Autumn Colours – Nature's Canvas is a Silk Parasol

The Adaptive Value of Autumn Foliage

Abstract

The variety and widespread nature of leaf colour change in autumn has led to investigation of the biochemical pathways and compounds responsible. The synthesis of bright red colouration initiated by longer nights prior to leaf abscission in deciduous species points to some adaptive value for this expensive ephemeral trait. It is hypothesized that during the breakdown of the unstable chlorophyll and the dismantling of the nutrient-rich photosynthetic apparatus, red anthocyanins provide a more biochemically parsimonious alternative to the elaborate xanthophyll system. This alternative enables leaves to screen out excess light energy and circumvent photooxidative damage to leaf cells, while allowing photosynthesis to persist at low rates in support of metabolic processes and phloem loading required for nutrient resorption from leaves.

Introduction

People continue to marvel at the spectacle of familiar green woods and local trees changing into a coat of blazing colours in autumn. Scientific investigations beginning in the 19th century (see Wheldale 1916) have led to a very good understanding of **how** this occurs. Research continues today in the fields of physiology, biochemistry, and molecular genetics to further elucidate the complex signalling pathways and mechanisms involved.

During the growing season, healthy leaves are green, and appear so due to the high concentrations of chlorophyll within the chloroplasts, organelles which act as microscopic factories converting water and carbon dioxide into carbohydrates and oxygen, using the energy in specific wavelengths of sunlight. Chlorophyll efficiently absorbs red and blue light during this process, but reflects or transmits the green light we observe. In autumn the chlorophyll breaks down and leaves show the yellow and orange colours of carotenoids already present in chloroplasts, but previously invisible because of the overwhelming green of the chlorophyll. In many species, new flavonoid pigments called anthocyanins are synthesized during this period imparting a

Robert D. Guy and Jodie Krakowski.
Department of Forest Sciences, Faculty of Forestry, University of British Columbia,
2424 Main Mall, Vancouver, BC, Canada, V6T 1Z4.
Corresponding author: guy@interchg.ubc.ca

red colouration, becoming purple as the pH increases (the compounds react with the cellular solution producing a visible colour change). These compounds are stored in vacuoles in the mesophyll and/or epidermal cells of leaves and fruits (Hrazdina et al., 1982).

Explaining **why** leaves develop brilliant hues in the autumn is not so straightforward. One North American aboriginal legend claims that when mighty ancestral hunters slew the celestial Spirit Bear, commemorated in the constellation, his red blood caused the tree leaves to redden in sympathy (Philp 2001). Jack Frost, charged with comprehensively painting every leaf with the onset of frost, would probably be relieved at recent developments in plant physiology which point to the adaptive value of leaf colour change in the autumn. His innocence is proven by the observation that leaves often change colour before temperatures reach the freezing point. Several environmental cues interact with the physiology of leaves to induce colour change well before the damaging temperatures of autumn arrive. Plant biologists and ecologists have proposed several direct fitness benefits of this transient adaptation.

Chlorophyll is a complex molecule. It is responsible for the vast majority of light capture to power carbon fixation in plants. Chlorophyll *a* and *b* molecules are associated with light harvesting complex proteins, which act as antennae funnelling light energy into photosystems I and II (Figure 1). Electrons, removed from water by the oxygen-evolving complex, are then propelled through these photosystems in a series of dozens of oxidation and reduction reactions that constitute the "photosynthetic electron transport chain". Proton (H^+) transport driven by the flow of electrons, in combination with the release of protons from water, creates a pH gradient across chloroplast membranes. The pH gradient is harnessed to make ATP (an energy currency) while the electrons are ultimately used to reduce NADP to NADPH. These products of the "light reactions" are consumed by the Calvin cycle, which, through numerous chemical steps, "fixes" CO_2 into the products of photosynthesis.

Photosynthesis ultimately produces carbon and energy stores available to the plant in the form of sugar, or stored in plastids such as chloroplasts as starch grains. These reserves provide the means by which all higher functions of the plant can occur: cellular division and repair, growth, nutrient uptake reproduction, translocation, etc..

Although ideally suited to their primary role, chlorophyll molecules easily break down due to their inherent instability, especially under the high-intensity photon bombardment of sunlight. The photons stimulate chlorophyll molecules to release excited electrons, disrupting the molecular bonds which hold the component atoms together. This is an exothermic reaction, after which the molecules achieve a more stable state in another form. This photooxidation of chlorophyll takes place throughout the leaf's green life. Normally, the chlorophyll thus destroyed is replaced by newly synthesized chlorophyll. In autumn, however, the synthesis of replacement chlorophyll stops.

Environmental triggers contribute to autumn colour change

In addition to providing the driving energy for photosynthesis, light influences the timing, magnitude and degree of leaf colour change and not only by destroying chlorophyll. Brighter sunlight tends to produce the most vivid colours, primarily when temperatures are low. Leaf age is also a factor, since the physiology and functions inherent in younger leaves differ from older leaves and they are less apt (or "competent") in responding to the longer nights and lower temperatures of autumn. Younger leaves, therefore, turn colour after mature leaves on the same tree (Figure 2). The foliage of *Larix lyallii* (sub-alpine larch) turns colour later into the autumn in years where leaf emergence has been delayed by cold spring weather (Worrall, 1993). On the other hand, drought and nutrient stress (Schaberg et al., 2003) contribute to earlier fading of green and the appearance of other colours. Often it is the tissues immediately adjacent to the veins that are the last to turn colour (Figure 3).

A reddening of foliage and other green tissues is not restricted to the autumn or to deciduous trees (Steyn et al., 2002). Even *Pinus banksiana* (jack pine) seedlings become stained with purple in the autumn (Nozzolillo et al., 2002). Other examples include the frequent bright reddish or purple tinge in many high-elevation plant species emerging through brilliant white snow, the red "snow algae" in montane and alpine sites, and the reddish cast in the winter foliage of several conifers (especially the *Taxaceae*, including the yews and redwoods, and *Cupressaceae*, including the cypresses) (Weger et al., 1993; Han et al., 2003). Many sun-exposed plants will also redden in summer in response to drought, nutrient or salt stress (Figure 4).

The interaction between the two stressors of high light and near-freezing temperatures has a more pronounced effect than either factor individually. This is easily observed: leaves at the top and outer edges of a canopy (unless they're young!), subject to the strongest light intensity, turn far brighter colours than shaded leaves (Feild et al., 2001). This suite of phenomena points towards a role for autumn pigmentation in **photoprotection**.

Natural history enthusiasts have long noted that leaves vary in colour, intensity and rate of change. This has been found among and within stands of trees of the same age, among parts of the same tree, even on different sides of a single leaf. Ramets of *Populus tremuloides* (trembling aspen) clones, where each individual tree is actually an aboveground shoot of a single root system, and thus all represent clones of a single genotype, have also been noted to vary widely in the same respect (Figure 5; Chang et al., 1989). Year to year variation was found in the peak colours and chemical signatures of different compounds within the same tree: yellow pigments were always detected, even in trees with green, orange or red foliage, while red pigments were only evident in red and orange leaves, and only expressed in some years (Chang et al., 1989). This variable and facultative expression of autumn colours may be correlated with environmental factors such as temperature and moisture availability.

Preparations for winter

A quick glance at the profusion of nature's ebullience may cause one to wonder, 'why bother?'. These leaves are on the brink of imminent death – they will soon fall off, and assume new functions as fodder or fertilizer as they decompose. However, the leaf still has one critically important function before this occurs. Large amounts of nutritive reserves must be recovered for winter storage so they can boost the array of activity which begins with new growth each spring.

Phloem-loading

When fully functional, deciduous leaves are rich in nitrogen, sulphur, potassium, phosphorus and numerous other essential plant nutrients. The main role of these elements, in free form or as components of proteins and other cellular constituents, is for photosynthesis. Nutrients are in short supply in most soils and it is therefore advantageous for plants to resorb and recycle

them. Indeed, over one-third of the yearly nitrogen and phosphorous requirements of forest trees are typically met this way. Studies show that following longer nights, nitrogen-containing amino acids and other nutrient-rich compounds move into leaf veins and then through the petiole, to be stored in the living bark (which includes the phloem) over winter (Greenwood et al., 1986). This translocation process is driven by osmotic gradients in the phloem created by the amount of dissolved solutes. The only way materials can exit leaves back to the stem is via this process, called phloem-loading. If available sugar is completely consumed and not replaced by photosynthesis, then transport will not be possible.

Phloem is a vascular tissue whose function is to move the products of photosynthesis and other phytochemicals throughout the plant, from their production site (source) to where they will be consumed or stored (sink). This movement depends on the active (energy-requiring) loading of sugars or sugar alcohols into phloem sieve and companion cells at the source end, and passive unloading at the sink end. Water follows by osmosis, generating a pressure gradient that pushes the phloem sap along. The sugar concentration of phloem sap is on the order of 15-25%. Hence large amounts of photosynthate are required.

A plant's ability to transport material through the phloem requires a functioning photosynthetic system to provide the sugar and energy needed for phloem-loading. Researchers have shown the existing energy reserves of leaves, consisting of sugars and stored starches primarily in the plastids, are too meagre to account for the recovery of leaf reserves without ongoing photosynthesis. The plant therefore faces a conundrum: at the same time enzymatic machinery is to be dismantled for seasonal recycling, some pieces of equipment must remain functioning to provide the energy and raw materials for this process.

Photoprotection

Normally functioning photosynthetic mechanisms dissipate light energy in excess of photosynthetic requirements. Light energy not captured for photosynthesis or otherwise diverted presents a danger to cells by reacting with unstable molecules and releasing free oxygen radicals, which then begin a series of oxidation reactions, damaging the cell (Yamasaki 1997). This type of damage due to light is called **photooxidation**. In particular, permanent

damage may be incurred by photosystem II as a result of excessive photon barrage. In leaves, the photosynthetic apparatus itself is the main source of these radicals.

If the speed of the carbon reactions is restricted by environmental stress (e.g., drought, poor nutrition, low temperatures), or if more light energy is absorbed than the photosystems are capable of processing, then the photosynthetic electron transport chain may become "over-reduced". Under these conditions of high excitation pressure, excess electrons may flow to oxygen (O_2) to produce superoxide (O_2^*) and other highly reactive radicals. These radicals destroy membranes and other cellular components on contact. Plants have efficient enzymatic systems for detoxifying these radicals, but these systems may be overwhelmed under high light, low temperature conditions. The risk will be especially high if light penetrates more deeply into canopies and leaf tissues as chlorophyll begins to degrade and leaves abscise. As summer ends, photosystems I and II, the chlorophyll-containing components of the photosynthetic apparatus, and the proteins of Calvin cycle are beginning to be dismantled and can no longer fully utilize the abundant light energy. Low temperatures, especially at dawn, exacerbate the situation by inhibiting remaining Calvin cycle activity (Figure 1). The leaf must rely on the properties of alternative pigments, some of which are already present in the photosynthetic complexes but were not previously visible due to masking by the strong green of chlorophyll.

First and most common are the **carotenoids** which absorb blue to green light and reflect yellow to orange wavelengths. The carotenoids include carotenes such as lutein (a brilliant red pigment) and xanthopylls such as zeaxanthin (which gives corn its yellow colour). Carotenoids, and especially zeaxanthin, are able to accept energy from chlorophyll and dissipate it safely as heat. Zeaxanthin is synthesized from another xanthophyll, violaxanthin, via the xanthophyll cycle. The amount of zeaxanthin present in a leaf at any one time is dynamically regulated by this pathway and may change within minutes (Demmig-Adams and Adams, 1992). The enzymes in the xanthophyll cycle are less efficient at low temperatures, but, depending on the species and whether the leaf is adapted to shade or sun, the presence of these pigments may be sufficient to prevent photooxidation and protect the senescent leaf for the remaining tasks at hand (Demmig-Adams and Adams, 1992).

The complex and energetically expensive xanthophyll cycle is a finely-tuned and highly sophisticated system. The simpler, although less precisely regulated, alternative for plants is to utilize **anthocyanins** or other screening compounds that block the light before it reaches chlorophyll (Figure 1). These molecules absorb higher-energy blue light and reflect or transmit lower-energy red light, so tissues with anthocyanins appear red to purple. Unlike the xanthophyll cycle, anthocyanins require no enzymes to function and are energetically much less costly to the plant to produce and maintain. Like the carotenoids, energy absorbed by anthocyanins is simply lost as heat. They are also effective antioxidants (Neill and Gould, 2003). Thus, this group of phytopigments acts as a molecular sunscreen or parasol to greatly reduce the amount of light impinging on remaining chlorophyll, preventing the initiation of unstable redox reaction chains and the release of damaging free oxygen radicals within the cell.

For plants which can potentially synthesize both xanthophylls and anthocyanins, there is clearly an advantage in the latter, cheaper compound, especially as leaves become more stressed and biochemical pathways less stable. Thus the vermillion and scarlet hues deepen as autumn progresses.

Adaptive benefits of colour change

Many different explanations have been proposed for the occurrence of autumn colour change in leaves. The association with light availability was noted very early on (Wheldale, 1916). Previously scientists thought that the synthesis of these chemicals did not have any evolutionary benefit, but it is highly improbable that such a persistent and widespread phenomenon would be selectively neutral. The distribution and frequency of autumn colour change suggests that this response evolved in many plant taxa independently, which infers it has some fitness benefit (e.g., Jaenike 2001). Similarly, a theory that compounds producing autumn colour were serving waste functions, emptying vacuoles of toxic products prior to leaf abscission (Ford 1986) seems unlikely on the same grounds. Red, orange or purple colours in fruit and possibly adjacent leaves are thought to provide a signal to herbivores that seeds are developmentally ready for dispersal, but many leaves that change colour have wind-dispersed fruit, are too immature to reproduce, or change colour long after seeds are dispersed.

An interesting recent hypothesis proposed that red leaves afford some

protection against aphid herbivory, suggesting that coevolution led to host specificity based on visual leaf colour cues as a signal mechanism for tree health during autumn oviposition (Archetti 2000; Hamilton and Brown, 2001). While many genera and species were reviewed, this does not take into account oviposition at other times and herbivory by other organisms; in autumn leaf herbivory in general is quite low.

As reviewed here, recent physiological explanations for autumn anthocyanin production focus on its role in capturing light and preventing photooxidative damage to the photosynthetic apparatus, especially during stress induced by low temperatures during autumn (Smillie and Hetherington, 1999; Hoch et al., 2001). Weger et al. (1993) proposed a similar role for winter rhodoxanthin in red cedar. The more efficient operation of anthocyanins at low temperatures relative to chlorophyll also suggests an adaptive role. Localized anthocyanin and rhodoxanthin expression at leaf surfaces which receive the most sunlight substantiates a protective role for these compounds (Gould et al., 1995; Feild et al., 2001; Hoch et al., 2001).

DO try this at home!

Simply appreciating nature's grandeur is eminently rewarding for those lucky enough to live in temperate continental climates featuring deciduous forests. The most spectacular examples are found in North America: the forests of New England, the Canadian maritime region and Quebec are major tourist attractions in autumn. These changes, although more subtle, can also be observed in some deciduous conifers. In the Rockies and Cascades, golden yellow stands of sub-alpine larch make for particularly enchanting and popular hiking destinations (Figure 6). Angiosperms such as *Betula* (birches), *Liriodendron tulipifera* (tulip trees) and most *Populus* (poplars, cottonwoods and aspens) turn yellow before becoming brown; even in these trees it is simple to observe which parts of the tree change colour first.

Research has demonstrated that ecological successional roles also influence the timing and expression of autumn colour: pioneer species, which colonize disturbed habitats and tend to grow rapidly, are adapted to maximize carbon capture in high light environments by inherent photoprotection mechanisms (Hoch et al., 2001). These species generally have less spectacular colours than the more shade tolerant species which typically grow in older forests.

There is a simple experiment anyone can do to test and observe these physiological changes and the effects of the environment on their expression. This works especially well on species with dramatic autumn changes, such as *Liquidambar styraciflua* (sweetgum), *Rhus* (sumac), *Cornus* (dogwood) or *Acer saccharum* (sugar maple). Before the leaves begin to change colour, cover up a portion of a leaf, still attached to the tree, with a piece of opaque material, such as thick paper. Do this on both sides of the leaf and secure it with a paper clip. An alternative approach is to cover the leaf with an image drawn in black on transparent film. Wait until the rest of the leaves on the branch show their autumn pigmentation and remove the masking: the covered portion should retain the yellow carotenoid colours, and little or no green since sustained chlorophyll synthesis requires direct light. You can even add an element of creative design or stencil mysterious messages (Figure 7) along your favourite wooded trail!

Bibliography

Archetti, M. 2000. The origin of autumn colours by coevolution. Journal of Theoretical Biology 205:625-630.

Chang, K.-G., Fechner, G.H., and Schroeder, H.A. 1989. Anthocyanins in autumn leaves of quaking aspen. Forest Science 35:229-236.

Demmig-Adams, B., and Adams, W.W. III. 1992. Photoprotection and other responses of plants to high light stress. Annual Review of Plant Physiology and Plant Molecular Biology 43:599-626.

Feild, T.S., Lee, D.W., and Holbrook, N.M. 2001. Why leaves turn red in autumn. The role of anthocyanins in senescing leaves of red-osier dogwood. Plant Physiology 127:566-574.

Ford, B.J. 1986. A theory of excretion in higher plants. Journal of Biological Education 20:251-254.

Gould, K.S., Kuhn, D.N., Lee, D.W., and Oberlauer, S.F. 1995. Why leaves are sometimes red. Nature 378:241-242.

Greenwood, J.S., Stinissen, H.M., Peumans, W.J., and Chrispeels, M.J. 1986. *Sambucus nigra* agglutinin is located in protein bodies in the phloem parenchyma of the bark. Planta 167:275-278.

Hamilton, W.D., and Brown, S.P. 2001. Autumn tree colours as a handicap signal. Proceedings of the Royal Society of London, B 1489-1493.

Han, Q., Shinohara, K., Kakubari, Y., and Mukai, Y. 2003. Photoprotective role of rhodoxanthin during cold acclimation in *Cryptomeria japonica*. Plant, Cell

and Environment 26:715-723.

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

Hrazdina, G., Marx, G.A., and Hoch, H.C. 1982. Distribution of secondary plant metabolites and their biosynthetic enzymes in pea (*Pisum sativum* L.) leaves. Plant Physiology 70:745-748.

Jaenike, J. 2001. Sex chromosome meiotic drive. Annual Review of Ecology and Systematics 32:25-49.

Neill, S.O., and Gould, K.S. 2003. Anthocyanins in leaves: light attenuators or antioxidants? Functional Plant Biology 30:865-873.

Nozzolillo, C., Isabelle, P., Andersen, O.M., and Abou-Zaid, M. 2002. Anthocyanins of jack pine (*Pinus banksiana*) seedlings. Canadian Journal of Botany 80:796-801.

Philp, J. 2001. Why leaves change color. University of Maine Cooperative Extension Bulletin #7078.

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

Smillie, R.M., and Hetherington, S.E. 1999. Photoabatement by anthocyanin shields photosynthetic systems from light stress. Photosynthetica 36:451-463.

Steyn, W.J., Wand, S.J.E., Holcroft, D.M., and Jacobs, G. 2002. Anthocyanins in vegetative tissues: a proposed unified function in protoprotection. New Phytologist 155:349-361

Weger, H.G., Silim, S.N., and Guy, R.D. 1993. Photosynthetic acclimation to low temperature by western red cedar seedlings. Plant, Cell and Environment 16:711-717.

Wheldale, M. 1916. The anthocyanin pigments of plants. Cambridge University Press, Cambridge, UK. 318 pp.

Worrall, J. 1993. Temperature effect on bud-burst and leaf fall in subalpine larch. Journal of Sustainable Forestry 1:1-18.

Yamasaki, H. 1997. A function of colour. Trends in Plant Science 2:7-8.
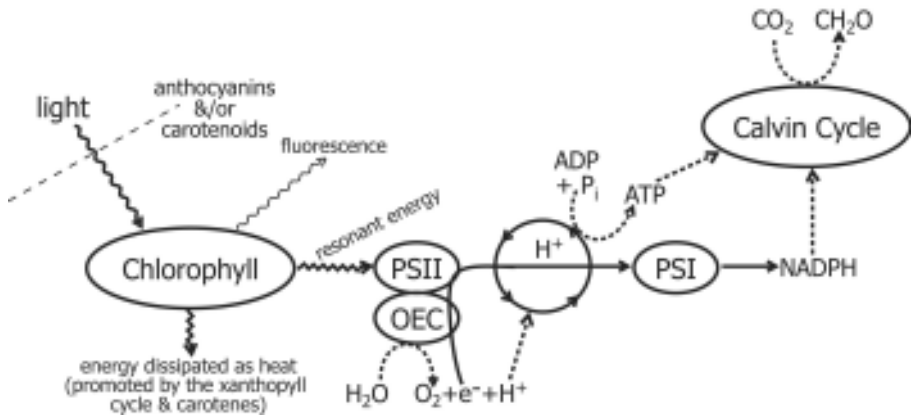
Figure 1. Simplified diagram of photosynthetic apparatus. PS I and II are photosystem I and II, respectively; OEC is the oxygen-evolving complex; P$_i$ is inorganic phosphate; e$^-$ represents electrons; H$^+$ represents protons; CH$_2$O represents carbohydrate products of photosynthesis.

Photos: Rob Guy

Figure 2. Colour changes later in younger leaves.
Figure 3. Isolated tissues turn before areas adjacent to major veins in this *Acer rubrum* (red maple) leaf.

Figure 4. a) anthocyanin in autumn foliage of *Acer palmatum* (Japanese maple), b) astaxanthin in *Chlamydomonas nivalis* (red snow algae), c) rhodoxanthin in western *Thuja plicata* (western red cedar), d) betacyanin in salt-adapted *Salicornia europaea* subsp. *rubra* (samphire).

Figure 5. Carotenoids in autumn *Populus tremuloides* (aspen) foliage.
Figure 6. Autumn foliage of *Larix lyallii* (sub-alpine larch).

Photo: Rob Guy

Figure 7. The name of the first author's eldest son, Lachlan, "stencilled" onto *Euonymus alatus* (winged Euonymus).