Autumn Leaf Colors

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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) Antioxidant protection for chlorophyll system as it is closed down for the season.
4) Regulate osmotic changes in senescing leaves 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.

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.

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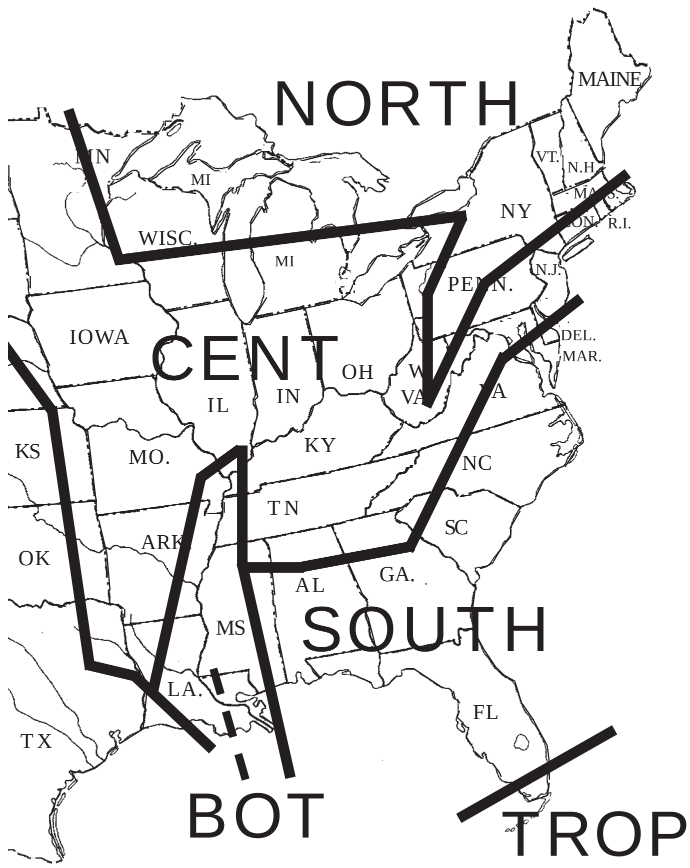

BOT = bottomland hardwoods -- cottonwood, gums, baldcypress, oaks
CENT = central hardwoods -- oaks, maples, cherry, yellow poplar, walnut
NORTH = Northern hardwoods -- maples, beech, birches
SOUTH = Southern oaks and pines -- yellow pines, southern oaks, sweetgum
TROP = tropical hardwoods -- mangrove,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

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

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.

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

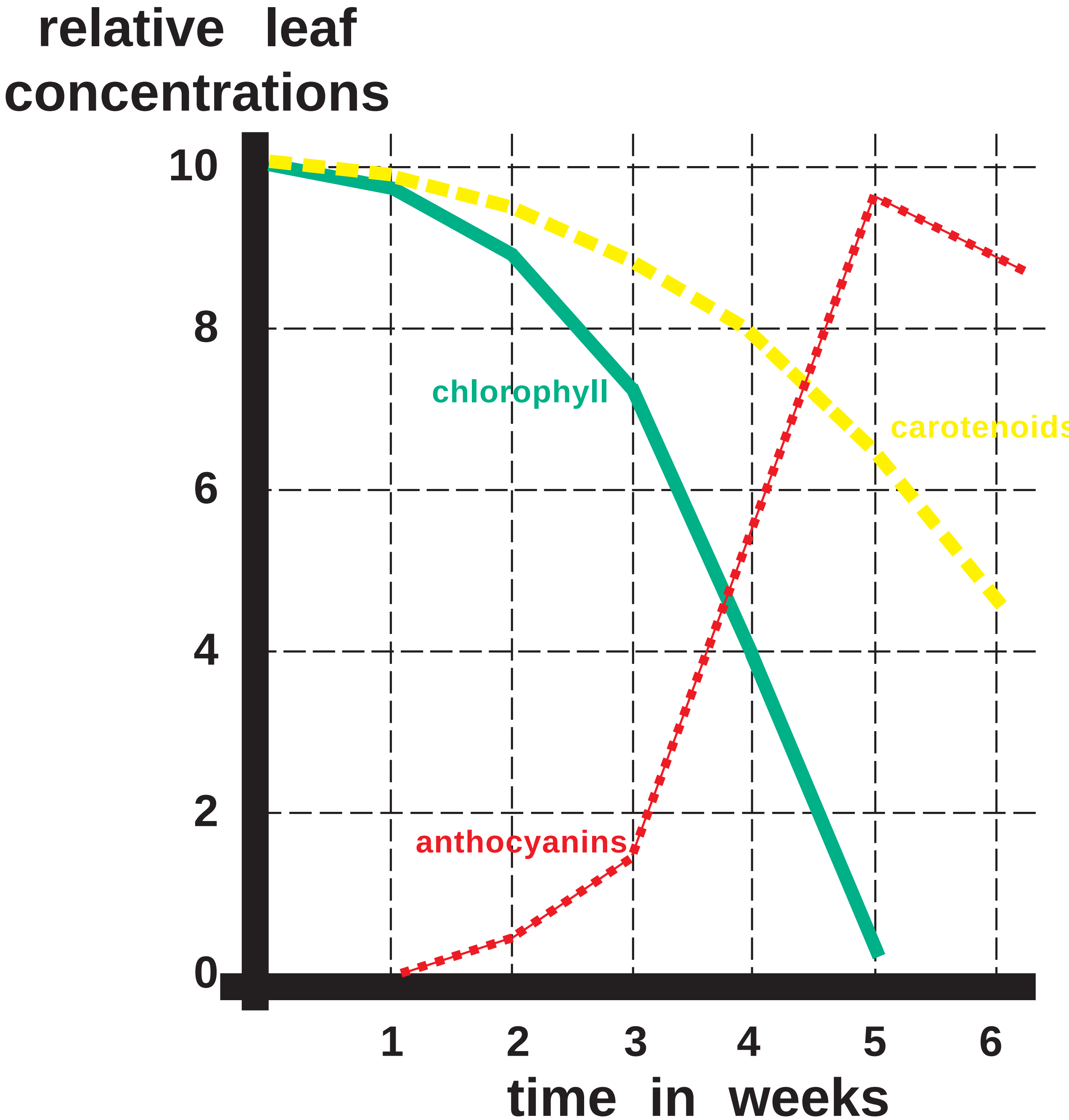

Figure 2: Relative change in primary tree leaf pigment concentrations over the fall senescence period.

(partially derived from Matile 2000)

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.

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). Figure 4.

The colors of tree rest and impending leaf 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.

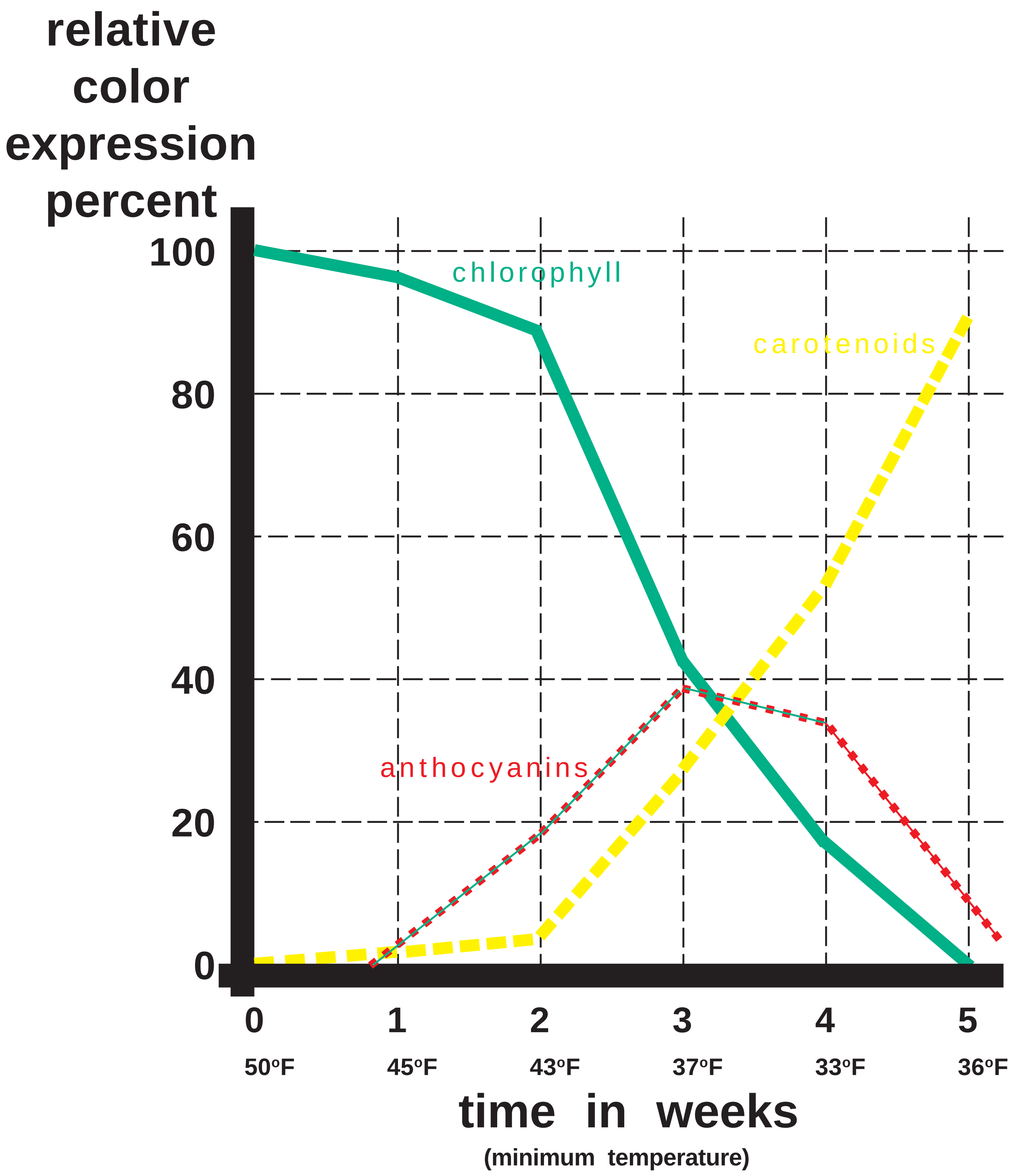

Figure 3: Relative color expression changes in a stand of sugar maple (*Acer saccharum*) trees in the Northeastern United States over one senescence period. (after Schaberg et.al. 2003)

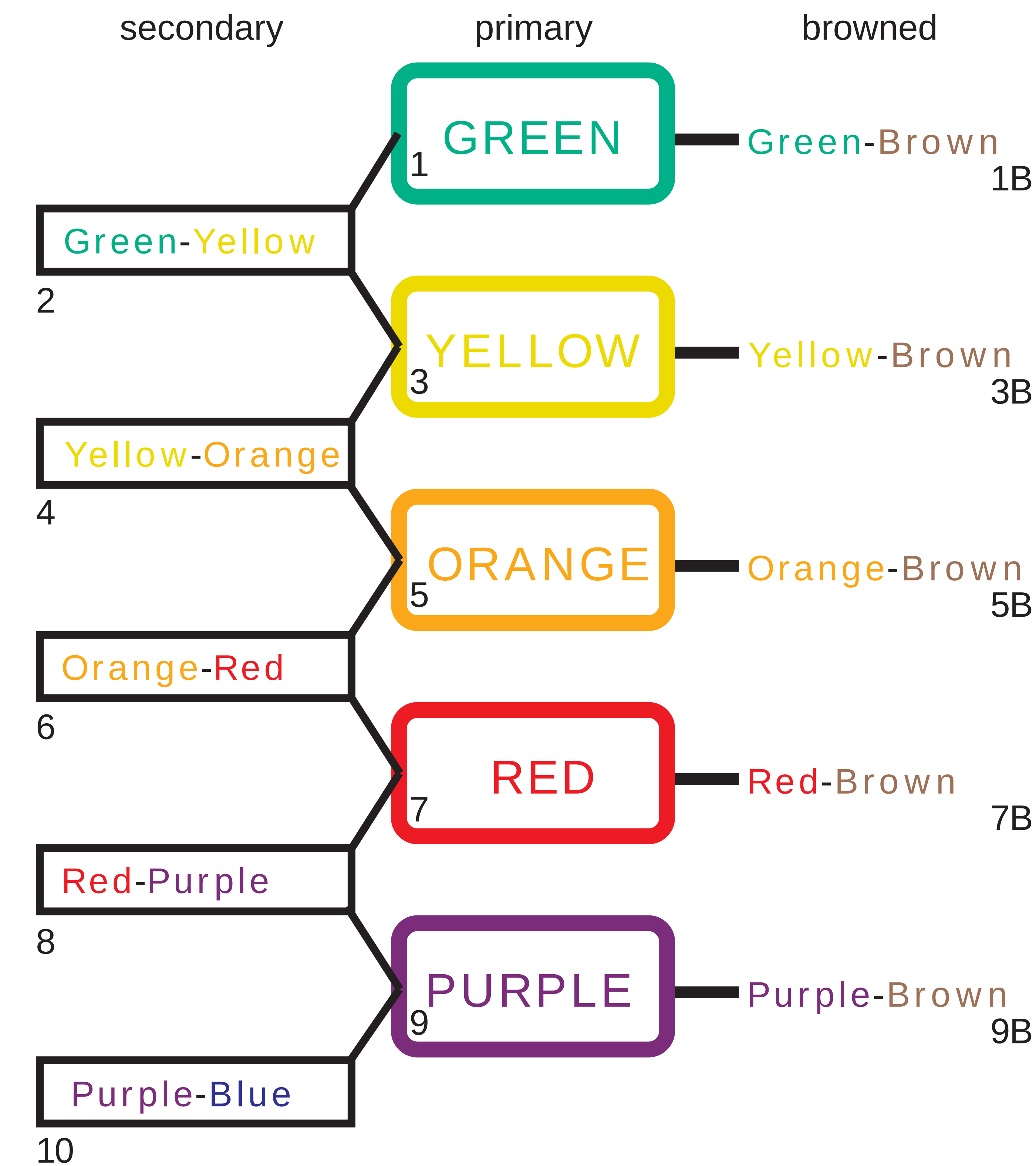

Figure 4: The 15 primary, seconday, and browned autumn tree colors with associated Coder Leaf Color Code values. Each color is modified by light (L) / dark (A), and by