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A Brief History of Leaf Color

The purpose of this introductory chapter is to provide a general survey to readers from various backgrounds about how we have thought about leaf properties related to their interactions with light. For example, questions such as "is it colored because of how light contacts the surface or because some colors of light are absorbed by particular materials?" These questions aroused curiosity about how the nature of interactions with light influences leaf properties, such as observations of leaf color differences on the upper and lower foliar surfaces or why leaves change color in the fall. Investigations from Aristotle up to the 19th century focused on the causes of leaf color and its variation and how these relate to how leaves function. Finally, we introduce some of the earliest studies on the physical mechanisms for the color patterns observed. As the chemical properties of leaves became known, researchers began to show close linkages between the three-dimensional structures that result from their anatomical and morphological patterns, the patterns of light absorption and scattering across the electromagnetic spectrum, and the associated physiological processes related to carbon, water, and nutrient budgets. The modern study of leaf optics really began with the 20th century. The evolving understanding of the botanical characteristics of leaves provides a context to understanding their optical processes.

For a long time, plants have been considered primarily from the point of view of utility and medicinal use. Historically, Assyrians, Egyptians, Chinese, and Indians recorded information about the external and internal characteristics of plants, but their descriptions were often fragmented or enigmatic. Greek philosophers contributed to the early development of botany as a science. It appears likely that the study of leaf optics began with a desire to understand the color of foliage. Little is known about Aristotle‘s work on the nature of plants (384–322 BC). In the *De Coloribus*, he identified four colors corresponding to the four elements: earth (black), air (white), fire (yellow), and water (blue). Aristotle described the changes in the color of plants during their development, maturity, and decay, although the passages at issue are not easy to interpret:

> . . . stagnant waters, and hence also sap in plants, are yellow green (χλωρον) at first, but next, when darkened by the rays of the sun, they become grass green (ποωδεζ) . . . When grass green water, including the sap in plants, is mixed with the rays of the sun, it is to some extent darkened . . . Furthermore, as the black in plants gradually weakens, grass green reverts to yellow green again.

Around 300 BC, Aristotle's student, Theophrastus (371–286 BC), produced the first work describing plant leaves in his encyclopaedia *De Historia Plantarum*, which we know from the Latin translation in the second half of the 15th century by Teodoro Gaza. For instance, he noticed differences in color between the upper and lower surfaces of some species (Hort, 1916):

Now all leaves differ as to their upper and under surfaces; and in most trees the upper surfaces are greener and smoother, as they have the fibres and veins in the under surfaces, even as the human hand has its "lines" but even the upper surface of the leaf of the olive is sometimes whiter and less smooth.

(book 1, chap. 10)

In the French translation, Suzanne Amigues remarks that the symmetry of the two comparisons is apparent (Amigues, 2003). Generally, "the upper surfaces are greener and smoother" than the lower surfaces. The upper surface of the olive leaf is a little rough and gray-green, the lower surface silky and silver-green: it is greener and less rough above than below. Compared to the upper surface of other species which are green and smooth, the olive leaf is "whiter and less smooth". Three centuries later, Pliny the Elder textually repeats the same words in his *Naturalis Historia* (Pliny the Elder, 1855):

These trees [elm, lime, olive, white poplar and willow] also present in their leaves the same difference that is to be observed in those of all the rest: the underside, which looks toward the ground, is of a green grassy colour, and has a smooth surface; while the veins, the callous skin, and the articulations, lie upon the upper face, the veins making incision in the parts beneath, like those to be seen upon the human hand. The leaf of the olive is whiter above, and not so smooth.

(book 16, chap. 36)

The late Renaissance period coincides with renewed interest in botanical medicines in the early botanic gardens of Leiden (1577), Montpellier (1593), and Heidelberg (1597) and their botanical descriptions in herbals, for example, the *De Historia Stirpium* of Leonhart Fuchs (1542) or the *Kitab-i hasha'ish* ("The book of herbs") published in 1595 (Figure 1.1). The latter is actually a Persian translation of the *De materia medica* of the Hellenistic scholar Dioscorides written in the 1st century AD.

In chapter 8 of the Notebooks of Leonardo da Vinci (Richter, 1970), *Botany for Painters and Elements of Landscape Painting*, probably written between 1513 and 1515, we find the earliest reference on the interaction of light with plant leaves. Although this chapter is less famous than his chapter 7, *On the Proportions and in the Movements of the Human Figure*, it is considered of similar biological significance. Da Vinci attempts to provide scientific explanations for why things look as they do and sets up rules to guide artists in representing trees. In particular, he explains how the colors of leaves should look in sunlight and in shade (Figure 1.2). The proportions of light and shade depend on the position of the leaf in relation to the Sun and the viewer. Seen from below, a concave leaf surface will be partly in shade and partly transparent, while the upper exposed surface is in light.

Da Vinci also noted that light reflected from the darkest leaves approximated the color of the atmosphere (Figure 1.3) because light on the illuminated portion combines the blueness of the atmosphere with the dark hue of the leaf to reflect a blue color. Yellow-green leaves do not reflect blue but combine the reflected blue of the atmosphere with the yellow of the leaf to appear yellow-green.

In the 17th and 18th centuries, scientists began to study the origin of green color in plants, which is widespread in the plant kingdom. In *Experiments and Considerations Touching Colours*, the famous British scientist Robert Boyle raised the question of leaf color and especially its changes throughout the seasons (Boyle, 1664):

First I have been willing to leave unmentioned the most part of those phenomena of colours, that Nature presents us of her own accord such as the different colours that [ ] appear upon the fading of flowers and leaves, [ ] etc. together with a thousand other obvious instances of the changes of colours.

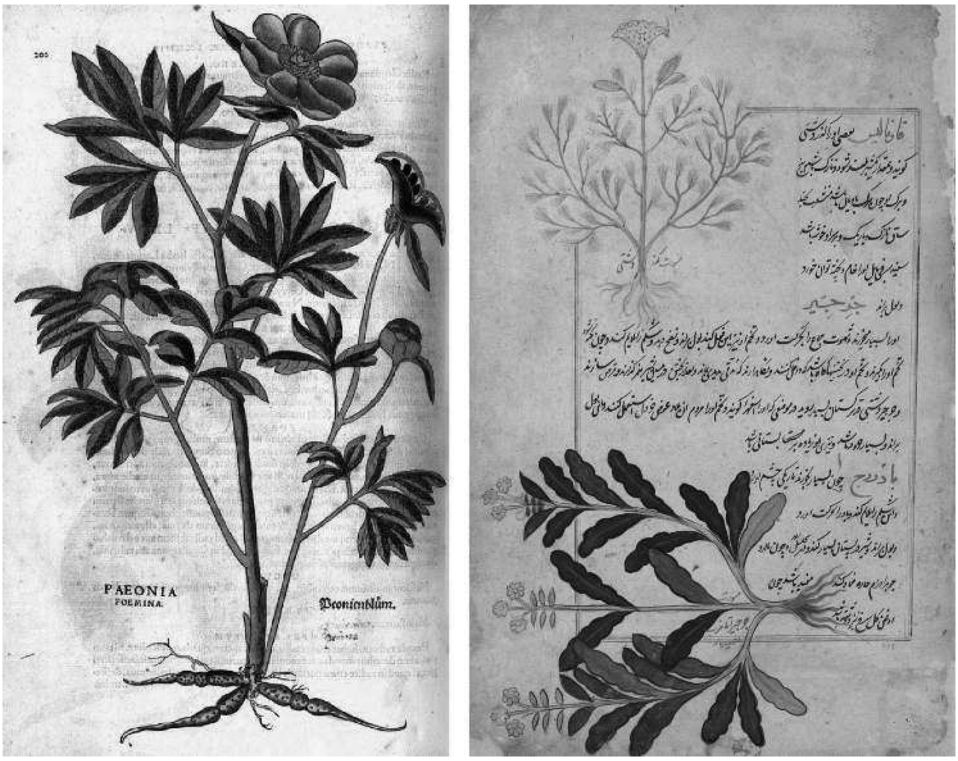

Figure 1.1 Illustrations of leaf structures: (left) from the *De historia Stirpium*; and (right) from the *Kitab-i hasha'ish* depicting bifacial leaf color. (A black and white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

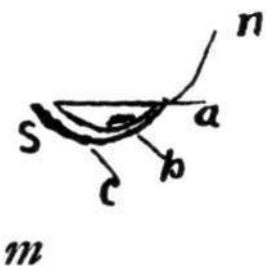

Figure 1.2 Proportion of light and shade in a leaf as seen by Da Vinci: "Sometimes a leaf has three accidents [of light] that is: shade, lustre [reflected light] and transparency [transmitted light]. Thus, if the light were at *n* as regards the leaf *s*, and the eye at *m*, it would see *a* in full light, *b* in shadow and *c* transparent" (Richter, 1970).

Later, he ponders why the two sides of some leaves display a notable disparity of colors that is revealed "when a breath of wind passes though them". However, Boyle does not consider light, but only thinks of colored matter. His theory of colors is quite different from that of Descartes, Newton, or Hooke, whose approaches were more physical: in his famous book *Optiks*, Newton (1704) explained the color of objects in terms of light interacting with them: "These colours arise from hence, that some natural bodies reflect some sorts of rays, other sorts more copiously than the rest".

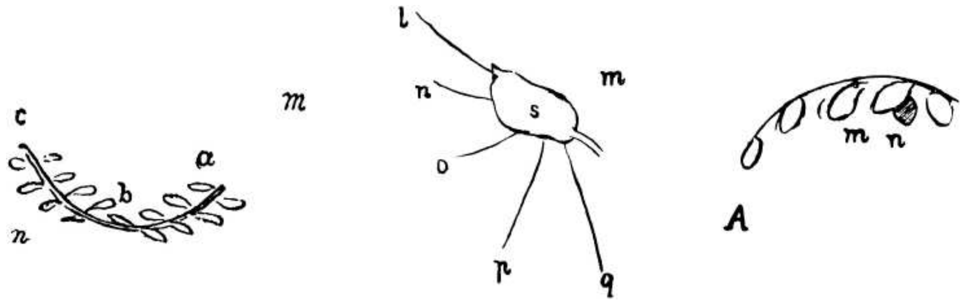

Figure 1.3 The gradations of shade and color in leaves as seen by Da Vinci: "If the light comes from *m* and the eye is at *n* the eye will see the colour of the leaves *a b* all affected by the colour of *m* – that is of the atmosphere; and *b c* will be seen from the underside as transparent, with a beautiful green colour verging on yellow. If *m* is the luminous body lighting up the leaf *s* all the eyes that see the underside of this leaf will see it of a beautiful light green, being transparent. In very many cases the positions of the leaves will be without shadow [or in full light], and their underside will be transparent and the right side lustrous [reflecting light]" (Richter, 1970).

Newton used prisms to prove that white light was actually made up of waves of different colors; then he showed that objects appear to be certain colors because they absorb and reflect different amounts and wavelengths of light. Newton surprisingly barely mentioned plant leaves or flowers in his book. For instance, Delaval (1774) only found one observation concerning the degradations of the green in the plants that fade. He was convinced that Newton's results obtained on transparent natural bodies, like glass, water, and air, were applicable to opaque bodies, and that a lack of experiments prevented him from discovering the origin of color in the animal and plant worlds.

In parallel, the chemists of the 17th and 18th centuries prepared "infusions of plants into several sorts of liquors" to extract their coloring principles or they burned leaves in the open air, assuming that the ash that remained after combustion contained these substances. Some, like the German physicians Johann Joachim Becher, in *Physica Subterranea* (Becher, 1669), and Georg Ernst Stahl, in *Opusculum Chymico-Physico-Medicum* (Stahl, 1715), attribute the green color of leaves to iron. While he was appointed counselor of mines for Saxony, in the heart of Germany, Johann Friedrich Henckel published *Flora Saturnisans* where he studied the chemical similarities between plants and minerals (Henckel, 1760). However, he could not make up his mind whether leaf color was due to iron or copper. He noted that M. L'Abbé de Vallemont had heard that tree leaves in the vicinity of gold mines have a golden color that is produced by ground exhalations. And to prove it, he relates this passage from Boyle: "Folia arborum saepiùs aureo colore obducta inveniri ab auri fodinarum exhalationibus metallicis". However, Lemery (1706) wonders about the presence of iron in plants: does it naturally occur or is it formed when plants are burnt to ashes? He is inclined to favor the first hypothesis:

> Le fer étant répandu en abondance dans toutes sortes de terres, & pouvant être aisément dissous par les premières liqueurs salines qui l'arrosent [ ]; ces liqueurs montant ensuite par la chaleur du Soleil dans les tuyaux des plantes pour les nourrir & les faire croître: ces liqueurs, dis-je, portent naturellement avec elles le fer donc elles se sont chargées.[1]

[1] Iron is abundantly present in all kinds of soils, and is easily dissolved by the first saline liquors that water it []; these liquors then go up by the heat of the Sun in the tubes of the plants to feed them and to make them grow: these liquors, I say, naturally carry with them iron they are laden with.

By vitrifying this ash, M. le Comte de Mouroux produced a stable dark green glass (Mouroux, 1770). He confirmed that the elements which cause the green color are independent of the body in which they are embedded. However, other authors showed that the color of the glass might be rather due to the temperature applied during the vitrification process. Mouroux also mentions a new theory expressed by Benjamin Franklin:

> I have been rather inclined to think that the fluid fire as well as the fluid air, is attracted by plants in their growths and becomes consolidated with the other materials of which they are formed and makes a great part of their substance.
>
> *(Franklin, 1751)*

and concludes that, with the help of this *fire*, plants receive a vital principle and the development of color. Note that although these theories were supported by several similar experiments, the results sometimes contradict each other (e.g., Delafolie, 1774; Achard, 1778; Morozzo, 1782).

The natural variation of colors observed in flowers and leaves was also attributed to the mixing of sulfurs with different salts contained in the sieve cells. In a discourse read at the Royal Society of London on 3 May 1677, the English physician Nehemiah Grew seems to confirm these early observations (Grew, 1682):

> I suppose therefore, that not only green, but all the colours of plants, are a kind of precipitate, resulting from the concurrence of the saline parts of the air, with the saline and sulphurious parts of the plant.

He explains that he could extract the green color of leaves with olive oil, but not with water. At the instigation of the Academy (understood to be the French *Académie Royale des Sciences* created in 1666), a complete chemical analysis of 1400 plant species was undertaken to know their nature, properties, and uses. They were found to contain common substances, in particular sulfurs, which at that time were suspected by chemists to be the cause of color. Thus Geoffroy (1707) notes: “le vert qui est la couleur la plus ordinaire des feuilles, est vraisemblablement l’effet d’une huile raréfiée dans les feuilles, & mêlée avec les sels volatiles & fixes de la sève”.[2] He also explains why leaves turn red in autumn by the beginning of the cold season: the pores and channels of the sieve cells stop flowing, so the sap is retained in the leaves where it turns sour; the acid that is produced destroys the alkali that is behind the green color, and the remaining sulfurs cause the red color. Senebier (1783), who was struck by the co-occurrence between leaf greenness and carbon fixation under the action of solar radiation, hypothesized that carbon was the cause of the green color. In 1809, he was the first to show that green matter was located in the parenchyma cells. Sulfur, iron, copper, gold, or carbon: at the end of the 18th century, physicists (or alchemists) were actually still in disagreement about the origin of color in leaves and other plant organs. But is chemistry the right way to unveil the secrets of plants?

The dominant influence of light on leaf color was recognized for the first time by the 17th-century English naturalist and botanist John Ray who noted that only light affects the green color of plants and that leaves turn white in darkness (Ray, 1686); if the plants that have been grown in the dark under an opaque vase are returned to the light, the leaves soon lose their white hue, and eventually assume their natural color; the rapidity with which they become green, and the intensity of their color, will be in proportion to the amount of light to which they are exposed. Ray made sure that this phenomenon was due neither to the deprivation of the air nor to the influence of heat. The evolution of current ideas on

[2] Green, which is the most ordinary color of the leaves, is probably the effect of a rarefied oil in the leaves, which is mixed with the volatile and fixed salts of the sap.

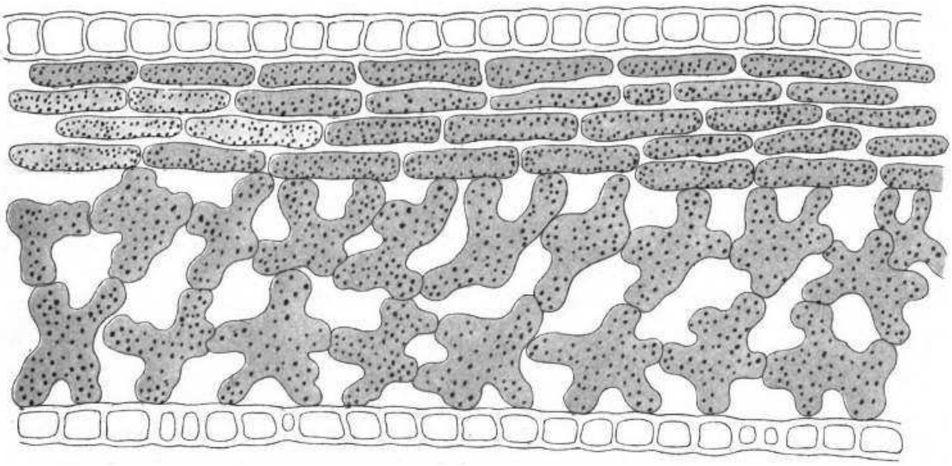

Figure 1.4 Cross-section of a European dogs tooth (*Erythronium dens-canis*) leaf. The epidermal cells are colorless; the upper mesophyll is made of elongated cylindrical cells that contain "granular" and "gelatinous" chlorophyll; the cytoplasm is either red or colorless, as it contains erythrophyll, the red coloring matter of leaves, or not; the white areas are due to the interposition of a thin air layer between the epidermis and the upper mesophyll (Morren, 1858a). (A black and white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

leaf color is inseparable from photosynthesis and the discovery of leaf pigments (for a comprehensive review, see Govindjee and Krogmann, 2004, and Hill, 2012). Joseph Priestley, an English chemist, initiated the experimental study of photosynthesis by discovering oxygen (termed dephlogisticated air) in 1774 and published his findings the same year (Priestley, 1774). He showed that oxygen could be produced by plants and support respiration in animals. He was followed by Jan Ingen-Housz who showed that light was essential to photosynthesis (Ingen-Housz, 1779), Jean Senebier who discovered that CO_2 was required for photosynthetic growth (Senebier, 1783), and Nicholas-Théodore de Saussure who highlighted the role of water (de Saussure, 1804). Finally, the German physicist Julius Robert von Mayer defined photosynthesis in his second publication using the principle of conservation of energy (Mayer, 1845). He showed that light energy from the Sun was stored as chemical energy in products formed during photosynthesis. The theory of native metals (iron, copper, gold, etc.) or non-metallic elements occurring in the native state (carbon, sulfur, etc.) to explain leaf color lost momentum for the benefit of green substances, first called "gelatinous green matter", green starch", "viridine", "resin", or "chromule". These substances can be found in the form of granules or in the amorphous state (Figure 1.4).

The word "chlorophyll" came from French in the early 19th century. It was made up from the Greek words *chloros* "light green" and *phyllon* "leaf" by two French pharmacists, Pelletier and Caventou (1817). It is ironic to note that they did not make a big deal of this name: "nous n'avons aucun droit pour nommer une substance connue depuis longtemps, et à l'histoire de laquelle nous n'avons ajouté que quelques faits; cependant nous proposerons, sans y mettre aucune importance le nom de chlorophylle".[3] Originally, all pigments were referred to as

[3] We have no right to name a substance known for a long time, and to the history of which we have added only a few facts; however, we will propose, without putting any importance on it, the name chlorophyll.

chlorophyll. The term anthocyanin (*anthos* being Greek for flower, and *kyanos* for blue) has been used since Marquart (1835) to represent the coloring matter that is responsible for the various colors found in flowers, fruits, and autumn foliage. Note that it has been long called erythrophyll (*eruthros* being Greek for red). Berzelius (1837a, 1837b) named the yellow pigments obtained from the autumn leaves xanthophylls (*xanthos* being Greek for yellow). According to these authors, anthocyanin and xanthophyll were considered as a counterpart to chlorophyll and assumed to be the result of a metamorphosis of chlorophyll under the effect of solar radiation (Phipson, 1858). It seems that chemists had trouble extracting and purifying leaf pigments (Filhol, 1865). For instance, without pure chlorophyll extract they could not make a judgment on the nature of chlorophyll: is it a pure substance or a mixture of several? Verdeil (1851) announced that chlorophyll was related to the coloring matter of blood, and as such, it contained iron. Fremy (1860, 1865) has ascertained that it was composed of two coloring principles, one a yellow called phylloxanthin, the other a blue called phyllocyanin. Later, Sorby (1872) identified two chlorophyll pigments, but the identification of different leaf pigments was only resolved in the 20th century. Scientists ran into another snag with the evolution of leaf color in the fall that occurs during leaf senescence (Macaire-Princep, 1828; Berzelius, 1837c; Morren, 1858a,1858b, 1858c), but also periodically in evergreen leaves (Mohl, 1837, 1838). Morren (1858a), who reviewed all the past and current theories explaining plant color, lamented the fact that this subject had only interested scientists in passing, but had rarely given rise to specific studies. In the middle of the 19th century, the main pigments that produce leaf colors – green, yellow, red, brown, etc. – are named, although their molecular formulas were not identified.

The second half of the 19th century is devoted to the more difficult study of their structure and evolution and, in connection with this, their relationship with the physical environment of growing plants. Once achieved, scientists rapidly started to study their intrinsic optical properties, in particular the absorption and fluorescence emission of chlorophyll. Brewster (1834) focused the Sun's light by a lens and he studied its dispersion by an English laurel (*Prunus laurocerasus*) leaf solution obtained by *absolute alcohol* (pure ethanol) extraction. The light transmitted through the solution was analysed by a prism. He wrote:

> we shall observe a spectrum of the most beautiful kind. In place of seeing the green space with a portion of blue on one side and yellow on the other, as the Newtonian theory would lead us to expect, we perceive a spectrum divided into several coloured bands of unequal breadths, and having their colours greatly changed by absorption. . .

as illustrated in Figure 1.5.

In the same article, Brewster described for the first time a very remarkable phenomenon, which he designated as *internal dispersion* and which is a major discovery in plant physiology: chlorophyll fluorescence emission. He experimentally showed an emission of red light in an alcohol extract of laurel (*Prunus laurocerasus*) leaves: "In making a strong beam of the Sun's light pass through the green fluid, I was surprised to observe that its colour was a brilliant red, complementary to the green". Even if leaf optical properties naturally included blue and red fluorescence, fluorescence is a world apart which has already given rise to many books and hundreds of dedicated articles, due to the close link between fluorescence and photosynthesis. For this reason, we will only mention it occasionally in this book. Twenty years after Brewster, Stokes (1852a) made a new experiment of light dispersion

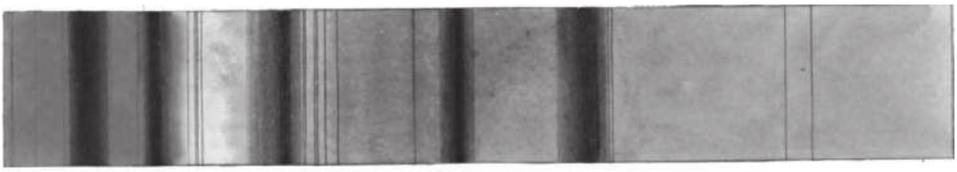

Figure 1.5 Decomposition of light by a solution of an English laurel green leaf showing several main absorption bands (from Brewster (1834), *Transactions of the Royal Society of Edinburgh*. Copyright © 1834 with permission from Cambridge University Press). (A black and white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

with a solution of common nettle (*Urtica dioica*) leaf. He used a candle as an illumination source and found five absorption bands situated in the blue (No. 5), in the green-yellow (No. 4), in the yellow (No. 3), and in the red (Nos. 1 and 2). He also probably mentions the first experiment dedicated to the measurement of a leaf transmittance spectrum:

It should be noted that although the absorption produced by leaf-green is best studied in a solution, its leading characters may be observed very well by merely placing a green leaf behind a slit, as near as possible to the flame of a candle, and then viewing the slit through a prism.

Brewster (1855) translated Newton's statements for a leaf as follows:

> The leaf of a plant, for example, appeared green in the white light of day, because it had the property of reflecting green light in greater abundance than any other. When the leaf was placed in homogeneous red light, it no longer appeared green, because there were no green rays in the red [ ] The green leaf, for example, stops or absorbs the red, blue and violet rays of the white light which falls upon it, and reflects and transmits only those which compose its peculiar green.

He and other authors undertook an extensive investigation of absorption spectroscopy and demonstrated linkages between vegetal colors and the absorption spectrum of plant leaf extracts (e.g., Ångström, 1853, 1854; Salm-Horstmar, 1854, 1855a, 1855b, 1856; Harting, 1855; Landrin, 1864; Hagenbach, 1870; Sorby, 1871a; Chautard, 1872; Schönn, 1872; Palmer, 1877a, 1877b; Timiriazeff, 1903; Ursprung, 1918). In particular, they studied the evolution over time of leaf pigment content and therefore of leaf color (e.g., Sorby, 1871b, 1884; Martin and Thomas, 1887; Gauthier, 1906).

Leaf extrinsic optical properties were first measured at the dawn of the 20th century, to answer the question of storage of solar energy in green plants. Scientists entered the era of quantitative data through the parallel development of measuring instruments. It is interesting to note that the earliest papers on leaf optical properties addressed the question of radiative energy exchange between plant leaves and their surrounding environment. The French physicist Edmond Becquerel, who discovered evidence of radioactivity, was the first to attack the question of storage of solar energy in green plants (Becquerel, 1868). Following this early work, Timiriazeff (1903), in a long article titled *The cosmical function of the green plant*, showed that the absorptance of direct sunlight by leaves, called the *economic coefficient*, was approximately 25%, an obviously underestimated value. As cited by Ansari and Loomis (1959), the earliest information regarding leaf temperatures dates from the mid-1870s when Askenasy (1875) held a mercury thermometer against the surface of thin leaves of *Sempervivum* and observed that leaves in sunlight were 4 to 5°C warmer than the surrounding air. More accurate determinations have been made by means of type-T (copper-constantan) or type-K (chromel-alumel) thermocouples and potentiometers. The thermocouple

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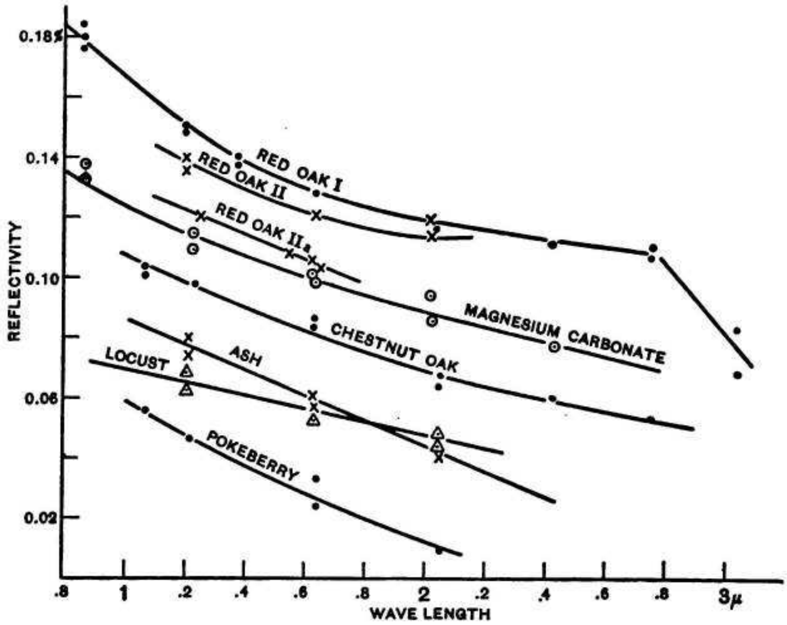

Figure 1.6 Reflecting power of green leaves (from Coblentz (1913), *Bulletin of the Bureau of Standards*. Copyright © 1913 with permission from the National Institute of Standards and Technology).

may be threaded through the mesophyll, inserted into the midrib, or glued to the underside of the leaf under experiment. Nevertheless, a good contact between leaf and junction is required to accurately measure leaf temperature. This article opened the way to new fields of applications in leaf radiative budget (e.g., Maquenne, 1880; Brown, 1905; Brown and Escombe, 1905; A.M.S., 1909; Clum, 1926).

In his studies of the *reflecting power* of matte surfaces, Coblentz (1913) published the first measurements of the reflection of visible radiation from leaf surfaces, undertaken in May 1908. At that time he used a bolometer, a mirror spectrometer, and a fluorite prism. The green leaves of nine plant species were illuminated at an angle of incidence of 45° with a Nernst glower, an obsolete device for providing a continuous source of infrared radiation from 2 to 14 micrometers. The curves of *reflecting power* show a regular decrease in reflection of energy of between 0.9 μm and 3.0 μm, which is true overall (Figure 1.6). However, these curves are difficult to interpret due to the poor spectral resolution, and the low near-infrared values do not seem to be realistic. Coblentz also provided the transmittance of plant leaves for the first time: about 20% of the energy, a definitely overestimated value, was found to pass through common lilac (*Syringa vulgaris*) and black locust (*Robinia pseudoacacia*) leaves at 600 nm.

The description of leaf optical properties in terms of physical processes, that is absorption of light by photosynthetic pigments and diffusion at the air–cell wall interfaces (Figure 1.7), is often attributed to Willstätter and Stoll (1918), who shrewdly understood that photosynthesis could not be reduced to a biochemical reaction.

Using a prism spectrophotometer and magnesium carbonate ($MgCO_3$) as a photometric standard surface, Shull (1928, 1929) measured the reflectance spectrum of the upper and lower surfaces of

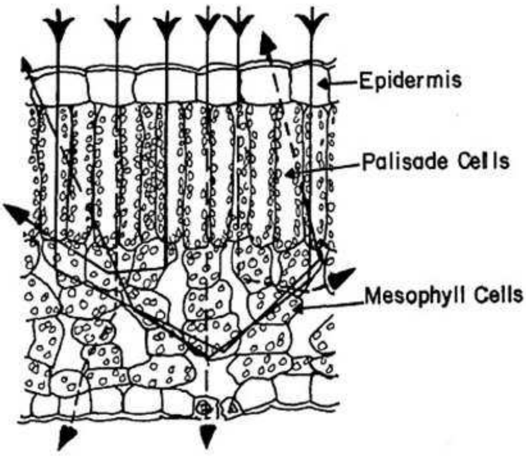

Figure 1.7 Schematic drawing depicting the Willstätter and Stoll (1918, p. 123) theory on the pathway of light through a dorsiventral leaf of *Acer negundo* (adapted from Sinclair et al. (1973), *Agronomy Journal*. Copyright © 1973 with permission from the American Society of Agronomy).

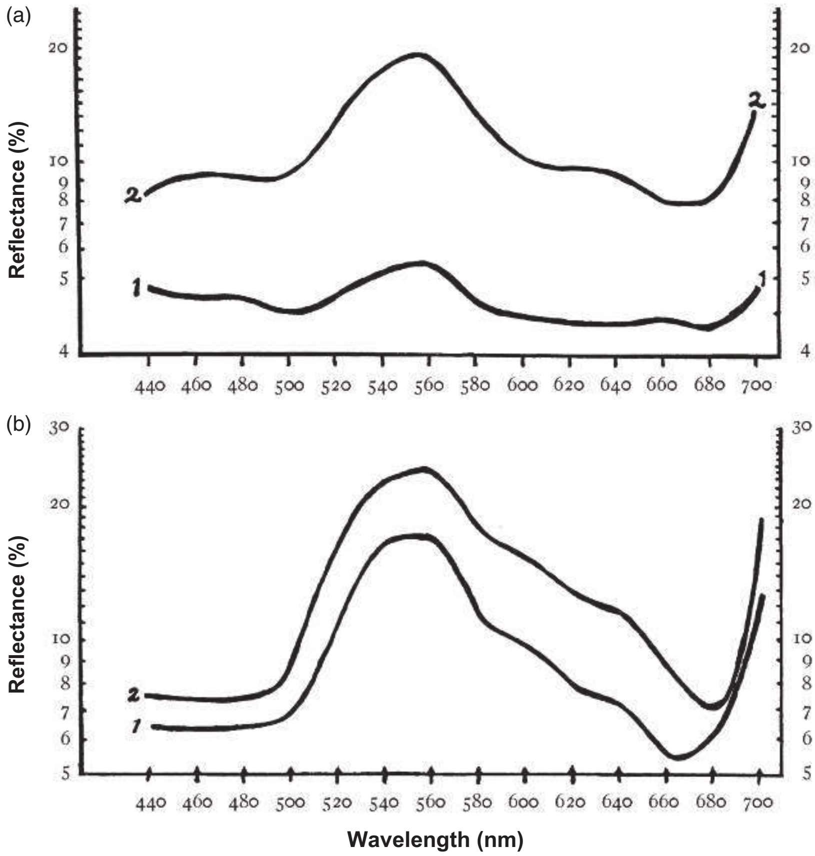

Figure 1.8 Reflection curves for leaves of: (a) rhododendron (1) and jonquil (2); (b) violet (1) and iris (2) (from Shull (1929), *Botanical Gazette*. Copyright © 1929 with permission from the University of Chicago Press).

a number of leaves from 430 nm to 700 nm (Figure 1.8). His results clearly indicate a maximum reflectance at approximately 550 nm (green) and a minimum reflectance between 660 nm and 680 nm (red) corresponding approximately to the maximum absorption band of chlorophyll. Unfortunately the spectra stop before the near-infrared plateau. The work of Shull initiated a series of articles on the monochromatic reflection of plant leaves. As reported by Billings and Morris (1951), it took almost 20 years and the improvement of monochromatic spectrophotometers before one could measure reflectance spectra continuously from the visible to the near infrared. The results of Rabideau et al. (1946) showed a sharp rise in reflectance starting at about 675 nm and continuing to a plateau of about 50% extending from about 750 nm to 850 nm, the limit of their observations. The advent, around 1940, of sensitive photographic film in the near infrared had already highlighted a much higher reflectance of plant leaves in this spectral range.

The applications of such studies are numerous and cover many scientific disciplines, from plant physiology (photosynthesis and photomorphogenesis) to remote sensing in the optical domain (environmental studies, precision farming, and ecology). Most papers have focused on the leaf spectral properties (hemispherical reflectance and transmittance) in connection with their biochemical content (chlorophyll, water, dry matter, etc.) and their anatomical structure. For instance, plant stress resulting from an insect attack or a nitrogen deficiency induces degradation of the leaf chlorophyll content, which has repercussions on the leaf optical properties: the reflectance and transmittance increase over the whole visible spectrum. This relation between cause and effect allows the estimation of leaf biochemistry – the chlorophyll content in this particular case – by establishing empirical relationships between the variable of interest and the leaf reflectance or transmittance, or better still, by directly using a physical model. It is now well established that leaf reflectance and transmittance are closely related to the biochemical content and anatomical structure, which depend on the plant species and, of course, on many environmental factors. Quantitative relations between these optical properties and these biophysical characteristics were empirically established in the second half of the 20th century: for example, stress can involve degradation of the chlorophyll pigments which, in turn, will cause an increase in reflectance and transmittance in the visible. In parallel, radiative transfer models were used to simulate these physical processes and estimate leaf biochemical composition.