptions by species.

Unveiling

Overpowering greens of summer foliage come from chlorophyll pigments. Green colors can hide and dilute other colors. As chlorophyll contents decline in fall, other pigments are revealed or produced in tree leaves. As different pigments are fading, being produced, or changing inside leaves, a host of dynamic color changes result. Taken altogether, the various coloring agents can yield an almost infinite combination of leaf colors. The primary colorants of fall tree leaves are carotenoid and flavonoid pigments mixed over a variable brown background.

There are many tree colors. The bright, long lasting oil paints-like colors are carotene pigments producing intense red, orange, and yellow. A chemical associate of the carotenes are xanthophylls which produce yellow and tan colors. The short-lived, highly variable watercolor-like colors are anthocyanin pigments producing soft red, pink, purple and blue. Tannins are common water soluble colorants that produce medium and dark browns. The base color of tree leaf components are light brown. In some tree leaves there are pale cream colors and blueing agents which impact color expression. Figure 4.

Perceiving Fall

The forest landscape and trees have five major pigment color sets which can define autumn colors. (Table 1) These tree pigments have chemical structures which modify light as it passes bye or is reflected away. Some wavelengths of light are absorbed by these pigments due to physical and chemical properties. Each pigment has a single or several peak wavelengths of light which are absorbed, with the rest of the wavelengths relatively unimpacted.

Humans see these unabsorbed wavelengths of light in the visual spectrum as a dominant color. Color can only be observed by a human in the visible spectrum wavelengths of roughly 380nm (violet) to 730nm (red). The wavelength number is a measure taken in nanometers (nm), or a billionth of an meter. People with modified color vision (various types of “color-blindness”) will still register light across the visible wavelengths but not always perceive a color, or the same color as everyone else. Color is truly in the eye, mind, and genes of the beholder.

Describing Colors

Tree fall leaf colors can be categorized into 15 Coder Leaf Color Code values. These values are a numeric code defining general color expression in autumn tree leaves. The primary colors of autumn trees are green (1), yellow (3), orange (5), red (7), and purple (9). Each of these primary tree colors combine to yield the secondary colors of green-yellow (2), yellow-orange (4), orange-red (6), red-purple (8), and purple-blue (10). Each primary tree color category can also be modified by browning (B). All color descriptions / coding can also be further modified along the gradients of light (L) / dark (A), and by intense (I) / dull (U). See Figure 18 in Appendix 1 for color definitions. See Table 5 in Appendix 1 for a summary of the dominant autumn colors expressed over the landscape.

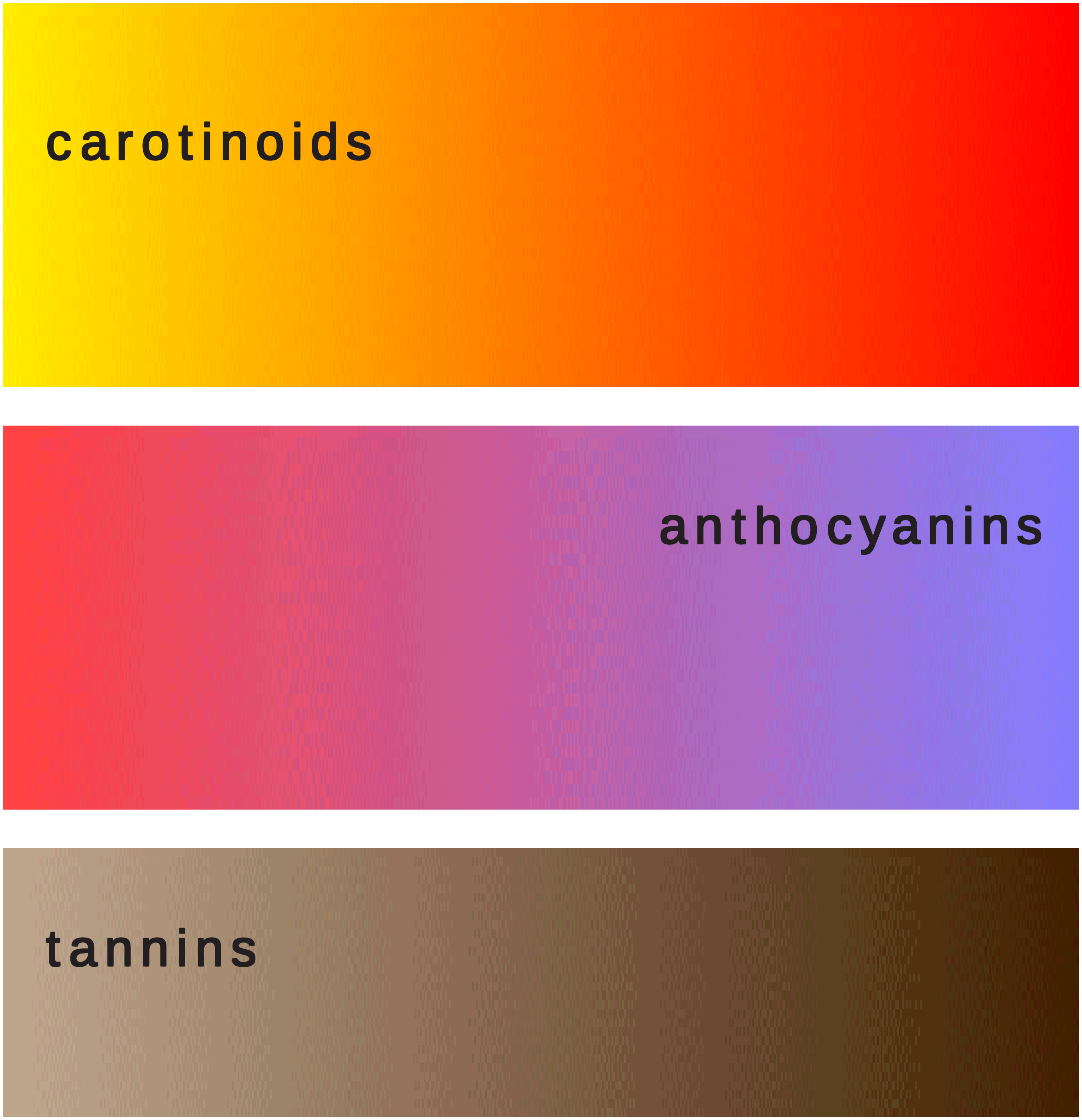


Figure 4: Graphical color expression range of the three major pigment groups in Fall senescing trees. Note white/cream color blending and brightening agents will impact color expression, as will chlorophyll green.

Table 1: Pigments groups responsible for major color expression in trees during Fall senescence.

1. Chlorophylls

2. Carotenoids
   - A. Carotenes
   - B. Xanthophylls

3. Flavonoids
   - A. Flavones & Flavonols
   - B. Anthocyanins
   - C. Proanthocyanidins (condensed tannins)

4. Tannins (sugared tannins)

5. Betalins (betacyanins & betaxanthins)

Chlorophyll Green

Chlorophylls are the green color pigments seen in tree leaves. Chlorophyll is the centerpiece (literally and figuratively) of light capture and food production in trees. Chlorophyll is bound to special membranes inside chloroplasts within leaf cells. Chloroplasts are transformed through senescence into gerontaplasts, or aged chloroplasts with declining chlorophyll maintenance machinery. Chlorophyll has a medium green color (it absorbs red and blue wavelengths of light) and is produced in such quantities as to dominate or mask other leaf pigments.

Chlorophyll is a light gathering antenna consisting of a porphyrin ring "head" structure with a magnesium atom center, and a long phytol "tail" (tetrapyrrole). It is chemically similar to the iron containing haem pigment of animal blood, and to vitamin B12. Chlorophyll is expensive for tree cells to make, difficult to maintain, and easily torn apart by far blue and ultraviolet light. In most tree leaf cells, a chlorophyll molecule only exists for an average of 26 hours, depending on the biological environment of the leaf. Chlorophyll is only produced when leaf tissues are stimulated by light.

A's & B's

The two types of chlorophyll in trees are called chlorophyll "a" (*chla*) and chlorophyll "b" (*chlb*). Chlorophyll b differs from chlorophyll a by having an additional double bonded oxygen atom attached to one corner, making *chlb* absorb slightly different wavelengths of light than *chla*. *Chlb* is called the shade chlorophyll and *chla* is called the full sun chlorophyll, even though both are present in any tree leaf with only the proportion of molecules changing. For example, the *chla / chlb* ratio in shaded tree leaves is about 2.5, where this ratio is about 4.2 in full sun leaves, on average.

If light excites chlorophyll, the energy captured can be quickly stolen by cellular machinery and used to make food. If chlorophyll is excited by light and can not quickly hand-off the energy to other cellular machinery, a highly reactive form of oxygen and peroxides can be generated which disrupt and destroy cell membranes. Tree leaf cells have several means for protecting chlorophyll molecules and for quenching any misdirected energy to minimize internal damage. Several types of colored pigments assist in this process. Some of these protective pigments are seen as Fall leaf colors.

Killing Chlorophyll

In senescence, chlorophyll is detoxified and broken-down. This process occurs along a material conserving pathway. Chlorophyll b is converted to chlorophyll a providing a spike of chlorophyll a and slightly changing leaf color to a darker green. Sometimes this deepening green color can be noticed just before yellowing begins in late Summer / early Fall. Figure 5. Next the long phytol tail is cut-off chlorophyll followed by the magnesium atom being liberated and shipped away. Finally, the large ring structure (porphyrin) of the chlorophyll head is straightened out. All these now colorless building blocks of chlorophyll are stored, further broken down, and shipped out of the leaf.

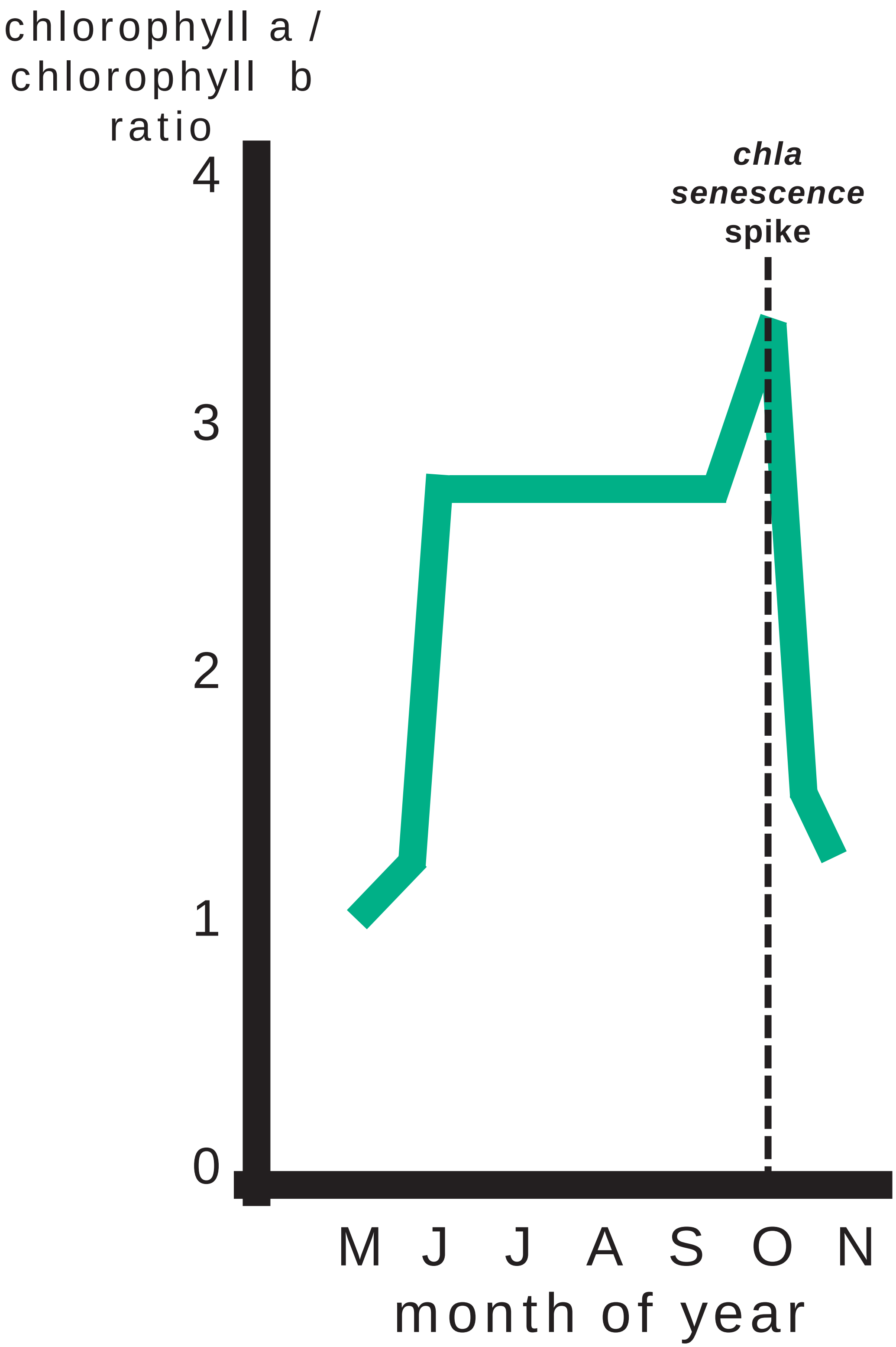


Figure 5: Change of chlorophyll ratio *(chla / chlb)* in mixed oak leaves over time. (from Sanger, 1971)

Carotenoid Oil Paints

Carotenoids (isoprenoids / tetra-terpenes) are some of the most common pigments made by plants and microbes, and stolen by animals. Carotenoids were discovered in 1831, and found to be essential to plants and always found in tree leaves. Carotenoids are non-nitrogen containing, fat-soluble pigments contained on membranes inside plastids, either with chlorophyll (in chloroplasts) or by themselves (in chromoplasts). Carotenoids are represented by more than 700 pigments - each presenting a slightly different color.

Carotenoids are tough, "oil paint-like" pigments that are familiar in everyday things such as the color of carrots, corn, bananas, egg yolks, and butter. Animals conserve and use a number of the carotenoids in their own coloration. Some chickens are fed yellow carotenoids to produce a pleasing golden-yellow skin color. To see a common set of carotenoid pigments, just lay a piece of cardboard over green grass for a few days. The grass will lose its chlorophyll, leaving the yellow of the carotenoids behind.

Tough Color

Carotenoids are built with forty carbons strung together and are called tetraterpenes (40C). Other important plant materials come from this same chemical line including the sesquiterpene (15C) abscisic acid (ABA), and many types of diterpene (20C) gibberellic acids. Both groups are important plant growth regulators. The carotenoids all share a long carbon chain structure which has alternating single and double carbon bonds (conjugated) with or without two types of terminal rings or loops.

Carotenoids are energy-expensive for a tree to manufacture and not easily broken apart. Unlike chlorophylls which are only manufactured or maintained when light is present, carotenoids can be generated in the dark. Carotenoids do more than just add color, they play three critical functions within tree leaves: blocking excessive light from sensitive chlorophyll systems; harvesting light beyond chlorophyll wavelengths; and, quenching energy paths leading to free radicals.

Light Antenna

The light capturing and processing machinery in a tree are dependent upon chlorophyll. Carotenoids help protect the light gathering system of trees from overexposure to light especially blocking some blue and violet light which damage chlorophyll molecules. Carotenoids, being more stable and tougher than chlorophyll, helps shield valuable but fragile chlorophyll. In other words, carotenoids function as a sunscreen in leaves.

Carotenoids act as antenna for capturing certain wavelengths of light. Because the carotenoids and chlorophylls are attached to membranes close to each other, the carotenoids can easily transfer any captured energy to chlorophyll molecules. This "assessory pigment" role for carotenoids helps to funnel more energy to chlorophylls to process. Alternatively, when chlorophyll captures energy and can not quickly pass it onto surrounding energy conserving machinery, carotenoids can remove this energy, preventing chlorophyll damage. Carotenoids vent energy away, disposing of extra energy as heat. If not vented away, unused energy would generate damaging oxygen radicals.

Anti-Oxidant

Probably the most important role for carotenoids in a tree is preventing light powered oxidation (destruction) of chlorophyll, surrounding molecules, and membranes by oxygen radicals. This type of oxidation can be extremely damaging to the light capture system and individual cells in a leaf. Carotenoids function as an anti-photo-oxidant. Anywhere in the tree where there is chlorophyll, light, and oxygen, carotenoids are pre-positioned to help protect light gathering systems from damage. Figure 6.

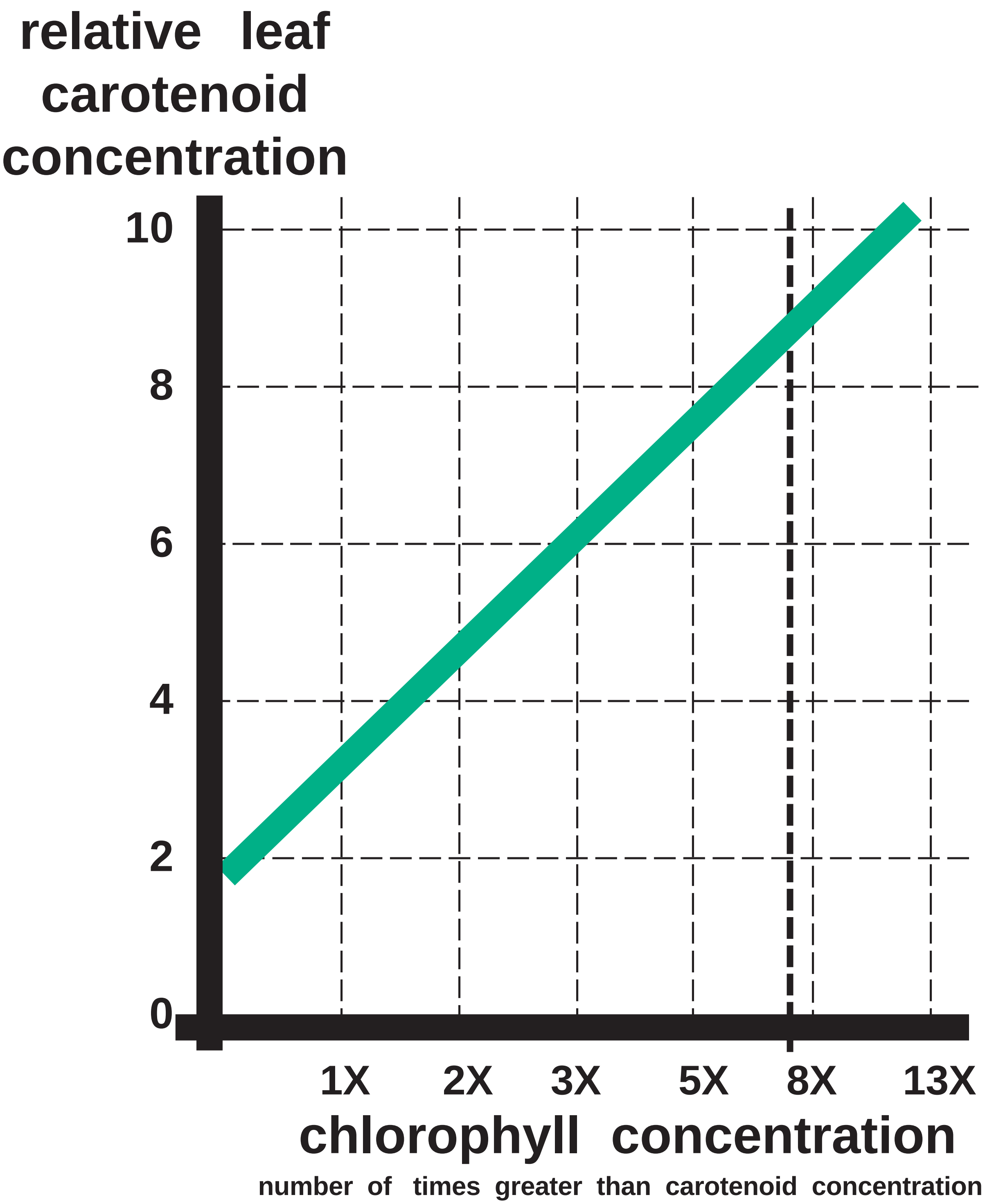


Figure 6: Estimated relative chlorophyll concentrations compared with carotenoid concentrations in tree leaves. Left of the bold dashed line are senescence levels of chlorophyll.

(derived from Lee et.al. 2003)

With & Without Oxygen

Carotenoid pigments comes in two forms, non-oxygenated forms called carotenes and oxygenated (alcohol) forms called xanthophylls. The pigment color expressed by carotenes and xanthophylls depend upon light wavelengths absorbed as shown in Table 2. Most carotenoids have three closely clustered light absorption peaks which cover an absorption range averaging roughly 70nm.

Carotenoids brightly color many tree parts with red, orange and yellow. The amount of carotenoids present in leaves is roughly one-twelfth the amount of chlorophyll present at the beginning of senescence. Figure 6. Xanthophylls comprise roughly 66-75% of all carotenoids in a leaf. Carotenoids usually outlive chlorophyll pigments by 3-5 weeks in tree leaves. New carotenoid pigments are also manufactured as leaf, light, and temperature conditions change.

Carotene Orange

Carotenes range in color from bright oil-paint-like yellow, orange, red-orange, and red. They are the pigments coloring oranges, tomatoes, carrots, pineapples, citrus, paprika, apples, saffron stigmas, strawberry, yams, mangoes, apricots, peaches, sweet potatoes, and pumpkins. The carotenes are long carbon chains with two, one or no carbon loops on their ends, like all carotenoids. For example, lycopene (pinkish-red) helps generate the bright red color of tomatoes and has no terminal loops.

A carotene with one terminal beta loop on the carbon chain is called a gamma form (a pink pigment and precursor to beta-carotene). A long chain of carbons with two identical beta loops on each end is called the beta form (orange colored beta-carotene). The delta form (yellow-orange pigment) has one alpha loop on its carbon chain (precursor to alpha-carotene). Two alpha loops on each end of the carbon chain is the alpha form (alpha-carotene, a yellow pigment).

Every tree species and individual may generate different amounts of different carotenes. Each carotene differs every so slightly from its chemical family members, but these small differences change light reflectance and so color expressed. Generally, beta-carotene is most common in chloroplasts and the lycopene is most common in chromoplasts. Both gamma-carotene and alpha-carotene are precursors to vitamin A (20C), a product of a split carotene and essential for animals.

Reflected Colors

Carotenes serve to protect chlorophyll from too much or the wrong wavelengths of light, and so act as a selective filter. *Chla* has general light absorption peaks around 670nm and 430nm. *Chlb* has general light absorption peaks around 640nm and 460nm, just inside the *chla* peaks allowing it to be more efficient in the shade of *chla*. Beta-carotene (orange) has absorption peaks between 420nm and 480nm, shielding chlorophyll from too much light at the blue end of the spectrum.

Every carotene theoretically, due to the long chain of carbons, can exist chemically as many hundreds of different isomers (i.e. 1,056 isomers for lycopene; 272 isomers for beta-carotene). In the tree, only one or two isomers usually exist. Extracting carotenes from tree cells usually disrupts and changes the isomer mix. The most common of the carotenes include pro-lycopene (orange), lycopene (pinkish-red), neuroporene (yellow), torlene (red), tetradehydrolycopene (red), zeta-carotene (pale yellow), gamma-carotene (pink), delta-carotene (yellowish orange), beta-carotene (orange), and alpha-carotene (yellow). There has been a number of positive human health values associated with consumption of many of the carotenes.

Table 2: Color expressed, average peak absorption wavelength (nm), and primary absorption wavelength range (nm) for a variety of carotene and xanthophyll pigments.

color expressed	average absorption peak	absorption range
clear / colorless	--	<360
pale yellow	400	378-425
yellow	443	414-475
yellow-orange	451	421-488
orange	455	432-490
pink	469	435-505
red	494 nm	451-540 nm

Xanthophyll Yellow

Xanthophyll (phylloxanthin) pigments were discovered in plants in 1837. As mentioned above, xanthophylls are oxygenated carotenoids. Xanthophylls are more strongly bound to cell membranes and more polar chemically than carotene carotenoids. Light is not needed to initiate or maintain xanthophyll pigments. Xanthophylls generate yellow, gold, yellow-tan, and yellow-orange colors in trees. They are found pigmenting marigold petals, citrus, peaches, nectarines, and papayas. The bright red of peppers are from capsanthin and capsorubin, unique red xanthophylls with modified end loops on each molecule. Animals can not generate xanthophylls and must utilize ingested plant pigments for coloration of feathers, egg yolks, and eye color, for example.

Cycling Up Protection

Xanthophylls are an important component of the light harvesting machinery in tree leaf chloroplasts. They absorb light in wavelengths chlorophylls can not and pass captured energy to primary chlorophyll reactions centers. Xanthophylls also serve a photo-protective role, protecting other tissues and the photosynthesis process from overexposure to light by acting as a filter of blue spectrum light and actively dissipating extra energy captured but not used. A part of this specialized progressive protective process is called the xanthophyll cycle.

In tree leaf cells much of the xanthophyll in the morning is in the form of a large violaxanthin pigment pool within plastids. As light intensity and ultraviolet light increases, violaxanthin (yellow) is converted to antheraxanthin (yellow) which provides greater light screening and cell protection. As sunlight intensity peaks, zeaxanthin (orange) is generated from antheraxanthin providing even more protection for photosynthetic machinery. Cells become more acidic at high light intensities which facilitates the quickening of the xanthophyll cycle toward zeaxanthin. Overnight most of the xanthophylls are converted back to violaxanthin. Xanthophylls (specifically zeaxanthin) have also been cited as a blue light sensor for stomate opening in the morning and for helping tree tissues sense directional differences in lighting, generating phototropism (directional growth response to light).

Naming Names

Some of the xanthophylls include flavoxanthin, rubixanthin, rhodoxanthin, canthaxanthin, zeaxanthin (orange), alpha- and beta-cryptoxanthin (yellow-orange pigments converted to Vitamin A in animals), zeinoxanthin (yellow), fucoxanthin, canthaxanthin, and astaxanthin (red), violaxanthin (yellow), lutein (yellow), neoxanthin (yellow), and antheraxanthin (yellow). Not all xanthophylls are involved with every xanthophyll-cited task within a tree leaf. Violaxanthin and lutein (yellow pigments) help capture light energy for photosynthesis (photosystem II) and dissipate excess energy for chlorophyll. Neoxanthin (yellow) does not capture light nor can it dissipate energy by eliminating energized radicals.

Lycopene (straight-line pinkish-red pigment) is the starting point for both carotenes and xanthophylls using two physiological processes. One process uses lycopene to generate beta-carotene with its two identical end rings eventually forming a number of xanthophylls. The other process generates alpha-carotene with its two different end rings eventually forming the xanthophyll lutein. As in the carotenes, small differences in end rings can change color expression. Lutein (yellow) and zeaxanthin (orange) are the same except for two bonds on one end ring.

Flavonoid Water Colors

There are more than 7,000 flavonoids -- phenolic compounds (having carbon rings) discovered in 1664. The pigment forms are found in angiosperms, especially in fruits and flowers, and in gymnosperms. All are water soluble and found dissolved in the cell vacuole solution. The flavonoids are here divided into two primary tree pigment groups: flavones and flavonols (pale yellow, cream, ivory, white, colorless); and, anthocyanins (dark yellow, orange, red, blue, pink, purple).

Flavo-Pale

Flavones and flavonols (sometimes called the "yellow flavonoids") are unique materials found in small amounts in tree leaves. They absorb selectively in the ultraviolet part of the spectrum, never interfering with photosynthetically active radiation wavelengths. They absorb much farther into the far blue end of the spectrum than anthocyanins. Some generate the yellows (chalcones) and bright yellows (aurones) of flowers. Many are visible to humans only when concentrated, then appearing milky or cloudy. Flavones and flavonols are visible to insects and utilized in some flowers to facilitate insect pollination. The value of flavones and flavonols to tree leaves are as selective light filters, filtering out the damaging UV light while allowing valuable wavelengths into cell machinery.

Some of the colorless flavone and flavonol pigments are maintained in cells and converted into anthocyanins when needed for protection of young tissues or of senescing tissues in Fall. The color expression value of flavones and flavonols are in how other colors are softened or modified. White creamy coloration provides additional depth and breadth for other colors. Colorless flavones and flavonols can form pigment complexes with highly colored anthocyanins and metal ions to form unique colors in a process called copigmentation. Some of the vivid blues arise from this process.

Anthocyanin Purple

Anthocyanins (meaning "blue paint" or "blue flower") are one form of water soluble ("watercolor-like") plant pigment discovered in 1913. They are usually concentrated just under the upper epidermis in the palisade parenchyma cells of the leaf. Anthocyanins are stored inside cell vacuoles and sometimes isolated in protein inclusions within vacuoles called anthocyanoplasts. In Fall, anthocyanins are synthesized in leaf cells from a pool of colorless flavonoids in vacuoles. Figure 7. They do not have nitrogen chemical components and so do not interact with nitrogen mobilization in the leaf. Anthocyanins are common in all trees and found in other terrestrial plants. These pigments are not essential to trees but perform many important functions. There are more than 630 anthocyanins known.

Anthocyanins are the pigments found in bronzed or dark-leaved trees in Summer. Anthocyanins also color some tree flowers, fruits, and new tissues. The red colored blush of new growth in many trees is the result of anthocyanin pigments. Anthocyanins make cherries, cranberries, and apples red while making grapes, blueberries and plums blue. The range of colors is great, producing dark yellow, orange, red, crimson, scarlet, dark red, blue, violet, pink, purple, burgundy, and purple-red colors. Anthocyanins can also be colorless.

Chameleon Changes

Each anthocyanin does not have a single base color. Color ranges widely depending upon conditions of the cell where dissolved over the course of the senescence season. Anthocyanins are not stable for long periods dissolved in the cell solution. Anthocyanins change color as cells age. They are sometimes mistaken for the water soluble betalain alkaloid pigments found in beet roots, spinach leaves and rhubarb stalks.

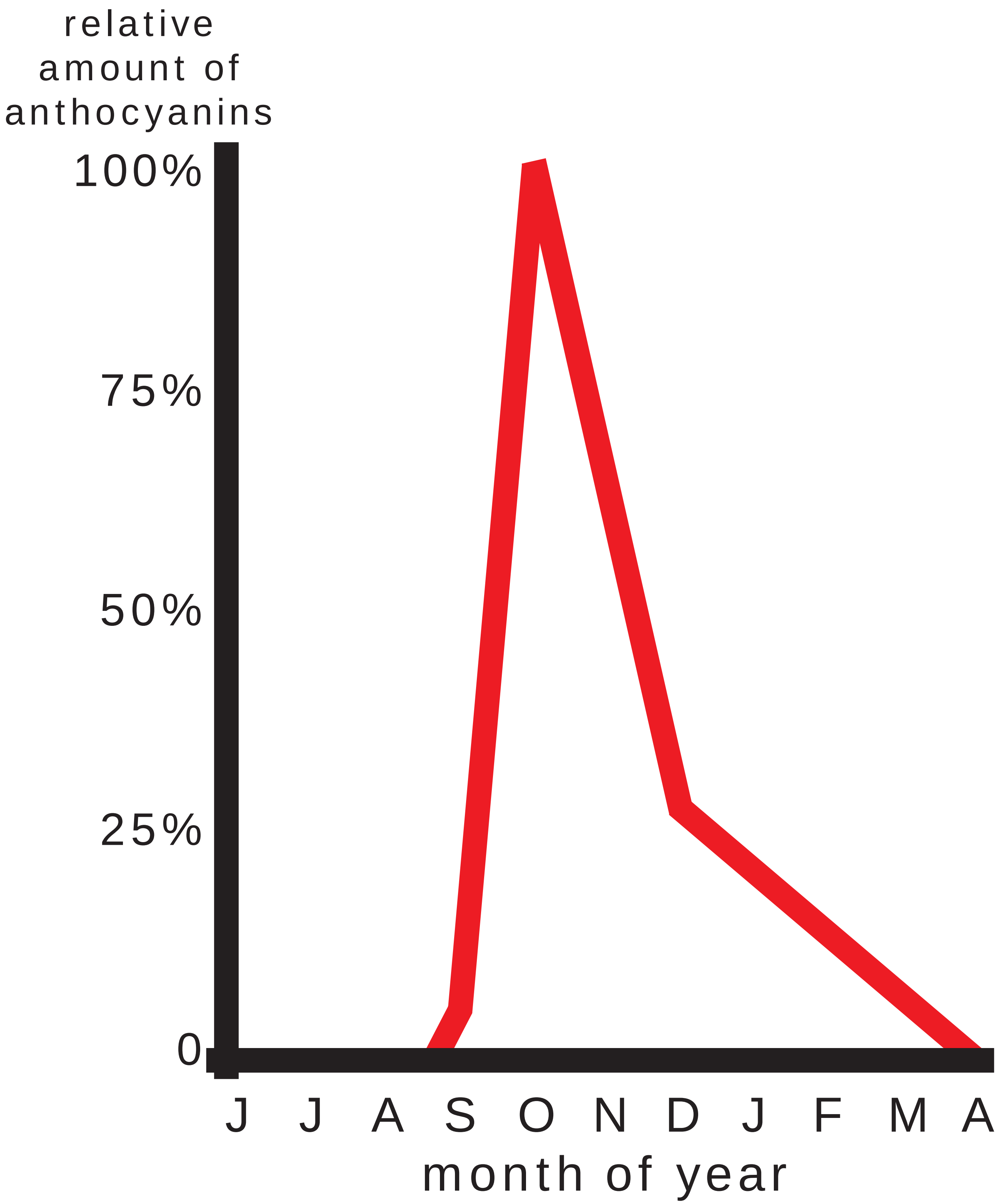


Figure 7: Changes of anthocyanins in oak leaves over time. (from Sanger, 1971)

Technically, there are two forms in the tree, usually not clearly differentiated: anthocyanins have a sugar attached; anthocyanidins are the pigment rings without a sugar attached. Usually glucose or rhamnose are the sugars comprising an anthocyanin. The sugar attachments make the anthocyanin more water soluble (and osmotically active / water conserving / frost resistive), and shifts the color of the pigment farther toward the blue end of the spectrum. Senescence greatly increased starch breakdown and sugar mobilization. Sugars greatly increasing within leaf cells in Fall include sucrose, fructose and glucose as anthocyanins concentrations peak.

Protective Services

In senescing leaves, anthocyanins serve a protective role. Anthocyanins provide sun-blocking, light filtering, and antioxidant services within leaf tissues containing chlorophyll. They can be induced in tissues by stress (cold, light, pests, element deficiency). Young shoots of Spring and senescing tissues in Fall may be colored with anthocyanins for protection. Summer leaves usually do not generate anthocyanins, but succulent shoots, petioles, and buds may show anthocyanin coloration. Anthocyanins help absorb damaging free radicals generated by inefficient photosynthesis reactions. Anthocyanins also provide limited protection against radiative frost damage while conserving leaf water.

Anthocyanins minimize photo-destruction of cell machinery by blocking damaging wavelengths of light in the 475-575nm wavelength range. Anthocyanins in tree leaves function as “blue blockers,” filtering out ultraviolet (UV) light to protect surrounding tissues from UV damage. Anthocyanins are generated following two pathways inside trees -- one initiated by ultraviolet light (UV) light reducing flavones, and one with no light required from a clear material called leuco-anthocyanin. Senescing leaves in full sun generate and maintain anthocyanins to assure successful reabsorption of valuable leaf materials.

Band on the Titanic

Anthocyanins are generated in response to many leaf stress conditions. One stress initiating anthocyanin production is essential element shortages. Senescence processes in a tree attempt to recover valuable nitrogen, sulfur, potassium, and phosphorus (and other elements) from leaves before leaves are abscised. As element deficiencies develop in a leaf, protective anthocyanins are generated to shelter the declining remnants of cell processes and machinery. Senescence is a living tissue process and requires some food production as fuel. Some waning level of photosynthesis is critical through the Fall, and anthocyanins help protect this last food production and remobilization process.

As starch is being dismantled into sugars, and sugars are being transported out of the leaf, anthocyanin content and forms greatly increase. Because anthocyanins are bound to a sugar molecule (the combined unit is called a glycoside) within a cell, sugar supplies are required for anthocyanin production and presentation. In Fall as low temperatures and a developing abscission layer slow material movement out of leaves, sugar enrichment and anthocyanin production result.

Red & Blue States

Every tree and species will have a different combination of anthocyanins generated depending upon genetic and environmental interactions. For example, as senescence of leaves continue into the Fall, cells become more acidic. As pH within a leaf becomes more acidic, the same anthocyanins become more red while a more basic pH in cells (early season cell contents) will generate more blue color expression from the same anthocyanins. The amount and form of iron (Fe) and aluminum (Al) in leaf cells also modify the range of anthocyanin colors.

Anthocyanins have a standard color gradient ranging across dark red, red, orange-red, purple-red, purple, bluish-purple, and blue. The chemical modifications which shift color along this color range are summarized in three statements: 1) as chemical attachments to the basic molecule change from OH (hydroxyl) to OCH (methyl), the color expressed becomes bluer; 2) as more small chemical attachments are added to the molecule, the color expressed becomes bluer; and, 3) the more basic cellular pH the bluer color expressed. See Table 3.

Variability!

Anthocyanin contents vary greatly from year to year in tree leaves while carotenoids stay relatively constant. Seasonal environmental and biological differences greatly change anthocyanin formation and color expression. Anthocyanin formation is greatly increased by, and color expression is impacted by:

-- leaf deficiency of nitrogen (N), boron (B), sulfur (S), potassium (K), and phosphorus (P);
-- water content (drying);
-- salt content (increasing);
-- starch to sugar conversion rate (accelerating);
-- sugar content (high);
-- ultraviolet (UV) light intensity (bright sunshine);
-- cool temperatures (non-freezing);
-- reduced precipitation (dry weather) causing less leaching of leaf materials;
-- wounding or infection of tissues
-- number of OH and OCH chemical attachments (more blue);
-- presences of chelating metals like aluminum (Al) and iron (Fe) (more blue);
-- presence of flavone or flavonol pigments (cloud and soften);
-- pH of cell vacuole (acid = red); and,
-- method of storage and cell shape.

Table 3: Example of colors expressed for selected anthocyanins with different chemical attachments (OH = hydroxyl group; OCH = methyl group), and at different cellular pH values.

name	attachments	pH 5 acid	pH 7 neutral	pH 9 basic
pelargonidin	1OH	dark red	orange-red	purple
cyanidin	2OH	red	purple-red	bluish-purple
delphinidin	3OH	purple	bluish-purple	blue
peonidin	1OH/1OCH	dark red	red	purple-red
petunidin	1OH/2OCH	red	purple-red	blue

Tannin Khaki

The death of leaf cells form oxidative products which are dark in color (melanins). These brown materials are various forms of phenolics like tannins. Tannins are found within and around leaf cells. Tannin, or tannic acid, was used to tan leather in the past concentrated from wood and bark. Tannins are water soluble and help color black tea. Tannins give red wine a darker color and a bitter taste. Tannins can be orange-brown, amber, yellow-brown, pale yellow, and light to medium brown in color. Tannins are polymers of phenolic rings combined in complex ways and found in two general forms in trees leaves: condensed and sugared.

Condensed tannins are laid side by side and can be precursors of anthocyanins (proanthocyanidins) under strong acidic conditions. Sugared tannins, or hydrolyzable tannins, are complexly interconnected with each other and sugars in small pieces. These two groups of tannins are not related to each other in how each are formed. From a color standpoint, they both generate dark colors. The sugared tannins are more water soluble than condensed tannins, and can form anthocyanins under weak acidic conditions. Tannins are reactive materials and can bind proteins together, disabling critical cellular, decay and digestive enzymes. Because tannins are dangerous to cell proteins, they are kept in cell vacuoles till cell death.

Betalain Special Red

Betalains (betacyanins or chromo-alkaloids) are water soluble, bright, alkaloid pigments stored in cell vacuoles. They were discovered in 1919. Betalains, like anthocyanins, are not essential to tree cells. Betalains are found in only one order of angiosperms called the *Caryophyllales* (*Chenopodiales*) and in some basidiomycete fungi. Within the *Caryophyllales* order there are several plant families, including the *Caryophyllaceae* and *Molluginaceae* which do not have betalains. If a plant has betalains, they will not have anthocyanins, and if they have anthocyanins they will not have betalain pigments. Trees with betalains are generally from the Mediterranean basin, Madagascar, and South Asia. Trees with betalain pigments are usually salt and drought tolerant.

Common plants with betalains include many carnivorous plants like pitcher plants, cactus, many succulents, seagrapes, pokeweed, jojoba, smartweed, sorrel, dock, buckwheat, rhubarb, salttree, bougainvillea, portulaca, ombu-tree, spinach, sugar beets and beets. The shirt-staining, water soluble pigment of a cut beet root is a betalain, not an anthocyanin. Notably, the carnations, pinks, campions and mouse-ears within this order of plants have anthocyanins not betalains.

Betalains are made from the amino acid tyrosine and has four carbon rings, many oxygens, and two nitrogens. Light is not required for inducing or producing this pigment. As an alkaloid, it is kept out of the way in the vacuoles of cells tethered to a sugar. Because it contains nitrogen, the pigment is part of a reabsorption process in the senescing leaf. Like anthocyanins, betalains reflect different colors depending upon pH conditions in the cell. Betalains are red to violet under basic pH conditions (called betacyanins), and yellow to orange under acidic pH conditions (called betaxanthins). Betalains have little impact on fall foliage coloration in the trees of Eastern North America, but can be found in understory and forest edge plants.

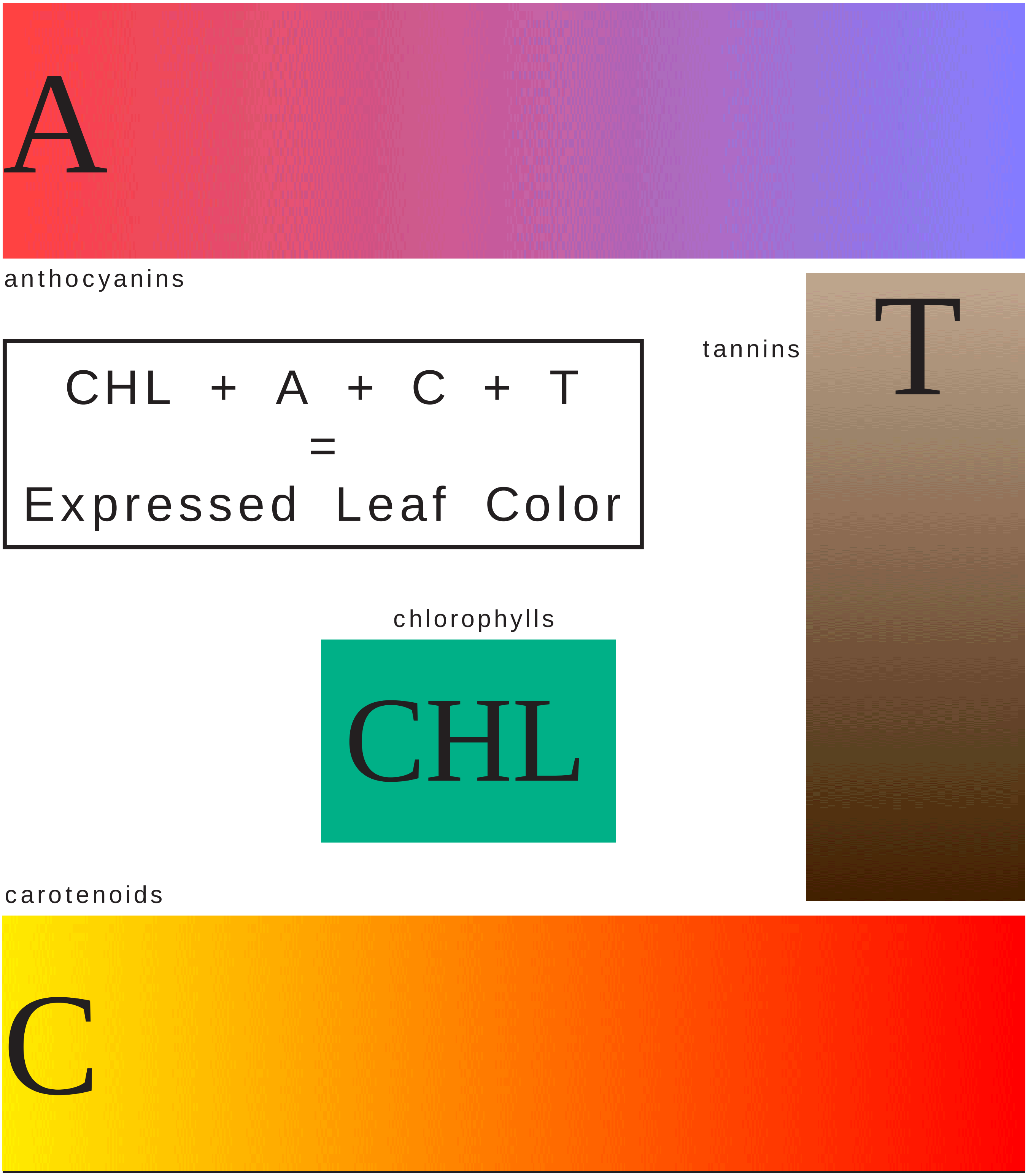
Pigment Summary

Fall colors herald Winter and approach of a following Spring. No new or unique mechanisms are used in generating fall colors, just pigments and colorants trees use for other functions.

The “watercolor,” “oil paint,” and “earth tone” colors all provide a fantastic show that humans around the temperate areas of the globe have long appreciated. Figure 8.

The chemistry of tree life can be colorful !

Figure 8: Generalized color range for major pigments comprising the autumn tree color expression palette.



Leaf Abscission

When leaves become inefficient and unable to produce food and growth regulators, a process of shutting-down and sealing-off begins. Trees shed many parts besides leaves, including fruit, flowers, bud scales, trichomes, twigs, and bark. The mechanism of tissue shedding has two components – active and passive. The active part is development of an abscission zone. Tree tissues, like leaves, are actively prepared for removal through biological and mechanical means. The passive part of tissue shedding is development of structurally weak areas along which force can be concentrated and tissues torn away by the environment. In other words, some tissues have cells which are forcibly broken apart, while other tissues have built-in weak zones which allow these tissues to be ripped away.

Shedding

Trees are shedding organisms. Trees shed inefficient or dead tissues internally as heartwood. Trees also shed tissues to the outside as root turnover, leaf and twig abscission, bark shedding, and through general compartmentalization. Shedding allows trees to maintain the most effective and efficient tissues to assure survival. If internal allocation problems or external environmental damage occurs, trees can eliminate unmaintainable living mass through shedding.

Leaf fall at the beginning of the dormant season in deciduous trees is one of the most visible of all shedding processes. By carefully examining fallen leaves and the leaf scars from where each fell, several things are apparent. The wound is usually smooth with vascular tissue ends clearly visible. The wound looks as though the leaf snapped-off in one catastrophic moment. Actually, leaf abscission is the culmination of many events and actions by the tree and within the environment.

End of Senescence

Abscission is the last step in a planned senescence process within tree leaves. Senescence is a series of events which allow trees to conserve resources, prepare for a resting period, and shed inefficient tissues. Senescence is not a disruptive series of unrelated events cued by worsening climatic factors. Senescence is a highly ordered and carefully controlled set of steps initiated in preparation for a resting stage in above-ground portions of a tree.

Near the end of the senescence process, designed fracture or failure lines develop at the base of tissues to be shed, like leaves. These prearranged fracture lines allow leaves to tear away without exposing the tree to additional damage. Leaf abscission is part of a process which allows the tree to seal-off tissues which will soon be killed or consumed by the environment. Trees use a senescence sequence to systematically remove valuable resources from leaves before they die. Once the resources are recaptured by the tree, dead and dying leaf tissues can then be shed. Frosts and heavy freezes at night, or sustained below-freezing air temperatures, quickly damage living cells in leaf blades and petioles. Once killed, all the resources leaf cells possess are unavailable for reabsorption into the tree.

Abscission Zones

Abscission zones occur at the base of leaf petioles and at the base of leaflets. Figure 9. Abscission zones are designed to allow for leaf shedding. Leaves are shed through a number of biological actions which weaken cell walls and initiate cells tearing away from one another. Abscission zones are composed of three critical portions: A) a cell wall degradation area; B) a shear force generation area; and, C) a tree protection zone. All three abscission zone portions are required for successful leaf shedding and effective tree survival. Most abscission zones are pre-positioned to facilitate shedding. Abscission zones may not be needed or used, but they are set-up to act as a potential barrier and boundary.

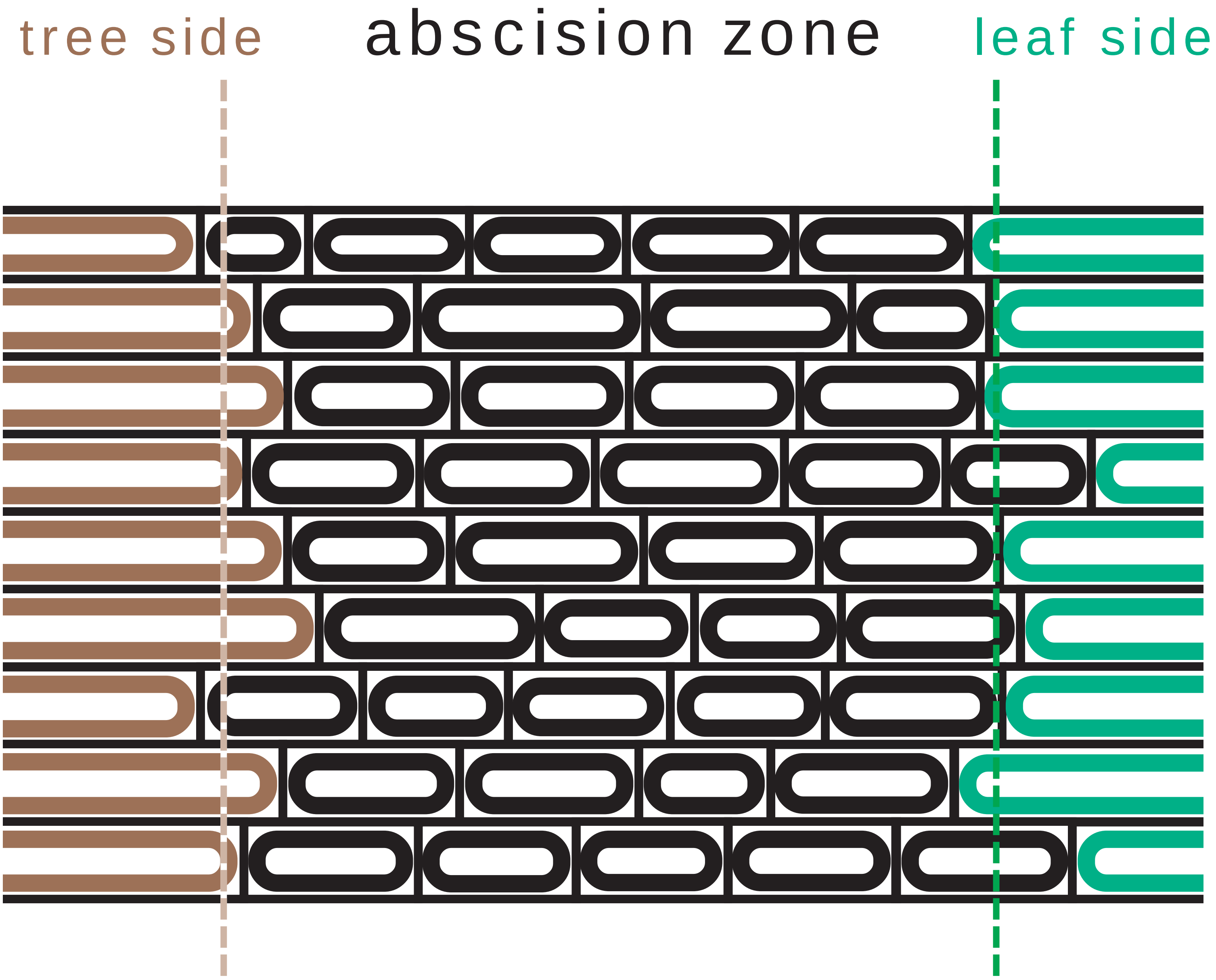


Figure 9: Two-dimensional diagram showing shorter cells in a leaf base abscision zone.

Wall Weakening

The abscission process begins with growth regulator signals initiating cellular changes. Abscission zone cells secrete pectinase and cellulase (wall degradation enzymes). These enzymes degrade the strength of the middle lamella and primary wall between cells. Figure 10. The middle lamella, the “glue” which holds cells together, begins to dissolve in the abscision zone.

At the same time, surrounding primary walls begin to swell from changes in chemical components. Calcium bridges across cell wall materials are removed. Cell wall changes are caused by enzymes and other materials deposited in cell walls produced by surrounding living cells. The cells in the abscission zone are dense with cytoplasm and organelles. Each cell is actively respiring and using energy to produce abscission materials. These cells remain alive and active until abscission.

More Wall Changes

As cell wall interconnections are weakened, water pressure within thin walled cells (turgor pressure in parenchyma) cause these cells to expand. As cells expand, they generate shear forces by pushing and pulling on surrounding weakened walls. Mechanically, fracture lines begin to develop between cell walls. In addition to internal forces, gravity and wind tugging on leaves help fracture lines grow.

As cell walls pull apart from one another, this open wound is being closed by deposition of blocking materials and protective compounds on the tree side. A strong protective boundary zone is prepared to defend remaining tree tissues from the environment and pests. Tyloses, suberin, lignin and other protective boundary-setting materials are developed and deposited on the tree side of the abscission zone. Figure 11.

Passive & Active

In the abscission zone, xylem elements and epidermis cell walls are either not degraded or are slow to weaken. These cells usually must be torn, stretched, or broken physically after connections between surrounding cells have been already fractured. Many types of circumstances like gravity, wind, precipitation and animal actions can break apart any remaining connected tissues and allow leaf fall.

The abscission process does require cell respiration and turgor pressure control. Breakdown of select carbohydrates, loss of small but key carbohydrate and protein wall components, increase of pectinase and cellulase enzymes, and removal of calcium wall connectors lead to wall weakening. As cells walls weaken further, parenchyma cells continue to osmotically expand, generating tremendous shear pressure on surrounding cell wall connections. Water is needed to generate this shear force. Rainfall or irrigation after an extended droughty period may lead to immediate leaf fall.

Control Mechanism

Auxin is a primary growth regulator produced in the leaf and slowly transported toward the leaf stem base through living cells. As long as auxin is effectively being transported across the abscission zone, abscission zone cells remain unreactive. As auxin production begins to wane in fall and auxin transport rates begin to decline due to less auxin availability, damage to living cells transporting auxin, and/or accelerating infection or wounding of living tissues by pests, cell wall changes are initiated.

Cell wall changes increasingly inhibit auxin transport, increase auxin concentrations on the leaf side, and accelerate ethylene production. Small amounts of ethylene hasten abscission zone development. ABA (abscisic acid), responsible (in part) for dormancy on-set in the leaf, stimulates ethylene production and inhibits auxin transport further.

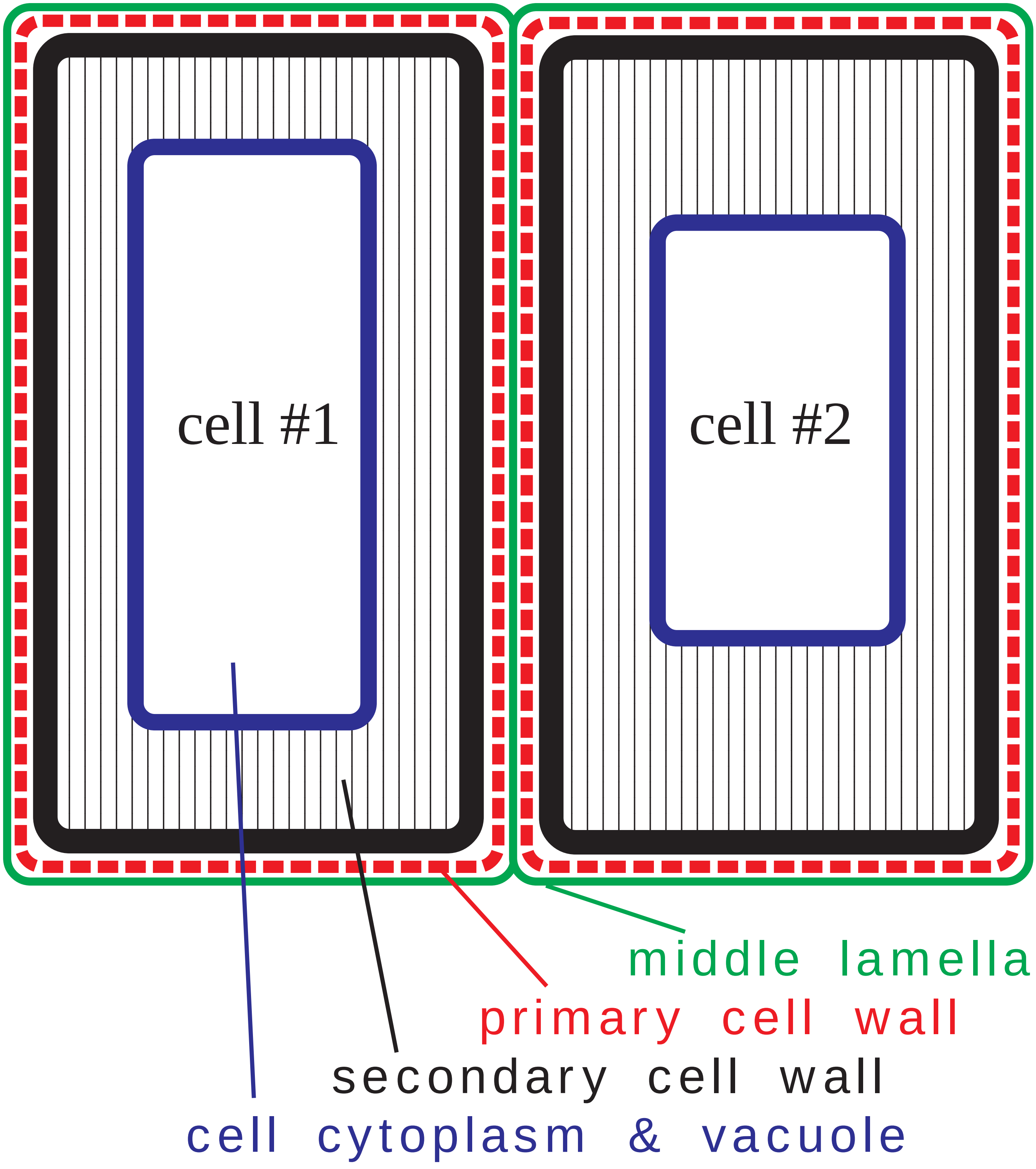


Figure 10: Two-dimensional diagram showing wall components of adjoining cells.

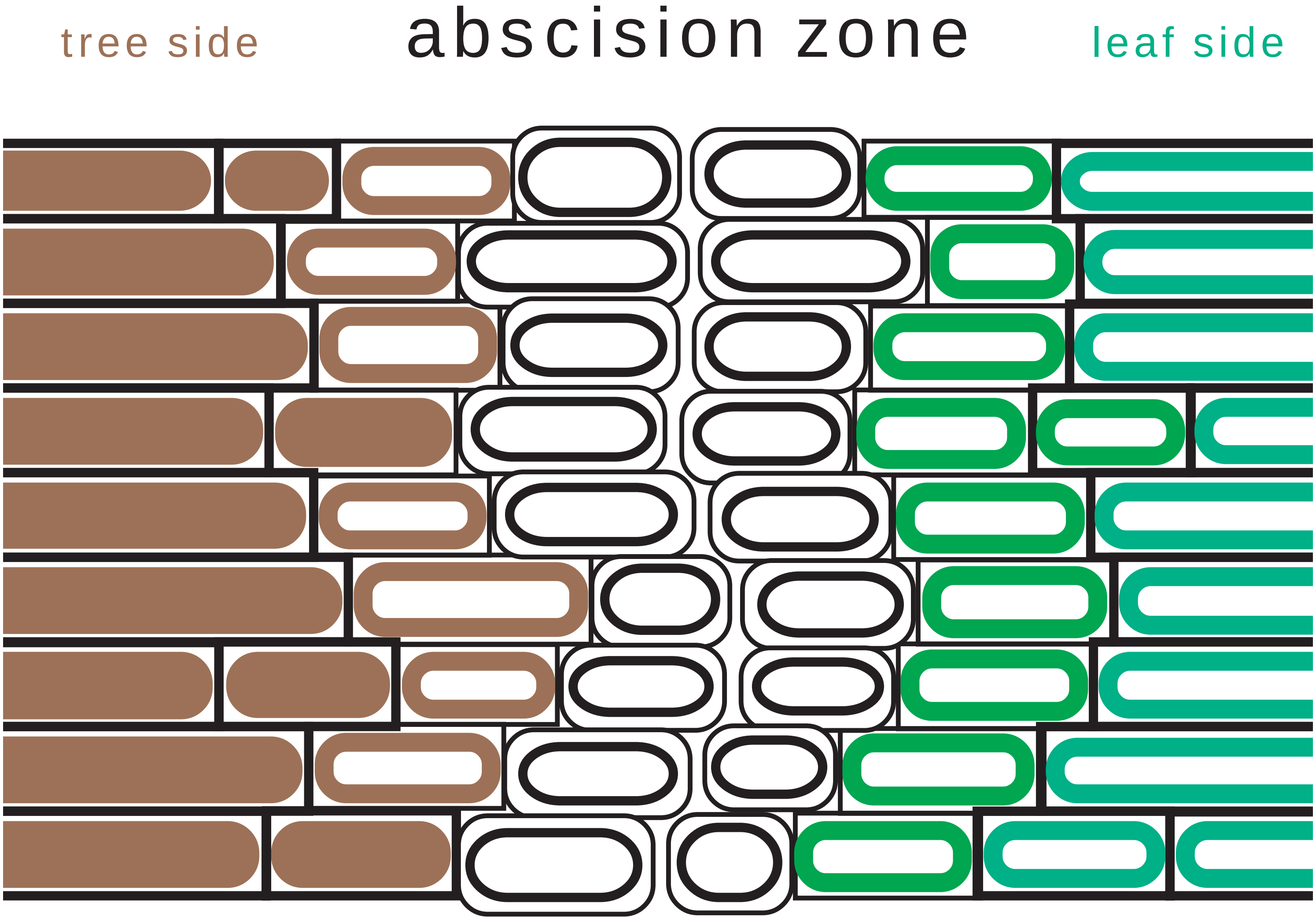


Figure 11: Two-dimensional diagram showing cells in a leaf base abscision zone with a fracture line between cells. Note tree protection zone on the tree side, wall degradation areas, and cell expansion zone all disrupting cell-to-cell connections.

In The Zone

Abscission zones in trees can be between 5-40 cells wide. Within this abscission zone only 1-3 cells will disconnect from each other. Cells in the abscission zone are the same types as found elsewhere in the tree. But, abscission zone cells tend to be smaller, more densely packed, with no intercellular spaces, less lignin, and have remained in a cell division phase longer than surrounding cells. Additional cell divisions in this zone prepares these cells for later abscission processes. Starch is stored in the abscission zone cells to assist in generating turgor pressure and enzymes for wall degradation.

In most abscision zones there is a single fault line which develops and is accentuated by additional wall degradations. Cells adjacent to fault line cells will have weakened walls also, allowing any fractures to propagate along several paths for short distances. Rarely, several full fault lines occur leaving the abscission wound ragged-looking. Fault lines follow the path of the middle lamella between cells.

Tree Responses

Deciduous trees do not loose all their leaves at once or just in the Fall. The larger and stronger any connecting xylem elements through the abscission zone, the longer leaves may be held on the tree. Some species do not fully set an abscission layer until early Winter. In other species, shear forces are not concentrated in the abscission zone until the beginning of the Spring growth period. Juvenile trees may not establish effective abscission zones at all and hold dead leaves throughout the 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.

The End?

Leaves are discarded by their trees to assure valuable resources are conserved, and in order to protect the tree. Leaves are designed to be disposable and pass through a senescence process which ends with abscission. Leaf abscission is both an active and passive process designed to seal-off and shed old tissues. Abscission of tissues help trees survive another year.

Color Surfing

The desire of people to see the best tree colors nature has to offer means estimating a time of peak color expression. This estimation process is fraught with problems because predictions are only as good as weather forecasts, tree health, and good chance allows. Human eyesight and color recognition also play a strong role in judging the quality and quantity of landscape color. Additionally, it is not necessarily the single tree and its colored leaves we most appreciate. As annual flowers may be massed together to yield a spectacular color show, trees can be seen as massed across a landscape in fall. The large swathes of tree colors blanketing autumn landscapes can be fantastic.

A Good Thing

Across a forested or tree-covered landscape, human color perceptions differ as much as tree colors. Some people enjoy and notice the early high contrast yellow stages of coloration. Others most appreciate the diversity of colors during the orange color peak. For other people, deep reds and purples of late Fall represent the best color presentations. Actually, the best colors are ones you can see and enjoy. Even people with limited color perception (color-blind) can enjoy the differences in texture and color contrasts developed in Fall. Any excuse for communing with trees and forests in search of autumn colors is a good thing.

Color Conditions

Fall colors are generated when chlorophyll is destroyed and other pigments are revealed or manufactured. Any climatic, site, or tree feature that modifies pigments will impact Fall colors. Probably most important to strong color presentations are the weather patterns of the preceding Summer and Fall. In some trees (most notably with ring-porus wood architecture), even events early in the previous Spring can affect this year’s Fall colors. The best conditions for Fall tree colors are: cool night temperatures with no freezes or frosts; warm, bright, unclouded sunny days; no drenching rains or wind storms; and, slight drought conditions in the last half of the growing season and on into the fall. Table 4.

Healthy Trees!

As in all life-associated functions, a healthy tree is needed for best color expression. A simple summary of good color conditions would be cool (not freezing), sunny, and dry. Fall rain fronts, long overcast periods, and extended periods of high humidity diminish color presentation. So do strong wind storms that blow leaves from trees. Wet and humid growing seasons lead to many leaf infections, premature leaf abscision, and leaching of materials from leaves. Heavy fertilizer applications of nitrogen and phosphorus can mute color expression, maintain chlorophyll longer into the season until a killing frost, or initiate leaf abscision from pests colonizing and damaging late season leaves. Freezing temperature and hard frosts stop color formation dead.

Table 4: Process summary steps in developing leaf color from late Summer to late Fall.

Leaf color formation is a natural process in trees.

Short days & cool nights of Fall bring changes to trees.

Green colored light-capture systems decline.

Turning-off leaves, green colors fade, reveal hidden colors.

Natural senscence reveals old colors & makes new colors.

Best colors come with cool, dry, and bright sunny days.

Frost, freeze, clouds, storms & rain hurt color expression.

Oil-paint-like colors = carotenoids (reds, oranges, yellows).

Watercolor-like colors = anthocyanins (reds, purples, blues).

Earth-tone-like colors = tannins (tans, browns).

Many different color combinations produced.
See Appendix 1.

Leaves sealed-off from tree & environment knocks off.

Fall colors not last gasp, but first breath of next Spring.

Color Pattern Development

Figures 12-16 are maps which help project color expression during Fall across the Eastern United States based upon historic weather measures. Figure 12 shows the month when the average sunshine hours decrease to 180 for the Eastern United States. This average value of sunshine hours tends to initiate senescence processes in trees. Figure 13 shows the month when the average daily temperature of 50°F is reached in Eastern North America. This average temperature pushes senescence along.

Figure 14 is similar to Figure 13. Figure 14 shows the progression of average minimum daily temperatures of 50°F across the Eastern United States. Figure 15 shows the average first 32°F temperature occurring by the end of each month across the Eastern United States. Figure 16 summarizes climatic and topographic values, showing the Appalachian range combined with the average daily temperatures on an annual basis. Note on Figure 16, it takes between and 1 and 1.5 weeks for color expression to move Southward for every 5°F of average temperature change.

Prediction Features

Key features of predicting fall tree colors and their peaks are:

1) leaf volume -- how many leaves are entering the color season still attached to their trees as compared to normal;

2) leaf health -- how damaged and disrupted are leaf surfaces from pest and environmental problems;

3) long-range weather forecasts for temperature, sunlight/cloudiness, and precipitation over the color period and the preceding few months;

4) actual temperature and precipitation over the last half the growing season, the whole growing season and the previous year's growing season;

5) key tree species timing and extent of color expression (species with premature and early leaf senescence); and,

6) historical record examination of peak color days from the past decade.

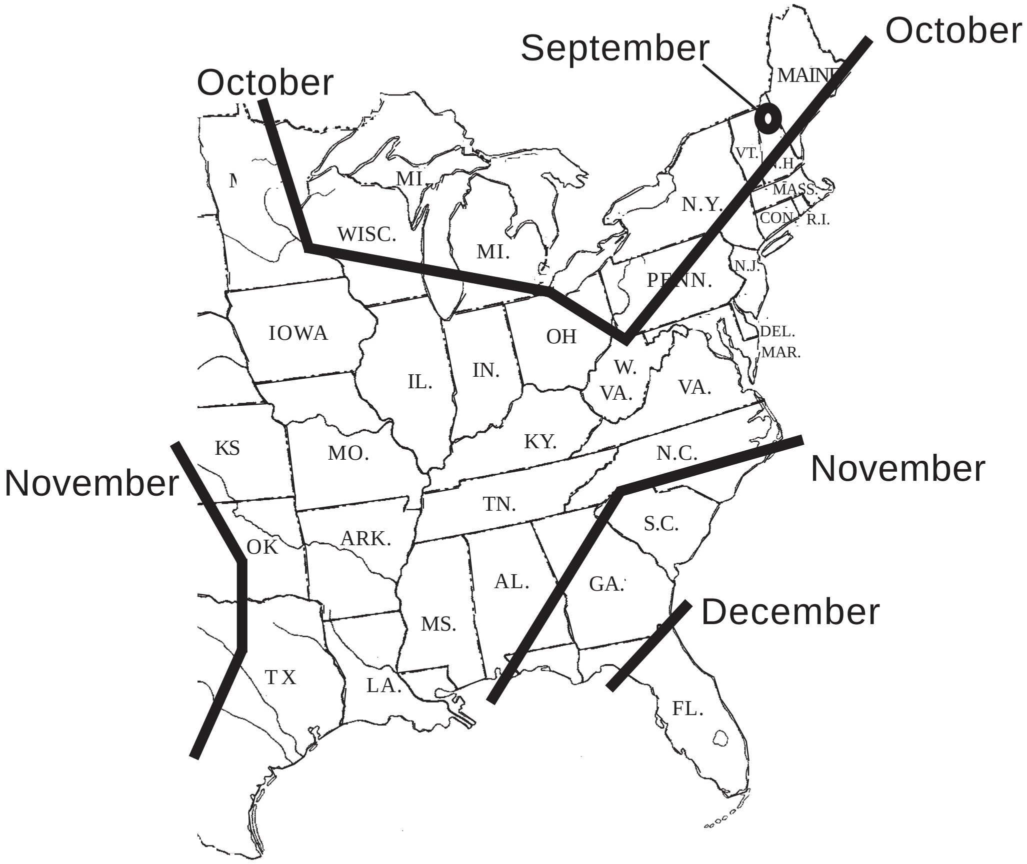


Figure 12: Average monthly progression of 180 sunshine hours South across the Eastern United States.

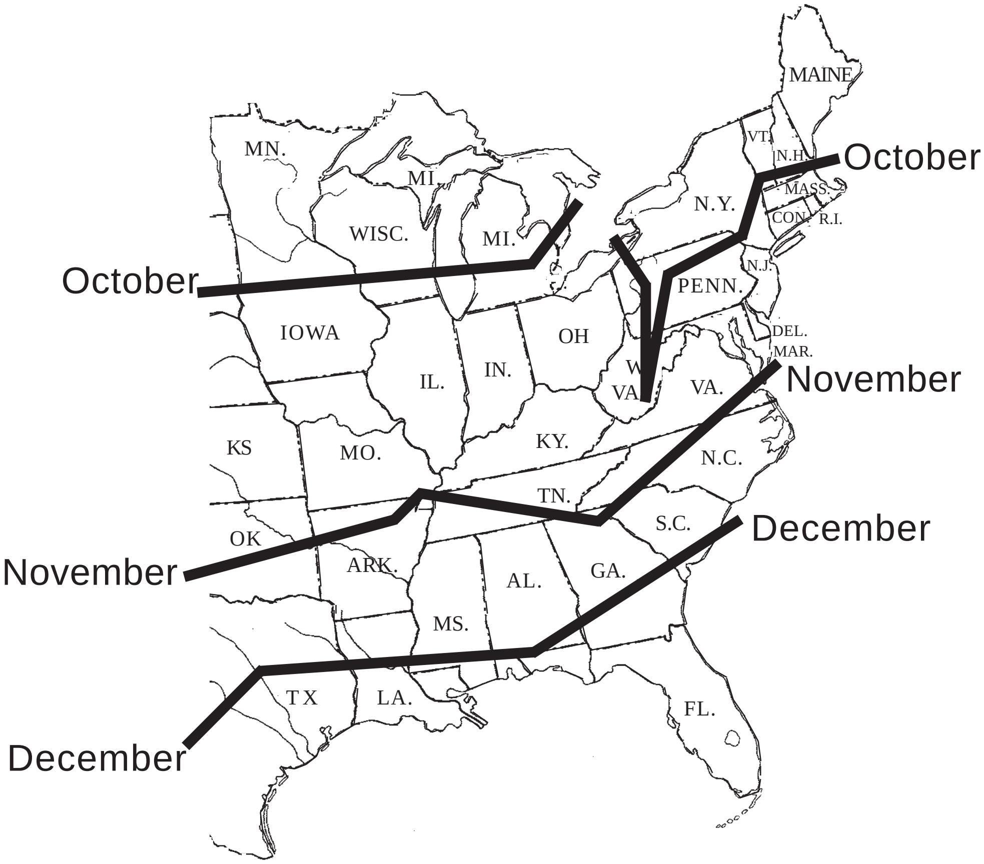


Figure 13: Average daily temperature of 50°F progression South across the Eastern United States in autumn.

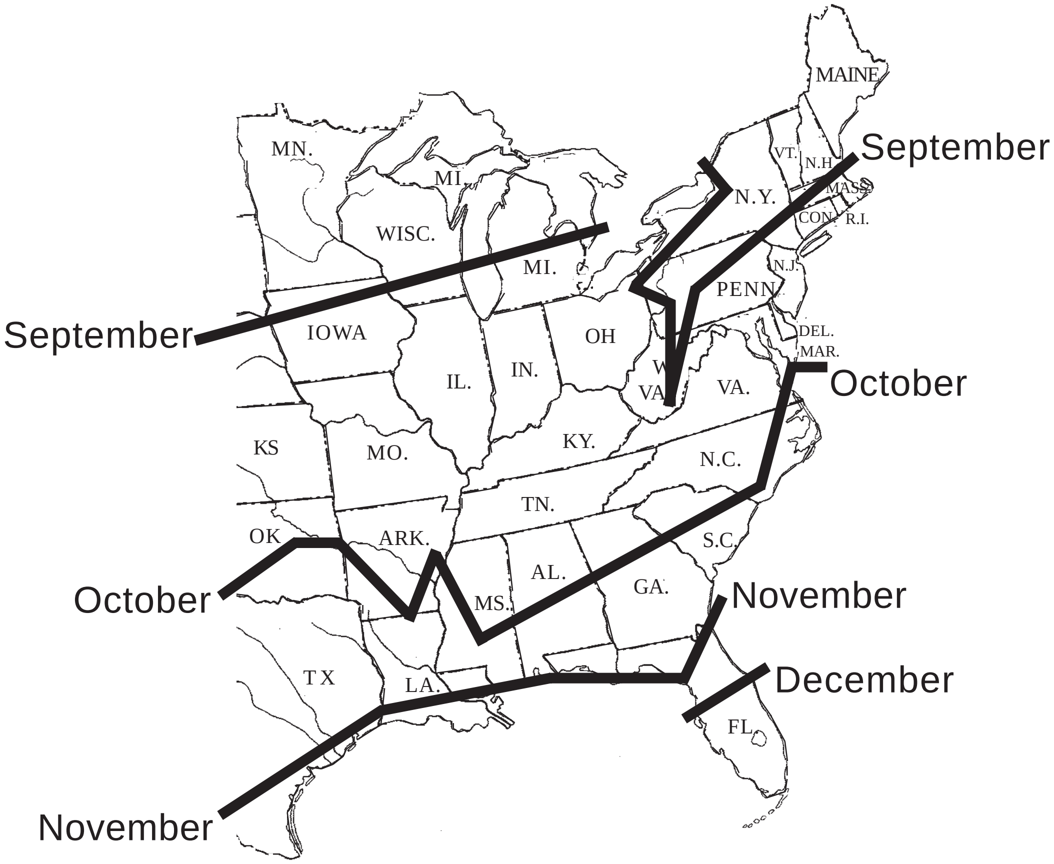


Figure 14: Average daily minimum temperature of 50°F progression South across the Eastern United States in autumn.

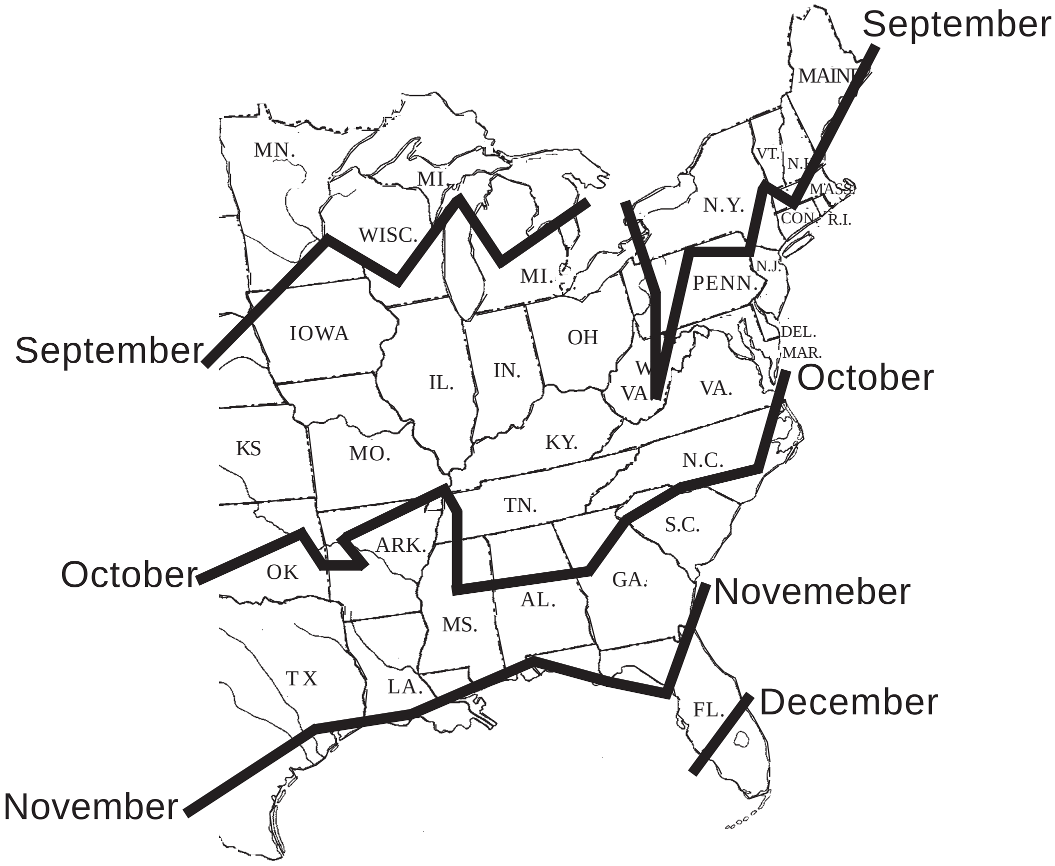


Figure 15: Progression of the average first 32°F temperature occurring across the Eastern United States by the end of each month.

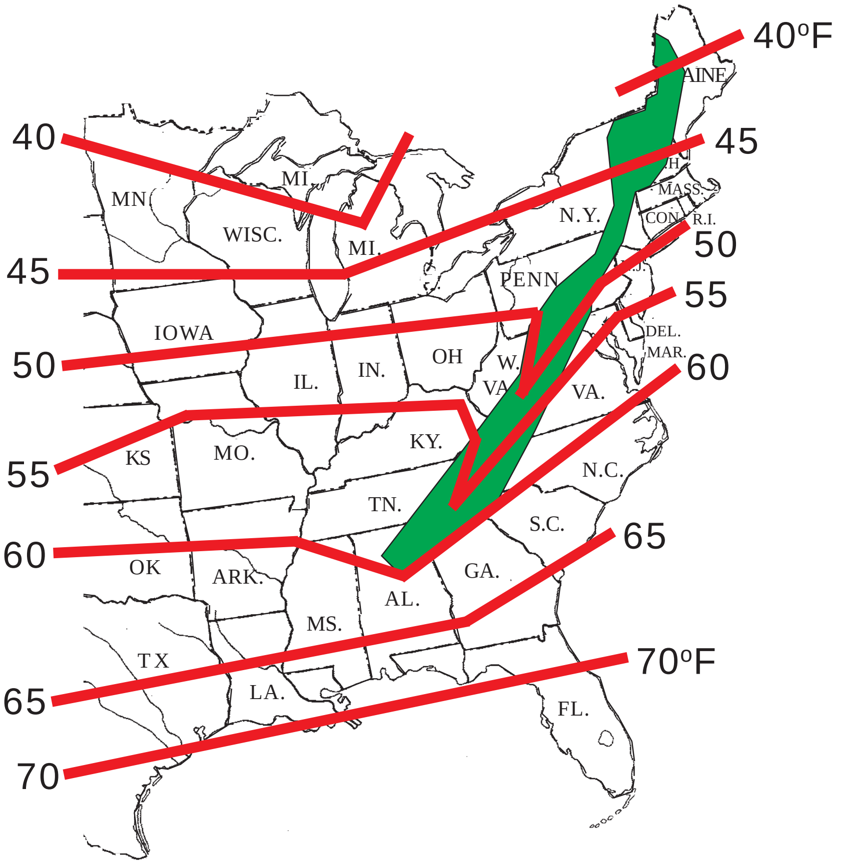


Figure 16: Map providing the area of the Appalachian mountains (in solid green), and the annual average daily temperatures in degrees (^{o}F in red solid lines).

Catching Waves

To understand landscape-level fall coloration in the Southeastern United States, a simple flow and wave model (Coder Leaf Color Propagation Model) can be used. Coloration changes begin at high altitudes and latitudes, and observationally flow down-slope and southward. Visualizing color waves sweeping over the landscape can help in explaining color changes, and associated environmental changes, occurring in Fall. Tree coloration advances in three primary waves in mixed hardwood forests.

Peaks

The first wave is yellow dominated. The second wave is orange. The third and final wave is red. Each wave, depending upon location is separated from the next wave by anywhere from six to sixteen days. Most humans consider peak color occurring just as the orange wave sweeps bye. After the red wave hits, the landscape slowly fades to brown. Figure 17.

Color Quenching

As color waves move southward, conditions yielding the best color expression are less and less present and not as strongly impacting on trees. The color waves eventually pass southward and are quenched in the evergreen forests of the Southern coastal plains. As fall progresses, the last pigments fade and the leaves fall away to carpet and enrich the forest floor. Even as this year’s leaves are raked, tree buds have next year’s leaves set to grow. Life processes continue in the rest of the tree to ensure surviving Winter. Fall colors represent not a last gasp, but a first breath of a new spring. Next year with spring bud break, chlorophyll veils will again come out with Fall colors hidden beneath their surfaces.

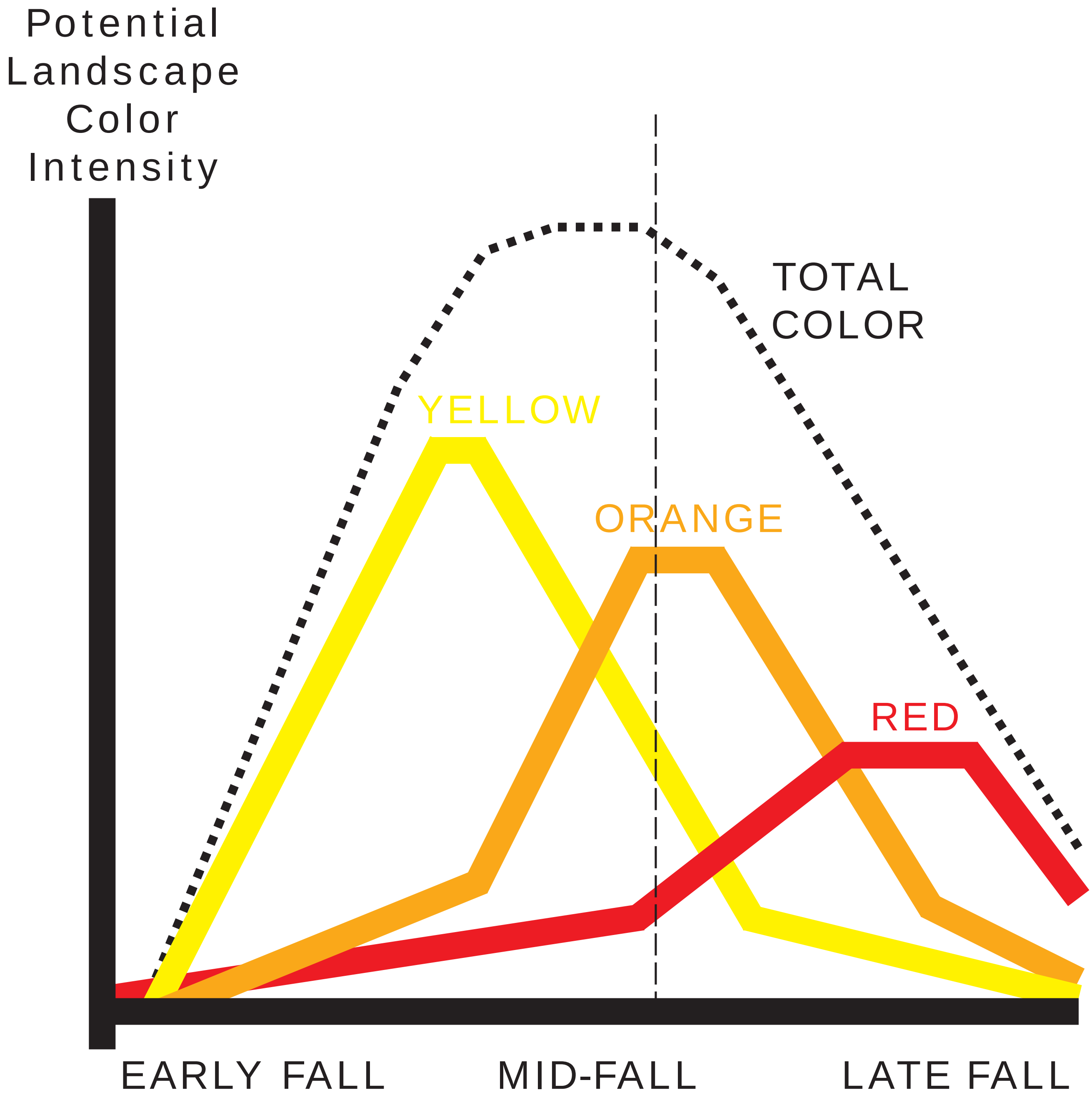


Figure 17: Principle landscape color waves from the Coder Leaf Color Propagation Model. Most people consider peak color at dashed line over the orange peak.

Summary

Best tree color presentations are the
additive effects and good fortunes of both
healthy trees and perfect climatic conditions.

See Appendix 1 for ideal tree
species color expression.

With so many different events leading to great tree color,
only a few years have a perfect combination
for best autumn color expression.

Selected Literature

Archetti, M. & S.P. Brown. 2004. The coevolution theory of autumn colours. Proceeding of the Royal Society of London (Series B) 271:1219-1223.

Close, D.C. & C.L. Beadle. 2003. The ecophysiology of foliar anthocyanin. Botanical Review 69(2):149-161.

Chalker-Scott, L. 1999. Environmental significance of anthocyanins in plant stress responses. Photochemistry and Photobiology 70(1):1-9.

Cuttriss, A. & B. Pogson. 2004. Carotenoids. Pages 57-91 in Davies, K. (editor). **Plant Pigments and Their Manipulations** (Annual Plant Reviews Volume 14). CRC Press, Boca Raton, FL, USA. Pp.352.

Hagen, S.B., S. Debeausse, N.G. Yoccoz, & I. Folstad. 2004. Autumn coloration as a signal of tree condition. Proceedings of the Royal Society of London -- Biological Sciences 271(Supplement 4):S184-S185.

Hoch, W.A., E.L. Singsaas, & B.H. McCown. 2003. Resorption protection -- anthocyanins facilitate nutrient recovery in autumn by shielding leaves from potentially damaging light levels. Plant Physiology 133:1296-1305.

Hoch, W.A., E.L. Zeldin, & B.H. McCown. 2001. Physiological significance of anthocyanins during autumnal leaf senescence. Tree Physiology 21:1-8.

Koike, T. 1990. Autumn coloring, photosynthesis performance and leaf development of deciduous broad-leaved trees in relation to forest succession. Tree Physiology 7:21-32.

Lee, D.W., J. O'Keefe, N.M. Holbrook, & T.S. Feild. 2003. Pigment dynamics and autumn leaf senescence in a New England deciduous forest, eastern USA. Ecological Research 18:677-694.

Matile, P. 2000. Biochemistry of Indian Summer: Physiology of autumnal leaf coloration. Experimental Gerontology 35:145-158.

Rolshausen, G. & H.M. Schaefer. 2007. Do aphids paint trees red (or yellow) -- can herbivore resistance or photoprotection explain colourful leaves in autumn? Plant Ecology 191:77-84.

Sanger, J.E. 1971. Quantitative investigations of leaf pigments from their inception in buds through autumn coloration to decomposition in falling leaves. Ecology 52(6):1075-1089.

Schaberg, P.G., A.K. van den Berg, P.F. Murakami, J.B. Shane, & J.R. Donnelly. 2003. Factors influencing red expression in autumn foliage of sugar maple trees. Tree Physiology 23:325-333.

Schwinn, K.E. & K.M. Davies. 2004. Flavonoids. Pages 92-149 in Davies, K. (editor). **Plant Pigments and Their Manipulations** (Annual Plant Reviews Volume 14). CRC Press, Boca Raton, FL, USA. Pp.352.

Taiz, L. & E. Zeiger. 1991. **Plant Physiology.** Benjamin / Cummings Publishing Company, Redwood City, CA, USA. Pp.565.

Tanner, G. 2004. Condensed tannins. Pages 150-186 in Davies, K. (editor). **Plant Pigments and Their Manipulations** (Annual Plant Reviews Volume 14). CRC Press, Boca Raton, FL, USA. Pp.352.

Wilkinson, D.M., T.N. Sherratt, D.M. Phillip, S.D. Wratten, A.F.G. Dixon, & A.J. Young. 2002. The adaptive significance of autumn leaf colours. Oikos 99:402-407.

Willows, R.D. 2004. Chlorophylls. Pages 23-56 in Davies, K. (editor). **Plant Pigments and Their Manipulations** (Annual Plant Reviews Volume 14). CRC Press, Boca Raton, FL, USA. Pp.352.

Zryd, J-P. & L. Christinet. 2004. Betalains. Pages 185-213 in Davies, K. (editor). **Plant Pigments and Their Manipulations** (Annual Plant Reviews Volume 14). CRC Press, Boca Raton, FL, USA. Pp.352.

Appendix 1:

Autumn colors of selected trees in the Southeastern United States.

Scientific name, common name, and fall color range are provided for tree species found in the Southeastern United States. Colors were placed into basic wavelength categories. Color descriptions which are hyphenated denote a first dominant color modified by the second listed color. No metallic, artistic, or whimsical color descriptions are used. Color intensity and purity change across the color expression season. Early in the season chlorophyll green will taint color expression. Late in the season or after severe frosts, dead tissue's brown colors will modify colors expressed. Average color expression as observed by the author or cited for each tree species is listed following the Coder Leaf Color Code values presented in Figure 18. Table 5 summarizes the range of colors from the tree species listed in Appendix 1.

scientific name	**common name**	**color expressed**
Acer barbatum	Florida maple	4
Acer buergerianum	trident maple	3 5 7 8
Acer ginnala	amur maple	3 7
Acer leucoderme	chalk maple	3 3B 5 7
Acer negundo	boxelder	3 3B
Acer nigrum	black maple	3 7
Acer palmatum	Japanese maple	7
Acer pensylvanicum	striped maple	3
Acer platanoides	Norway maple	3 5
Acer rubrum	red maple	3 5 7
Acer saccharinum	silver maple	3 3B 5
Acer saccharum	sugar maple	3 5 7
Aesculus flava	yellow buckeye	5
Aesculus glabra	Ohio buckeye	3 5
Aesculus hippocastanum	horsechestnut	3 3B
Aesculus octandra	yellow buckeye	3
Aesculus parviflora	bottlebrush buckeye	3
Aesculus pavia	red buckeye	3
Aesculus sylvatica	painted buckeye	3 5
Ailanthus altissima	tree-of-heaven	3
Alnus glutinosa	European alder	3B
Amelanchier arborea	serviceberry	4 5
Aralia spinosa	devil's walkingstick	3 3B
Asimina triloba	pawpaw	3
Betula alleghaniensis	yellow birch	3
Betula lenta	sweet birch	3 4
Betula nigra	river birch	3
Broussonetia papyrifera	paper mulberry	2
Carpinus caroliniana	blue-beech	3 5 7
Carya cordiformis	bitternut hickory	4

scientific name	common name	color expressed
Carya glabra	pignut hickory	3 4
Carya ovata	shagbark hickory	4
Carya tomentosa	mockernut hickory	4
Castanea dentata	chestnut	3 5
Castanea mollissima	Chinese chestnut	3 3B
Catalpa bignonioides	Southern catalpa	2
Celtic laevigata	sugarberry	3
Celtis occidentalis	hackberry	3
Cercis canadensis	redbud	2 3
Chionanthus virginicus	fringe tree	3
Cladrastis kentukea	yellowwood	3 4
Clethra acuminata	cinnamon clethra	3
Clethra alnifolia	pepperbush	3B
Cornus alternifolia	alternate-leaf dogwood	8
Cornus amomum	silky dogwood	9B
Cornus florida	dogwood	7 8
Cornus kousa	Kousa dogwood	7 8
Corylus americana	filbert	2 7B
Cotinus obovatus	smoketree	5 7
Crataegus calpodendron	pear hawthorn	5 7
Crataegus crus-galli	cockspur hawthorn	5 6 8
Crataegus mollis	downy hawthorn	4 6
Crataegus phaenopyrum	Washington hawthorn	5 7
Crataegus viridis	green hawthorn	7
Diospyros virginiana	persimmon	3 5 7
Elliottia racemosa	Georgia plume	3B 6
Euonymus americanus	strawberry bush	7
Euonymus atropurpureus	burningbush	3 5 7
Fagus grandifolia	American beech	3 3B
Fagus sylvatica	European beech	3B 7
Franklinia alatamaha	Franklinia	5 7 8
Fraxinus americana	white ask	3 7 7B 8
Fraxinus pennsylvanica	green ash	3 9
Ginkgo biloba	ginkgo	3
Gleditsiav triacanthos	honeylocust	3
Gymnocladus dioicus	Kentucky coffeetree	3
Hamamelis virginiana	witch hazel	3 4
Helesia diptera	two-winged silverbell	3
Helesia parviflora	little silverbell	3
Helesia tetraptera	Carolina silverbell	3
Juglans nigra	black walnut	3 3B
Koelreuteria paniculata	goldenraintree	3 4

scientific name	**common name**	**color expressed**
Lagerstroemia indica	crapemyrtle	4 7
Lindera benzoin	spicebush	3
Liquidambar styraciflua	sweetgum	3 5 7 8 9
Liriodendron tulipifera	yellow-poplar	3 4
Maclura pomifera	Osage orange	3
Magnolia acuminata	cucumber magnolia	4 7B
Magnolia fraseri	Fraser magnolia	3 3B
Metasequoia glyptostroboides	dawn redwood	5B 7B
Morus alba	white mulberry	3
Morus rubra	red mulberry	3
Nyssa sylvatica	blackgum	5 7 9
Ostrya virginiana	ironwood	3 5
Oxydendrum arboreum	sourwood	7
Parthenocissus quinquefolia	Virginia creeper	5 7
Pistacia chinensis	pistache	5 6
Platanus occidentalis	sycamore	3B 4
Populus deltoides	cottonwood	3
Prunus pensylvanica	fire cherry	3 5 7 8
Prunus serotina	black cherry	2 4 5 7
Prunus virginiana	chokecherry	3
Ptelea trifoliata	hoptree	3
Pyrus calleryana	ornamental pears	5 7 9
Quercus acutissima	sawtooth oak	3 3B
Quercus alba	white oak	3 3B 7 7B
Quercus bicolor	swamp white oak	7
Quercus chapmanii	Chapman oak	3 5 7
Quercus coccinea	scarlet oak	7
Quercus ellipsoidalis	northern pin oak	3B 7B
Quercus falcata	Southern red oak	3B 7B
Quercus falcata var. pagodifolia	cherrybark oak	2 3B
Quercus imbricaria	shingle oak	3B 7B
Quercus incana	bluejack oak	7B
Quercus laevis	turkey oak	7
Quercus lyrata	overcup oak	3B 7B
Quercus macrocarpa	bur oak	3 3B
Quercus marilandica	blackjack oak	3B 5B 7B
Quercus michauxii	swamp chestnut oak	5B 7B
Quercus montana (prinus)	chestnut oak	3B 4 7
Quercus muehlenbergii	chinkapin oak	7B
Quercus nigra	water oak	3B 4B
Quercus nuttallii	Nuttall oak	7B
Quercus oglethorpensis	Oglethorpe oak	7
Quercus palustris	pin oak	7 7B
Quercus phellos	willow oak	3B
Quercus robur	English oak	7 7B

scientific name	**common name**	**color expressed**
Quercus rubra	red oak	7 7B
Quercus shumardii	Shumard oak	7 7B
Quercus stellata	post oak	3B 7
Quercus velutina	black oak	3B 7 7B
Rhus (Toxicodendron) vernix	poison sumac	3 5 7
Rhus aromatica	fragrant sumac red	7B
Rhus copallina	winged sumac	7 8
Rhus glabra	smooth sumac	7
Rhus radicans	poison ivy	3 5 7
Rhus typhina	staghorn sumac	5 7
Robinia pseudoacacia	black locust	3
Salix nigra	black willow	3
Sambucus canadensis	elder	3
Sapium sebiferum	tallowtree	7
Sassafras albidum	sassafras	3 5 7
Sophora japonica	pagodatree	3
Sorbus americana	American mountain-ash	4 8
Styrax americanus	Amrican snowbell	2
Taxodium ascendens	pondcypress	7 7B
Taxodium distichum	baldcypress	5B 7B
Tilia americana	basswood	3 5B
Tilia cordaya	littleleaf linden	3
Ulmus alata	winged elm	3 4
Ulmus americana	American elm	4
Ulmus parvifolia	lacebark elm	3 7 8
Ulmus rubra	red elm	3 3B
Vaccinium arboreum	sparkleberry	8
Viburnum dentatum	arrowwood	7
Viburnum lentago	nannyberry	5 7
Viburnum nudum	possumhaw	7
Viburnum prunifolium	blackhaw	6 7 8
Viburnum rufidulum	rusty blackhaw	3B 7
Vitis rotundifolia	muscadine grape	3
Wisteria frutescens	American wisteria	3
Zelkova serrata	zelkova	3B 5B

Literature Sources for Appendix 1

Bell, C.R. & A.H. Lindsey. 1990. **Fall Color and Woodland Harvests.** Laurel Hill Press, Chapel Hill, NC. Pp.184.
Dirr, M.A. 1998. **Manual of Woody Landscape Plants.** Stipes Publishing, Champaign IL. Pp.1187.
Kirkman, L.K., C.L. Brown, & D.J. Leopold. 2007. **Native Trees of the Southeast.** Timber Press, Portland, Oregon. Pp.370.
Little, E.L. 1984. **Audubon Society Field Guide to North American Trees** (Eastern). Alfred A. Knopf, New York. Pp.714.

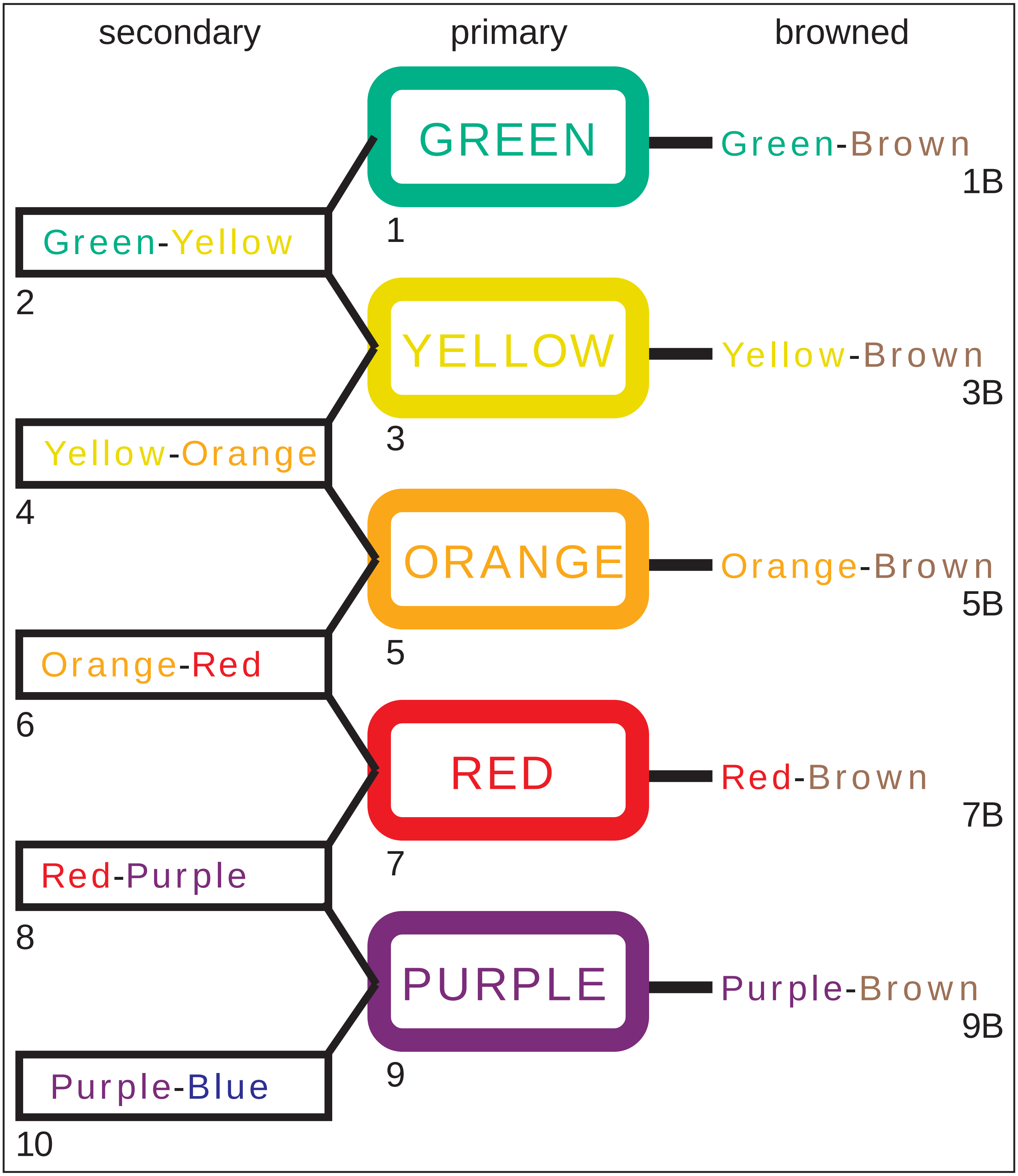


Figure 18: The 15 primary, seconday, and browned autumn tree colors with associated Coder Leaf Color Code values.

Each color modified by light (L) / dark (A), & intense (I) / dull (U).

Table 5: The distribution of colors among tree species listed in Appendix 1 -- Figure 18.

CODE #	COLOR	PERCENT
1	GREEN	0
1B	Green-Brown	0
2	Green-Yellow	6%
3	YELLOW	28%
3B	Yellow-Brown	10%
4	Yellow-Orange	7%
5	ORANGE	12%
5B	Orange-Brown	2%
6	Orange-Red	2%
7	RED	20%
7B	Red-Brown	7%
8	Red-Purple	5%
9	PURPLE	1%
9B	Purple-Brown	0
10	Purple-Blue	0