Chemical Research on Plant Growth

A translation of Théodore de Saussure's Recherches chimiques sur la Végétation

Translated, with an Introduction, by Jane F. Hill

Springer

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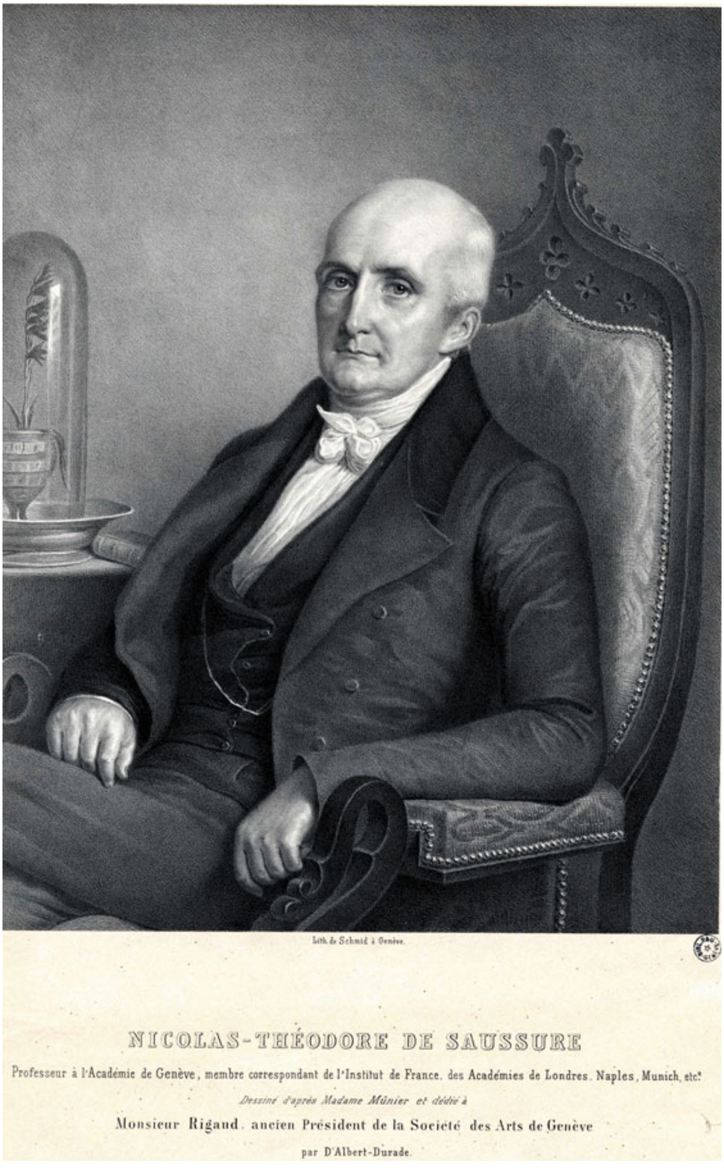

Portrait of Théodore de Saussure. On the table at his side is a "recipient", or receptacle, that encloses a plant; this was an experimental set-up that he used for studying gas exchange between plants and atmosphere of varying composition. (Image courtesy of Bibliothèque de Genève, Centre d'iconographie genevoise)

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Foreword

Théodore de Saussure was the last of the early pioneers of photosynthesis research. He filled in the gaps in the basic understanding of photosynthesis and presented the first concise summary of the field in his 1804 book *Recherches chimiques sur la Végétation,* which is translated into English here for the first time.

De Saussure's work was built on the achievements of his predecessors in plant-nutrition research. In the early 17th century, Jan van Helmont had shown that plants obtain very little of their dry matter from the soil, contrary to the prevailing view. Van Helmont concluded, instead, that plant dry matter is composed mostly of "transmuted" water rather than of soil. In the early 18th century, Stephen Hales demonstrated that "air" is fixed in plant matter, but, at the time he was working, knowledge of the atmosphere was so limited that he was unable to distinguish one kind of gas from another. In the early 1770s, Joseph Priestley discovered the fundamental fact that plants and animals exist in an interdependent relationship mediated by gases: Plants "purify" air that has been "vitiated", or corrupted, by the breathing of animals or burning of candles, and that animals, in turn, thrive in the restored air. In the last quarter of the 18th century, Antoine-Laurent Lavoisier and his colleagues made great strides in chemistry, which enabled rapid advances in knowledge about photosynthesis and plant nutrition during this period. The discovery that the atmosphere is not a homogeneous substance but instead is composed of a number of gases was of great importance for this unfolding understanding of plant nutrition. At about this same time, Jan Ingen-Housz established that light is necessary for plants to thrive and to produce oxygen, and Jean Senebier provided the insight that carbon dioxide is taken up in the production of oxygen by plants.

De Saussure showed that water is a component of plant dry matter (a fact that van Helmont had inferred but not conclusively demonstrated), thus enabling completion of the basic, overall equation of photosynthesis. De Saussure also showed that plant carbon comes mainly from atmospheric carbon dioxide rather than organic carbon in the soil. Further, he showed that plants obtain their minerals from the soil rather than from "transmutations" of other substances by a vital force within the plant, and that minerals are essential for plant growth.

Two German translations of de Saussure's book appeared during the 19th century. This first English translation now makes it readily accessible for English-speaking students, researchers, and other readers who are not familiar with French or German.

Jane F. Hill, known to me for several years as an accomplished historian of photosynthesis research, has written a beautiful introduction for this book (see Translator's Introduction) that places de Saussure's book in a historical context. This introduction, as well as additional supplementary material in the book, incorporates editorial and other suggestions that I made on draft versions of the manuscript. The introduction provides an account of the gradual replacement of primitive ideas about plant nutrition by the more accurate information supplied by the early pioneers, culminating in the work of the last of these early researchers, de Saussure. The fate of the book is also addressed, beginning with its positive initial reception, which was followed by neglect of its fundamental conclusions until their revival by Jean-Baptiste Boussingault and Justus von Liebig in the mid-19th century. The introduction describes how, despite some errors due to the relatively primitive state of knowledge and experimental methodology in de Saussure's day, the book is now widely recognized as a classic and a basic document in the development of the understanding of photosynthesis and plant nutrition. Finally, the life and scientific career of de Saussure are traced in detail.

In Chap. 10, Jane F. Hill presents succinct summaries of each of the nine chapters of de Saussure's book; in addition, she has provided at the end of the book three very important appendices, which provide conversions of units of measurements, a glossary of terms, and fleshed-out bibliography for most of the approximately 100 authors cited by de Saussure in his text.

I end this *Foreword* by making a reference to the Preface (pp. xxiii–xxvi), and three editorials (pp. 5–35) in a 2005 book *Discoveries in Photosynthesis*, edited by Govindjee, J. T. Beatty, H. Gest, and J. F. Allen, Springer, Dordrecht; they provide a link to the many discoveries and discoverers in photosynthesis research since de Saussure's pioneering work.

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Preface to the Original de Saussure Book

The object of the research that occupies me in this work is the influence of water, air, and humus on plant growth. I do not pretend, however, to fathom all aspects of this immense subject. I address the questions that can be decided by experiment and forgo those that can give rise only to conjectures. In natural history, the facts alone lead to the truth. In following this route, one is forced to acknowledge that the discovery of the means used by nature for the development of plants and for the composition of their substance must remain beyond our grasp for a long time. The solution of these questions often requires information that we do not have. It requires exact procedures for the analysis of plants and a full knowledge of their organization.

The functions of water and gases in the nutrition of plants, and the changes that plants produce in their atmosphere, are the subjects that I have investigated most deeply. The observations of Priestley, Senebier, and Ingen-Housz opened the road that I have traveled, but they did not attain the goal that I set myself. If imagination has sometimes filled the gaps that they left, it is by conjectures whose inadequacy has always been shown by their unintelligibility and inconsistency. For my eudiometric tests, I used either potassium sulfide [“*sulfide of potash*”] or phosphorus.[1] These procedures allowed me to achieve in my analyses an accuracy that the nitrous gas eudiometer used by my predecessors could not attain.

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[1] In this work, when I have given readings of the phosphorus eudiometer, they have always been cleared of the error that nitrogen gas can introduce through the expansion it undergoes in dissolving the phosphorus. Berthollet determined precisely the correction that this expansion requires. There is, however, a case in which this correction should be negligible: it is when the condensation of oxygen gas is observed at the precise moment at which it has reached its maximum, or when the phosphorus ceases to give off white vapors. In this operation, the nitrogen gas begins to expand only when it contains no more oxygen gas. In the first moments of the disappearance of the oxygen gas, the expansion of the nitrogen gas is undetectable. The expansion usually only reaches its extreme limit 24 hours after the complete absorption of the oxygen gas.
For these experiments, I used rapid combustion and the bent tube indicated by Giobert (*Analyse des Eaux de Vaudier*). I tilt the eudiometer when the phosphorus is melting, so that the phosphorus flows and spreads over the full length of the tube. With this procedure, the analysis of air is completed in less than half an hour, and at this time needs no correction.

My research leads me to conclude that water and air contribute more to the formation of the dry matter of plants growing in a fertile soil than does even the humus matter that they absorb in aqueous solution through their roots.

I also focus on a subject that has given rise only to hypotheses: the origin of the ash of plants. I investigate, through numerous experiments, the principles by which these ashes vary, in both amount and composition, depending on the season and the nature of the plants and their different parts. This work brought me several new observations, which show that all the questions that I have just stated can be resolved without attributing to vegetation creative forces and transmutations contrary to known observations.

In experiments on plant growth, so many diverse and unforeseen factors tend to influence the results that one should never fail to report all the accompanying circumstances. The details I provide on this subject will serve to determine the degree of confidence that can be placed in my research. They will prevent contradictions that arise from differences in method. They will explain errors that I cannot flatter myself to have avoided in a series of long, difficult experiments, whose results are perhaps applicable only to the species of plants that I examined. The path that I set upon is without doubt dry and fatiguing, but if one considers that the goal towards which it is directed is the improvement of agriculture, one will bear with its difficulties and excuse its shortcomings.

Acknowledgments

The translator gratefully acknowledges her deep indebtedness to a number of individuals who offered encouragement and support during the course of this project and who consented to read critically, review, or proofread the entire manuscript or parts of it. First, I want especially to thank Govindjee, Professor Emeritus, Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, IL, USA, without whose encouragement and help this book would not have been possible, and whose advice, editing, and insightful comments were invaluable.

I am also indebted to Mary Ellen Bowden and Robert Kenworthy, of the Chemical Heritage Foundation, Philadelphia, PA, USA, for their generous assistance with chemical terminology.

Others to whom I am deeply grateful include Marilyn Schiff for her unfailing encouragement and for advice on French usage; and Anita Baker-Blocker, Dennis G. Baker, and Barbara Wolanin for critical readings and comments on various parts of the manuscript.

I could never have completed this project without the tremendous encouragement and support of my husband, William A. Hill, whose tireless and careful proofreading of drafts was of immeasurable value and is deeply appreciated.

The staffs of various libraries were of great assistance in helping track down reference works, especially older works, of limited accessibility, cited by Théodore de Saussure in his book. I am particularly indebted to Eric Frazier, Reference Librarian, Rare Book and Special Collections Division, Library of Congress, Washington, D.C., USA, for generous help in finding many of these obscure references. Staffs at a number of other libraries also provided valuable assistance: National Library of Medicine, Bethesda, Maryland, USA; American University Library, Washington, D.C., USA; United States Department of Agriculture, National Agricultural Library, Beltsville, Maryland, USA; Public Library System of Montgomery County, Maryland, USA; Bibliothèque de Genève, Geneva, Switzerland; Bibliothèque nationale de France, Paris, France; and Biblioteca Accademia delle Scienze, Turin, Italy.

Translator's Introduction

Summary: In his 1804 book, *Recherches chimiques sur la Végétation*, Théodore de Saussure amalgamated his own research results with the findings of earlier investigators of photosynthesis to produce the first concise summation of the basic facts of plant nutrition. Important advances that he contributed to the overall knowledge in the field were that water is incorporated into the dry matter of plants; that plant carbon is derived from the carbon dioxide of the air, not from humus or soil; that the minerals in plants are absorbed from the soil, not created by a vital force; and that minerals are essential to plant growth.

In an introduction written by the translator, de Saussure's book is placed in historical context and details of his life are presented. In addition, the translator has provided a glossary of terms and a list of de Saussure's more than 100 citations, with fuller reference details than were given in the original book.

Key words: Théodore de Saussure; photosynthesis; plant nutrition; history of science; early pioneers of photosynthesis research; plant mineral nutrition; roles of carbon dioxide, water, and minerals in plant growth and development; chemical revolution; agricultural chemistry; 18^{th}- and 19^{th}-century agricultural science, agronomy, and soil science; "humus" theory of plant nutrition; historical importance of *Recherches chimiques sur la Végétation*; reference details for literature cited by de Saussure; chemical equation of photosynthesis

Between the early 17th and early 19th centuries, pioneering researchers unraveled the fundamentals of photosynthesis and plant nutrition. The last of these pioneers, plant physiologist Théodore de Saussure (1767–1845), of Geneva, Switzerland, consolidated his own findings with the contributions of earlier researchers to provide the first concise, unified concept of photosynthesis and the physiology of plant nutrition in his book, *Recherches chimiques sur la Végétation* (de Saussure 1804a). De Saussure's most important findings were that plants incorporate water into their dry substance; that they obtain their carbon from the atmosphere, not from humus in the soil, as many others thought; and that their minerals come from the soil, not from "transmutations" of other elements within the plants, as was widely believed at the time. He also showed that minerals are essential to growth, and he performed the most detailed analyses of the minerals in plant ash to that date. De Saussure's demonstration that plants incorporate water enabled completion of the basic, overall chemical equation of photosynthesis, which states that, from the simple, inorganic substances water and carbon dioxide, plants, using the energy of sunlight, produce fixed carbon, with the liberation of oxygen gas.

Recherches chimiques sur la Végétation met with initial acclaim and was soon translated into German (de Saussure 1805), but the book's fundamental conclusions were then ignored for the next several decades. In the mid-19th century, the book's worth was re-established, ensuring de Saussure an enduring reputation.

Throughout the 19th century, even during the decades of eclipse, chemists and plant scientists, including some of the most illustrious in the field, cited the book extensively for various purposes (e.g., Thaer 1809–1812; Davy 1813; Keith 1816; Liebig 1840; Schleiden 1842; Boussingault 1860–1891; von Sachs 1875; Pfeffer 1881; Aikman 1894). Late in that century, after the book's conclusions had once again been recognized, it was translated into German a second time (de Saussure 1890). During the 20th and early 21st centuries, English-language writers on photosynthesis and other aspects of plant science, agriculture, and the history of chemistry praised the book highly, and many of them quoted passages that they had translated into English (e.g., Harvey-Gibson 1919; Sherman 1933; Browne 1944; Reed 1949; Nash 1952; Gabriel and Fogel 1955; Partington 1962; Aulie 1970; Morton 1981; Arnon 1991; Magiels 2010). A facsimile edition of the original French text was published in 1957, and a second facsimile edition appeared in 2010. Despite the book's widely acknowledged importance, however, the full text has not been available in English until now.

Plant Nutrition Concepts Before the Pioneering Research on Photosynthesis[1]

Advances in the knowledge of both chemistry and plant nutrition were long hampered by vague, untested assumptions, such as the idea that one substance could be "transmuted" into another. This concept had been invoked since the alchemical Middle Ages, not only in connection with the attempt to change base metals into gold, but also as an all-purpose explanation for a wide range of natural phenomena. Scientific advances were also hindered by the doctrine, which had persisted from the time of Aristotle (384–322 B.C.), that all matter is composed of just four elements: earth, air, fire, and water. In addition, a vital force was thought to control processes within organisms, operating differently from the principles that govern nonliving matter.

With knowledge so limited, plants were understandably thought to obtain all their nutrients from the soil through their roots, which were seen as somewhat analogous to animal mouths. This view persisted into the late 18th century in many quarters, even as experimental evidence was accumulating showing that air and possibly water, in addition to soil, contributed to plant nutrition. English agricultural writer and farmer Jethro Tull (1674–1741), in his widely read book *The New Horse-Houghing*

[1] The term "photosynthesis" did not originate until the late 19th century (see Gest 2002).

Husbandry (1731 and many subsequent editions), popularized this view, with his advocacy of an agricultural system based on pulverizing the soil to such a fine powder that the particles could easily be taken in by plant roots.

In a detailed discussion of early ideas about plant nutrition, Browne (1944, p. 256) credits German physician and chemist Georg Ernst Stahl[2] (1660–1734) with making the first attempt at a scientific explanation of soil fertility, especially the benefits of organic manures. Stahl attributed soil fertility to an oily or fatty principle (a "phlogistic fatness"). Similarly, Külbel (1741) assumed that the main source of plant fertility was a fatty magma ("*magma unguinosum*") occurring in humus. Other promulgators of this concept of soil fertility included Home (1757), Wallerius (1761, per Browne 1944, p. 256), and Dundonald (1795).

The idea soon arose that humus had to be brought into solution by oxidation and fermentation before it could be used by plants (Browne 1944, p. 256), and out of this idea grew the "humus theory" of plant nutrition, which held that plants obtain their carbon from water-soluble organic matter in the soil (Waksman 1936; Russell 1976; Feller and Boulaine 1987; Boulaine 1994; van der Ploeg et al. 1999; Feller and Manlay 2001). Although some fertilizers, such as salts and lime, were acknowledged to promote plant growth, they were thought only to aid the decomposition of humus and the dissolution of organic matter in the soil water (van der Ploeg et al. 1999, p. 1057).

Often intertwined with the humus theory was the idea that a vital force in the plant created the minerals that had long been detected in plant ash. These minerals were thought to originate by transmutation of other constituents of plant matter (van der Ploeg et al. 1999, p. 1057), not from the external environment.

Contributions to Knowledge of Plant Nutrition and Physiology by the Photosynthesis Pioneers who Preceded Théodore de Saussure[3]

One hundred years before Külbel (1741) posited a fatty magma as the main source of plant fertility, Flemish physician Jan van Helmont[4] (1579–1644) took the first

[2] Stahl is best remembered for his advocacy of the phlogiston theory of chemistry, which held sway during the 18th century before it was upended by the chemical revolution late in that century.

[3] Publications focusing on the work of the early pioneers of research on photosynthesis and plant nutrition include Rabinowitch (1945, Vol. 1, Chap. 1); Nash (1952); Rabinowitch and Govindjee (1969, see Introduction); Hill (1970); Rabinowitch (1971); Egerton (2008); Magiels (2010); and Hill (2012). The early pioneers are treated within the larger context of the history of chemistry by Partington (1957, 1962) and Ihde (1964); within the context of agricultural chemistry by Browne (1944); and within the context of soil science by Russell (1976). Overviews of photosynthesis research that go beyond the era of the early pioneers, up to various later dates, include von Sachs (1875, 1890 English translation); Spoehr (1919); Sherman (1933); Morton (1981); Höxtermann (1992); Huzisige and Ke (1993); Govindjee and Gest (2002); Govindjee et al. (2003); Govindjee et al. (2004); Govindjee and Krogmann (2004); Morton (2008); and Nickelsen (2010).

[4] For more on van Helmont, see Redgrove and Redgrove (1922), Harvey (1929), Pagel (1972), and Newman and Principe (2002), among many other sources.

major step towards a broader, more accurate view of plant nutrition. He was the first to demonstrate convincingly that soil could not be the only source of plant nutrients. He planted a 5-pound willow tree in an earthen pot in which he had placed 200 pounds of oven-dried soil, and covered this vessel with a perforated lead shield to exclude foreign matter. He added only water to the pot for 5 years. After removing the tree from the soil and re-weighing it (without the leaves that had been shed during the 5-year period), and also weighing the re-dried soil, he found that the tree had gained about 164 pounds and the soil had lost only 2 ounces. From these results, van Helmont concluded that the solid substance of plants is formed not of soil, but instead entirely of water (one of the four Aristotelian elements) that has been transmuted into solid matter, or "earth" (another of the Aristotelian elements). Van Helmont's experiment was briefly reported in a posthumously published collection of his writings (van Helmont 1648). Although he was correct in his conclusion that water is an important component of plant dry matter, he did not prove a role for water (an achievement belonging to Théodore de Saussure, 150 years later), and he mistakenly ruled out soil and the atmosphere as other sources of plant nutrients. He did establish, though, how little of their solid matter plants derive from the soil (Hill 1970).

The first experimental evidence showing that soil does play a role in plant nutrition was provided at the end of the 17th century, by English naturalist and geologist John Woodward (1665–1728). Woodward (1699) showed that plants grown in water containing impurities or soil gained more weight than did plants grown in distilled water. He concluded that the impurities or soil were the essential nutrient and that water was merely a vehicle carrying them into the plant.

Also in the late 17th century came evidence that air might be involved in plant nutrition, when the first-ever comprehensive studies of plant anatomy were undertaken, by Malpighi (1675–1679) and Grew (1682). They found that leaves contain minute pores (stomata) in their surfaces and have internal structural features that appeared capable of functioning as air ducts. Then, in the early 18th century, the first functional evidence was found for the involvement of gases in plant life: Stephen Hales[5] (1677–1761), an English physiologist, chemist, and cleric, reported in his classic book *Vegetable Staticks* (1727) that "air" becomes "fixt" (solidified) in plant dry matter and thereby loses its "elastick" (gaseous) state. Because Hales accepted the prevailing doctrine that all matter is composed of the four Aristotelian elements, however, he did not distinguish one kind of gas from another.

During the late 18th century, the understanding of photosynthesis progressed rapidly, as the chemical revolution yielded both new chemical knowledge and improved experimental techniques that could be applied to the study of plant nutrition and physiology. In turn, research in plant nutrition contributed to knowledge of chemistry (see Partington 1962; Ihde 1964). Of the many European natural philosophers who contributed to the dramatic advances in chemistry during that period, the

[5] For biographies of Hales, see Clark-Kennedy (1929) and Allan and Schofield (1980).

French researchers and theorists, led by Antoine-Laurent Lavoisier[6] (1743–1794), stand out. Although Lavoisier did not advance the understanding of photosynthesis directly, his work helped make rapid progress in that field possible. For example, in 1770, Lavoisier took an early step towards overthrowing the doctrine of transmutation when he showed, through an experiment with water in a vessel, that the water was not transmuted into earth, or dry substance. He thereby cast doubt on van Helmont's conclusion that plant dry matter consists of transmuted water. Lavoisier also played a key role in establishing that there is a broad array of chemical elements, which are definable much more precisely than the four, all-encompassing, Aristotelian elements. To qualify as an element, a substance had to be shown to persist through complex chemical reactions and not be decomposed into more fundamental substances.

Another chemical advance important for photosynthesis research was the isolation of individual gases and the determination of their composition. This work was made possible by improved methods of catching gases, transferring them from vessel to vessel, and studying their properties (Rabinowitch 1971). Much of this work in "pneumatic" chemistry was done by British researchers during the third quarter of the 18th century (see Ihde 1964, Chap. 1). The work was greatly aided by the development of a piece of equipment, the pneumatic trough, which consisted of a receiver, or vessel, inverted in a bath of water or mercury to trap gases.[7]

The first gas to be isolated was carbon dioxide. It had originally been discovered by van Helmont (1648), who did not appreciate its significance. The gas was rediscovered in 1754 by Scottish physician Joseph Black (1728–1799), who called it "fixed air" (1756). Hydrogen was discovered by Henry Cavendish (1731–1810) in 1766, and nitrogen by three separate researchers in the early 1770s (see discussion by Partington 1962, p. 222, pp. 263–265).

English chemist and theologian Joseph Priestley[8] (1733–1804) broadened awareness that the atmosphere has a functional role in living organisms, with his startling discovery that plants "restore" air that has been "injured" by the burning of a candle or the breathing of an animal (1772, p. 168). Priestley, however, could not explain the relationship.

Priestley also developed a chemical technique, which he called the "nitrous air test" (but which actually used nitric oxide), to measure the degree of "purity" of a gas sample (1772, pp. 210–216).[9] The nitrous air test came to be widely used by

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[6] Biographies and other treatments of Lavoisier include McKie (1952); Guerlac (1961, 1975); Holmes (1985, 1998); Donovan (1993); Poirier (1996); and Bell (2005).

[7] For a history and description of the pneumatic trough, see Badash (1964) and Parascandola and Ihde (1969).

[8] For a comprehensive treatment of Priestley, see the two-volume biography by Schofield (1997, 2004).

[9] The nitrous air test was based on the reaction between oxygen and nitric oxide (NO), a colorless, insoluble gas. The solubility of the reaction product, nitrogen dioxide (NO_2), in water caused a decrease in the volume of the gas phase and thus provided a measure of the amount of oxygen in the original sample (see discussions by Conant 1950; Nash 1952; Partington 1962; Ihde 1964). De Saussure used the nitrous air test in some of his work with gases and plants, although by

18th-century chemists. Although Priestley did not realize it when he developed it, this was a test for oxygen, a gas that he himself was to discover only two years later, in a nonbiological context (see Priestley 1775). He named his new gas "dephlogisticated air" (as distinguished from "phlogisticated," or "bad," air). Lavoisier (1778) renamed the gas "*oxygine*"—i.e., oxygen.

The discovery of oxygen was the central event that enabled Lavoisier to overthrow the older, phlogiston theory of chemistry, which had dominated through most of the century (Conant 1950, p. 49), in favor of a new, more scientifically based, oxygen chemistry. The phlogiston theory, promulgated by Stahl (see Partington 1957, pp. 85–89), held that combustible materials contain an "inflammable principle," called "phlogiston," which is transferred to the atmosphere upon burning or, in the case of metals, upon calcination. Once the atmosphere had become "phlogisticated," or saturated with phlogiston, it could support no additional burning or calcination, nor could it support animal life, because respiration was presumed to saturate the air with phlogiston given off by slow burning within the animal body. In combustion and respiration, then, the role of phlogiston was essentially the converse of the role that oxygen was shown to play.[10] Armed with the new knowledge of oxygen, Lavoisier (1783) launched a vigorous attack on the phlogiston theory. He and his colleagues (de Morveau et al. 1787) revised and modernized chemical terminology, removing the phlogiston-associated language. Soon thereafter, Lavoisier set forth his new approach to chemistry in his pioneering book *Traité élémentaire de Chimie* (1789). Most of the chemical elements recognized in this book are still accepted today.

Late-18th-century chemical discoveries that were especially important for the understanding of plant and animal physiology included: the finding that fixed air (carbon dioxide) is composed of carbon and oxygen (Lavoisier 1781); that water, rather than being an element, is a compound of hydrogen and oxygen (see discussion by Partington 1962, p. 344 ff); and that fixed air is different from "mephitic" air (nitrogen) (see Partington 1962, p. 263). In physiology, animal respiration was demonstrated to be a process of oxidation that provides heat for the body (Lavoisier 1777; Lavoisier and de la Place 1780).[11]

Lavoisier developed the technique of analyzing organic substances by combustion (Holmes 1985, Chap. 9), and used it to analyze spirit of wine (alcohol), olive oil, and wax (1784). He noted (1789, 1790 English translation, p. 123) that the "true" constituent elements of plants are hydrogen, oxygen, and carbon.

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the mid-1780s, this technique of "eudiometry," or measurement of oxygen-gas content, had been largely abandoned as imprecise and unreliable (Golinski 1992, p. 93). In his research on plants, de Saussure preferred to use phosphorus or potassium sulfide in his eudiometric tests. For the history of the development of eudiometric methods, see Benedict (1912), Golinski (1992, pp. 117–128), and Magiels (2010, Chap. 4).

[10] See Conant (1950) and Nash (1952) for detailed discussion of the phlogiston theory and its upending by oxygen chemistry.

[11] For details about Lavoisier's findings in physiology, see Holmes (1985).

A major advance in the understanding of photosynthesis itself came in 1779, when, during a single summer of research, Dutch physician Jan Ingen-Housz (1730–1799) made the critical discovery that sunlight is essential for plants to thrive. Based on this pivotal finding, Ingen-Housz has been credited by some (e.g., Gest 1997; Magiels 2010) with the discovery of photosynthesis.[12] Ingen-Housz (1779) reported his results during the autumn immediately following his summer of work.

Ingen-Housz achieved his important insight about light partly because he used an innovative experimental set-up. Priestley's experiments were done on whole plants. Ingen-Housz, however, made use of a 1754 observation by naturalist Charles Bonnet (1720–1793) that bubbles form on leaves that are submerged in water. Bonnet had not recognized their significance but, with the benefit of the increase in knowledge of gases over the intervening years, Ingen-Housz was able to demonstrate that the bubbles consist of dephlogisticated air and that only illuminated leaves produce this gas. Ingen-Housz had no idea of the identity of the starting material for the production of dephlogisticated air, however, instead invoking a vague "transmutation," excited by light, within submerged leaves, and a different process—a withdrawal of phlogiston from the air—by plants in aerial environments.

Ingen-Housz also showed that the non-green parts of plants, and the green parts when not illuminated, produce fixed air. Thus he discovered respiration in plants, two years after Lavoisier (1777) had reported it in animals. Priestley, in contrast, with his use of whole plants, had difficulty obtaining clear results in his later experiments because his experimental material contained both non-green, carbon dioxide-producing tissues and green, oxygen-producing ones and because he did not understand the requirement for light in photosynthesis. Ingen-Housz noted that production of dephlogisticated air by plants during the day exceeded their production of fixed air by night, so that overall the improvement of the atmosphere during the day far outweighed its vitiation, or corruption, at night (1779, p. 47).

Swiss clergyman and naturalist Jean Senebier[13] (1742–1809) contributed the next major insight on photosynthesis. He repeated many of Ingen-Housz's experiments, with mostly similar results, and he did not always give Ingen-Housz due credit (Magiels 2010), but Senebier (1782) was the first to establish that fixed air is consumed in a plant's production of dephlogisticated air. Senebier (1782, 1783) also found that the amount of dephlogisticated air produced is roughly proportional to the amount of fixed air available to the plant. (This was a line of research that de Saussure was to expand upon and refine.) Further, Senebier (1782) pinpointed the green, fleshy parts of leaves (the parenchyma) as the sites where fixed air is transformed into dephlogisticated air.

[12] Rabinowitch and Govindjee (1969, p. 7) conclude that each of the early pioneers made an invaluable contribution to the understanding of photosynthesis and that "there is fame enough to share among them".

[13] Kottler (1973) provides a comprehensive historical description of the scientific contributions of Senebier.

In contrast to Ingen-Housz, Senebier considered the production of fixed air by plants to be an indication of stress or disease caused by the unnatural growing conditions in experimental situations, rather than a natural process carried out by all plants. This subject became a major area of contention between the two men.

During the final two decades of the 18th century, Ingen-Housz (1787, 1789, 1796) and Senebier (1783, 1788, 1791, 1792, 1800) revised their views, speculated, and quarreled about various aspects of plant metabolism.[14] The two men agreed that carbon has a nutritional role in plants: Senebier (1791, p. 164; and 1800, Vol. 3, p. 151) stated that carbon combines with plant constituents, and Ingen-Housz (1796, p. 4) concluded that plants derive some of their most essential substances—such as their acids, oils, and mucilages—from the two elements that compose carbon dioxide (or carbonic acid, as it was then called). They disagreed about the source of plant carbon, however, right to the end: Ingen-Housz (1796) attacked the humus theory, conjecturing that plants growing in the open air obtain almost all of their carbon from the atmosphere, whereas Senebier (1800, Vol. 3, p. 148 ff) clung to the idea that they obtain it through their roots, from carbon dioxide dissolved in the soil solution. The quantitative data necessary to settle the matter would be supplied by de Saussure.

Senebier, in his writings on fixed air, initiated an error of interpretation that was to be perpetuated by Ingen-Housz (1796), de Saussure, and many others, for some 150 years. This was the idea that the oxygen liberated in photosynthesis comes from carbon dioxide rather than from water. This view seemed logical based on the close equivalence between the volumes of carbon dioxide absorbed and oxygen released. The idea is often attributed to Ingen-Housz (1796)—by, for example, Arnon (1971, 1991); and Raven, Evert and Eichhorn (1999)—but, although Ingen-Housz briefly stated this view in 1796, he confusingly also mentioned water as a source of oxygen, and, more importantly, it was not Ingen-Housz, but Senebier, who earlier had done many, repetitious studies and analyses that suggested carbon dioxide as the precursor of the oxygen released. Senebier's very verbosity may have eclipsed his findings, and Ingen-Housz, with his concise summary of the field in 1796, was more easily read and comprehended (Hill 2012, p. 792). It is now known that water, not carbon dioxide, is the source of the oxygen gas liberated in green-plant photosynthesis.

At century's end, unresolved questions also remained about the source of plant nitrogen and hydrogen. Lavoisier (1784) had found that plant matter contained abundant hydrogen, and Berthollet (1785) had found nitrogen in both plants and animals, but from what source did plants obtain these two important nutrients?[15] Because the most logical source of plant hydrogen was water, there was conjecture (by, e.g., Berthollet 1786; Senebier 1792) that plants obtain it from that liquid. Senebier's opinion (1792, p. 208) was based on his demonstration that plants transpire much

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[14] See Nash (1952) for a detailed, comparative account of the ideas of Ingen-Housz and Senebier during this period.

[15] Adequate concentrations of the four major nutrients in dry plant tissue are now considered to be, by weight, 45 % carbon, 45 % oxygen, 6 % hydrogen, and 1.5 % nitrogen (Stout 1961, as cited by Raven et al. 1999, p. 728).

less water than they take in through their roots. The contribution of water to plant dry matter was to be established by de Saussure.

For plant nitrogen, the most logical source seemed to be the large reservoir in the atmosphere, which is approximately four-fifths nitrogen gas, by volume. Ingen-Housz (1796) believed in an atmospheric source, but Senebier (1800, Vol. 3, p. 159) thought that it came from the soil, along with the carbonic acid that he also believed was absorbed from there. Senebier failed to establish that soil was the source, however, and de Saussure, although speculating correctly against gaseous nitrogen as the source, did not settle the matter.

In addition, neither Ingen-Housz nor Senebier clarified the source of plant minerals. The idea that a vital force within plants formed these substances was still prevalent when these two researchers completed their work. Senebier (1791, p. 252) pondered the question of vital force versus environment, but did not provide an answer.

Although both Ingen-Housz and Senebier clung to the phlogiston concept until late in life, both of them eventually re-interpreted their findings, to a large extent, in terms of Lavoisier's chemical system. Senebier probably adopted the new system about 1789 (Smeaton 1978); Priestley never did.[16]

Of the later publications by Senebier and Ingen-Housz, it was Ingen-Housz (1796) that was the most succinct and that, according to Nash (1952, p. 105), provided "a fair approximation to the conceptual scheme that we now hold to be correct.... [A] view representing a closer approach to our present conceptual scheme was not proposed until 1804" (in de Saussure's book). Ingen-Housz (1796), in an appendix to an obscure British government publication, presents the first formulation of plant nutrition and the photosynthetic process in accordance with the new chemical theory (Rabinowitch 1945). Although not entirely consistent in his terminology, Ingen-Housz mostly used "carbonic acid" rather than "fixed air," and "oxygen" or "vital air" rather than "dephlogisticated air." He used "carbon," but also sometimes "coal," for the element. His scheme, however, included only brief mention of the idea of the decomposition of water, and he paid scant attention to a possible nutritional role for minerals or to the question of how plants obtained minerals.

Thus, at the dawn of the 19th century, with the contributions of Priestley, Ingen-Housz, and Senebier completed, quantitative data on photosynthesis and plant nutrition were still incomplete and critical questions remained.

De Saussure Provides Extensive Quantitative Data to Address the Important Questions

The position of the Swiss plant physiologist Théodore de Saussure in the history of the early research on photosynthesis has been compared to that of Jan van Helmont, as both were transitional figures: Van Helmont was an alchemist, but he addressed

[16] See Holmes (2000), however, for the view that Priestley's concept of phlogiston was only loosely allied with older phlogiston theories.

subjects that became major fields of study in the burst of chemical and plant physiological research of the late 18th century. De Saussure, in turn, completed the basic experimental work and provided a unified theoretical interpretation of the field; he also opened the way for further experiment and advances in knowledge (Nash 1952, p. 106).

Younger than his immediate predecessors, Théodore de Saussure did not have to labor under the weight of the phlogiston theory, because, by the time of his research, that theory had largely been replaced by Lavoisier's new chemistry. In accepting the new chemistry as a young man, Théodore was probably following the lead of his father, the noted scientist Horace-Bénédict de Saussure (1740–1799), who as early as 1788 adopted the new system and was probably the first scientist in Geneva to do so (Smeaton 1978).

With his more modern outlook, Théodore de Saussure recognized from the start that a facile recourse to the "transmutation" of one kind of substance into another as an explanation of natural phenomena was no longer tenable. Instead, he approached problem-solving analytically, designing experiments that were carefully targeted to answer important physiological questions of the day. He followed Lavoisier's lead and used a balance-sheet approach, carefully recording his quantitative results. He was thus able to build quantitatively on his predecessors' qualitative observations. Naturally a cautious man, not given to extravagant speculation as were his immediate predecessors in the field, he stuck to facts as revealed by experiments.

In many of his experiments, de Saussure used whole plants, which he was careful to maintain in a normal, healthy state. Unlike his predecessors, he did not simply observe whether the plants thrived or wilted, but measured their weight gain, and he did not merely determine whether the air "improved," but measured the amounts of its gaseous constituents. Also unlike his predecessors, he made liberal use of controls, comparable samples for determining quantities of substances in the initial plant material, and repetition of experiments with different plant species or plant organs. He made errors, some due to the primitive experimental techniques of his time, and others—of interpretation—due to the still-rudimentary state of knowledge. Nevertheless, he was able, through his thorough and wide-ranging investigations, to come close to identifying the sources of most of the major elements found in mature plants, and to determine the paths by which plants obtained them.

Some of the important questions de Saussure addressed—and the conclusions that he reached based on his experiments—were:

1. What is the quantitative relationship between the carbon dioxide taken in and the oxygen released by green plants in the light?
   De Saussure found that, under many conditions, there was a close equivalence between these quantities, but that in general somewhat more carbon dioxide was taken in than oxygen released.[17] This led him to conclude that plants retain, in their substance, a small amount of residual oxygen from the carbon dioxide. He

[17] The finding that the carbon dioxide taken up exceeded the oxygen released may be attributable to a slow reaction of oxygen with the chemicals in the particular eudiometric tests de Saussure used (Morton 1981, p. 360, note 74).

often found, erroneously, that plants released a small amount of nitrogen gas to the atmosphere.

De Saussure's findings supported Ingen-Housz's view that, in ordinary air and with exposure to light, the uptake of oxygen and emission of carbon dioxide are, in a healthy plant as a whole, invariably exceeded by the uptake of carbon dioxide and emission of oxygen. These two processes (photosynthesis and respiration), although directly opposed, seemed to be inextricably linked in plant metabolism.

2. Do plants obtain their carbon mainly from the soil or the atmosphere?

   Using experimental plants grown with their roots in distilled water and their shoots in the open air, de Saussure provided the first convincing demonstration that plants assimilate carbon mainly from atmospheric sources. This was a major blow to the humus theory. He dealt that theory a further blow by showing that carbon is proportionally more abundant in the humus than in the plants whose decomposition gave rise to the humus, due to the loss of hydrogen and oxygen, in the form of water, from the humus. If plants were taking a large amount of carbon from the soil, he reasoned, there should be a decrease, not an increase, in the carbon in the humus. Further, he found that, in humus extracts, which are the soluble part of the humus and the only part available to plants, there is too little solid substance to account for the dry weight gained by plants that are growing and developing in the humus. Further, he found that, in atmospheres to which he had added a limited amount of extra carbon dioxide, plants in the sun gained more in dry weight than they did in ordinary air.

3. Does some of the oxygen released by green plants in the light come from the decomposition of water?

   De Saussure evaluated other authors' claims that some of the oxygen released by plants comes from water rather than carbon dioxide. He generally found no evidence for this. In the case of a plant growing in a normal day/night cycle, in an oxygen-free atmosphere, the plant may release several times its own volume of oxygen gas, but de Saussure did not consider this an indication of the breakdown of water, with release of the water's oxygen. Instead, he reasoned that the plant, having had no contact with oxygen gas during its early stages of growth, formed carbon dioxide entirely from the carbon and oxygen of its own substance and then decomposed it. In contrast, this same plant, at least if it was not fleshy and was growing in an atmosphere that already contained oxygen, did not form carbon dioxide entirely from its own substance but instead combined its carbon with the oxygen in the atmosphere. The plant's decomposition of this carbon dioxide simply returned to the atmosphere the free oxygen that had been there at the start. Because he found no net increase in atmospheric oxygen content under these conditions, he concluded that plants did not add oxygen to the atmosphere by a direct decomposition of water.

4. Does atmospheric oxygen combine directly with plant constituents other than carbon?

   De Saussure found that atmospheric oxygen generally reacts only with the carbon of the plant, forming carbon dioxide gas. These findings countered some previous researchers' assertions, such as the claim that oxygen combines directly with substances in a germinating seed to produce sugar. He based this conclusion on his finding of a near-equivalence between the volumes of oxygen taken up and carbon dioxide released, both in germinating seeds and in more-developed plants. Leaves exposed to an alternating day/night regime, in a receptacle filled with ordinary air, consumed oxygen at night but restored it by an approximately equal volume of carbon dioxide during the day. He also found that atmospheric oxygen gas is not fixed in the tissues of dead or fermenting plants or plant substances (such as wine that is fermenting to vinegar), during the early stages, nor does it combine with plant hydrogen to form water. He concluded that the sole role of oxygen in these stages is to combine with plant carbon, yielding carbon dioxide gas.

5. Is the presence of oxygen gas necessary for plants to break down carbon dioxide and to grow?
   Plants, de Saussure found, need oxygen gas in their atmospheres in order to be able to break down carbon dioxide (i.e., to photosynthesize) and to grow. Plants can survive in environments lacking oxygen gas only if they are able to produce free oxygen through the decomposition of carbon dioxide that they form entirely from their own tissues. Even plants that can survive in an atmosphere of pure nitrogen gas, however, die there if carbon dioxide is added to that atmosphere in concentrations that would have allowed plant growth in an ordinary atmosphere. (He also determined that plants do not absorb nitrogen, hydrogen, or carbon monoxide gases.)
   Like Ingen-Housz, de Saussure concluded that the union of atmospheric oxygen with plant carbon (i.e., respiration) is a normal plant process and not, as Senebier had thought, an indication of unnatural growing conditions or of plant stress or disease. He considered respiration to perform the same function in plants as in animals, that is, to bring about a release of heat, through the combination of atmospheric oxygen with the carbon of the organism. He noted that plants' release of heat often went undetected. De Saussure was unable to develop as clear an interpretation of the metabolic role of oxygen in plants as he was of carbon dioxide, as noted by Nash (1952, p. 110).
6. Do plants fix the elemental components of water in their dry substance?
   In regard to a possible role for water in plant nutrition, de Saussure reasoned—quite plausibly, but, as it turned out, incorrectly—that, because the amount of oxygen the plant loses to the atmosphere is approximately equal to the amount of oxygen in the carbon dioxide that the plant takes in, the most likely source for most of the oxygen assimilated by plants is water. He also reasoned—correctly, in this case—that water is probably the source of the hydrogen in plant dry matter. He showed experimentally that growing plants do, indeed, assimilate water (although not as much as he thought, since they assimilate only the hydrogen, the oxygen coming from the carbon dioxide). He thus confirmed van Helmont's guess that water is an important component of plant dry matter. Many consider de Saussure's recognition of the role of water to be his single greatest contribution to the understanding of plant nutrition (Nash 1952, p. 113). He provided the

additional, important insight that the weights of hydrogen and oxygen in a plant cannot be increased substantially unless the weight of carbon is simultaneously increased. By linking the incorporation of carbon and water, he foreshadowed the discovery of plant carbohydrates, but in his day, of course, there was no knowledge of organic carbon compounds (Naef 1987, p. 336).

7. Do plants form and release water?
   De Saussure found that water was formed and released during some processes within living plants, such as in seed germination, and also in some processes occurring in nonliving plants and plant products. For example, when atmospheric oxygen combined with the carbon of humus or of wood extracts and formed carbon dioxide, water was also produced. This water, however, was generally composed from hydrogen and oxygen already contained within the dry substance of the plant or plant product, not from the combination of atmospheric oxygen gas directly with the hydrogen of the substance. He believed that the later stages of fermentation presented a possible exception to this pattern, in that atmospheric oxygen combined directly with plant hydrogen.
8. Are the minerals that are found in plant ash created by a vital force within the plant or do they come from the soil?
   De Saussure demonstrated that mineral substances disappeared from test solutions in which plants were immersed by their roots, and that these substances reappeared, in roughly the same proportions as they were absorbed, in the incineration products (ash) of the plants. He thereby showed that the minerals in plants do not owe their presence to a transmutation of carbon or other elements by a vital force. Further, he demonstrated that roots do not absorb all solutes in the same proportions, and that they absorb more of the water of solution than they do any of its solutes.
   De Saussure's analyses of plant ash were the most accurate and extensive performed up to that time, and his tabulations of the percentages of the various minerals in the ash were the first of their kind (Browne 1944, p. 200). His analyses revealed all of the minerals now known to be plant macronutrients, except sulfur. He found traces of other minerals, in amounts too small for him to analyze quantitatively.[18]
   Another of de Saussure's important findings was that the composition of plant ash reflects the mineral composition of the soil in which the plants have grown. He thereby showed that humus does, after all, play a role in plant life—not as a carbon source, but as a mineral source. In addition, he found that mineral concentrations in plants vary among different species, among different tissues, and with plant

[18] Nine essential plant macronutrients are now known: carbon, oxygen, hydrogen, nitrogen, potassium, calcium, magnesium, phosphorus, and sulfur. Adequate concentrations of the last four of these nutrients in plant dry tissue are 1 % or less. In addition, there are eight known essential plant micronutrients: chlorine, iron, boron, manganese, zinc, copper, nickel, and molybdenum (Stout 1961, as cited in Raven et al. 1999, p. 728).