Chapter 2
In Pursuit of a Pathway (1843–1918)

> If we try to nail down the present state of our scientific views on the assimilation of carbon in the chlorophyllous parts of plants, we are forced to confess that [...] in this fundamental question of plant physiology we are still at the stage of discussing the possible and the probable.[1]

The quote above succinctly characterises the state of photosynthesis research in the second half of the nineteenth century. The author of this quote openly acknowledged that so little was known about photosynthesis that the formulation of "hypotheses", which in this case were taken to be equivalent to "speculations", seemed to be the only, and, therefore, justified, resort. The body of knowledge at the time, concerning organic reactions in general and the processes in the living organism in particular, was scant and the methods available went hardly beyond input–output measurements without any means to access the stages in-between. This situation was not to change for decades to come. Even as late as 1925 the British plant physiologist Walter Stiles still maintained, in his monograph on carbon assimilation in plants, that "the nature of the intermediate substance or substances formed in photosynthesis is a subject on which [...] our real knowledge is practically negligible".[2]

Yet, photosynthesis still attracted the attention of a number of scientists, some of which concerned themselves with possible mechanisms and pathways of photosynthesis, as will be introduced in this chapter. The period analysed stretches from 1843, the year in which the German organic chemist Justus Liebig brought forward a rudimentary idea of the photosynthetic mechanism—the first attempt to account for photosynthesis in terms of a chemical pathway—until 1918, the date of publication of the voluminous monograph compiled by the German organic chemist Richard Willstätter together with his Swiss collaborator Arthur Stoll. Finding the biochemical pathway for the reduction of carbon dioxide to the stage of carbohydrates in plants was no trivial task given the situation described above. The main topic of this chapter is to elaborate the characteristic features of the models that chemists came up with and to spell out the chemists' strategies to deal with the enormous methodical

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[1] Reinke (1882, p. 289).

[2] Stiles (1925, p. 193).

difficulties. The highly critical attitude held by several plant physiologists in view of this methodology provides evidence for the fact that the chemists' strategies were deeply embedded in a specific research context and community that complied to conventions which were far from universally accepted.

2.1   The Nineteenth-Century Conception of Photosynthesis

"The leaves and other green parts of a plant absorb carbonic acid, and emit an equal volume of oxygen", the German organic chemist Justus Liebig, a towering figure at the time, maintained in 1842.[3] He thereby captured one of the central features of photosynthesis that had been generally known since the work of Joseph Priestley and others in the eighteenth century: the gas exchange that took place in the green parts of plants. Liebig went on to explain in some detail how the assimilated carbon then might be used in the plant to synthesise a wide range of compounds, primarily, he thought, carbohydrates. The latter was confirmed in the early 1860s by the German plant physiologist Julius Sachs, who identified starch—a polysaccharide—as the first distinctly recognisable product of photosynthesis.[4] It was also clear that sunlight was related to this process: in 1845, the German physician Julius R. Mayer described the plant as a reservoir of "solar force", which the plant absorbs and then transforms into a different type of force that Mayer called "chemical potential" ("*chemische Differenz*"). The latter would then be used, Mayer suggested, in the plant's growth and metabolism.[5] The resulting, widespread notion of photosynthesis—or "carbon assimilation", as it was usually referred to at the time—was extremely stable, up to the late 1920s.[6] A characteristic formulation is provided in the following lines, which were published in an encyclopedia for the German educated middle class of 1907:

> Assimilation in the botanical sense of the word is the formation of carbohydrates from carbonic acid and water while oxygen is released. This process is limited to the chlorophyllous assimilation system (assimilation tissue) and requires the involvement of sunlight.[7]

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[3] Liebig (1842, p. 24). In 1845, Liebig was ennobled and, henceforth, became known as Justus *von* Liebig. Further literature on Liebig will be cited below, when his specific photosynthesis model is being discussed.

[4] See Sachs (1862, 1864) for the original papers; the most informative biographical work on Sachs still is Pringsheim (1932).

[5] See Mayer (1845, particularly pp. 37–42). On Mayer's contribution to the discussion of physical forces ("*Kräfte*"), see Caneva (1993); Smith (2003).

[6] See, for example, the definition in the textbook by Heinrich Schroeder in 1928: "Carbonic acid assimilation (photoenergetic assimilation) [. . .] is the specific ability of the chlorophyllous plant to reductively synthesise organic compounds—in the first step carbohydrates—from carbonic acid (carbon dioxide and water) by using radiant energy, while, at the same time, releasing oxygen". Schroeder (1928, p. 653); paragraph 1a. All translations into English, if not otherwise declared, are by the author (K.N.). See also Gest (2002) for a brief history of the term "photosynthesis" and its definitions.
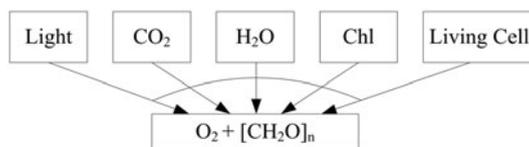
[7] Anonymous (1907a).

Fig. 2.1 The elementary one-step model of photosynthesis: the basic consensus on the causal factors of the overall process from the mid-nineteenth century until the beginning of the twentieth century.

Carbon dioxide (mostly taken to enter the reaction in the form of carbonic acid) and water, absorbed from the atmosphere and the soil, were taken as the starting materials of the process, which, in the green cells of plants, were then converted, under the influence of light, into carbohydrates and oxygen. From the work of Henri Dutrochet, Julius Sachs and others, chlorophyll pigments were known to play a crucial role in this process, although the precise character of this role was highly disputed.[8] Equally disputed was the reason for the fact that photosynthesis stopped as soon as the cell was damaged; the "living cell", or some specific aspect of it (usually suspected to be either some part of the protoplasm or a structural component), also seemed to be a necessary factor.

This (rather limited) body of knowledge on the mechanism of photosynthesis can be conceived of as a simplistic, one-step model, which is visualised in graph form in Fig. 2.1.[9] Molecular oxygen and carbohydrates, the general chemical formula of which is $[CH_2O]_n$, were taken to be the effects of a process in which carbon dioxide and water, light, chlorophyll ("Chl" in the figure) and the "living cell" acted as causally relevant factors—yet, how these factors interacted with each other was highly debated. Given the complexity of the process, everybody knew that, of course, a great many different steps were required to reach the final stage of photosynthesis, passing through a wide range of intermediate compounds. Photosynthesis researchers agreed neither on the order of the processes involved nor on the question as to which of these processes were light driven and which were not. Yet, everyone was aware that, in whatever way the more complex model would be drawn up, the basic causal links that are represented in the basic one-step model had to be accounted for some way or another. This made it the starting point for all investigations of the photosynthetic process in the period under study and, therefore, also for the subject of this chapter.

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[8] Dutrochet (1837); Sachs (1864).

[9] This notation is largely in line with the wide-spread conventions of representing causal graphs; see, e.g., Pearl (2000); Baumgartner and Graßhoff (2004). However, in contrast to the more rigid use of this notation, in this book no metaphysical commitment is implied concerning the factors included in these graphs. Specifically, while causal graphs usually name "events" as relata of the causal links, the adequacy of this interpretation for representing biochemical mechanisms, which rather outline the interaction of concrete entities, is doubtful.

2.2   Finding the Chemical Mechanism

The community that accepted this limited knowledge of photosynthesis as a common denominator is not easy to define. Already in the nineteenth century, photosynthesis research spread over a range of different disciplines, as was observed in one of the first monographs on the subject matter, published in 1925. The author, Walter Stiles, maintained that "the processes taking place in the green leaf, which involve the absorption of carbon dioxide from the air and the manufacture of carbohydrates from it and the water supplied by the soil [. . .] are among the very few problems of botany which have attracted the attention of workers in other fields".[10] The methods of research taken to be necessary to make any progress at all in elucidating photosynthesis included microscopical anatomy, experimental physiology as well as analytical and theoretical chemistry.[11] This range of techniques corresponded to the range of very different aspects of the process to be considered. The structural prerequisites of photosynthesis, for instance, were studied by plant anatomists and morphologists, who tried to explore the close relationship between the morphology of the leaf and its functional requirements;[12] others investigated the development, organisation and distribution of chloroplasts in the green organs of plants.[13] Plant physiologists concentrated on the influences of several macro-parameters on the process, such as light intensity, temperature and carbon dioxide concentration; while the effects that the incident illumination had on the pigments were mainly explored by physicists, who were interested in the mechanism of light absorption and the chemical efficiency of rays.[14] The question of the (bio)chemical mechanism of photosynthesis, finally, was predominantly, if not exclusively, the domain of chemists; and this is the aspect of photosynthesis research that I shall focus upon in the following sections.

It was primarily a number of German nineteenth-century chemists who felt attracted to the problem of the photosynthetic mechanism and who tried to elucidate as far as possible the course of events by which in the leaves of plants carbon dioxide (in its dissolved condition, that is, as carbonic acid) was worked with water into sugar.[15] From the point of view of chemistry, there were two key questions to be answered in this search for the pathway of photosynthesis: (1) How was carbon dioxide, a highly stable compound, reduced? This question was closely related to the release of oxygen, as reduction still was mostly conceived of as oxygen disposal. However, the second question immediately followed: (2) How were the one-carbon units that

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[10] Stiles (1925, p. 1).

[11] Cf. Reinke (1882, pp. 290–291).

[12] See, e.g., Haberlandt (1881, 1884).

[13] See, von Mohl (1837) for a seminal contribution along these lines.

[14] These early photochemical studies were greatly inspired by the new technique of photography; see, e.g., Boberlin (1993).

[15] On the development of physiological chemistry, or: chemical physiology, in Germany and elsewhere, see Höxtermann (2007b); Holmes (1985); Kohler (1982); Fruton (1972a). On the general situation of chemistry in Germany around 1900, see Johnson (1990).

(presumably) resulted from the carbon dioxide reduction joined together to form large molecules such as sugars?

Above all, it was the first question that puzzled the chemists, as carbon dioxide was one of the most chemically inert molecules known to exist: How could this molecule be made to undergo complex reactions without exposing it to extremely high temperatures or atmospheric pressure? In the following sections of this chapter, the main approaches developed by the nineteenth-century chemists involved in photosynthesis research will be described in terms of background, content, evidence and their relationship to each other. Although some of these approaches are well-known—notably Adolf von Baeyer's formaldehyde model—no in-depth comparative analysis has yet been undertaken, so that some detail is required in order to understand the dynamics of this line of research.[16]

2.2.1 *Justus Liebig and the Organic Acid Model*

It was the aforementioned Justus Liebig who first put forward a possible pathway for the process of photosynthesis.[17] Liebig started to think about this theme around 1840, that is, when he began to consider the impact of chemical knowledge to problems within the domain of life processes: an interest that was at least partly stimulated by the increasing demand at the time in Germany to improve the foundations of agriculture.[18] One of the first results of this line of thinking was the highly influential book *Chemistry in its Applications to Agriculture and Physiology* (1840), which was translated almost immediately in several languages and went through numerous editions.[19] Therein, Liebig emphatically propagated that it was high time to integrate chemical methods and concepts into the study of plants and their internal functioning, among others: his method of studying metabolic changes in terms of input–output balances.[20]

Liebig found the investigation of plants as it was practiced (or so he thought) by his colleagues in the botany departments deeply unsatisfying: "In botany the talent and labour of inquirers has been wholly spent in the examination of form and structure: chemistry and physics have not been allowed to sit in council upon the

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[16] See, e.g., Florkin (1977, pp. 147–151), for a discussion of Baeyer's formaldehyde hypothesis. The latter is also treated in Rabinowitch (1945, pp. 255–260), in which Baeyer's approach is compared with Liebig's point of view.

[17] For Liebig's biography, see Brock (1997).

[18] Cf. Allen (1975, pp. 154–157). On Liebig and his influence on agricultural science, see also Rossiter (1975).

[19] The original German version was published as Liebig (1840).

[20] On the integration of chemical and physical methods and concepts into botanical research during the nineteenth century see, e.g., the contributions to Hoppe (1997b) and Janko and Strbánová (1991).

explanation of the most simple processes"[21] Liebig complained. Yet, the botanists were unable to solve the central issues of inquiry, Liebig went on, because they lacked the skills to perform the necessary experiments, "it being an art which can be learned accurately only in the chemical laboratory".[22] Liebig's arrogance in this matter, in combination with his far-reaching ignorance of the actual state of plant physiology at the time (he seems to have taken his knowledge of the field from one single textbook), did not go unnoticed, as is documented in the reactions by, for example, the renowned plant physiologist Matthias J. Schleiden, who was never shy of polemics, and the equally distinguished Hugo von Mohl.[23] If Liebig chastised the plant physiologists for their lack of knowledge in chemistry, Hugo von Mohl wrote, Liebig's lack of knowledge of plants and their organisation surely would have to be considered equally disadvantageous. Mohl was ready to admit that the study of plants, insofar as it was of an experimental nature, was "more in the sphere of the chemist than of the botanist". However, Liebig's own suggestion to solve the pertinent problems presented "splendid evidence for the proposition that chemistry has not yet found out much more than nothing at all about the chemical processes in the interior of plants".[24]

In fact, Liebig's plea for experimental research in physiology and his pride on the chemists' achievements in this respect should not be overrated. Liebig was able to quantitatively determine what the plants took in and what they gave off; yet, like everybody else in the field, he lacked the techniques to investigate the processes that went on within the organism. Liebig nevertheless developed a proposal, which was first brought forward in a publication of 1843, while he repeated the principal idea in a number of other places, among those, several editions of his own chemistry textbook.[25] (A slightly simplified reconstruction of Liebig's model, in the form of a graph, is given in Fig. 2.2) This is how Liebig introduced his suggestion:

> If one considers that unripe fruit, for example, grapes, cannot be enjoyed due to their high acid content; that in sunlight these fruits behave in the same way as leaves, namely, that they are capable of absorbing carbonic acid and releasing oxygen; that at the same time as the acids decrease, the sugars increase: in view of these points, one cannot reject the idea that the carbon of the organic acids in unripe fruit becomes part of the sugars in ripe fruit; that, therefore, the acid is transformed into sugar, effected by the release of oxygen and the components' absorption of water.[26]

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[21] Cited: 2nd edition, Liebig (1842, pp. 37–38).

[22] Liebig (1842, pp. 39–40).

[23] See Werner and Holmes (2002) for a detailed analysis of this controversy; Werner (2001) describes how Alexander von Humboldt tried to resolve the disagreement.

[24] Cited Werner and Holmes (2002, pp. 436–438). Mohl's defence was published as von Mohl (1843).

[25] For the first version, see Liebig (1843); see also Florkin (1977, p. 147); Stiles (1925, p. 194); Schroeder (1917, pp. 2–3), and Rabinowitch (1945, p. 255).
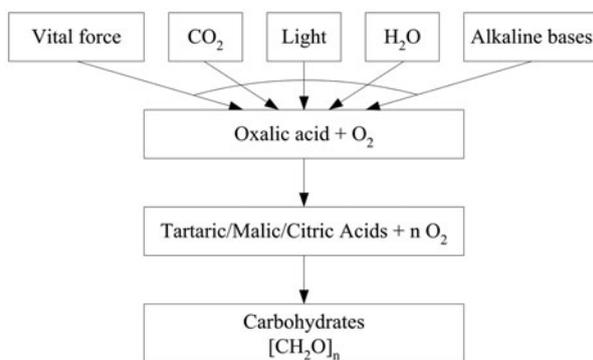
[26] Liebig (1843, pp. 61–62).

Fig. 2.2 The different processes involved in photosynthesis according to the organic acid hypothesis, which was originally proposed by Liebig (1843). The precise sequence of organic acids was unclear.

Starting from the observation that fruits gradually sweeten as they ripen, Liebig surmised that the tartaric, citric, malic, etc. acids in fruits might be the intermediates on the pathway from carbonic acid to sugar. And since all these acids were usually found in leaves in the form of their ions combined with the ions of alkalis, such as potassium or calcium, to a salt, Liebig concluded that these alkalis played a crucial role in the process too. (He took this to be the reason for the fact that plants would not grow without a minimal amount of these alkaline substances being available, either in the natural soil itself or added in the form of artificial fertilisers).

Liebig's account of the actual sequence of acids in the pathway of photosynthesis was rather vague, although he suggested that initially oxalic acid might be produced from carbonic acid by the release of oxygen—given the presence of an alkaline base, light and some hypothetical vital force. The latter was his interpretation of the unspecified "living cell" factor that was mentioned earlier, since the vital force was thought to fade away when the living organism was damaged or destroyed.[27] Liebig thought that, in later stages, oxalic acid might be reduced to tartaric, malic or citric acid, from which carbohydrates were then formed, thereby releasing additional oxygen. Thus, Liebig postulated a stepwise path from carbonic acid to carbohydrates via compounds that became increasingly poor in oxygen and rich in hydrogen. Some empirical support was taken from the fact that, in the presence of alkali and at high temperatures, the decomposition of oxalic, tartaric and citric acids to carbon dioxide had been observed in the test tube by the French chemist J. L. Gay-Lussac; and in view of this finding, Liebig considered it entirely feasible that the reverse reaction could take place in plant cells.[28] (Note that this assumption of reversibility was, at the time,

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[27] See Schroeder (1917, p. 2). Although, in many instances, Liebig rejected the practice of using a vital force as an explanatory factor, he still acknowledged that there were some phenomena that could not be explained without this force. On Liebig's position between reductionism and vitalism, see Lipman (1967) or Hall (1980). See also Caneva (1993) on this point.

[28] Liebig (1843, p. 63).

only supported by the observation that there were some inorganic reactions, notably in the context of metal combustion, that were found to work in both directions, while very little was known about the behaviour of organic compounds).

Liebig was also rather cautious when it came to describing how this sequence of reaction in plants might be brought about. He skipped the questions of possible sources of hydrogen or of the potential roles for chlorophyll and light in the process, and he did not even touch upon the problem of how carbohydrates might be formed from the organic acids. Liebig had never been afraid of formulating sweeping hypotheses on the course of metabolism without going into any much detail.[29] Yet despite the lack of detail, the principal idea of Liebig's model—that organic acids were the intermediates in the gradual reduction of carbon dioxide to carbohydrates— was still being debated in the 1920s, even though both the vital force and alkalis had by then been abandoned as relevant factors of the process. The main points in favour of Liebig's model were: *first*, that it was, in fact, possible to construct a stoichiometrically plausible pathway from carbon dioxide to carbohydrates through the stages of various organic acids; and, *second*, that this approach provided an explanation for the fact that organic acids were found in surprising abundance in all parts of the plant, while nobody had been able, up to then, to identify their physiological function.[30]

2.2.2 Adolf von Baeyer and the Formaldehyde Model

One could hardly say that Liebig's proposal aroused either passionate interest or decisive rejection among his contemporaries. In fact, it was only in 1870 that a serious alternative was being advanced by the German organic chemist Adolf von Baeyer. In essence, Baeyer's model comprised the assumption that the first reduction product of photosynthetic assimilation was formaldehyde: a small (and highly noxious) organic molecule, which resulted, Baeyer surmised, from the photolysis of carbon dioxide in the presence of water, light and chlorophyll, while at the same time oxygen was released. As we shall see in later chapters of this book, even far into the 1930s, parts of this hypothesis were still counted among the most promising candidates for a photosynthesis model.[31]

It is worth taking a quick look at Baeyer's general preoccupations at this time.[32] He is, of course, particularly renowned for his research on the plant dye indigo: Baeyer

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[29] See Werner (2001). Werner and Holmes (2002) provides an analysis of the dispute between Liebig and Matthias Schleiden and Hugo von Mohl on this point.

[30] Many of these acids are central intermediates of cellular respiration, namely, of the citric acid cycle, as is well-known today. As Liebig rejected the thought that there was respiration in plants, this explanation was not even conceptually available to him.

[31] See on Baeyer's model and its broad reception also Nickelsen and Graßhoff (2011).

[32] See Baeyer (1905) for his autobiography. Further information on his life and work is provided by Klemm (1953) and in Baeyer (1966).

successfully synthesised this important dye in the test tube in 1880, and by 1883 he had completely elucidated the molecule's structure. (Baeyer was awarded the 1905 Nobel Prize in Chemistry, in part because of these achievements.) However, around 1870, Baeyer was also interested in condensation reactions, and he achieved a major breakthrough in 1872 when he succeeded in carrying out the poly-condensation of phenol and formaldehyde. Formaldehyde had been discovered in 1855 by the Russian chemist Alexander M. Butlerov and had since become a product of central interest in the field of organic chemistry. Baeyer based his photosynthesis model on empirical evidence that Butlerov had presented in 1861: on heating trioxymethylene (a condensation product of formaldehyde which today is known as 1,3,5-trioxane) in an alkaline medium, a viscous fluid was produced, which seemed to have some of the properties of sugar.[33] Baeyer took this as the starting point for his proposal of how carbohydrates were synthesised in living plants. In a short paper devoted not even entirely to the problem of carbon assimilation Baeyer made the following argument:

> The general assumption in regard to the formation of sugar and related bodies in the plant is that, under the action of light, carbon dioxide is gradually reduced in the green parts [of a plant] and by subsequent synthesis is converted into sugar. [...] Butlerov's discovery provides the key [to the alternative assumption that sugar is formed directly from carbon dioxide], and it is indeed surprising that it has up to now been so little utilised by plant physiologists.
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> The similarity that exists between the blood pigment and the chlorophyll has often been referred to; it is also probable that chlorophyll as well as haemoglobin binds carbon monoxide. Now, when sunlight strikes the chlorophyll, which is surrounded by CO_2, the carbon dioxide appears to undergo the same dissociation as at higher temperatures: oxygen escapes and carbon monoxide remains bound to the chlorophyll. The simplest reduction of carbon monoxide is to the aldehyde of formic acid—it only needs to take up hydrogen, $CO + H_2 = COH_2$. Under the influence of the contents of the cells, as well as through the alkalines, this aldehyde is then converted into sugar. [...] Glycerol could, in addition, be formed by the condensation of three molecules and the subsequent reduction of the thus formed glyceric aldehyde.[34]

According to this proposal, the carbon reduction in photosynthesis consisted of several processes, which are reconstructed in Fig. 2.3. First, carbon dioxide binds to the chlorophyll, which is shown as [Chl–CO_2] in the figure; in this state and under the influence of light the carbon dioxide is reduced to carbon monoxide, upon which oxygen escapes. Baeyer justified the assumption of this step by referring to the structural similarity between chlorophyll and haemoglobin: since the latter was known to bind carbon dioxide, it was reasonable to assume, he thought, that chlorophyll could do so as well. The carbon monoxide is then reduced further to formaldehyde by the bonding of either molecular hydrogen or two atoms of hydrogen from other sources (which were not specified). Thus, in contrast to the conceptualisation of the

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[33] See Butlerov (1861). The episode is also discussed in Stiles (1925, p. 194); Florkin (1977, p. 147); and Rabinowitch (1945, p. 255).

[34] Quoted in Stiles (1925, p. 194); also in Florkin (1977, pp. 147–148). Translation provided by Jörgensen and Stiles (1917), with minor changes introduced by the author, K.N. For the German original, see Baeyer (1870, pp. 67–68).
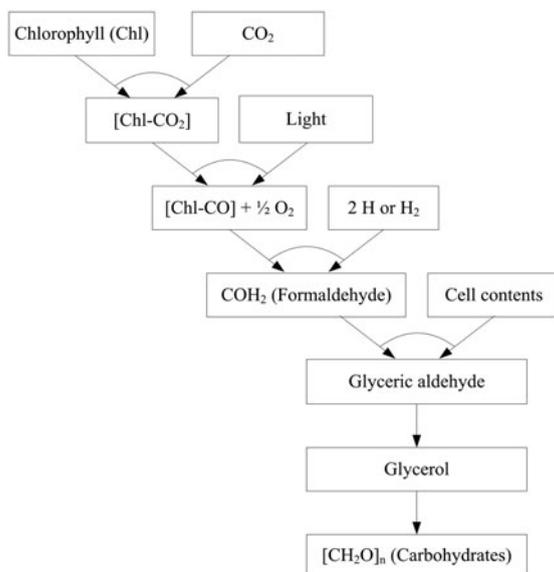
**Fig. 2.3** The processes involved in photosynthesis according to Baeyer's formaldehyde model (1870).

process in the organic acid hypothesis, the actual reduction of carbon dioxide to the oxidation state of sugars (which was instantiated in formaldehyde) was assumed by Baeyer to occur without the formation of any intermediates. In subsequent reactions, the formaldehyde was then thought to produce carbohydrates—a process that was presumably promoted somehow by the contents of the cell. Baeyer hypothesised, for example, that the first sugar product might still be associated with the components of the cell, and that it would only later be released as sucrose, starch or cellulose.[35] However, before Baeyer presented his own point of view, he dismissed the organic acid hypothesis:

> The intermediate steps [of the gradual reduction process] have been sought in the organic acids—formic acid, oxalic acid, tartaric acid, etc.—which can be regarded as the reduction products of carbon dioxide. According to this opinion, at those times when the green parts of the plant are most strongly subjected to the action of the sun's rays, a strong accumulation of acids should take place, and these should then gradually give way to sugar. As far as I know, this has never been observed, and when it is remembered that in the plant sugars and their anhydrides are found under all circumstances, whereas the presence of acids varies according to the type of plant, the particular part and its age, then the opinion already often put forward, that the sugar is formed directly from the carbon dioxide, increases in probability.[36]

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[35] Baeyer (1870, p. 68).

[36] Quoted in Stiles (1925, p. 194); also in Florkin (1977, pp. 147–148). Translation provided by Jörgensen and Stiles (1917). For the original German text, see Baeyer (1870, pp. 67–68).

Hence, Baeyer's main objection to the organic acid hypothesis was that one of its (conjectured) empirical consequences, namely the accumulation of intermediate products at times of strong photosynthetic action, had, as yet, not been observed. Furthermore, Baeyer pointed out that the acid content of a plant was strongly dependent on parameters that were probably not connected to photosynthesis—such as the species, the part of the plant, the time of year, and so on—which did not tie in with the assumption that these acids were the intermediates of the general photosynthesis pathway. At the same time, Baeyer stressed that he was able to propose a much easier and more direct pathway than Liebig had done: "Indeed, it would be difficult to attain the goal so easily through a gradual synthesis following the other theory!"[37] As a matter of fact, his proposal does seem pretty straightforward if one writes it down as a formula:

$$CO + 2\,H \longrightarrow COH_2 \; (= \text{formaldehyde})$$
$$n\,[COH_2] \longrightarrow [CH_2O]_n \; (= \text{carbohydrates})$$
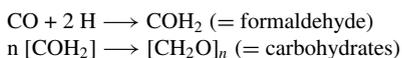
Put into prose: if carbon monoxide is formed, you only need to add two atoms of hydrogen to arrive at formaldehyde. The latter is already very close to the basic unit of carbohydrates (which is $[CH_2O]$), so that in order to form carbohydrates the formaldehyde only needs to be slightly rearranged and its units multiplied (in condensation reactions); and finally the resulting glyceric aldehyde would be transformed into a sugar—although Baeyer never explicitly discussed this additional complication. In fact, after this short contribution, barely fleshed out on a couple of pages, Baeyer never again returned to the subject matter.

2.2.3   Testing and Modification

While the reception of Liebig's model had been rather lukewarm, Baeyer's contribution undoubtedly sparked off a lively discussion. Over the decades between the two proposals the audience for the theme had dramatically multiplied: physiological (and agricultural) chemistry, or biochemistry as it was later called, had become a field of growing interest.[38] In 1861, the first independent institute of physiological chemistry had been founded in Tübingen, Germany, headed by Felix Hoppe-Seyler, who, in 1877, had started the first journal of the field, the *Zeitschrift für physiologische Chemie*. In the first issue Hoppe-Seyler confidently stated that "biochemistry [...] has grown to a science that has not only placed itself on a par with biophysics, but in activity and success competes with it for rank".[39] The importance of metabolic

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[37] Baeyer (1870, p. 68).

[38] On the uneasy relation between "pure" and "applied" chemistry (such as, e.g., agricultural and animal chemistry) in the decades around 1900, see Johnson (1990, pp. 25–27).

[39] Quoted in Fruton (1972a, p. 8). On the history of metabolism studies in the early twentieth century, see Holmes (1986). An exemplary reconstruction of the roots of (plant) biochemistry in botanical research is given in Höxtermann and Sucker (1989).

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Models of Biochemical Mechanisms, 1840-1960
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