Contributions

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History of Ecological Sciences, Part 43: Plant Physiology, 1800s

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Plant geography and plant physiology were two foundations upon which plant ecology arose during the later 1800s. Plant geographers Alexander von Humboldt, Hewett Watson, Joseph Hooker, and de Candolle, father and son, were discussed in previous parts of this history. Building on the outstanding experimental studies on plant growth conducted during the 1700s, and on Antoine Lavoisier's chemical revolution, botanists, agronomists, and chemists established a flourishing plant physiology during the 1800s. Scientists in Britain, France, Germany, and Switzerland led the way.

Two poorly developed theories accepted at the beginning of the 1800s, humus as fertilizer and vitalism, became discredited during the 1800s. Humus was disintegrated plant matter, which varied in composition from place to place, intermixed with topsoil. It was different from animal manure, though both seemed to have similar effects. There was a long tradition of using humus as fertilizer. Two early founders of agricultural chemistry were Scotsman Francis Home (1719–1813) and Swede Johan Gottschalk Wallerius (1709–1785). Home, a physician and later a medical professor at the University of Edinburgh, published his important *Principles of Agriculture and Vegetation* in 1757. USDA agronomist Charles Browne nicely summarized Home's book in his *Source Book of Agricultural Chemistry* (1944:117–126). Wallerius was Sweden's first professor of chemistry, at Uppsala University (Partington 1962:169–172, Boklund 1976, Frängsmyr 1985:6). Wallerius' *Agriculturae Fundamenta Chemica* (1761) appeared in both Latin and Swedish, as a dissertation defended by his student, Count Gustavus Adolphus Gyllenborg, and bibliographies list it under either name. Its similarity to Home's *Principles* makes it likely that Wallerius was indebted to Home's book (Browne 1944:128).

The earliest discussion of humus that Browne quotes (in translation, Browne 1944:130–131) is from *Agriculturae Fundamenta Chemica*, which Browne also summarized (Browne 1944:126–134). Wallerius had not invented the humus term or concept, but his understanding of it seemed to be what

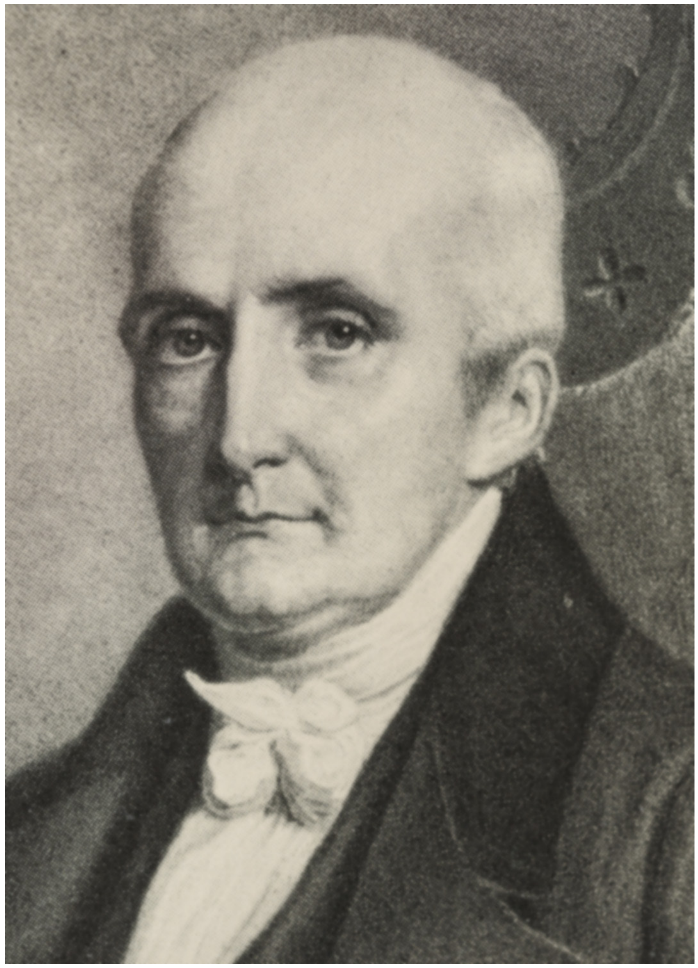


Fig. 1. Nicolas-Théodore de Saussure. Trembley 1987:433.

was generally accepted (Waksman 1942). Both Browne (1944:208, 211) and botany historian Alan Morton (1981:392–393) viewed the humus theory as impeding understanding, and as leaving room for vitalism. We will see, however, that when mycorrhiza on roots are involved, something like a humus theory was invoked.

We reach the 1800s, where we left off in Part 28 (Egerton 2008:169), with the *Recherches chimiques sur la végétation* (1804) by Genevan Nicolas-Théodore de Saussure (1767–1845). He was indebted not just to Lavoisier and plant experimentalists of the 1700s, but also to his own father, Horace Bénédict de Saussure, a prominent geologist with serious interests in botany and meteorology (Carozzi 2005). The elder Saussure trained his son to be his assistant (Hart 1930, Pilet 1975).

Although Saussure's *Recherches* apparently lacks a modern edition, more recent authors provide discussions and/or quotations in English or French (Browne 1944:193–202, Weevers 1949:6–7, Gabriel and Fogel 1955:338–342, Nash 1957:225–231, Morton 1981:338–342, Buchs 1987:171–180, Naef 1987:333–337, Magnin-Gonze 2004:160–161). Saussure was the most sophisticated experimentalist thus far in the history of botany (Sachs 1890:497–502, Reed 1942:215, 241–242). Where his predecessors had been content to record whether a plant did well or poorly under experimental conditions, he measured how well or poorly they did, and compared that result with measurements on control plants or plants in other experiments. Plants grow faster in air enriched by carbon dioxide, but only to a maximum of 8% carbon dioxide; at a higher percentage, plants do poorly. Where his predecessors tried something to see what happened, he designed experiments to test hypotheses. His experimental techniques and equipment represented advances that later physiologists copied.

Saussure sometimes refined experiments conducted by his predecessors. For example, Van Helmont had conducted an experiment in which he weighed a tub of dirt into which he planted a willow stem, and five years later he removed the tree and found the amount of dirt was the same (Egerton 2004:209). Van Helmont thought he had proved that the tree gained all its weight from rain or distilled water that he added, not noticing the possibility that it absorbed gases from the air, despite his having coined the word "gas" (Egerton 2004:209). That 1600s fallacy had been corrected during the 1700s, but Saussure added that van Helmont's scale had not been precise enough to detect minute amounts of minerals that his tree absorbed from the earth. When plants are removed from where they grow, minerals within them are also removed, causing a loss of soil fertility. Saussure also resolved some past disputes left hanging by his predecessors. Priestley and Ingen-Housz had thought that nitrogen was absorbed by plants from the air; Senebier was skeptical, but had not found a way to settle the argument. Saussure did so by showing that only oxygen and carbon dioxide were absorbed from the air. Although he realized that nitrogen in the air was not absorbed by plants, he thought atmospheric ammonia might be (Saussure 1804:207, Partington 1962:283–284, Aulie 1970*b*:453).

Saussure's goal was to gain a comprehensive understanding of plant physiology. He developed a conceptual scheme that allowed him to assign the source and route of supply of every major element that chemical analysis discovered in mature plants (Nash 1957:431, Partington 1964:311, Fussell 1971:154). He was the first to make regular analyses of plant ashes, and his were the most accurate and extensive analyses yet attempted. He found that not all the oxygen and hydrogen in plants could come from air, and therefore he concluded that water was a major nutrient of plants and not just a medium for transferring material from soil to roots. He recognized that plant liberation of carbon dioxide at night indicated a fundamental similarity to animal respiration, studied by Lavoisier (Morton 1981:338). No experimentalist is infallible, and occasionally he was less diligent than he should have been. He overlooked sulfur in the ashes. Another example: since the red variety of *Atriplex hortensis* produces as much oxygen as the green variety, he concluded green color was not essential for growth, when he might have seen with a microscope green cells below the red epidermis of red leaves (Sachs 1890:503, Morton 1981:340–341). *Recherches* was a pivotal book: it culminated past researches and potentially opened doors for the future. Yet Morton (1981:392) thought that "The basis of plant nutrition seemed to have been so thoroughly settled by de Saussure that for a long time botanists gave the subject no serious attention." Sachs (1890:508) attributed the lack of progress to the deadening influence of vitalism theory. Both authors were thinking of Continental chemical studies on plants.

In Britain, the physiological approach by Thomas Andrew Knight (1759–1838) was more physical than

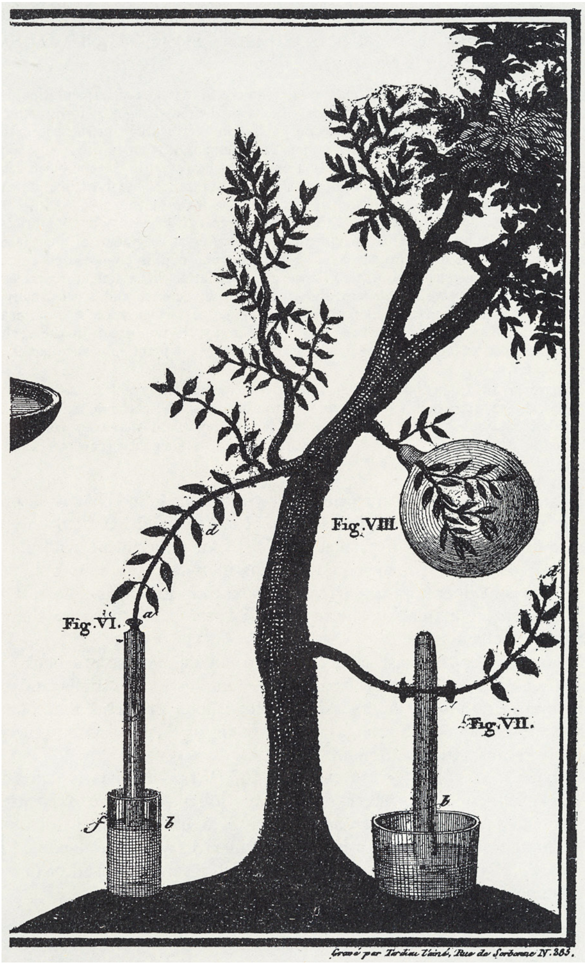


Fig. 2. Apparatus to determine the changes effected in the composition of air by a twig stripped of some leaves (Fig. VI), by the leafless part of a branch (Fig. VII), and by leaves in an enclosed amount of air (Fig. VIII). Saussure 1804; from Browne 1944:195.

chemical. He graduated from Oxford University and assumed management of his brother Richard Payne Knight's 10,000-acre estate (Simpkins 1973, Browne 2004, Elliott 2004). He began experiments on improving the breeds of fruits, vegetables, and cattle, which led to correspondence with botanist Sir Joseph Banks (1743–1820), president of the Royal Society of London (Knight 2004*a*). He sent Banks 23 reports on his agricultural experiments, which Banks published in the Royal Society's *Philosophical Transactions* (1795–1812), but *The Banks Letters* (Dawson 1958:496–509, 906) lists and summarizes 97 letters that Knight wrote to him. Knight's early experiments on the movement of sap in trees were less decisive than he had hoped, because they were not informed by an adequate general theory of physiology (Harvey-Gibson 1919:82–83, Reed 1942:176). Knight's most important discovery was geotropism (1806), named by Julius Sachs in 1868 (Harvey-Gibson 1919:83–87, Singer 1959:376–377, Morton 1981:390). Knight attached germinating seeds to rapidly rotating discs—some experiments with horizontal and others with vertical discs—attached to a water wheel in a stream.

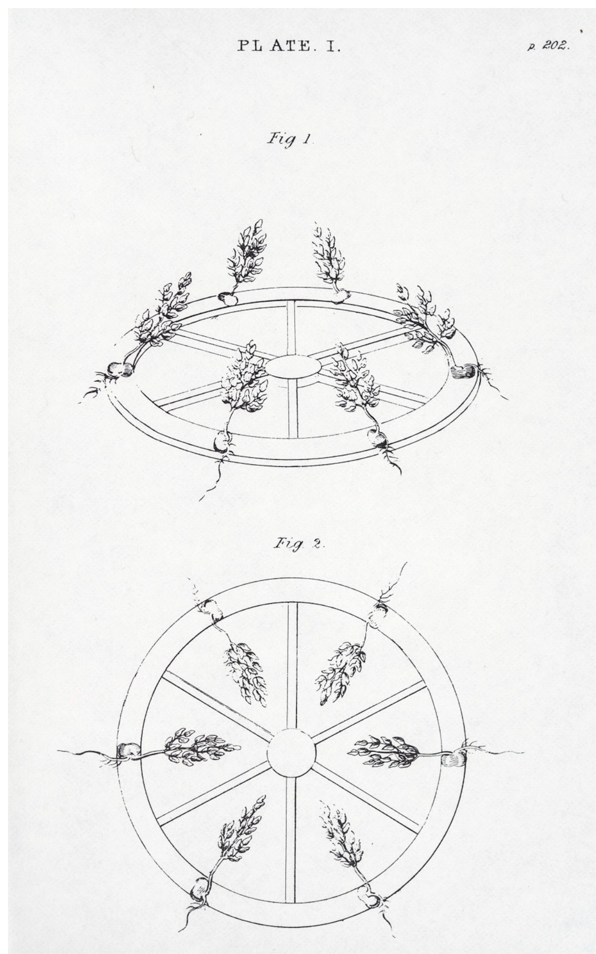


Fig. 3. Knight's experimental design to study geotropism. Davy 1839, VII: facing 202, 1972.

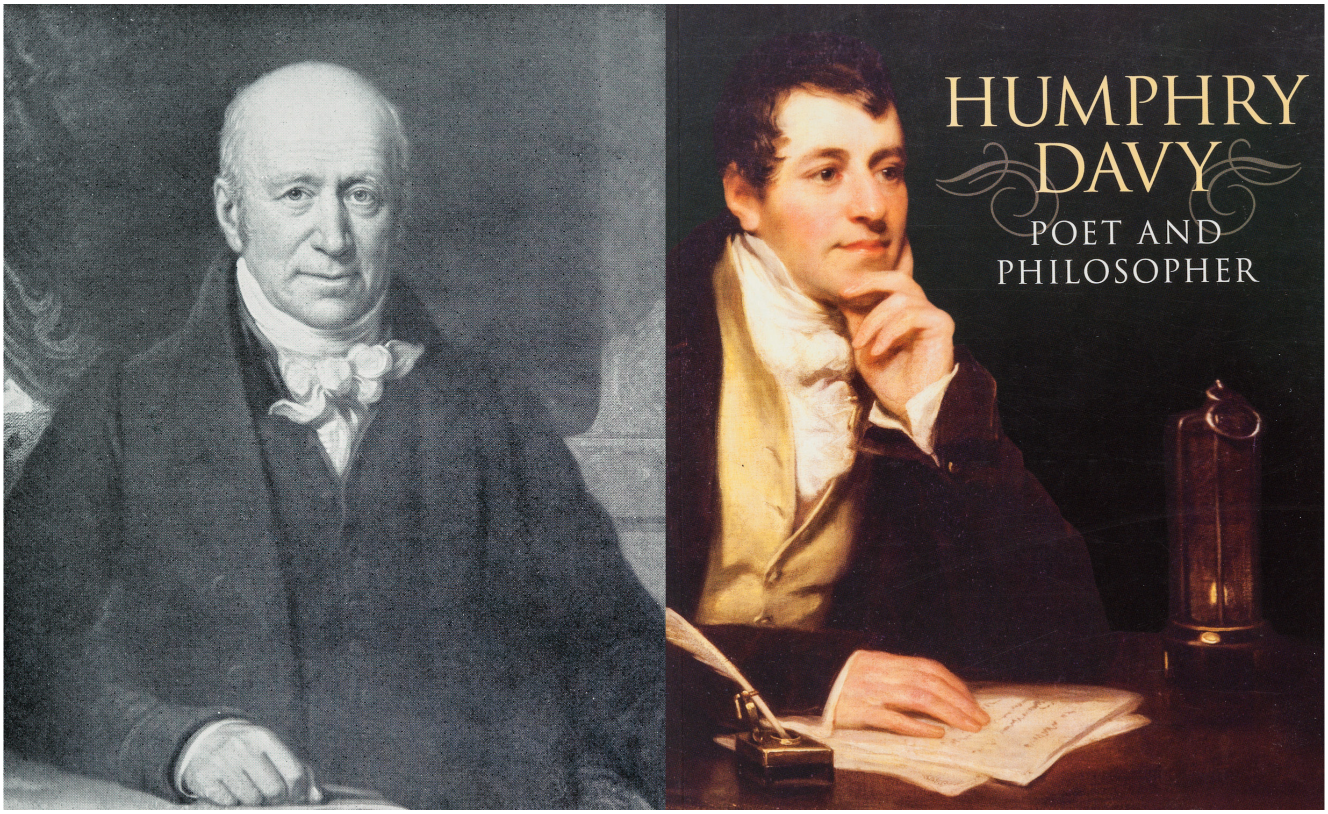


Fig. 4. (a) Thomas Andrew Knight. Simmonds 1954: Fig. 127. (b) Humphry Davy, 1821. By Thomas Philips. National Portrait Gallery, London. Thorpe 2007: cover.

He discovered that roots have positive and stems have negative geotropism. Sachs named Knight's experimental device a klinostat. In 1811 Knight showed that roots can be diverted from the vertical by moist earth, and in 1812 he showed also that tendrils of *Vitis* and *Ampelopsis* show negative heliotropism (Sachs 1890:549). Many of his papers on experiments were collected and republished posthumously (Knight 1841).

Humphry Davy (1778–1829) was a successful chemist as both researcher and public lecturer at the Royal Institution in London (Jones 1871:312–403, Treneer 1963, Ihde 1964:127–131, Partington 1964:32–39, Hartley 1966, Russell 1966:66–76, Knight 1971, 1992, 2004*b*, Fullmer 2000, Tuttle 2004). He became famous by being first to use electrolysis to separate certain compounds not previously decomposed, and thus discovered sodium, potassium, calcium, strontium, barium, magnesium, and chlorine. In 1802, before de Saussure's *Recherches* was published, the Board of Agriculture asked him to teach a course on agricultural chemistry. Since there was a substantial overlap in members of the Board and Proprietors of the Royal Institution, that diversion from pure to practical chemistry was easily arranged (Wilmot 1990:23). Davy taught the course from 1802 through 1812, revising his lectures yearly, and published his lectures as *Elements of Agricultural Chemistry* (1813), which was an important synthesis of more than 100 previous studies, including the works of both de Saussure and Knight. Davy

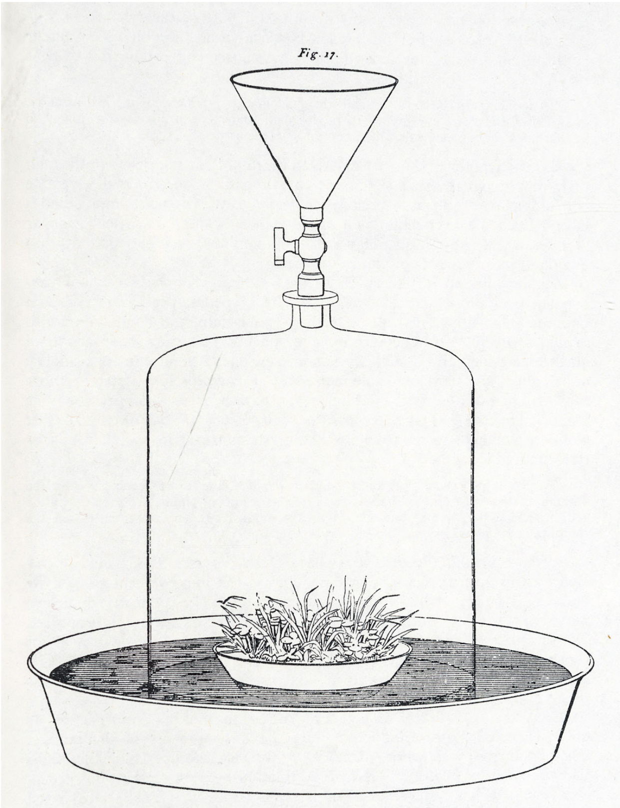


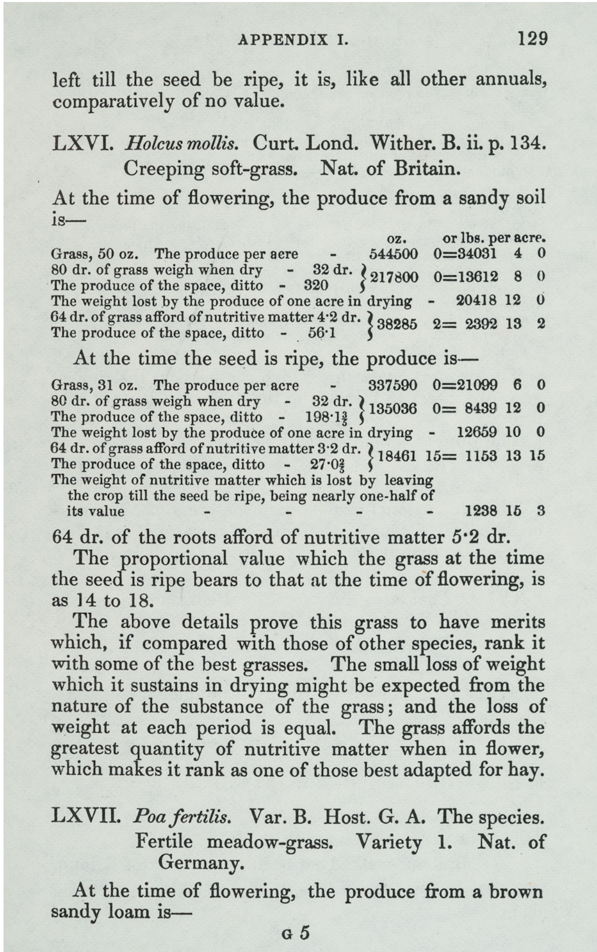
Fig. 5. Davy's apparatus for studying the gases evolved by meadow grass. Browne 1944:209.

and Knight became close friends, and Davy dedicated the fourth edition of *Elements* (1827) to Knight. *Elements* went through six English and five American editions and was translated into German (1814), Italian (1815), and French (1819). It was the most popular book ever written on the subject (Miles 1961:128).

Davy divided *Elements* into eight lectures, and if he read one per evening, they were long evenings. Browne (1944:205–210) summarized *Elements*, including two illustrations. Lecture 1 was introductory, partly historical. Lecture 2 discussed gravity (Knight's work, Fig. 3 above), heat, light, electricity, and plant substances. Lecture 3 was on plant organization—roots, trunks, branches, leaves, flowers, seeds—and plant compounds. Lecture 4 was on soils, their analysis and improvements. In 1805 the Board of Agriculture provided a laboratory near the Royal Institution for such analyses, and Davy designed equipment for analyses that is preserved in the History of Science Museum, Oxford University (Knight 1992:47).

Lecture 5 was on the atmosphere and its influence on plant growth and seed germination. Lecture 6 was ostensibly on "manures of vegetable and animal origin," but mostly on animal manures, and rather than using actual plants as manures, he grew plants in various plant substances, like sugar water, mucilage, and tanning solution. Lecture 7 was on mineral or fossil manures, and he discussed experiments—some of which were his own—using as fertilizers calcium carbonate, quicklime, slaked lime, dolomite, gypsum, peat ash, calcium phosphate, and the salts of sodium, potassium, and ammonia. Lecture 8 was on improvements of land by burning, irrigation, fallowing, crop rotation, and pasturage. An appendix provides data that the Duke of Bedford had his gardener, George Simpson, at Woburn Abbey, collect at field trials on which forage species were most nutritious as livestock feed (Davy 1839, VIII:89–141). Simpson's extensive data were quite precise (Fig. 6), but Davy was only able to make a few imprecise comments about them (Davy 1839, VIII:144–148). Davy is credited with making agricultural chemistry into a coherent subject, but he deemphasized mineral fertilizers (Wilmot 1990:26). Davy's support for humus theory was a negative influence (Browne 1944:208, 211, Morton 1981:392–393).

The popularity of Davy's *Elements of Agricultural Chemistry* began to wane in 1835, when an English translation of Chaptal's *Chimie appliquée à l'agriculture* appeared (Miles 1961:133). As a scientist-educator, Jean Antoine Chaptal (1756–1832) was as capable as Hermbstädt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left till the seed be ripe, it is, like all other annuals, comparatively of no value.

LXVI. *Holcus mollis.* Curt. Lond. Wither. B. ii. p. 134. Creeping soft-grass. Nat. of Britain.

At the time of flowering, the produce from a sandy soil is—

	oz.	or lbs. per acre.		
Grass, 50 oz. The produce per acre -	544500	0=34031	4	0
80 dr. of grass weigh when dry - 32 dr. / The produce of the space, ditto - 320	217800	0=13612	8	0
The weight lost by the produce of one acre in drying -		20418	12	0
64 dr. of grass afford of nutritive matter 4·2 dr. / The produce of the space, ditto - 56·1	38285	2= 2392	13	2

At the time the seed is ripe, the produce is—

Grass, 31 oz. The produce per acre -	337590	0=21099	6	0
80 dr. of grass weigh when dry - 32 dr. / The produce of the space, ditto - $198{\cdot}1\frac{3}{5}$	135036	0= 8439	12	0
The weight lost by the produce of one acre in drying -		12659	10	0
64 dr. of grass afford of nutritive matter 3·2 dr. / The produce of the space, ditto - $27{\cdot}0\frac{2}{5}$	18461	15= 1153	13	15
The weight of nutritive matter which is lost by leaving the crop till the seed be ripe, being nearly one-half of its value - - - -		1238	15	3

64 dr. of the roots afford of nutritive matter 5·2 dr.

The proportional value which the grass at the time the seed is ripe bears to that at the time of flowering, is as 14 to 18.

The above details prove this grass to have merits which, if compared with those of other species, rank it with some of the best grasses. The small loss of weight which it sustains in drying might be expected from the nature of the substance of the grass; and the loss of weight at each period is equal. The grass affords the greatest quantity of nutritive matter when in flower, which makes it rank as one of those best adapted for hay.

LXVII. *Poa fertilis.* Var. B. Host. G. A. The species. Fertile meadow-grass. Variety 1. Nat. of Germany.

At the time of flowering, the produce from a brown sandy loam is—

G 5

Fig. 6. George Simpson's field data for *Holcus mollis*, number 66 of 97 species he analyzed for Davy. Curt. Lond. = William Curtis, *Flora Londinensis* (two volumes, London, 1798). Wither. B. = William Withering, *Botanical Arrangements* (four volumes, London, 1801). Davy 1839, VIII:129.

(see the discussion on Hermbstädt below) and Davy, but he was also a prominent government official under Napoleon (Browne 1944:183–189, Crosland 1971, Matagne 1999:38–39). Chaptal obtained a doctorate in medicine at Montpellier and then went to Paris for further study, but soon became more interested in chemistry. He became wealthy, partly by marriage and by a large gift from an uncle, and also by investing in chemical industries. On an estate in the Loire Valley, he raised sheep and sugar beets. He published the first edition of his *Élémens de chimie* (three volumes, 1790) a year before Hermbstädt published his comparable work. Surprisingly, Hermbstädt not only translated Lavoisier into German, but also Chaptal. Others translated Chaptal's *Élémens* into English, Italian, and Spanish. Part 4 of the *Élémens* was on the chemistry of plants (149 pages) and animals (88 pages). While this work was very popular, in 1823 Chaptal published *Chimie appliquée à l'agriculture* (two volumes, edition 2, 1829), which became his most popular work and was translated, as mentioned above, into English (1835, three American editions) and German.

French chemists Pierre-Joseph Pelletier (1788–1842) and Joseph-Bienaimé Caventou (1795–1877) studied the chemistry of plants, including green pigment in leaves, naming this compound chlorophyll (1817) (Reed 1942:197, Delépine 1951, Partington 1964:241–243, Berman 1971, 1974). University of Utrecht Professor of Chemistry Geradus Johannes Mulder (1802–1880) continued these studies in the

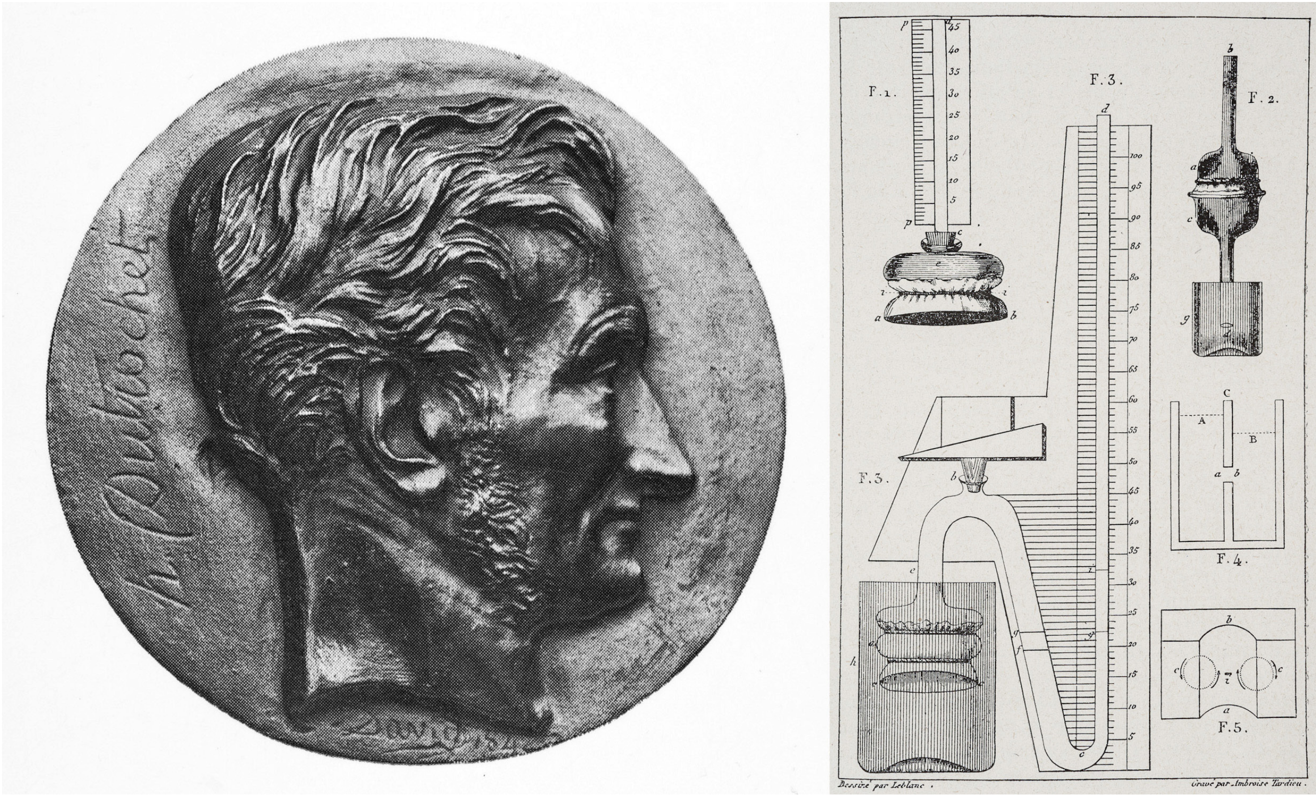

Fig. 7. (a) Henri Dutrochet. Medallion by David d'Angers. (b) Endosmometer. Dutrochet 1837. Carls 1954:164.

1830s and correctly analyzed phytol (Reed 1942:167, Browne 1944:252–262, Partington 1964:319–320, Snelders 1974:558). In 1851, University of Tübingen Professor of Botany Hugh von Mohl (1805–1872), who had coined the term protoplasm and founded *Botanische Zeitung* (1842), discovered that chlorophyll does not occur throughout green cells, but occurs in granules (now chloroplasts) (Reed 1942:166, Weevers 1949:9, Klein 1974). Chlorophyll was a complex substance that was slowly elucidated in the later 1800s and early 1900s, when four constituents were separated (Reed 1942:197–199).

René-Joachim-Henri Dutrochet (1776–1847) grew up in an aristocratic family during the French Revolution (Kruta 1971, Schiller and Schiller 1975:5–21, Aron 1990). After participating in revolutionary conflicts, he studied medicine in Paris, 1802–1806, and then became an army medical officer. After contracting typhoid, he retired from the army and later turned to biological research. In 1831 he became a member of the Académie des Sciences. He studied both animal and plant physiology; his *Recherches anatomiques et physiologiques sur la structure intime des animaux et des végétaux et sur leur motilité* (1824) contained an early defense of the cell theory (translated by Gabriel and Fogel 1955:6–9), though his studies were not precise enough to establish it (Harris 1999:27–31). His discovery of osmosis and his studies on gas exchanges between organisms and their environments were relevant to all forms of life (Sachs 1890:508–514, Reed 1942:176, Carles 1954:163–174, Schiller and Schiller 1975:27–60, Morton

1981:390–392, Magnin-Gonze 2004:180–181). He synthesized almost three decades of research in his *Mémoires pour server a l'histoire anatomique et physiologique des végétaux et des animaux* (1837). His discussion of the similarity between plant and insect respiration is translated by Bodenheimer (1958:378–379).

Dutrochet fastened membranes to a perforated metal disc and attached a mercury monometer, creating the first osmometer, with which he measured osmotic pressure. He concluded that osmotic pressure increases with the density of the substance on the opposite side of the membrane from water, though he overlooked concentration of the substance as a cause. He decided that osmosis causes water uptake by roots and sap movement. He also studied the response of leaves of the sensitive plant *Mimosa pudica* to touch, and he used a thermo-electric apparatus to measure heat produced by growing shoots. He believed his findings undermined vitalism. He developed an experimental test that later became standard: growing *Elodea* in water with light but varying other environmental factors and assessing gas bubbles generated (Weeves 1949:9). Dutrochet's studies were the best physiological investigations between 1804 and 1840, but they were not studied as carefully as they deserved (Sachs 1890:514). Von Mohl further clarified osmosis in plants (Reed 1942:177–178).

In Prussia, agricultural chemists and related workers wanted to increase crop productivity. Berlin professor of chemistry Sigismund Friedrich Hermbstädt (1760–1833) published a three-volume chemistry textbook for his students in 1791, and then translated Lavoisier's *Traité élémentaire de chimie* (1789) into German (1792). He taught chemistry at the Berlin Medico-Surgical College and other institutions, but when Wilhelm Humboldt established the University of Berlin (now Humboldt University) in 1810, Hermbstädt became professor of technology, which included agricultural chemistry (Kerstein 1978). He had founded the *Archive der Agriculturchemie* in 1803 and published seven volumes before it ended in 1818. It published such illustrious authors as Saussure and Alexander von Humboldt. Hermbstädt also published in it his own experiments with different fertilizers for crops (Browne 1944:189–192). Studies on agricultural chemistry were also being conducted by agronomist Albrecht Daniel Thaer (1752–1828), who became head of the Institute for Agriculture in Möglin, wrote a four-volume treatise, *Grundsätze der rationellen Landwirtschaft* (Berlin, 1809–1812), and also taught at the University of Berlin, 1810–1818. Thaer's bibliography, which numbers each edition of his works and includes foreign translations, runs to 429 titles (Klemm and Meyer 1968:196–228). Agricultural chemist Heinrich Einhof (1778–1808) became professor of chemistry at Möglin, and he published analyses of plant products and humus in *Archiv der Agriculturchemie* (Browne 1944:178–183, Partington 1964:252). Thaer published Einhof's *Grundriss der Chemie für Landwirthe* (1808) soon after Einhof's death.

Gustav S. Schübler (1787–1834) was the founder of soil physics (Browne 1944:225–231). He studied science and medicine at the Universities of Tübingen and Vienna, practiced medicine in Stuttgart, then taught at a new agricultural institute near Bern, Switzerland, 1812–1817, before returning to teach at Tübingen. His *Grundsätze der Agricultur-chemie in näheraer Beziehung auf land- und forstwirthschaftliche Gewerbe* (Fundamentals of Agricultural Chemistry with special reference to practical farming and forestry, 1830) devoted 170 pages to soils and fertilizers and 67 pages to analysis of plant products. His classification of soils was partly physical and partly chemical: quartz sand, sandy limestone, earthy gypsum, powdered calcium carbonate, potter's clay, loamy clay, humus, loam of cultivated fields. He also divided soils into heavy and light soils.

Sachs discussed three works that synthesized plant physiology during the 1830s. The best was the first: *Physiologie végétale* (three volumes, over 1600 pages, 1832, German, 1833–1835) by Augustin-Pyramus de Candolle (1778–1841), who was discussed (regarding phytogeography) in Part 34 of this study (Egerton 2010:26–29). He was the most productive botanist of his time, and *Physiologie végétale* was the second part of his *Cours de botanique*. It proved to be more popular than the first part, *Organographie végétale* (two volumes, 888 pages, 1827), and the Royal Society of London awarded him a medal for it (Candolle 2004:440). Sachs (1890:515–516) grumbled that Candolle sometimes buried "points of fundamental importance under a huge mass of facts and statements from other writers" and he "went off on a tangent with his idea of the contractile spongiole at the root tip" (Reed:1942:176), which tip supposedly sucked up solutions. Candolle did understand that the escape of water vapor from plants was related to the number of stomata, and that sunlight accelerates transpiration (Reed 1942:189–190).

Browne (1944:213) complained that "De Candolle's support of the humus theory [1832, III:1242–1243], because of the high standing of his authority, greatly delayed the acceptance of the mineral theory of plant nutrition." Browne (1944:213–214) also thought that de Candolle (1832, I:248–249) probably exaggerated the importance of root excretions as inhibitors of other plants, now called amensalism, the importance of which was still unclear in 1987 (Barbouret al. 1987:119). Candolle accepted a limited vitalism (Drouin 1994*a*, *b*).

Karl S. Sprengel (1787–1859) was an agricultural chemist whose work Browne (1944:231–239) considered very important, but historians of botany have ignored him. He studied under the agronomist Thaer. Sprengel managed several large estates in Saxony and Silesia for seven years, then took an agricultural tour through Germany, The Netherlands, France, and Switzerland. He next studied and taught at Göttingen University until 1831, taught at Collegium Carolinum in Brunswick, 1831–1839, and finally opened an agricultural academy at Regenwald. He wrote numerous articles, which he later incorporated into five of his books, which Browne discussed. He was skeptical of the humus theory of plant enrichment and studied its content and possible role (Ihde 1964:421, Partington 1964:310, 312). He listed (1845) 15 elements that he considered essential for healthy plant growth—oxygen, carbon, hydrogen, nitrogen, sulfur, phosphorus, chlorine, potassium, sodium, calcium, magnesium, aluminum, silicon, iron, and manganese—and five elements that might be essential—fluorine, iodine, bromine, lithium, and copper. The first three came from the air, and the rest from the soil. He thought that either too little or too much of some elements could inhibit growth. He analyzed and compared productive and unproductive soils, an example of which Browne quoted (Browne 1944:234). He classified soils into 18 groups and fertilizers into 6 groups and provided analyses of 180 soils from different parts of the world. He emphasized that different plant species have different mineral and soil needs. Browne summarized Sprengel's significance (1944:237)

> *Sprengel was thus recognized long before Liebig as a proposer of the doctrine of mineral fertilizers. Liebig (1862), always jealous of his own claims for this discovery, disputed this recognition on the basis of the great inaccuracy of Sprengel's analyses and also because he failed to distinguish between essential and unessential ash constituents. While this does not affect the priority of Sprengel's announcement, Liebig was perfectly correct in the main facts of his criticism.*

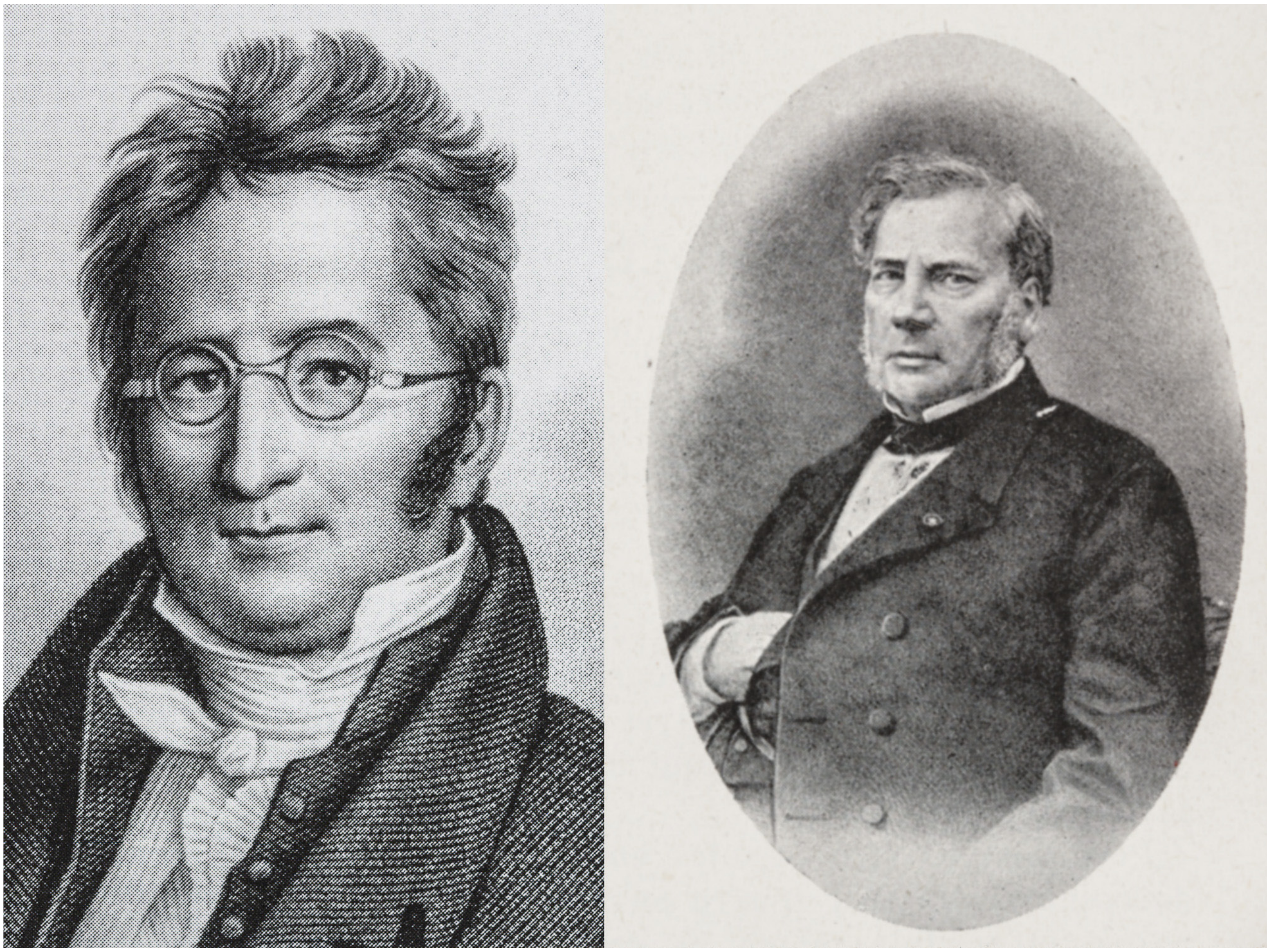

Fig. 8. (a) August Pyramus de Candolle. Trembley 1987:388. (b) Jean-Baptiste Boussingault. Carles 1954:154.

Browne added that Liebig's analyses were not flawless either.

The founding of agricultural experiment stations was an important addition to teaching agricultural sciences. Bossingault developed the first one in France, Lawes the second one in England, and others followed in Germany and the United States (Rossiter 1975, Finlay 1998).

Jean-Baptiste Boussingault (1802–1887) was a Parisian who had a rudimentary early education, but his mother gave him the money to buy Louis Thenard's *Traité de chimie* (four volumes, 1813–1816), and he taught himself chemistry. He attended public lectures at the Collège de France and then studied at a mining school (as Humboldt had). He spent the years 1821–1832 in geological, mineralogical, and meteorological researches in the Andes (Aulie 1970*a*, *b*, McCosh 1984). He published 25 scientific papers while in South America, and afterwards published 20 more articles on South America. His posthumous *Mémoires* (five volumes, 1892–1903) discussed his life only into 1832, perhaps inspired by his patron and friend Humboldt's *Personal Narrative*. Boussingault, like Saussure, brought to physiology from the physical sciences a sophistication in experimentation that runs through his work (Ihde 1964:422–423, Partington 1964:340–341). After returning to France, he married on 7 January 1835, and then taught chemistry at Lyon for half a year. His wife and her brother had inherited an estate at Bechelbronn in Alsace, and he became fascinated by the challenge of applying science to agricultural improvements (Browne 1944:239–252). German plant physiologist Sachs (1890:449) claimed that Boussingault "pursued the path of pure induction as contrasted with Liebig's deductive mode of proceeding, [and] gradually improved the method of experimenting on vegetation," and French plant physiologist Carles (1954:155) judged Boussingault to be the greatest agronomist of the 1800s. A prominent English historian of agriculture (Russell 1937:13) agreed: "to Boussingault belongs the honor of having introduced the method by which the new agricultural science was to be developed," and their judgment is echoed by McCosh (1984:xiii).

Theophrastos (*c.* 371–*c.* 287 B.C.) had reported that legumes, excepting chickpea, reinvigorated soil (Theophrastos 1916, II: Book 8, section 7, par. 2, pages 183–185; Theophrastos 1976–1990, II, Book 4, section 8, par. 2, page 273) and Pliny (AD 23–79) had reported that plowing under lupines enriches the soil (Plinius Secundus 1950, Book 17, ch. 6, pages 38–39). The Belgian practice of crop rotation was learned by Englishman Sir Richard Weston in 1644 and published in his *Discours of Husbandrie* (1650), but no one before Boussingault studied the practice scientifically (Russell 1966:37–38). He planned a series of crop rotations and studied this problem, 1836–1848, with special focus on where plants get nitrogen, in what form, and how it is assimilated (Aulie 1970*b*:422–445, McCosh 1984:68). He also compared the time taken by crops to mature at Bogata and Bechelbronn, measuring days between germination and maturation and also mean temperature. The several aspects of physiology, soils, and fertilizers that he studied are seen in his *Économie rurale considérée dans ses rapports avec la chimie, la physique et la météorologie* (two volumes, 1843–1844, second edition, 1851, German 1844, second edition, 1851, English 1845, Italian 1850). He was never satisfied with his understanding of the uptake and use of nitrogen by plants. Boussingault experimented on this by growing clover, peas, wheat, and oats in unfertilized soil and found that the clover and peas gained nitrogen, but the wheat and oats did not (1843–1844, I:82–83; cited from Browne 1944:244).

The agricultural press flourished in the 1800s, in both Europe and the United States. *The Cultivator*, a monthly edited by Joseph Buell at Albany, New York, for the years 1838–1839 provides a sample for both Britain and America, since he quoted extensively from British periodicals. It included accounts of livestock as well as crops, but only the latter are discussed here. In March 1838 Buell began discussing what he called "The New Husbandry," by which he meant sustainable agriculture rather than using up the land and moving on. It involved manuring, draining, good tillage, alternating crops, root culture, and substituting fallow crops for naked fallow. He acknowledged that "Philosophers have speculated for ages, as to what constitutes the food of plants," but felt that every farmer knew that animal or plant manure "constitute the true food of farm crops." However, "Mineral, fossil, and earthy substances, may meliorate the soil, and increase its capacities for the healthy development and maturity of plants…"

Justus Liebig (1803–1870) was one of the foremost chemists during the 1800s (Partington 1964:294–

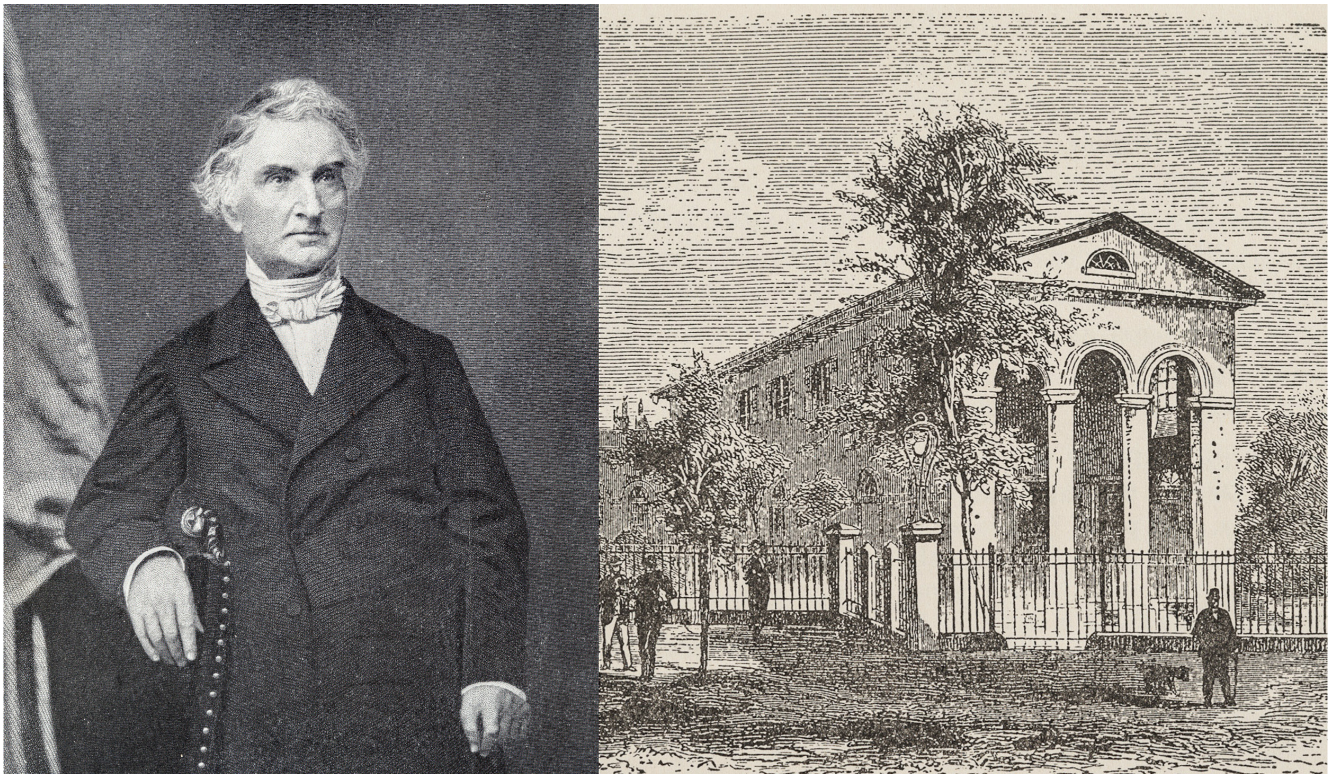

Fig. 9. (a) Justus Liebig. Moulton 1942: facing 1. (b) Liebig's laboratory building. Moulton 1942:6.

317, Holmes 1973, Brock 1997, Finlay 2000). He was the son of a chemist in Darmstadt who made drugs, dyes, and paints. He first studied chemistry in the universities of Bonn and Erlangen, but was dissatisfied with his training and obtained a grant to study in Paris. He received the instruction he sought from Joseph Louis Gay-Lussac.

Liebig was not only an outstanding researcher, publisher, and journal editor; he also revolutionized chemical education by emphasizing laboratory instruction and obtaining the first large-scale university laboratory (Browne 1942*a*:6, Ihde 1964:261–264). On the other hand, he was impulsive, polemical, and often had too many irons in the fire. These latter traits are evident in his work on agricultural chemistry (Browne 1942*a*, *b*, 1944:262–281). In Liebig's defense, there were certainly some bizarre ideas on plant physiology in the scientific literature. One was that plants use their vital force to create elements. The Berlin Academy of Science had awarded a prize in 1799 to J. C. Schrader for "demonstrating" this and had published his account in 1800. H. Braconnot had "confirmed" this finding in 1807. Schrader had published before Saussure's *Recherches* (1804) had appeared, but not so Braconnot. In 1838 a prize was offered at Göttingen for further proofs on this, and two researchers in Brunswick, A. F. W. Wiegmann and L. Polstorff, won the prize in 1840 for refuting the claim that plants create elements, though their study was not published until 1842, after Liebig's (Browne 1944:221-225).

In 1837 the British Association for the Advancement of Science invited Liebig to report at its 1840 meeting on the present state of organic chemistry. This invitation inspired him to write *Organic Chemistry in Its Applications to Agriculture and Physiology* (1840), published in German and translated into English by Liebig's former student, Lyon Playfair. It went through nine German editions and 19 editions in nine other languages (Paoloni 1968). He had conducted research on plant and animal substances, and ecologists remember him for his "law of the minimum," that every plant requires certain substances to grow, and if the minimal amount of any one of them is lacking, the plant cannot flourish (Liebig 1841, quoted in Odum and Odum 1959:88–89, Kormondy 1965:12–14). However, "Liebig's great prominence as an organic chemist did not qualify him in 1840 to become an authority on agricultural chemistry" (Browne 1942*a*:4). He was quick to criticize plant physiologists and agricultural chemists, but his own pronouncements were often vulnerable to counter-attacks. Alexander von Humboldt intervened to make peace between him and botanists Jacob Mathias Schleiden (1804–1881) and von Mohl (Werner 2001, Werner and Holmes 2002). Liebig mounted the most devastating attack yet on vitalism and the humus theory of plant nutrition (Waksman 1942, Brock 1997:147). Although he understood that atmospheric nitrogen was unavailable to plants, he found ammonia in rainwater and concluded that atmospheric ammonia via rain was a sufficient source for plants (Brock 1997:159), and he thought that the value of fertilizers was in their mineral, not nitrogen, content. However, Boussingault made exhaustive measurements of rainwater in 1853–1854, showing that the amount of ammonia in rainwater was very small compared to the needs of plants (Aulie 1970*b*:456–457).

Furthermore, John Bennet Lawes II (1814–1900) and Joseph Henry Gilbert (1817–1901), at the Rothamsted Experimental Station in England conducted a 12-year controversy with Liebig (despite Gilbert having received his Ph.D under Liebig) that led by 1855 to their showing that Liebig's mineral theory was wrong and that Boussingault's more balanced views on importance of minerals and nitrogen in fertilizer were correct (Aulie 1970*b*:454, 1974, Farrar 1973, Brock 1997:173, Finlay 2004*b*, Thompson 2004). Lawes inherited the Rothamsted estate at age eight. He attended Oxford University in 1832–1834 and left without a degree, but he studied chemistry there, and possibly botany, under Professor Charles Daubney (1795–1867), who taught both subjects (Thackray 1971, Desmond 1977:373–374, Goddard 2004, Oldroyd 2004). Lawes returned home and converted a fine bedroom into a chemistry laboratory (Russell 1942:164). His goal was to apply science to the improvement of agricultural productivity. He began with experiments similar to those that Daubney conducted at the Oxford Botanic Garden, in which some crops were grown continuously in the same plots and others were grown in crop rotation. In 1836–1838 Lawes used bone dust as a fertilizer for turnips, without effect, and in 1839–1840 he applied as fertilizer burnt bones and phosphate decomposed by sulfuric acid with very positive results. He then hired a chemist, Dobson, from University College, London, to assist in experiments. On 23 May 1842 Lawes patented his fertilizer made from bones, bone ash, and phosphorite, and he started a successful fertilizer business that provided funds to support his further researches (Russell 1942:168–169). In 1843 Dobson immigrated to Australia, and on 1 June Lawes hired Gilbert, who remained there for the rest of his life (Bottomley 1913, Farrar 1973, Desmond 1977:251, Finlay 2004*a*).

Another example of Liebig's reliance on chemistry rather than physiology is his claim that "any one of the alkaline bases may be submitted for another, the action of all being the same" (Leibig 1840:95, quoted from Browne 1944:268). Sprengel was delighted to set him right on this. Still other examples: Liebig thought decomposition of dead matter was a purely chemical process—slow combustion—

Fig. 10. Liebig's teaching laboratory and students. Published in 1842. Rossiter 1975:following 148.

and he concluded that the amount of ash obtained by incineration indicated the ingredients needed in commercial fertilizers. Because of such blunders, Browne (1944:269) concluded that Liebig's 1840 treatise was less finished than Boussingault's *Economie rurale* (1843–1844) was when it appeared. Boussingault was not just a chemist, like Liebig, but an agricultural chemist. Even so, Liebig did have a substantial impact, partly because of the challenge to others to either verify or refute some of his claims, but even more because his teachings and publications led to institutional growth of agricultural chemistry in both Germany (Schling-Brodersen 1992) and in the United States (Rossiter 1975). His influence on the growth of an agricultural research station in England at Rothamsted was less direct, but not negligible (Russell 1942, 1966:97–107). The first German edition of Liebig's *Organic Chemistry in Its Applications to Agriculture and Chemistry* (1840) had 195 pages; the seventh edition (1862), 1130 pages. Although its length had increased in earlier editions, the seventh edition was revised and expanded to improve Liebig's standing on this subject after much criticism (Finlay 1991, Brock 1997:177–179).

Julius Sachs (1832–1897), son of an impoverished draftsman-engraver in Breslau, Germany (Wroclaw, Poland), became an orphan in 1849. However, he had learned some of his father's skills and was hired by Czech medical biologist Jan Purkyne (1787–1869) to become his draftsman at the University of Prague. Sachs took courses at the University and in 1856 received his Ph. D. In 1857 he became lecturer in plant physiology and taught the first course on this subject in Germany. He taught in several other institutions until 1867, when he went to the University of Würzburg, where he remained (Pringsheim 1932, Bopp 1975, Magnin-Gonze 2004:194–195).

Fig. 11. Julius Sachs. Magnin-Gonze 2004:194.

Sachs acquired his scientific expertise not so much from formal education as from working with Purkyne (Nemec 1953). He did not form many close relationships, but he was an excellent lecturer and experimentalist who trained many of the leading plant physiologists of the next generation (Bower 1938:23, James 1969), including Francis Darwin, who became his father's assistant in botanical research (Ayres 2008).

Morton (1981:424) thought that Sachs launched the new physiology in 1859–1865, though Nemec (1953:214) noted that Sachs had already published 18 articles in 1853–1856, in a scientific journal, *Ziva*, which Purkyne edited, and that these articles became the nucleus for Sachs' *Lehrbuch der Botanik* (1868; fourth edition, 1874). Sachs became an evolutionist in 1854 (Nemec 1953:214). Sachs revived the technique of water culture in which he grew plants with the addition of mineral salts, which showed that plants needed neither humus nor silica (Weevers 1949). He showed that the essential mineral elements were potassium, calcium, magnesium, phosphorus (as phosphate), sulfur (as sulfate), and iron (in very small amounts), and that sodium, chlorine, and silicon, found in plant ash, were not essential. He further showed that plants can obtain nitrogen from both nitrates and ammonium, though nitrates were best. Sachs was the first to advance the understanding of carbon assimilation since Saussure. Sachs showed that starch is the first product of photosynthesis to be stored, from which other carbon compounds were formed, and that starch converts to sugar for transport to tissues beyond the leaf. He distinguished materials for growth (proteins, carbohydrates, fats) from reserve substances (starch, crystals, oil, etc.) and secreted substances (cellulose, lignin, wax, pigments, etc.), which Morton (1981:425–426) thought was "of the greatest value in developing a comprehensive view of plant metabolism…" Sachs also studied water and sap movement (Reed 1942:178–179), the effects of temperature and light on germination, growth, transpiration, chlorophyll formation, and the origin and growth of organs. From these studies came the concept of minimum, optimal, and maximum temperatures for growth and development. These findings were incorporated into his *Handbuch der Experimentalphysiologie der Pflanzen* (1865), which was Volume 4 of a *Handbuch der physiologischen Botanik*, which he published jointly with four other botanists. This collective work became the foundation for a flourishing science of plant physiology. Beginning about 1873, he studied geotropism, heliotropism, and hydrotropism. He felt condescending toward Darwin's contributions to plant physiology because of the simplicity of his methods (Morton 1981:427, 444, note 24). However, Sachs lacked

Darwin's caution and humility, which led Sachs to defend more erroneous hypotheses than Darwin ever did, including his attacks on natural selection as a mechanism of evolution (Bopp 1975:59). Nevertheless, modern plant physiology began with Sachs.

A famous French chemist, Louis Pasteur, also trained a plant physiologist, Jules Raulin (1836–1896), who made an important study of elements or compounds essential for growth (Carles 1954:161–162, portrait 154, 1975). Raulin studied under Pasteur at the École Normale Supérieure and later became his laboratory assistant. Raulin's "Études chimiques sur la vegetation" (1870, English extracts in Lechevalier and Solotorovsky 1965:347–358), which he researched for 10 years, was a doctoral dissertation. He chose common mold *Sterigmatocystis* (or *Aspergillus*) *niger* for his experimental subject. He found this species achieved best growth at 35°C at 70% humidity. The very specific compounds that he found best promoted growth are now combined into "Raulin's medium."

German physiologist Albert Bernhard Frank (1839–1900) possibly coined the term "Symbiotismus" (1877), and used it to describe the relationship between alga and fungus in lichens (Sapp 1994:6, Mitchell 2012), discovered symbiosis between fungi on tree roots, which he named "Mykorrhiza," and hornbeam (*Carpinus betulinus*) and beech (*Fagus sylvaticus*) trees (1885; discussed, with Frank's illustration reproduced, by Ainsworth 1976:100–101). Later (1887) he distinguished between ectotropic mycorrhiza of trees and endotropic mycorrhiza of Orchidaceae and Ericaceae. Still later, Frank (1894) explained the importance of mycorrhiza for forestry.

An understanding of nitrogen sources for plants remained incomplete. Marcello Malpighi (Egerton 2005:138–139) illustrated nodules on roots of legume *Vicia Faba* in *Anatome Plantarum* (Part 2, 1679) and stated they were not insect galls (Reed 1942:229). German agricultural chemists Hermann Hellriegel (1831–1895) and Hermann Wilfarth reported (1888) that (translated in Schadewaldt 1972:237)

> *leguminous plants, cooperating symbiotically with bacteria enclosed in nodules on their roots (*Rhizobium frank*), assimilate nitrogen from the air and convert it into a utilizable bound form.*

Wheat and oats lacked those nodules with bacteria and could not assimilate nitrogen from the air, though they could assimilate it from the soil, with crop rotation after a field had grown legumes. Hellriegel found that bacteria from clover could not produce nodules on lupine, and Nobbe and Hiltner (1898) concluded that each legume species has its own species of nodule-forming bacteria (Reed 1942:231). In 1929, Baldwin and Fred decided that six species of nitrogen-fixing bacteria exist, all in the genus *Rhizobium* (listed with hosts in Reed 1942:231). The nitrogen cycle of marine plants was as complex as on land, and attempts to apply land-plant explanations to marine plants had little success.

Plant physiology in the 1800s began (de Saussure) and ended with skillful experimentalists (Sachs and his students), but there were conflicting concepts and muddled ideas, including humus theory and vitalism, that slowed straightforward, steady progress. Besides those who investigated from the perspective of pure science, the needs of agriculture played an enormous role in furthering the study of plant growth. This involved both agricultural investigators and institutions. Liebig invaded the domains of plant physiology and agricultural chemistry with less initial success than he had expected, but his challenge was very stimulative of more and more precise research. The study of sexual reproduction in the nonflowering plants and fungi during the 1800s could be considered as part of plant physiology, but is not considered here. Morton (1981:394–404) provided a good summary of these important developments, though he omitted references.

Further reading

Historians of biology and of botany have not published much on the history of plant physiology in the 1880s. Howard S. Reed's *Short History of the Plant Sciences* (1942:176–265) has the most details known to me, written by a plant physiologist, as is Julius Sachs' *Geschichte der Botanik* (1875, English 1890), which remains useful. Alan Morton's *History of Botanical Science* (1981) is more concise than Reed's and more recent. Theodorus Weevers' *Fifty Years of Plant Physiology* (1949) ostensibly only covers the end of the 1800s, yet it has brief but helpful comments for the earlier 1800s. Useful on French contributions are Raoul Combes' *Histoire de la Biologie végétale en France* (1933) and J. Carles' article on the history of French plant physiology (Carles 1954). The important contributions made by agronomists have been documented more extensively. Charles Browne's *Source Book of Agricultural Chemistry* (1944:178–281) tells this story until the 1840s in some detail. Fussell's *Crop Nutrition* (1971) covers the same subject, being more up-to-date, but much briefer. John Russell's *History of Agricultural Science in Great Britain, 1620–1954* (1966) is a detailed survey of a leading country. Jean Boulaine's *Histoire de l'agronomie en France* (1992) includes the history of agricultural sciences, though it covers the 1800s in less than 100 pages. Simon Nightingale's historical bibliographical article, "Agriculture" (2000), provides recent references.

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