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Can a History of Photosynthesis be Grand?

A Review of *Explaining Photosynthesis: Models of Biochemical Mechanisms, 1840–1960*, by Kärin Nickelsen, Springer, 2015

Andre M. Hahn§

Kärin Nickelsen's *Explaining Photosynthesis* makes an important contribution to the history of the plant sciences by offering an in-depth historical and philosophical exploration of photosynthesis research from its beginnings in the 1840s on into its mid-twentieth-century "golden age." This trajectory traces how early diverse and open research programs gradually developed into more stable consensuses around methods and results through various heuristic and interdisciplinary strategies. Early photosynthesis research, like that of Justus Liebig and Adolf von Baeyer, was marked by "research opportunism" and "building-block" strategies. These early multidisciplinary approaches, while maintained to some degree, gradually developed into more fully engaged interdisciplinary strategies over subsequent research generations. These later approaches were exemplified in the mid-twentieth century by the Berkeley Group's work on dark reactions and the international efforts researching light reactions. While Nickelsen's focus on philosophical and sociological aspects differs from other histories of photosynthesis that focus on discovery, they share a common narrative form which develops towards a particular end. Rather than the accumulation of facts characteristic of discovery narratives, Nickelsen's narrative is characterized by the increasing sophistication of methods and models used to reflect photosynthetic phenomena.

KEYWORDS

historical narratives ● heuristic strategies ● interdisciplinary ● research groups

Kärin Nickelsen's *Explaining Photosynthesis: Models of Biochemical Mechanisms, 1840–1960* gives a much needed historical and philosophical account of one of the major research projects in modern plant sciences. This look at the scientific models of photosynthesis expands upon Nickelsen's previous work with eighteenth century botanical illustration which she viewed as a type of modeling activity (Nickelsen, 2006). Weaving between active research and the discourses around it, Nickelsen boldly attempts to find some bridge between the history of science and the philosophy of science by identifying heuristic strategies based on her historical representation of photosynthesis research. While philosophically productive and rich in historical content, Nickelsen's text demonstrates, in opposition to its stated intention, that the historian's goal of avoiding grand narratives may be incompatible with drawing philosophical conclusions based on historical work.

A major value of *Explaining Photosynthesis* is the detailed account it gives of key actors who have worked on the subject. These details, which comprise most of the book, would be attractive to those doing historical research on related topics such as the plant sciences, biochemistry, and biophysics in the late-nineteenth and early-twentieth centuries. They would also be of interest to plant scientists themselves who are interested in exploring successful and unsuccessful research strategies around photosynthesis and biochemistry. Philosophers of science reading the book could focus mainly on the introductory and concluding material

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§ 322 Milam Hall, 2520 SW Campus Way, Corvallis, OR 97331 USA
✉ E-mail: hahna@oregonstate.edu

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along with some of the concluding remarks in the second, fifth, and sixth chapters, as these are the most philosophically dense.

Nickelsen breaks down photosynthesis research into six periods that reach from the 1840s into the 1960s. The first, and longest period, begins shortly before Robert Mayer's recognition that plants convert light into chemical energy in 1845 and ends in 1918 with several models explaining the chemical pathway of photosynthesis. During this period, the beginning and end points of photosynthesis were well established: carbon dioxide and water converted under the influence of light into carbohydrates and oxygen. A result of analogical reasoning, this broad outline of photosynthesis mirrored models of respiration where oxygen is converted into carbon dioxide. Beyond the broad acceptance of this general understanding, researchers were less in agreement over the specifics of interaction and the intermediate processes. By 1918, each model had critics who would classify it as only speculative.

These disagreements, according to Nickelsen, were partly due to the highly multidisciplinary techniques used by researchers that, because of a lack of interest in connecting their conclusions, often did not become interdisciplinary. This situation was grounded in a research culture emerging around photosynthesis, one characterized by "research opportunism." In this culture, the possibility of solving the problem of photosynthesis was an interesting "side issue" on which scientists like Justus Liebig (1803–1873) and Adolf von Baeyer (1835–1917) could bring to bear methodologies from their central research projects (48–53). Liebig applied his intentions to improve agriculture through chemical methods by proposing acids found in unripe fruits as intermediaries between the uptake of carbon dioxide and the production of carbohydrates. Based on his work with condensation reactions, Baeyer proposed formaldehyde as the first step in this process. Many from the emerging field of biochemistry found Baeyer's proposal more promising than Leibig's. Even without any confirmation, Baeyer's suggestion of formaldehyde held its place in the mechanism of photosynthesis into the 1930s.

At this point, Nickelsen begins to extract information for philosophical analysis. One way she accomplishes this is through constructing a "prototype model" in order to describe the synthesis of four major models that attempted reconciliations of Liebig and Baeyer—those of Emil Erlenmeyer (1877), Emil Baur (1913), Georg Bredig (1914), and Richard Willstätter and Arthur Stoll (1918). Alongside her prototype model, Nickelsen also describes a "building-block strategy" in which researchers isolated localized processes into subunits, and arranged, added, or removed them in various ways (44–46). Each of these structures for analysis works in an opposite direction, illustrating the complexity of treating a topic both historically and philosophically. Nickelsen's prototype model leads her to describe *similarity*; the original four models shared characteristics that may be useful for assessing early research in other areas. They included: simplicity; conservatism with respect to the starting and ending points of the process, combined with speculative intermediary steps; and incompleteness embodying a researcher's narrow, yet well developed, laboratory and theoretical perspective. In contrast, applying the lens of the building-block strategy leads her to describe *differences*, where multiple models were kept in circulation and particular parts of them were debated. To explain the advantages of this strategy, Nickelsen uses Philip Kitcher's notion of "cognitive diversity" maintained by "altruistically rational agents" who advocate for and draw upon "inferior" theories in the hope that those theories will contribute to their own work (47). This juxtaposition of similarity and difference helps to highlight the variety of early models of photosynthesis while also providing more generalizable theoretical insights.

Moving on from the more chaotic situation of early research on photosynthesis, Nickelsen next turns her focus to Otto Warburg's (1883–1970) work during the 1910s and 1920s. Warburg's main contribution was to transfer the methodologies of manometry (biochemistry) and bolometry (photophysics) to photosynthesis research in order to produce more accurate measurements. Warburg used manometric methods to measure gas exchange and bolometry to measure radiation intensities in his father's lab at the *Physikalisch-Technische-Reichsanstalt* in Berlin. His time visiting Joseph Barcroft's laboratory at Cambridge led him to develop the "Warburg apparatus" which more accurately measured gas exchange and, eventually, led to the use of *Chlorella* as a "model organism" in photosynthesis experiments. Warburg's techniques ended in the construction of a model consisting of a "primary photochemical product" produced by the actions of light reacting with carbon dioxide derivatives and resulting in the release of oxygen. Nickelsen describes Warburg's overall strategy as a type of building-block strategy, where, through research opportunism, he transferred subunits from research carried out under his father and on his own regarding cell respiration to his research on photosynthesis. Unlike the earlier actors brought up by Nickelsen, Warburg continued to work on photosynthesis for the remainder of his career.

Warburg's later work ultimately had a less savory impact on photosynthesis research as he debated his former student Robert Emerson (1903–1959) over the maximum yield of quanta per photosynthetic unit (further explained below). Warburg had made early measurements that placed the yield around 4–5 in 1927. These numbers were not challenged until 1949 when William Arnold (1904–2001) published his research from the mid-1930s that suggested 8 quanta as a minimum, well over Warburg's maximum. This discrepancy caught the attention of others who sought to evaluate the differing results in order to reach an accurate number. As part of this attempt to reach a conclusion, Emerson invited Warburg to his laboratory at the University of Illinois in Urbana to sort out the discrepancies. This attempt was unsuccessful and only hardened Warburg's attachment to his own results, which had meanwhile crept all the way down to one quantum—a result he tied to Albert Einstein's photochemical equivalence law. Warburg's coauthor, Dean Burk (1904–1988), also used his connections at *The New York Times* to publish popular articles in support of these lower minimums. Despite the "propaganda campaign," by 1955 most researchers agreed on 8–10 quanta minimum (180). Through it all, Warburg was able to maintain his reputation in Germany as he controlled most of the relevant information. But when Melvin Calvin won the 1961 Nobel Prize for chemistry, it damaged Warburg's reputation as he was suddenly viewed as responsible for isolating Germany from the leading research on photosynthesis.

For Nickelsen, this controversy concerned disagreements over "fundamental assumptions and theoretical priorities" rather than merely over facts or methods. The utilization of non-epistemic factors like authority and defamation by Warburg and his supporters show that "The technical issue of finding the maximum quantum yield of photosynthesis in order to elucidate the photosynthetic mechanism developed into a battle of the Good and the Evil" (197–198). While Nickelsen's classification scheme is helpful here, it is slightly off target, as what she describes appears to be more a dispute over methods. Resorting to non-epistemic factors is not necessarily a sign of epistemic strategies being exhausted, though it may be a sign that those involved are unprepared to go deeper into the epistemic roots of their assumptions. Additionally, one could imagine more fundamental assumptions, such as disciplinary or paradigmatic ones, than are contained in this very specialized debate within photosynthesis research.

During the 1930s, parallel to the dispute over maximum yield on quanta, a more collegial endeavor between research groups in Berlin, Cambridge, Pasadena, and Chicago began looking at the generally accepted model that combined Warburg's work with that of Willstätter and Stoll's. Nickelsen again finds a good explanatory fit here for research opportunism, as physiology, biochemistry, and microbiology converge through more conferences, interdisciplinary groups, and imported techniques from physics and chemistry. But research became more than opportunistic as interest in photosynthesis research grew more and more defined and the understanding of photosynthesis became more complex over this period.

A significant result of these more collaborative endeavors was the development of the concept of the photosynthetic unit. Coined by Hans Gaffron (1902–1979) and Kurt Wohl (1896–1962) in 1936 to explain Emerson and Arnold's unexpected oxygen to chlorophyll ratio, the concept of the unit led to modifications in Cornelius B. van Niel's (1897–1985) generalized equation for photosynthesis. The various models proposed gradually led researchers away from a straightforward mechanistic understanding of photosynthesis that had characterized all earlier models, toward embracing a more complex picture to account for findings which were becoming increasingly difficult to reconcile.

For the remainder of her treatment, Nickelsen focuses on research surrounding dark and light reactions in photosynthesis from the late 1930s into the early 1960s. Alternating between light and dark conditions over differing intervals had been a way for researchers to affect photosynthetic rates since Emerson and Arnold first recognized the effect in 1932. The Berkeley group, headed by Melvin Calvin (1911–1997), sought to understand the mechanism behind this phenomenon while drawing heavily on the use of the cyclotron and radiotracer methods available at the time only at the University of California, Berkeley. As the group grew and became formalized, a broad range of topics came under discussion by representatives of many disciplines. Overall, the group developed four different photosynthesis models between 1948 and 1954. By 1954, Calvin presented the group's "definitive" model which, under slight modification, is still recognized at present. One aspect, at the time, that still needed to be reconciled was labeling. When Andrew A. Benson (b. 1917) helped fill these labeling gaps in Calvin's findings, Calvin "lost" Benson's results as he reviewed the manuscript. Soon after, Calvin asked Benson to leave the laboratory. Nickelsen implies that these machinations helped Calvin to be the sole recipient of the 1961 Nobel prize for biochemistry.

Beyond the possibility of scandalous acts by Calvin, Nickelsen finds that the methods of the Berkeley Group were often described as "first rate," as others rarely had access to the resources available to them

(246). Their weekly meetings featuring Calvin's very pointed questions were interdisciplinary and collaborative; that is, until after the 1954 paper. According to Nickelsen, coming up with new models so quickly involved three main "heuristic moves": transferring knowledge from different contexts, assuming biochemical reactions can run in reverse, and recombining structural formula with pencil and paper (248). Still, the group conservatively formed new hypotheses, with "more radical hypotheses" coming only when required by empirical evidence (250). For Nickelsen, the Berkeley Group recreated the geographically distributed pluralism of earlier photosynthesis research in the late-nineteenth and early-twentieth centuries.

Alongside the Berkeley Group's research on dark reactions came work on how, if at all, light reactions provided the "driving force" for dark reactions (252). As with dark reactions, the assumption that photosynthesis was merely the reverse process of respiration informed initial explorations into the actual mechanism. Additionally, the incorporation of findings on the significance of ATP led to the understanding of photophosphorylation while findings on cytochromes as an indicator of redox helped explain how chloroplast respiration differed from other types of green tissue. By 1959 chloroplasts were seen as using light energy to form ATP and cytochromes were thought to be part of electron transport chains that formed ATP. These findings contributed to the creation of the Z-scheme model which several research teams from Europe and the United States arrived at nearly simultaneously, using various methodologies and perspectives. This broad geography contrasted with the localized discoveries at Berkeley. In the end, Nickelsen describes the 1950s as the "golden age" of photosynthesis research, a period more focused and better equipped, both technologically and theoretically, than the earlier periods of extreme research opportunism.

One way to situate Nickelsen's work within the relatively small historiography of photosynthesis is through a comparison with historical sections located in larger works produced by researchers active in the field. This ends up creating telling juxtapositions. Earlier histories, like that by chemist E. C. C. Baly, still saw a bright future in the role of formaldehyde in carbohydrate production (Baly, 1940). Nickelsen's own coverage of this topic includes the inevitable discarding of formaldehyde as empirically unverified in the late 1930s, right as Baly was writing. More recent histories have foregrounded actors who appear in Nickelsen's work only briefly, while ignoring or downplaying prominent actors in *Explaining Photosynthesis*. For example, D. O. Hall and K. K. Rao highlight Frederick F. Blackman's interpretation of light-saturation curves implying a two-step mechanism of "light" and "dark" reactions. Nickelsen attributes this interpretation of the two reactions to Warburg, the central actor in her third chapter, who is not even mentioned by Hall and Rao (Hall and Rao, 1994). Warburg also fails to appear on R. P. F. Gregory's table of significant contributors to photosynthesis research, yet Blackman receives the same credit as he did from Hall and Rao (Gregory, 1989). Also telling is that, while not mentioning Warburg, Hall and Rao, and Gregory each mention Emerson and Arnold's work on photosynthetic unit ratios. As explained above, Nickelsen spends a lot of time detailing the controversy between Warburg and Emerson over this matter. The absence of Warburg from some historical work by photosynthesis researchers shows how complete the discrediting of his reputation was in the end. When Warburg begins to reappear in the literature, his role remains small, as, for example, "Emerson's own Professor" who was a biochemist and not as someone necessarily working on photosynthesis (Govindjee, 2000). These often brief accounts by scientists provide some details on their views of photosynthesis which are lacking in more comprehensive botanical histories (Morton, 1981). However, the most striking difference between Nickelsen and these researchers is in narrative perspective. Nickelsen's treatment, while also more thorough and detailed, looks at modeling as a scientific, philosophical, and social activity. In contrast, the researchers focus on events of discovery for their scientific significance regarding further research. All, however, take on a form of that could easily fit into a grand narrative.

Nickelsen may disagree with this last assessment as she very clearly attempts to frame her work as a history that lacks a grand narrative. In her concluding remarks she states that "The aim of this book was not to construct another grand narrative of discovery. The aim was to bring exactly those intricate details to the fore that undermine the very idea of such a narrative, that is, present the highly diverse approaches to elucidating the mechanism of photosynthesis, only some of which were to last; and to try and identify some recurrent heuristic strategies that scientists utilized when they were confronted with the inherent complexity of their subject matter: plants in light and darkness" (316). This self-assessment evokes Jean-François Lyotard's postmodern "crisis of narratives" arising from the conflict between narrative and scientific forms of knowledge (Lyotard, 1984). Yet, this conflict does not imply a strict separation between the two areas, as Lyotard still finds grand narratives operating in the form of state-supported narratives tied to the funding of science. In this case, the "mythic" or "epic" narrative remains to help justify spending while also providing motivation for scientists and winning over non-scientists to the cause of that research. Additionally, Stephen

Prickett has pointed to Lyotard's notion of the end of grand narratives in the postmodern era as itself a grand narrative (Prickett, 2002). So, on Lyotard's and Prickett's assessment, it may be more difficult to escape grand narratives than merely stating it as an accomplished feat.

By examining mathematical theories, Lyotard links the decline of continuous differentiable functions as viable models of knowledge and prediction, to the "little" narratives of scientific discourse. Here, characteristics of incompleteness, paradox, and discontinuity replace large-scale continuity, both in the explanations of scientific topics and the evolution of science itself. Lyotard's insights align with Nickelsen's description of her work as focusing on "crucial episodes and highlights" rather than "striving for completeness" (1). By striving for historical *incompleteness*, Nickelsen is able to create a space better suited for her philosophical ends: identifying overarching heuristics and analyzing them into specific strategies involved in constructing models of photosynthetic mechanisms. A good illustration of this is when Nickelsen constructs the prototype model to represent the state of photosynthesis research at the end of 1918. It is these types of generalizations, however helpful they may be philosophically and despite claims that they undermine grand narratives, that are the raw material of grand narratives. They do this by giving the impression of more unity than concretely existed at the time and implying a shared history among subsequent researchers. Nickelsen's presentation of alternative interpretive frames, like the building-block strategy, helps balance out the generalizing effects of the prototype model. Yet, these interpretations still maintain a certain independence from the narrative itself.

If we are really interested in not constructing grand narratives (and I am not completely convinced we should be), it would be helpful to explore the implications of various methods of historical representation. Painting in very broad strokes, three main types are readily apparent. First, despite the convention of representing historical research in roughly chronological order, some history is done backwards. In this case, historical actors are presented as striving, consciously or not, for a particular goal. In *Explaining Photosynthesis*, it is the goal of explaining photosynthesis with ever greater sophistication. The only real outcome of this method is some type of **teleological** narrative (green in figure 1) where the end point serves as a constrictive attractor toward which all other materials under consideration tend in varying degrees. Though it may offend certain sensibilities, a more honest textual representation of these histories may be a reverse chronological order that traces the roots of a historical event. The opposite and far less common method is to choose a starting point and trace it forward in time. This results in **protological** histories (blue), often in the form of reception histories (e.g. Rupke, 2008). These seem to be the surest way of avoiding a teleological narrative. While there are still constraints, there is more incentive to expand subjects and flush out novel connections. Under this method, loose ends that can appear in teleological narratives are not so much anomalies as they are demonstrations of diverse paths inherent in an original event. A third way is expanding the immediate **context** of a subject (yellow). Here more immediate influences are of interest, and there is greater possibility of exploring interdisciplinary connections at a particular moment, which may become too complex with the other two methods.

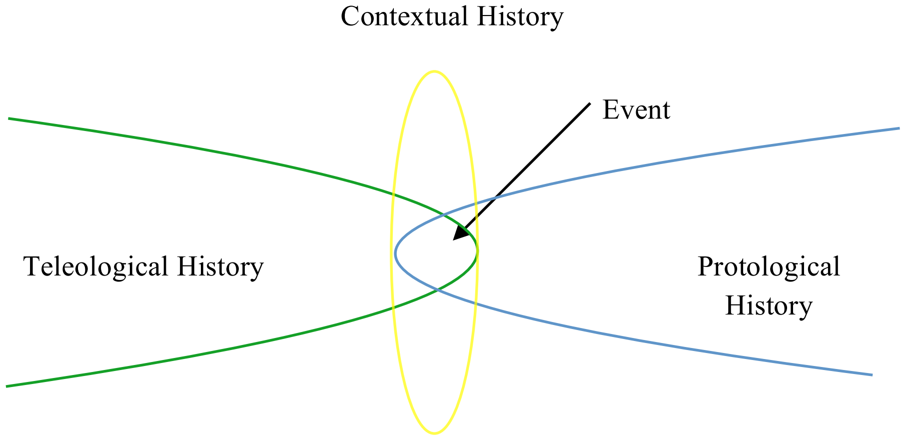

Figure 1

Nickelsen's representation combines a teleological narrative with a good amount of context and a few protological snippets. While contextual details may undermine particular teleological narratives, they often only point toward other potential narratives depending on one's perspective. The protological inclusion of "diverse approaches," as Nickelsen calls them, does not, in this case, undermine the larger narrative of photosynthesis research, but rather reinforces it by identifying successful and unsuccessful paths that ultimately approach the present consensus, or at least arrive near it. In Nickelsen's case, the narrative moves from early chaos toward more ordered and accurate understanding, and toward consensus about explaining photosynthesis.

So the question arises: should Nickelsen, and other historians, continue attempting to avoid grand narratives? *Explaining Photosynthesis* illustrates that this should not be the case. As a major contribution by a historian and philosopher, Nickelsen's text definitely breaks new ground, as she provides not only a history of photosynthesis research, but also a critical history that seeks to extract more generalizable philosophical and sociological lessons from the subject. Her narrative form fits well with this project, as it provides an end or goal, at least implicitly, in the gradually increasing sophistication of photosynthesis models. Without an end like this, any philosophical conclusions based on the history would be worth very little, since Nickelsen is looking for what strategies have worked toward that sophistication. The building-block strategy, research opportunism, and other strategies identified by Nickelsen appear as practical strategies for building such sophistication.

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