CONTRIBUTIONS

Commentary

A History of the Ecological Sciences, Part 28: Plant Growth Studies During the 1700s

During the 1600s naturalists made significant progress in describing and illustrating plant anatomy. Development of microscopes both stimulated and aided such studies. Foremost contributors were Marcello Malpighi (Adelmann 1966, I:384–417, 423–426, Belloni 1974), and Nehemiah Grew (Metcalfe 1972, LeFanu 1990), and to a lesser extent, Antoni van Leeuwenhoek (Egerton 2006*a*:54–55). They found minute pores (stomata) that seemed to indicate that plants interact with the air (Nash 1957:335). Achievements in plant physiology during the 1600s were more modest. Botanical researchers had established that over time a tree seedling in a tub with a weighed amount of dirt gains weight if watered regularly (apparently showing that wood came from water), and that cuttings from some plants gain weight if their stems are left in water (Egerton 2004). In 1724, Richard Bradley supported the hunch of two correspondents that plants draw nourishment from the air, and Jethro Tull ridiculed him for it (Egerton 2006*b*:120). A detailed documentary history by Leonard K. Nash, *Plants and the Atmosphere* (1957), includes a helpful flow chart of ideas and discoveries, 1650–1804, and Oliver Morton's book on photosynthesis and the economy of nature has a concise history of discoveries during the 1700s (2007:325–343).

Stephen Hales (1677–1761) is generally considered the founder of plant physiology (Clark-Kennedy 1929, Nash 1957:336–343, Guerlac 1972, Alan and Schofield 1980, Morton 1981:246–253, Harré 1983:52–58, Allan 2004), which relegates his predecessors to the status of precursors. He went to Cambridge University in 1696 and studied to become a clergyman. His interest in science was awakened in 1703 after William Stukeley arrived. Although Hales was 10 years older than Stukeley, they became close friends. Together they attended lectures and demonstrations in science, conducted various experiments, and went on field trips around Cambridge to collect plants, using John Ray's Cambridge flora (1660). Stukeley's map of where they collected survives and is reproduced, as is his portrait, by Clark-Kennedy (1929: Plates 3, 5). About 1706 Hales experimented on blood pressure in dogs. Yet his new scientific interests did not divert him from becoming a clergyman in 1709, at Teddington, a village on the Thames River (Clark-Kennedy 1929: Plate 14). In 1712–1713 he resumed experiments on blood pressure, and in 1718 he and Stukeley were elected fellows of the Royal Society of London.

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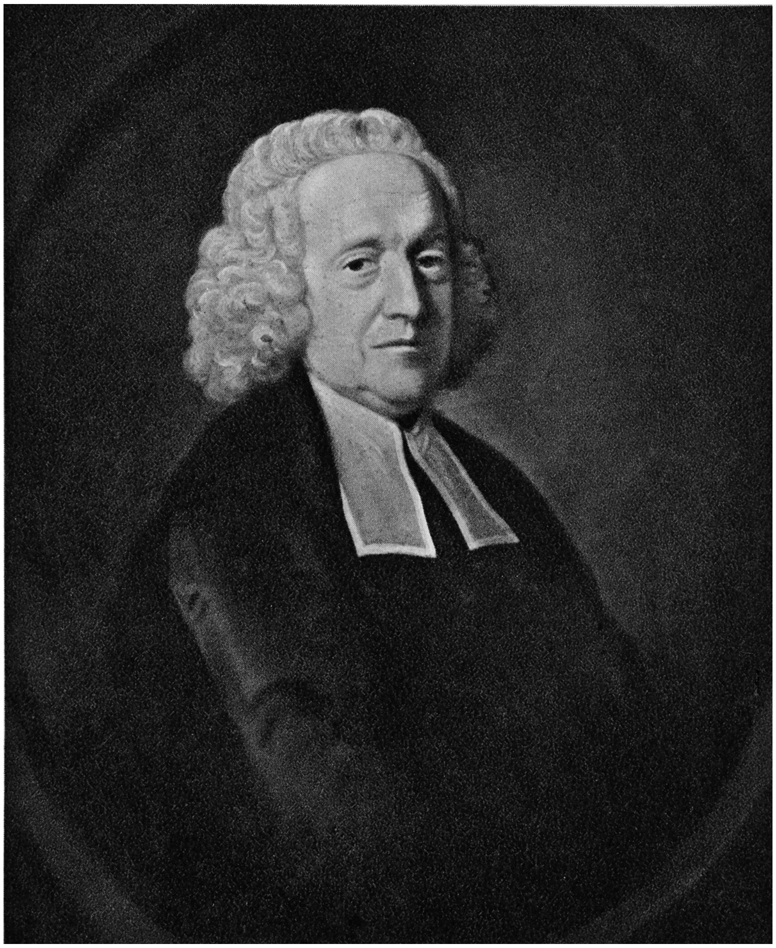

Fig. 1. Stephen Hales, age 81, by Thomas Hudson. National Portrait Gallery, London.

Hales was 50 when he published his first scientific work, *Vegetable Statics* (1727). His studies on blood pressure in mammals (besides dogs, he used two horses and a deer) had given him the idea to study the flow of sap in plants. The brief earlier experiments on the motion of sap in trees made by Willughby and Ray (1699; Egerton 2005:304) seem amateurish in comparison, and Richard Bradley's article (1716) hardly seems an improvement on theirs. Yet Hales' biographers suspect that Bradley's article may have nudged Hales in that direction, because "it raises many of the issues which Hales was to investigate: sap motion and possible circulation, root action, differentiation of function of bark layers, pith and wood, and variation in sap character" (Alan and Schofield 1980:31). From Hales' first experiment, begun on 3 July 1724, one sees why he was soon recognized as England's foremost living scientist (Newton having died in 1727). He explained how he measured the total leaf surface of an experimental sunflower plant 3.5 feet high (Hales 1961:2)

> *I cut off all the leaves of this plant, and laid them in five several parcels, according to their several sizes, and then measured the surface of a leaf of each parcel, by laying over it a large lattice made with threads, in which the little squares were ¼ of an inch each; by numbering of which I had the surface of the leaves in square inches, which multiplied by the number of leaves in*

the corresponding parcels, gave me the area of all the leaves; by which means I found the surface of the whole plant, above ground, to be equal to 5616 square inches, or 39 square feet.

He then measured the length of the root system. There were eight main roots, 15 inches long. He selected one of them with lateral rootlets attached and weighed it; then he measured its length plus the length of all rootlets; then he weighed the other seven main roots with rootlets attached and found that "the sum of the length of all the roots to be no less than 1448 feet. Next, he used a complex calculation to determine the surface area of all the roots, which was 15.8 square feet, which was three-eighths of the aboveground surface area. Finally, he measured the velocity of water movement in that plant, given the fact that it perspired 20 ounces of water in a 12-hour day. That was not the end of his experiment, but this summary and quotation illustrate his thoroughness. He found that his sunflower (before he dismantled it) "perspired"(now transpired) an average 1 lb., 4 oz. of water in 12 hours. His discovery of transpiration was of fundamental importance.

Was the water lost merely evaporated, or was there also root pressure pushing water up the stem? To find out (in Chapter 3), in experiment 34, on 30 March at 3 pm, he cut off a grapevine stalk 7 inches above the ground and attached a glass tube to it (the joint sealed with melted beeswax and turpentine). There was no action, so he filled the tube 2 feet high with water, which was absorbed by the stem down to 3 inches of the bottom by 8 pm. During the night, "it rained a small shower"(Hales 1961:57). At 6:30 am the water in the tube was 3 inches higher than it had been at 8 pm. The temperature was 43° (Fahrenheit). And so on, through experiment 39 and figures 17–20, to demonstrate the existence of root pressure.

Hales not only made important discoveries about

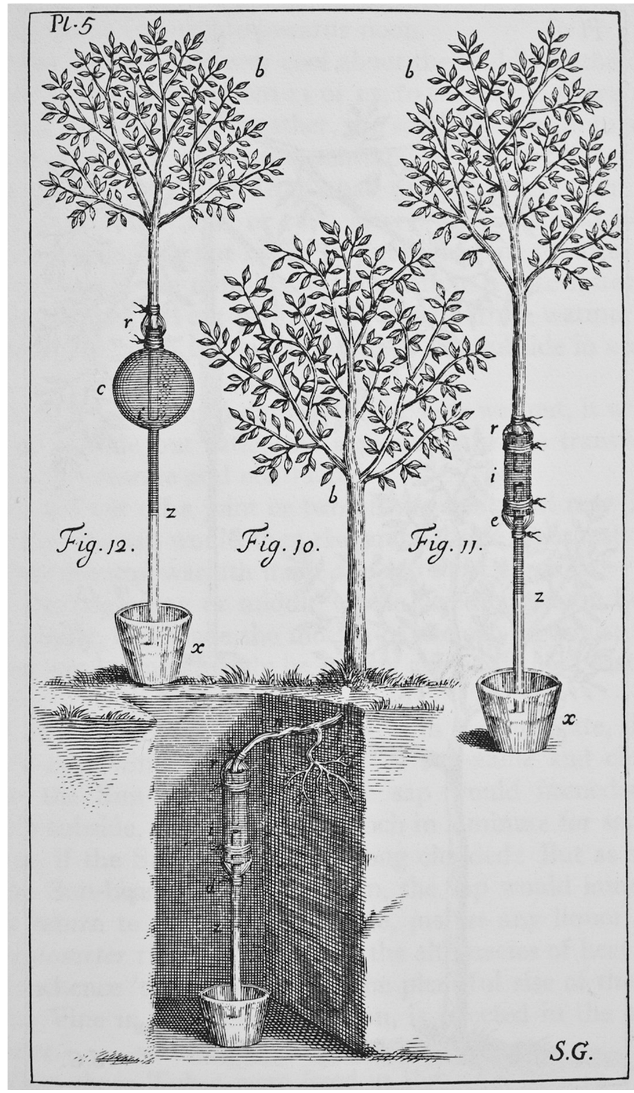

Fig. 2. Hales' figures 10, 11, and 12 illustrate his experiments 21, 22, and 25, respectively. Fig. 10 used a pear tree and Figs. 11 and 12 used apple trees.

water relations in plants, he also investigated plant interactions with air (Chapter 5). He acknowledged that both Grew and Malpighi had thought that air is carried in the largest vessels of wood. Perhaps that is why Hales studied stems rather than leaves. The vacuum pump had been developed in the 1600s and he used one in these experiments. Exactly what air is had not yet been determined, and so he did not explore the roles of oxygen and carbon dioxide. One historian of chemistry commented (Partington 1957:91)

> [Hales'] *chemical work—probably under Newton's influence—is entirely quantitative, and is a good example of the poor results obtained when the qualitative chemical characters of the substances investigated are neglected, but his experiments inspired both Black and Priestley.*

This is more concise than Partington's later conclusion (1962:112–122).

Like many a pioneering scientist, Hales had to invent not only experimental techniques, but also experimental equipment. He illustrated his experiments, described his equipment, and explained how to duplicate his experiments. His studies of airs may have arisen from his plant research, but those studies were not limited to plants. The vacuum pump was helpful, but insufficient. He therefore invented two versions of a pneumatic trough (Fig. 3). Hale's book was widely read and appreciated.

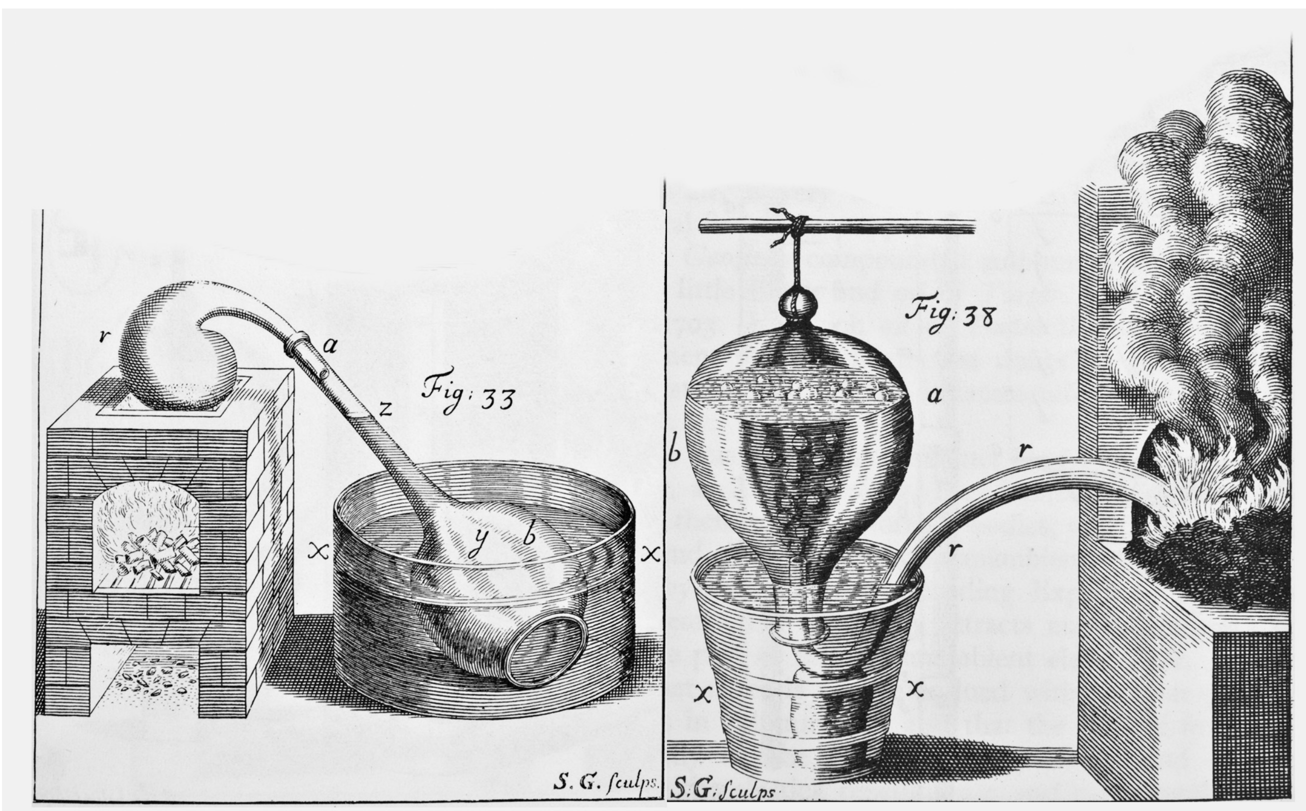

Fig. 3. Hale's pneumatic troughs; his figures 33 and 38 from Plates 15 and 17, respectively; r--r in fig. 38 is an "iron retort" made from a gun barrel in which one end was melted shut.

Buffon translated it into French (1735) and others translated it into German (1747) and Italian (1750). His investigative techniques and instruments helped stimulate a chemical revolution in the second half of the 1700s.

Previously, we saw that John Ray discussed tree ring growth in 1660 and explained that the side of a tree facing the equator grows faster than the opposite side (Egerton 2005:302). On 29 April 1749 Carl Linnaeus (Egerton 2007*a*) departed on his last exploration, to Skåne in southwestern Sweden. Just before reaching Kristianstad, he saw a recently-cut oak and marked the tree rings that were especially narrow and especially broad. Later, he consulted meteorological records and established that the narrow rings correlated with cool summers and the broad rings with warm summers (Linnaeus 1751:68–69, Caddy 1886–1887, II:356, Blunt 1971:196). This was a beginning of dendrochronology, though later developments were not indebted to these observations published in Swedish.

In 1754 a prominent Geneva naturalist, Charles Bonnet (1720–1793) published a book on the function of leaves in plants. His fame rests primarily on his demonstration of parthenogenesis in aphid, but after his eyesight declined, he shifted his research to this topic (Bonnet 1948:146–151). In a biographical article, a fellow Swiss, P. E. Pilet, claimed (1970:286)

> *In the* Researches*, Bonnet grouped five memoirs, all of which were of prime importance for plant biology: He precisely described the characteristics of the nutrition of leaves and of their transpiratory phenomena.*

However, a historian of photosynthesis (Nash 1957: chart at 362) concedes only that Bonnet confirmed Hales' opinion that plants have an important interaction with air, and that Bonnet made a significant observation which he misinterpreted. Recent historians of Geneva botany (Naef 1987:340–341) and general botany (Morton 1981:359, note 70) agree with Nash's assessment of Bonnet's work on plant growth.

Joseph Black (1728–1799) also benefited from Hales' book. He was the son of a Scottish wine merchant who lived in Bordeaux. In 1740 he went to school in Belfast, and about 1744 he entered the University of Glasgow and became the student assistant to the professor of chemistry. In 1752 he transferred to the University of Edinburgh, where he earned an M.D. degree in 1754 (Partington 1962:130–143, Ihde 1964:35–38, Guerlac 1970). His Latin dissertation was on a chemical subject, the effect of alkaline substances to relieve acid indigestion. After further experiments, he published his most important work: *Experiments Upon Magnesia Alba, Quicklime, and Some Other Alcaline Substances* (Black 1756, partly reprinted by Leicester and Klickstein 1952:81–91). The most important aspect of this research was an incidental discovery. He found a component of air he called "fixed air" (carbon dioxide), which he could identify by a lime water (aqueous calcium hydroxide) test which caused a white precipitate (calcium carbonate). He also found from experiments on birds and small mammals that fixed air did not support life or even the flame of a candle. Black's other important discoveries concern heat and are not relevant here, though of indirect ecological importance—latent heat and specific heat. Black's demonstration that ordinary air contained a particular kind of air that could be identified opened a door to the search for other kinds of air, and two other Englishmen soon walked through it.

Henry Cavendish (1731–1810) was the son of Lord Charles Cavendish, who himself conducted important research on heat, electricity, and magnetism. The son inherited wealth and devoted his life to scientific research (Jungnickel and McCormmach 1996, McCormmach 1971, 2004). He identified "inflammable air" (hydrogen) in 1766 (partly reprinted by Leicester and Klickstein 1952:134–142), which he thought might be the principle of fire, "phlogiston" (Partington 1962:302–362, Ihde 1964:38–40). Phlogiston was the vague "flammable principle," really a theory of combustion, that had grown uncritically since Georg Ernst Stahl (c.1660–1734), an influential physician–chemist (Partington 1961:653–686, L. S. King 1975, Teich 1982:363–368) had expounded it in his textbook, *Fundamenta Chymicae* (1723). A candle, for example, gives off phlogiston when it burns; if it burns in an enclosed space, it goes out when the air is saturated with phlogiston. Cavendish's most important discovery was the composition of water (1784; reprinted in Leicester and Klickstein 1952:142–153).

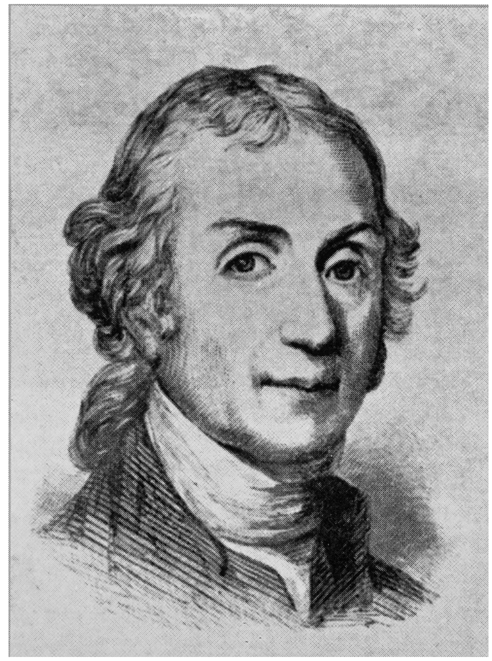

Fig. 4. Joseph Priestley about 1766.

In contrast to Cavendish, Joseph Priestley (1733–1804) was from a working-class family, but after his mother died, he lived with a childless aunt who was well off and paid for his education in a dissenting academy (Schofield 1997, Freimarck 1999, 2004a, b).

He was a very ambitious scholar who became a teacher until 1773, when the Earl of Shelburne asked him to become his librarian. Priestley had broad interests, including liberal politics and religion (he became a Unitarian minister), and science was only a serious hobby. His voluminous writings on politics and religion became controversial in a turbulent age. He was one of a dozen men of science who participated in an informal but important Lunar Society, begun in the 1760s, that met in Birmingham and lasted into the early 1800s (Schofield 1963, Uglow 2002). He began publishing on physics in 1767, and after a fourth edition of Hales' *Vegetable Staticks* appeared in 1769, Priestley began in 1770 similar studies on "airs" (Partington 1962:237–296, Ihde 1964:40–50, Priestley 1966, Schofield 1975, Hessenbruch 2000). From then on, he became preoccupied with researches on airs. He published his early results in a long article in the *Philosophical Transactions of the Royal Society* entitled "Observations on Different Kinds of Air" (1773 [dated 1772]). He began with Black's "fixed air." Cats and mice died in it and a candle went out in it. Sometimes plants also died, but if they did not die, they flourished in it. He first experimented with sprigs of mint, and later found that his discoveries were applicable to other plants. He realized this was an important discovery (Priestley 1773:193)

> *This observation led me to conclude, that plants, instead of affecting the air in the same manner*

with animal respiration, reverse the effects of breathing, and tend to keep the atmosphere sweet and wholesome, when it is become noxious, in consequence of animals living and breathing, or dying and putrefying in it.

However, he found that plants were less effective in restoring noxious air in winter than in summer. He had not yet discovered that sunlight gave plants the capacity to restore noxious air. In June 1772 he demonstrated his findings to his friends Benjamin Franklin and Sir John Pringle, and on 1 July he summarized further experiments in a letter to Franklin (Priestley 1966:104–105, Finger 2006:174–177). Priestley (1773:199) quoted Franklin's reply

> *That the vegetable creation should restore the air which is spoiled by the animal part of it, looks like a rational system, and seems to be of a piece with the rest* [of how nature works]. *Thus fire purifies water…by distillation, when it raises it in vapours, and lets it fall in rain; and further still by filtration, when, keeping it fluid, it suffers that rain to percolate the earth. We knew before, that putrid animal substances were converted into sweet vegetables, when mixed with the earth, and applied as manure; and now, it seems, that the same putrid substances, mixed with the air, have a similar effect. The strong thriving state of your mint in putrid air seems to shew that the air is mended by taking something from it, and not by adding to it.*

Franklin hoped this new discovery would "give some check to the rage of destroying trees that grow near houses…" We now know, of course, that Franklin was only half right in concluding that mint mended the air by taking something from it (CO_2), and not by adding to it, since a photosynthesizing plant does add oxygen to the air. Priestley further discovered (1773:217–218) that both plants and mice die in nitrous air.

Priestley's early experiments led to his being awarded the Royal Society's Copley medal in 1773. The president of the Royal Society, his friend Sir John Pringle, spoke at the presentation, and in doing so explained that winds take vitiated air to plants "for our relief, and for their nourishment" (Pringle 1774). Pringle's speech was published for a wider audience than read Priestley's scientific paper, and it publicized a new dimension to the balance of nature concept: air exhaled by animals is poisonous to other animals but stimulates plants, which, in turn, produce air that is good for animals.

Many of Priestley's experiments were collected into two works: *Experiments and Observations on Different Kinds of Airs* (three volumes, 1774–1777) and another three volumes under a similar title in 1779–1786. Priestley's most famous discovery was of "dephlogisticated air" (oxygen), which he collected on 1 August 1774 by heating mercuric oxide hot enough to separate the elements, and published his discovery in 1775 (Conant 1950:34–48, Leicester and Klickstein 1952:112–122, Partington 1962:256–262).

In spring and summer of 1778 Priestley conducted more experiments on plants that continued to give him mixed results, but he finally realized that dephlogisticated air was only produced by plants in sunlight; merely providing heat in the dark did not stimulate plants to purify air (quoted in Nash 1952:366). This research, published in 1779, still contained some confusion and so was not definitive (partly reprinted in Leicester and Klickstein 1952:122–125, Nash 1957:358–369).

His final report on his experiments on plant growth (Priestley 1790:247–347) cleared up some of his confusion, but since he never gave up the phlogiston theory, others who did give it up soon gained a better understanding than his (Teich 1982:368–373). The French Revolution began in 1789, and as it progressed, both Priestley's politics and religion became very unpopular in England. On the second anniversary of the storming of the Bastille, 14 July 1791, a Birmingham mob burned the Unitarian Meeting House and then the houses of Priestley and other dissenters. As the most reviled man in England, he fled to America in 1794.

Fig. 5. Jan Ingen-Housz in 1769, drawn by A. L. L., engraved by Cunego.

Jan Ingen-Housz (1730–1799) was the son of a prosperous Dutch merchant and pharmacist, and both father and son became friends with Sir John Pringle when he was stationed near their Brenda home with the British Army. Because the family was Catholic in a Protestant country, Ingen-Housz went to the Catholic University of Louvain in Belgium for his M.D. degree, *summa cum laude* in 1753. He then spent a year at the University of Leiden, probably upon Pringle's advice. Next, he practiced medicine in Brenda until his father died in 1764, and then moved to London. He became an expert at smallpox inoculation, and in 1768 George III recommended him to Empress Maria Theresa to inoculate her family. She appointed him court physician for life, and he lived in Vienna until 1788, though he frequently visited Paris and London. In 1788 he settled in Paris until the storming of the Bastille on 14 July 1789 alarmed him. He departed for Belgium and The Netherlands, where, as an Austrian courtier, he was viewed with suspicion, and so he returned to live in London (van der Pas 1973, Smit 1980, Ingen Housz 2005).

Ingen-Housz became interested in plant growth after reading Priestley's first article and Pringle's Royal Society speech when Priestley won the Copley Medal. However, his Austrian responsibilities prevented him from investigating the subject until the summer of 1779, which he spent in England and conducted the extensive experiments reported in *Experiments upon Vegetables, Discovering Their Great Power of Purifying the Common Air in the Sun-shine, and of Injuring it in the Shade and at Night* (1779; partly reprinted in Leicester and Klickstein 1952:125–133). He solved the mystery of Priestley's inconsistent results concerning plants restoring air (Partington 1962:278–280). Both Nash (1957:369–384) and Reed (1950) discuss Ingen-Housz's work, with extensive quotations from his book, and both Reed (1950:293) and Morton (1981:333) list Ingen-Housz's achievements; here is Morton's list (abridged, with modern chemical names)

1) Evolution of oxygen occurs only in light, in green parts of plants.

2) Evolution of oxygen ceases in the dark.

3) Carbon dioxide is produced by all parts of plants in darkness.

4) Production of oxygen in day far exceeds production of carbon dioxide at night.

5) Rate of oxygen production depends on the intensity of light.

6) Oxygen production depends on sunlight, not heat.

7) Oxygen is produced mainly on the lower surface of leaves.

Fig. 6. Jean Senebier.

In 1780 Ingen-Housz translated his book into French, and others translated it into Dutch and German. Priestley criticized some of Ingen-Housz's ideas, and in 1781 Ingen-Housz discussed with his friend, Benjamin Franklin, how to respond (Conley and Brewer-Anderson 1997:283–284, Schofield 2004:154–156, Chaplin 2006:282–283). Not only was he making his discoveries while Priestley was still working in the field; there were other newcomers with whom he conducted priority disputes (Smit 1980:129–131).

One of his competitors was the Geneva scholar Jean Senebier (1742–1809), who was a protégée of Bonnet (Bay 1931, Pilet 1975*b*, Naef 1987:330–333). Senebier (1782:3) provides a history of his early research on plants, indicating that he began in 1779. He was encouraged by publication of the French edition of Ingen-Housz's *Experiments* (1780). Ingen-Housz had discovered that in boiled distilled water a green leaf produces no "dephlogisticated air" [when water contains no CO_2, leaf produces no O_2], but he did not draw the important conclusion from this discovery that Senebier did.

They both knew that pump water was rich in "fixed air" (CO_2) and that plants produce much dephlogisticated air in pump water; therefore, Senebier concluded in his *Mémoires physico-chimiques sur l'influence de la lumière solaire pour modifier les étres des trios règnes de la nature et surtout ceux du règne vegetal* (1782) that fixed air must be present for plants to make dephlogisticated air. This was his most important discovery (Nash 1957:388–391, Morton 1981:334–336). Ingen-Housz considered Senebier's *Mémoires* to be "a copy of his own work from the evidence of the planning and sequence of the experiments performed, the eudiometric units used and the terminology" (Smit 1980:130). However, the acknowledged repetition of one scientist's experiments by another is not plagiarism. In 1782

Senebier announced he was unable to confirm Ingen-Housz's conclusion that plants vitiate the atmosphere at night, but in 1788 he admitted that his further experiments did confirm it, though he believed it less important than Ingen-Housz thought (Nash 1957:385–386). Furthermore, Senebier accepted some corrections from others, including Alessandro Volta, who convinced him that his belief in 1782 that "phlogisticated air" (N_2) mixed with "pure air" (O_2) formed "fixed air" (CO_2) was mistaken (Nash 1957:398, Partington 1962:280–283).

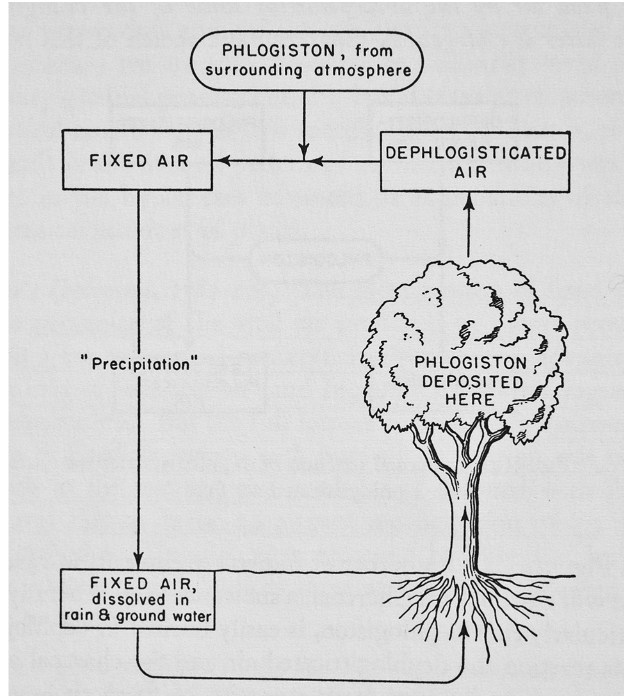

Fig. 7. Senebier's 1782 concept of plant–air interactions. Nash 1957:396.

Meanwhile, the conceptual framework in which chemists operated was being challenged in France by Antoine-Laurent Lavoisier (1743–1794), who followed in the Cartesian theoretical tradition, in contrast to the empirical English Baconians (McKie 1952, Partington 1962:363–495, Ihde 1964:57–88, Guerlac 1973, Poirier 1996, Crosland 2000, Holmes 2003). However, Lavoisier was happy to repeat experiments by Boyle, Hales, Black, Cavendish, and Priestley to see if he could reinterpret them. That English research included, but was not limited to, the study of plant growth. Lavoisier deliberately set out to destroy the phlogiston theory. The flaw that aroused his suspicion was that in the burning of wood, the residue weighed less than the original substrate, and in the burning of metal, the residue weighed more than the original substrate, yet both were explained in the same way—a loss of phlogiston. In the case of wood, phlogiston had a negative weight; in the case of metal, a positive weight. Lavoisier made little progress in his revolution until Priestley came to Paris two months after he had discovered "dephlogisticated air" in 1774 and told him about it. Lavoisier then took several missteps before conducting his crucial experiment in April 1776, demonstrating that common air is not a simple substance and that respirable air is only-one quarter of the whole. Lavoisier renamed "dephlogisticated, or respirable air," "oxygen" in the nomenclature revolution initiated by him and three associates (Guyton de Morveau et al. 1787; partly reprinted in Leicester and Klickstein 1952:180–192; see McKie 1962:188–197, Partington 1962:481–484). After performing much work on animal respiration, Lavoisier was inspired by Priestley and Senebier's experiments to study plant growth himself, and he advanced his own chemical understanding in doing so (Holmes 1985:313–314). Lavoisier's chemical revolution coincided with the French Revolution (Conant 1950, Donovan 1993, Mauskopf 2000, Gillispie 2004, Jackson 2005); his revolutionary textbook, *Traité élémentaire de chimie* (1789) appeared a month after the storming of the Bastille. While Priestley was fleeing to America because of the French Revolution, Lavoisier was literally losing his head because of it, a victim of the guillotine in the Reign of Terror.

Senebier accepted Lavoisier's new chemistry a year before Ingen-Housz did. In his *Expériences* *sur l'action de la lumière solaire dans la vegetation* (1788), Senebier adopted some of the new terms without, however, abandoning all of the old (Senebier 1788:288, translated in Nash 1957:404)

> *Since plants contain hydrogen whether they grow in sand, in sponge, or in powdered glass, it is evident that the plants do not obtain the hydrogen from these substances…light and water is indispensable to vegetation. Light does not contain inflammable air, while water does. Therefore it appears that one may believe that if some parts of plants relieve the water of its hydrogen, by combining with the latter, the oxygen must escape from the plant by the action of sunlight….*

Ingen-Housz had to accept the contributions of both Lavoisier and his rival, Senebier. By 1789, in the second volume of his revised *Expériences sur les vegetation*, he had accepted some of Lavoisier's chemistry and achieved an "impressively comprehensive interpretation of the chemical activities of plants…."(Nash 1957:413). However, he did not yet accept Senebier's claim that carbon dioxide is decomposed in green leaves and releases oxygen into the air. He finally accepted Senebier's claim in an obscure *Essay on the Food of Plants and the Renovation of Soils* (1796).

Ingen-Housz's coming up to speed in 1796 was like Priestley doing so in 1790: it was not crucial because the action was elsewhere—back to Geneva, with a new investigator. Nicolas-Théodore de Saussure (1767–1845) was the son of a leading Swiss natural philosopher, Horace Bénédict de Saussure (1740–1799), who was primarily a geologist (Carozzi 2005), but whose broad interests included botany and meteorology. Although the son received a formal education at l'Académie de Genève, he learned science from his father (Hart 1930, Pilet 1975*a*, Sigrist and Candaux 2001). If Hales was the founder of plant physiology, Nicolas de Saussure advanced it "from the simple exploration of facts to the status of a science, with its own basis of integrated theory and specific methodology" (Morton 1981:342). He never faced the challenge of unlearning phlogiston chemistry; he learned the new chemistry from the start. His first publication was an extensive "Essai sur cette question: la formation de l'acide carbonique est-elle essentielle à la vegetation?"(1797), published in the journal Lavoisier founded, *Annales de chimie*. De Saussure's article consolidated the understanding of respiration and carbon assimilation and prepared the way for his decisive *Recherces chimiques sur la végétation* (1804), which is the basis of Morton's just-quoted evaluation of his achievements, but which work came after the century being surveyed here (Buchs 1987:171–180).

In 1800, Erasmus Darwin (1731–1802) published *Phytologia*, a large book of 612 pages that included a detailed discussion of physiology. His main biographer, Desmond King-Hele (1999:334–335), insists that Darwin made important, but neglected, contributions to our understanding of photosynthesis, and he provides this quotation as proof (Darwin 1800:193–194, 1968:105)

> *This carbonic gas in its fluid state, or dissolved in water, not in its aerial or gaseous state, is the principal food of plants; as appears, because their solid fibres consists principally of carbon, and their fluids of water.*
>
> *Next to carbonic acid the aqueous acid, if it may be so called, or water, seems to afford the principal food of vegetables…when vegetable leaves are exposed to the sun's light, they seem to give up oxygen gas; but in the dark they give up carbonic acid, like the breath of animals.*

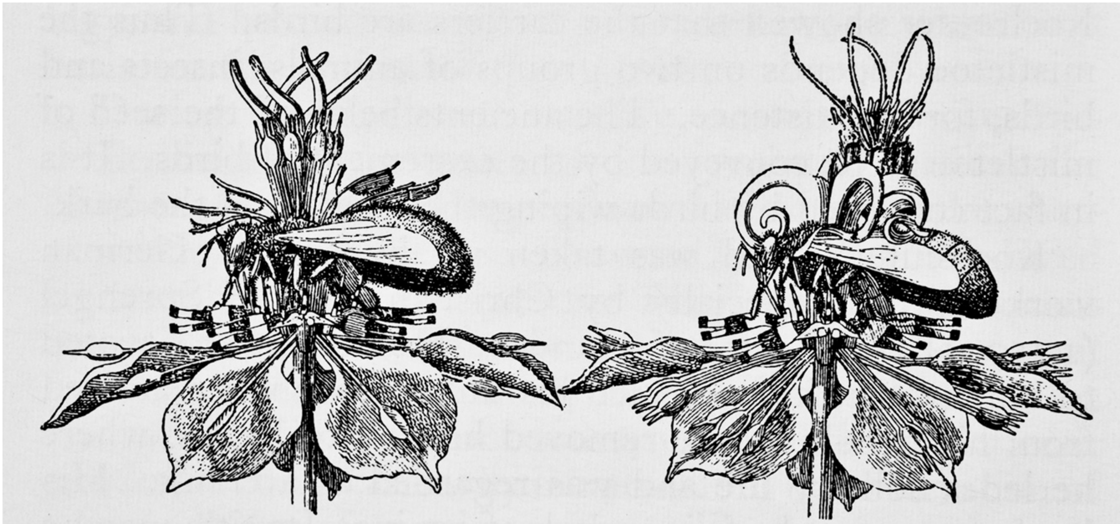

Fig. 8. Pollination of *Nigella arvensis*. Showing anthers just above a visiting bee in left drawing. After pollen is exhausted, anthers bend down and lie on petals and a bee then arriving has pistils bent over it to receive pollen. Sprengel 1793.

It would be fairer to credit Darwin with being well read in the botanical literature (McNeil 2004:203–204). The reason this discussion has been neglected is that it is not original (Darwin never said it was) and was not based upon experiments at a time when experimentation had become essential in plant physiology research. Darwin is better remembered for his ideas on evolution and on biological control of agricultural pests.

A very different aspect of plant growth studies concerned flowers. If petals were to protect fruit, why did they fall off so soon? Was nectar a waste product or nourishment for seeds? No one knew. As we saw in Part 25 (Egerton 2007*b*:256–257), Arthur Dobbs pointed out that when bees collect nectar they also pollinate flowers, but although his report appeared in the *Philosophical Transactions of the Royal Society of London* (1750), it went virtually unnoticed. In 1694, the German botanist Rudolph Jacob Camerarius had published experiments supporting the sexuality of plants hypothesis, and in the 1700s his conclusion was widely accepted (Morton 1981:214–220, 239–245). Nevertheless, the Imperial Academy of Sciences in St. Petersburg offered a prize for an essay on further experiments to demonstrate the sexuality of plants, and the German botanist Joseph Gottlieb Koelreuter (1733–1806) responded by conducting hybridization experiments, which he published in 1761–1766 (Olby 1973, Morton 1981:316–321). During these experiments he discovered that some flowers are structured for wind pollination and others for insect pollination. His work was better noticed than Dobbs' article, but insect pollination still did not make much of an impression. One of Koelreuter's readers was the German rector of a Lutheran school and amateur botanist, Christian Konrad Sprengel (1750–1816). He began studying *Geranium* in 1787, and he focused on pollination, rather than on hybridization as Koelreuter had (L. J. King 1975). Wanting to avoid the neglect that Koelreuter had experienced, he illustrated *Das entdeckte Geheimniss der Natur im Bau und in der Befruchatung der Blumen* (1793) with 25 copperplates containing 1117 drawings of 461 species.

Despite that, his work made little more impression on botanists than Koelreuter's had, and he abandoned a planned second volume on pollination. Lorch's brief talk on "History of theories on the function of nectar" (1964) ignores Koelreuter and is overly brief on Sprengel, but it is very good at showing how slowly the true function of nectar was accepted during the 1800s.

Plant growth studies in the 1700s focused mostly on interactions between plants and the atmosphere. No progress occurred in understanding the role of cambium (Lorch 1967:262–268). Progress that did occur depended on identifying the gases in the air and then documenting their roles in plant physiology. Hales, Priestley, Ingen–Housz, Senebier, and de Saussure were the leading investigators, with Lavoisier playing a significant role. They made substantial progress in clarifying the interactions between plants and the atmosphere. This occurred during the chemical revolution that Lavoisier led, and plant investigations both played a role in that revolution and benefited from it. Good progress occurred in the understanding of insect pollination, but it attracted little interest.

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