Leaf senescence and autumn leaf coloration

When viewed by astronauts, Earth is the blue planet. When imaged by Earth observation satellites, the planet is green. This reflects the fact that water and chlorophyll are the signatures of life in the solar system. Satellite images show the green color of vegetation ebbing and flowing with the seasons (**Fig. 1**). A whole season of the year in temperate regions is named for the fall of leaves that follows the seasonal replacement of chlorophyll with the yellows, oranges, reds, purples, and browns of autumn foliage. Such a global-scale biological event must surely have a purpose and a mechanism. We are now learning the *how* of color change in plants; the *why* is more elusive, but new insights from genetics and evolutionary biology are providing possible answers.

Light is essential for green plants, but can be harmful too. The small ephemeral weed *Arabidopsis thaliana* is botany's laboratory rat: a universally studied model organism that does just about everything

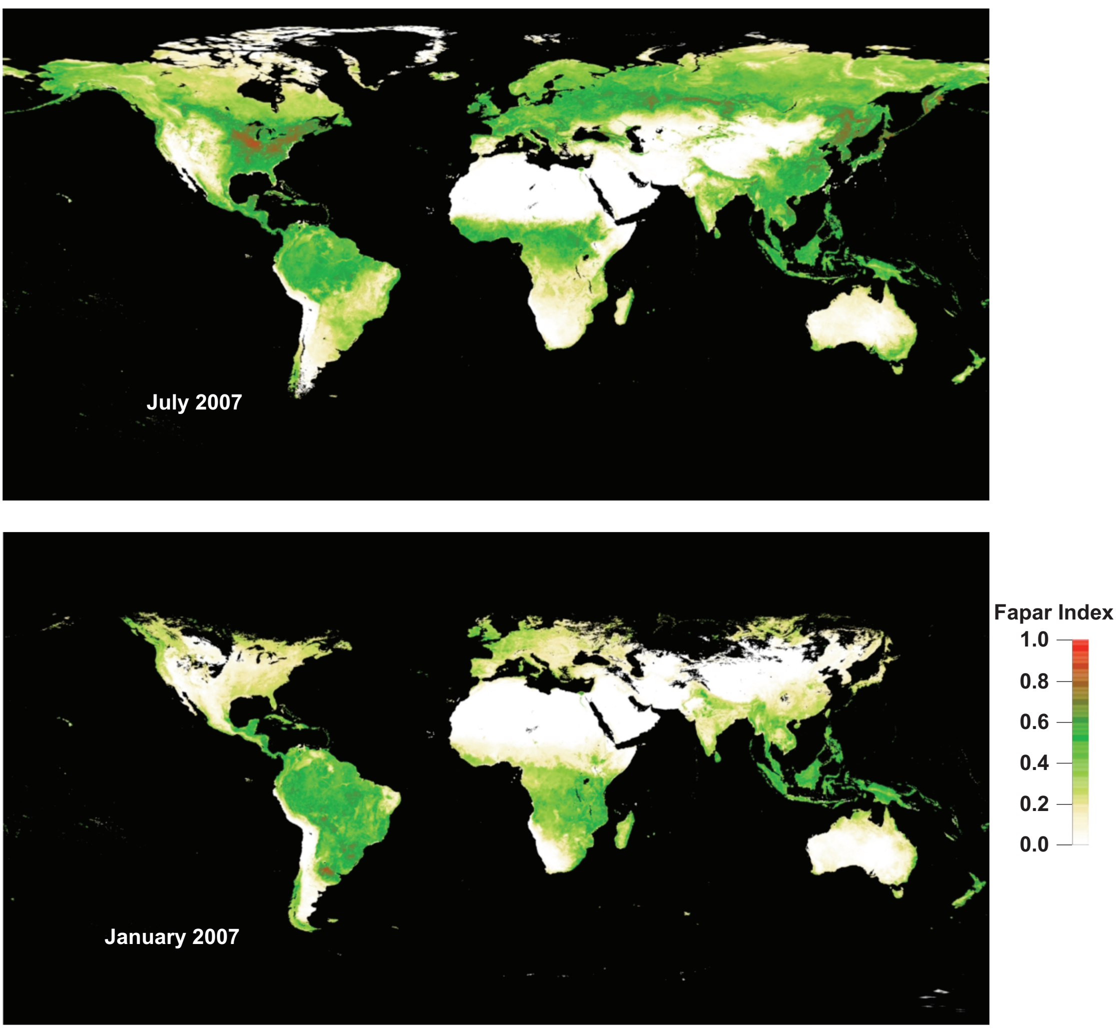

Fig. 1. Photosynthetic pigments of foliage on a global scale, measured by the Envisat satellite in Fapar units (Fapar = fraction of absorbed photosynthetically active radiation). The images are monthly averages comparing coverage in January and July 2007, showing the extent of seasonal variation in chlorophyll, particularly in northern temperate regions. (*Courtesy of European Space Agency Envisat satellite, MERIS data*)

a flowering plant should do, in an experimentally tractable way. Like those of trees and crop species, its leaves develop into the green solar panels that power growth through photosynthesis, then, when their productive job is done, they initiate senescence, turn yellow, and eventually die. There are many *Arabidopsis* mutants with alterations in genes controlling development, physiological function, and environmental response. Among these mutants is *acd2*, a genetic variant that suffers from lesions on older leaves in the light (**Fig. 2**). When the *acd2* gene was finally cloned and identified in 2001, it turned out to be an inactive form of a gene encoding red chlorophyll catabolite (RCC) reductase, an enzyme of chlorophyll breakdown. This provides a clue as to why plants take the trouble to expend physiological energy on changing the colors of leaves that are destined to die: chlorophyll and its derivatives, if not carefully processed by organized biochemical pathways in green cells, can be toxic when illuminated. The mutant's name, *acd2*, stands for *accelerated cell death*-2 and clearly expresses the consequences of disrupting pigment metabolism in senescing green tissues.

The behavior of *acd2* can be understood in evolutionary terms by considering how certain single-cell algae dispose of chlorophyll. If cultures of *Chlorella protothecoides* growing photosynthetically in the light are transferred to darkness and deprived of a nitrogen source, they turn yellow by a process that resembles the yellowing of senescing leaves. At the same time, the culture medium accumulates a red pigment that chemical analysis shows to be a chlorophyll derivative. A similar red chlorophyll catabolite (RCC) is an intermediate in the metabolism of chlorophyll during leaf senescence (Fig. 2). RCC is potentially harmful because it generates reactive oxygen species and free radicals that destroy the fabric of living cells. Single-cell aquatic plants deal with the threat from RCC by pumping it out of the cell. Multicellular land plants do not have this option and have evolved a detoxification mechanism that begins with the conversion of RCC to a colorless product by RCC reductase. In the mutant *acd2*, RCC reductase is missing. As a consequence, when chlorophyll is degraded, RCC builds up and mediates cell death in the light. The ultimate destination of the product of the RCC reductase reaction is the central vacuole, the large membrane-limited aqueous compartment that occupies most of the volume of the green cell. Sequestering products out of harm's way in the vacuole is a further detoxification measure employed by land plants. It seems that the progression from green to yellow that is characteristic of foliar senescence is a highly visible symptom of toxin disposal.

Recycling is a way of life for green plants. If eliminating chlorophyll is a hazardous business requiring stringent detoxification measures, why doesn't the plant simply abandon the pigment by dropping it unchanged within falling leaves? The answer is that the removal of chlorophyll is associated with, and necessary for, the salvage of protein nitrogen from the senescing leaf to support the development of young

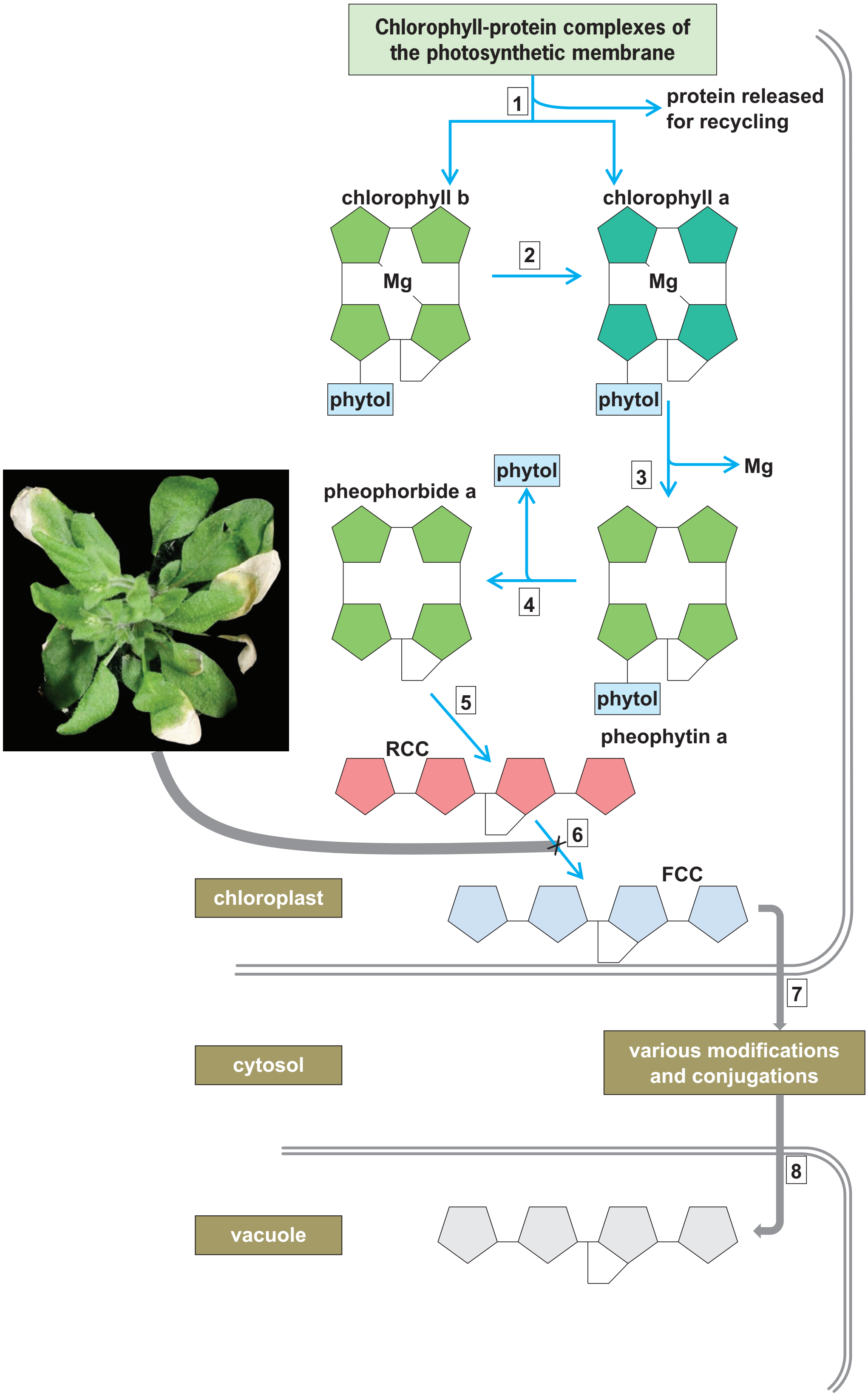

Fig. 2. The cellular mechanism of chlorophyll breakdown in plant senescence. The enzymes and transporters responsible for the sequence of biochemical transformations are as follows: [1] stay-green; [2] chlorophyll b reductase; [3] dechelation reaction; [4] pheophytinase; [5] pheophorbide a oxygenase; [6] RCC reductase; [7] ATP-dependent catabolite transporter; and [8] ABC transporter. The *Arabidopsis* mutant, *acd2*, is blocked at reaction [6] and suffers from light-dependent leaf lesions as a consequence of the anomalous buildup of the normally transient phototoxic intermediate RCC. (FCC = fluorescent chlorophyll catabolite.)

organs or storage tissues. In many crops and natural plant communities, nitrogen is an important limiting factor for growth and productivity. Senescence evolved as a way of liquidating the investment of nitrogen in green tissues when they become old and unproductive and reinvesting it in younger, better-adapted structures.

Most of the salvageable nitrogen in green cells is located in the chloroplasts (cell plastids occurring in the green parts of plants, containing chlorophyll pigments, and functioning in photosynthesis and protein synthesis). A large fraction of this protein is bound to chlorophyll. Chlorophyll (and protein) degradation begins with the controlled unpacking of pigment-protein complexes (Fig. 2). Observations on mutants indicate that nitrogen from pigment-binding proteins cannot be released and relocated to destination tissues unless chlorophyll is removed. For example, a mutant gene called *stay-green* (*sgr*) renders plants that carry it unable to deliver chlorophyll from pigment-protein complexes to the chlorophyll breakdown machinery. Such plants cannot mobilize chlorophyll-associated protein, which remains more or less unchanged in the leaf even as the nitrogen from other proteins is being recycled during senescence.

Yellow pigments are revealed during senescence. The picture that we are developing of color changes in senescing leaves is of the controlled detachment of chlorophylls from their nitrogen-rich binding proteins in chloroplast membranes, followed by a series of transformations via transient green and red intermediates, culminating in colorless end products that accumulate in the cell vacuole (Fig. 2). In ripening crops and many other species, green is replaced by golden yellow. Carotenoids, the chemical group responsible for the yellow and orange pigments of senescing foliage, are already present in green leaves and are unmasked as chlorophyll is removed. Some carotenoids are built into chlorophyll-protein complexes. As the complexes and chloroplast membranes are taken apart, carotenoids coalesce in intensely colored lipid-rich globules within the senescing chloroplast (**Fig. 3**). Leaves tend not to make more carotenoids during senescence; however, in other senescencelike processes such as the ripening of tomatoes, bell peppers, and other colorful fruit, substantial amounts of new carotenoids may be synthesized. Carotenoids are potent antioxidants, retained during leaf senescence as part of the cellular equipment defending against photodamage.

Some senescing leaves turn red. In many regions of the world, such as the forests of New England in the United States, senescing leaves turn spectacularly red. Anthocyanins, the chemical constituents commonly responsible for the fiery colors of autumnal foliage, are water-soluble pigments that (in contrast to the fat-soluble carotenoids) are actively synthesized by senescing photosynthetic tissues and accumulated in the vacuoles of leaf cells (Fig. 3). Genes for carotenoid synthesis are extremely ancient, exhibiting a high degree of conservation from flowering plants all the way to unicellular organisms resembling those present at the origin of life. On the other hand, recognizable genes for metabolism of anthocyanin-like compounds do not occur until the algae evolved, became integrated into development only once land plants began to appear, and are characteristic of the relatively recent (in evolutionary terms) flowering plant groups.

Autumn colors evolved to defend against a hostile environment. It has been suggested that anthocyanins are sunblockers, defending vulnerable tissues from the harmful effects of excess light. There is also evidence that anthocyanins can act as antioxidants. An alternative or additional explanation for the origin of foliar anthocyanin is coevolution. According to this hypothesis, autumn coloration is a signal of quality, directed at insects that migrate to the trees in autumn. The red color of foliage may be symptomatic of the plant's unsuitability as a host because of high levels of chemical defenses, of poor nutritional status, of imminent leaf fall, or of any other characteristic that would induce a lower fitness in the insects. Mathematical models based on signaling theory generally support the coevolution explanation and emphasize the significance of insect visual systems and behavior and of the nature of the link between leaf color, defense status, and plant vigor.

Outlook. In conclusion, researchers studying the meaning of color in senescing leaves are able to enjoy the pleasures of engaging with biological events that are both scientifically challenging and esthetically satisfying.

For background information *see* ABSCISSION; CAROTENOID; CHLOROPHYLL; COLOR; DECIDUOUS PLANTS; LEAF; PHOTOSYNTHESIS; PIGMENTATION; PLANT ANATOMY; PLANT PHYSIOLOGY; PLANT PIGMENT in the McGraw-Hill Encyclopedia of Science & Technology.

Howard Thomas

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Bibliography. M. Archetti et al., Unravelling the evolution of autumn colours: An interdisciplinary approach, *Trends Ecol. Evol.*, 24:166–173, 2009; H. Ougham et al., The control of chlorophyll catabolism and the status of yellowing as a biomarker of leaf senescence, *Plant Biol.*, 10(suppl. 1):4–14, 2008; H. J. Ougham, P. Morris, and H. Thomas, The colors of autumn leaves as symptoms of cellular recycling and defenses against environmental stresses, *Curr. Top. Dev. Biol.*, 66:135–160, 2005.

URLs

The Essence of Senescence

http://www.sidthomas.net/SenEssence/index.htm

Plant Biology: Senescence of Plant Leaves

http://www.plant-biology.com/Leaf-Senescence.php

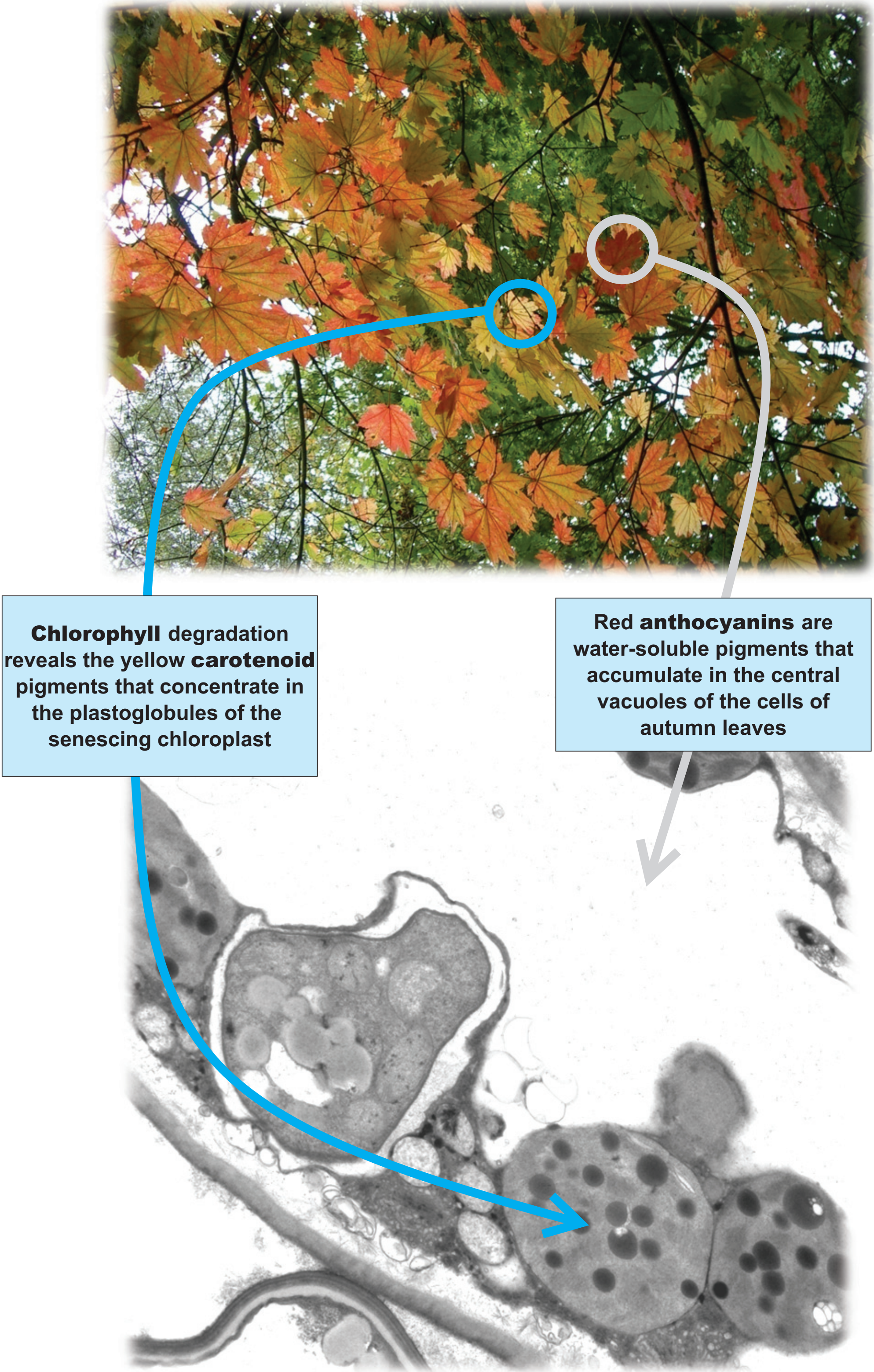

Fig. 3. Detail of the ultrastructure of a senescing cell showing the different locations of the yellow (carotenoid) and red (anthocyanin) pigments of autumn leaves.