



Minireview

## The conference at Airlie House in 1963

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### Abstract

In many ways, the 1963 conference at Airlie House was an unusual event. The meeting convincingly demonstrated that photosynthetic research, previously reported mostly at conferences of botany and/or plant physiology, had become an independent and important field of biological research. New techniques had been developed and yielded exciting new results. Electron transport, photophosphorylation and their coupling were the main topics. Also, intermediates of electron transport, the enzymes catalyzing the reactions, and the structure of the photosynthetic apparatus, were discussed. The conference came at a time, when abundant new data had been accumulated seeking a platform. The editors (Bessel Kok and André Jagendorf) of the proceedings wrote in their introduction: 'Every so often someone manages to remove another stone from the wall through which we all want to see, and the crowds tend to flock around the new peep hole.' Beyond the scientific program, the organizers astounded the participants with an unusual social program.

**Abbreviations:** DCMU – 3-(3,4-dichlorophenyl) 1,1 dimethylurea; DCPIP – 2,6-dichlorophenol indophenol; MRF – methaemoglobin reducing factor; NADP – nicotinamide adenine dinucleotide phosphate (at the time known as TPN, triphosphopyridine nucleotide); PPNR – photosynthetic pyridine nucleotide reductase

### Introduction

In the 1950s, the results of photosynthesis research were mostly reported in journals and at conferences of botany, plant physiology or related meetings. The conferences at Gatlinburg (Tennessee) in 1952 and 1955 (Gaffron et al. 1957) and the 'Light and Life' – meeting at the Johns Hopkins University (McElroy and Glass 1961), are examples. Just prior to the Airlie meeting, there was an international conference in Gif-sur-Yvette, France (see de Kouchkovsky 2002).

Since then, technology had advanced rapidly, particularly in fast reaction spectroscopy and chromatography. So did progress in the field. The conference at Airlie House was a consequence of this development. Primary topics were the mechanism of electron transport and photophosphorylation, the coupling of photophosphorylation to electron transport, the involvement of co-factors and enzymes in electron transport and the structure of the photosynthetic apparatus. The mechanism of CO<sub>2</sub> reduction seemed to be established with the work of Melvin Calvin and Andrew Benson. Some progress was reported by James A. Bassham, N.E. Tolbert, Martin Gibbs, C.P. Whittingham et al., William L. Ogren and David Krogmann and by Shigetoh Miyachi (Kok and Jagendorf 1963).

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Figure 1. Aerial view of Airlie House, near Warrenton, Virginia.

### The conference

Airlie House is a stately mansion near Warrenton, Virginia, some 70 km south of Washington, DC (Figure 1). The conference took place from 14 to 18 October 1963. Chairman was Bessel Kok. He was director of Biology at the Research Institute for Advanced Studies (RIAS) in Baltimore, Maryland. Organizer of the meeting was André T. Jagendorf, then Associate Professor in the Department of Biology at the Johns Hopkins University (JHU). At the time, the author was research assistant of B. Kok at RIAS and a student of chemistry at JHU.

One hundred thirty scientists, mostly senior researchers, participated in the conference. Some of them were accompanied by post-doctoral fellows. Doyens of the meeting were James Franck and Eugene I. Rabinowitch. Franck was Nobel-Prize winner of Physics in 1925 together with Gustav Hertz. He later turned to the more theoretical aspects of photosynthesis (Franck and Rosenberg 1963; Jerome L. Rosenberg, this issue). Rabinowitch had assembled most of the knowledge on photosynthesis up to the late 1950s in three remarkable books (Rabinowitch 1945, 1951, 1956).

During the conference, all lectures were held in a single session and in the same room. As usual, the lecturers had an allotted time. This time was set on a clock placed near the rostrum. When the time of a speaker was up, the clock gave off a penetrating shrill sound, that mercilessly interrupted the speech.

The proceedings of the conference were published in a book entitled 'Photosynthetic Mechanisms of Green Plants.' The book contains 77 articles on 758 typeset pages (Kok and Jagendorf 1963).

### The scientific program

The scientific program encompassed most fields of photosynthetic research that were current at the time. New and exciting results had accumulated. The organizers wanted that these reached an appropriate audience. As they said in their foreword: 'It was the feeling of the Committee that progress in the field since the last meeting of this kind warranted a summing up and organization of our newer information.' Many of the results reported at Airlie had obviously been published before in the primary literature.

#### Electron transport

As early as 1943, Emerson and Lewis, working with intact cells of *Chlorella*, reported that the quantum yield of oxygen evolution decreased sharply, when the wavelength of the actinic light exceeded 680 nm ('red drop'). Experiments of Emerson et al. (1957) showed that the poor quantum yield in this region could be stimulated with additional light of shorter wavelengths ('Emerson enhancement'). In the same year, Blinks (1957) described 'chromatic transients.' Taken together, these observations suggested the involvement of two light reactions in photosynthetic electron transport (see a historical perspective by Myers 2002).

At the Airlie conference, red drop, Emerson enhancement and chromatic transients were discussed intensively (Bannister and Vrooman 1963; Blinks 1963; Fork 1963; French 1963; Govindjee 1963; Myers 1963; Whittingham and Bishop 1963). Most photosynthetic organisms, including isolated chloroplasts exhibited these phenomena. Only photosynthetic bacteria showed neither of these effects (Govindjee 1963). Thus, the idea that two photosystems, named PS I and PS II, were operating in photosynthetic electron transport of green plants appeared to be established.

The theory of two light reactions involved the notion that each of the photosystems possesses its own pigment system. The pigments acted rather like an optical lens: hundreds of chlorophyll molecules collected the incoming light and focussed it into a trap. The probability of a favorable reaction was then greatly enhanced. Thus, a trap was a point in electron transport where the electro-chemical energy of the light was transformed into chemical energy.

In 1956, Kok showed that light absorbed primarily by, what was later called, PS I caused the oxidation of a pigment with an absorption maximum at 703 nm. He

called it P 700. He showed in 1959 that light primarily absorbed by, what was later called, PS II reversed this effect. At that time, he related this observation to the light effect discovered by Emerson. Some time later, Horst Witt and co-workers (Döring et al. 1969) reported an absorption change at 680 nm, which they called Chl.<sub>a</sub><sub>H</sub>; it was shown to be the trap pf PS II.

Based on thermodynamic arguments, Hill and Bendall (1960) proposed an electron transport scheme, involving two cytochromes.

Also Duysens et al. (1961) suggested a rudimentary 'series' scheme involving a cytochrome. They observed antagonistic effects of light absorbed in pigment systems I and II on the redox state of cytochrome *f* and suggested a process which moved, by light, electrons (or hydrogens) in two steps from a high to a low redox potential. In this scheme, Photosystem I oxidized a cytochrome, and Photosystem II reduced it. In turn, Photosystem I reduced an hitherto unknown electron acceptor, X (Duysens 1989). Forti et al. (1963) discussed the role of cytochrome *f* from a biochemical standpoint.

At Airlie, several graphic representations of the interaction between the two photosystems were offered: Duysens (1963) and Arnon (1963) pictured the light reactions as a zig-zag. Accordingly, the absorption of light transported electrons (or hydrogens) along a redox scale from approx. +0.8 to -0.4 eV. Horst Witt and co-workers (Rumberg et al. 1963) depicted practically the same interactions with circles and arrows. Kok (1963) produced a filigrane curlicue.

Two partial reactions of electron flow were described. The basis of these postulates was that the herbicide DCMU (3-(3,4-dichlorophenyl)-1,1 dimethylurea) inhibited electron transport completely. The reduction of NADP (nicotinamide adenine dinucleotide phosphate; at the time known as TPN, triphosphopyridine nucleotide) could, however, be restored with the addition of reduced DCPIP (dichlorophenol indophenol)/ascorbate (Vernon and Zaugg 1960). This reaction produced no oxygen. Hoch and Martin (1963) investigated the wavelength dependence of this reaction and established that it was due to Photosystem I only. Kok (1963) showed that P 700 was the trap in this system.

A second variant was cyclic electron transport. After inhibition with DCMU, chloroplasts with a co-factor, such as PMS (phenazine methosulfate), yielded a light-dependent synthesis of ATP without the evolution of oxygen. Apparently, the electron, instead of being transferred to an external acceptor, could cycle

back to an 'electron-deficient chlorophyll molecule' (Arnon 1963).

The details of PS II remained obscure. Duysens (1963) suggested that measurements of chlorophyll fluorescence reflected the activity of the trap. The mechanism of oxygen evolution was unknown.

#### *Intermediates and enzymes*

One consequence of these developments in electron transport was to search for substances connecting the light reactions and for enzymes that catalyzed them. Several soluble factors had been previously isolated from plants or chloroplasts. According to the reactions they catalyzed, they were named TPN-reducing factor (see discussion in Arnon 1963), methaemoglobin reducing factor (Davenport et al. 1952), PPNR (photosynthetic pyridine nucleotide reductase; Keelin et al 1963), or 'red enzyme' (Gewitz and Völker 1962). At the Airlie house conference, it was well established that all these factors were actually ferredoxin. Ferredoxin was involved in the reduction of NADP, and possibly acted as a switch between linear and cyclic electron transport (Arnon 1963).

Trebst et al. (1963) investigated a large number of derivatives of plastoquinone, since plastoquinone seemed to play a major role in the electron transport of Photosystem II. The isolation of plastocyanin (Kato and Takamiya 1963) was a unique new discovery.

#### *Coupling photophosphorylation to electron transport*

There was little doubt at that time, that photophosphorylation was coupled to electron transport. The question was how electron transport provided the energy of some 10–12 kcal/mol necessary for the formation of ATP. One theory suggested the existence of a hypothetical substance,  $\sim X$ . In contrast to a covalent bond, the squiggle was supposed to be a high energy bond, generated by electron transport. Its energy was supposed to somehow be used for the binding of the third  $P_i$  to ADP. This postulate explained neither how this bond was formed, nor how the energy supposed in the squiggle was utilized in phosphorylation, that is, the theory explained practically nothing. Efforts to isolate  $\sim X$  consistently failed.

Packer (1963) related structural changes in the chloroplast membranes, measured by light scattering, to photophosphorylation. His interpretation assumed



Figure 2. 'The sermon on the mound.' *Left of the tree:* Horst Witt (standing); Achim Trebst, and Mary Belle Allen (sitting). *Middle:* Jack Myers, Bessel Kok and William Arnold. *Right:* James Franck relaxing on a bench. *Far right:* George Hoch and Dan Arnon discussing the Z-scheme at the blackboard.

that the structure of the membranes in the light, took on a high energy conformation. Upon relaxation, the energy could be used as a source for phosphorylation.

In 1961, Peter Mitchell proposed a general chemiosmotic theory for the coupling of electron transport and phosphorylation based on the movement of  $H^+$  across membranes. Originally, Mitchell's theory was applied to mitochondria. At Airlie House, Jagendorf and Hind (1963) showed first experimental data, that this theory could also be applied to isolated chloroplasts. They observed a light-dependent movement of  $H^+$  ions across the chloroplast membrane. At the time, however, they could not decide whether a high-energy compound, structural changes in the chloroplast membrane or a proton gradient were responsible for the coupling of photophosphorylation to electron transport. The further developments and the amazing outcome of these experiments were amply described by Jagendorf (1998). In 1978, Peter Mitchell received the Nobel prize for his work.

### Structure

Research at the time was also concerned with the structure of the photosynthetic apparatus. The investigations were done with different methods, on various algal species and with isolated chloroplasts. In 1961, Menke had suggested that chloroplasts possess a lamellar fine structure. He named these elements 'thylakoids.' At Airlie House, Menke (1963) present-

ed a first model of this structure; however, this model could reveal an insight only to the initiated (see Menke 1990 for his Personal perspective). Further studies on the structure of chloroplasts were reported by Olson (1963) and Wolken (1963).

Rabinowitch (1963) discussed variations of a bilayer model. While his ideas were interesting, they went more or less unnoticed as they were not supported by experimental data.

### Social events

The rather isolated location of Airlie House and the relatively small number of participants was congenial to individual meetings and personal discussions among the participants. These mainly took place in the extended gardens of the place, in the rooms of the participants or at the bar.

At lunch time, there was an unofficial meeting in the garden. There was a bit of a hill. Gibbs (1963) called these meetings 'The sermon on the mound' (Figure 2).

A notable event happened on the last evening. In a ceremony, Giorgio Forti was crowned 'King of the Chloroplast.' Sitting on a green 'throne' on the small stage above the dining room, he wore a green cloak, a golden (paper) crown and a regal ring. Bessel Kok delivered a humorous introductory speech. The mood of

the audience was exuberant. They repeatedly chanted 'Forti-Forto-Fortissimo.'

'King' Giorgio presented to several participants, let me call them, personally-directed artifacts related to their recent work. They had been prepared by Bessel Kok with the help of his workshop. To receive the decorations, those honored came to the 'throne,' kneeled down and kissed Giorgio's ring. Forti described his own feelings during the ceremony in his personal perspective (Forti 1999).

During the ceremony, Eugene Rabinowitch received a scroll printed on (bogus) papyrus, designating him as 'prophet of photosynthesis.' Horst Witt, who had presented his view on the interaction of two light reactions with interacting wheels and arrows, was presented with wheels and arrows made of plywood. Dan Arnon received a six foot tall green arrow and a ball. The ball was to symbolize his ideas on cyclic phosphorylation. Steve Brody was given a plastic 'dumbell.' He had suggested that P 700 was a dimer. Gibbs had reported an asymmetry in the  $^{14}\text{C}$  distribution pattern of the reductive pentose-P-cycle. He received an asymmetric doll, half man and half woman. Hans Gaffron received a crook and a miter, the regalia of bishops. At the time, his co-worker was Norman Bishop.

A decoration had also been prepared for James Franck, however, he did not want to participate in the spectacle and was spared.

Figures 3 through 7 show some of the scientists attending the conference. A group photograph of most of the participants appears in the front of this special issue.



Figure 3. Leaving the auditorium for lunch. *Left to right:* Jack Myers, Bessel Kok, Steve Brody and Alexander Müller.



Figure 4. Relaxing during the midday break. *From left to right:* Jack Myers, Bessel Kok, James Franck and the author, Hans Rurainski.



Figure 5. *Left to right:* Norman Bishop, James Franck and Berger Mayne.

## Epilogue

The success of the Airlie meeting convinced many participants that a conference of this kind should be repeated on a regular, but more international, basis. Alas, this idea has never been realized.

To be sure, photosynthesis remained an independent and important field of biological research. Also, the idea of internationalizing such a meeting has been realized. But the field expanded rapidly in both numbers of topics and, necessarily, participants. The first 'International Congress of Photosynthesis' was held in Freudenstadt, Germany, in 1968. Since then the number of participants and the range of topics has increased steadily (Govindjee et al. 2002).

The last meeting since the writing of this paper was held in Brisbane in 2001 with approximately 1500 scientists attending.



Figure 6. Participants relaxing. Center: Larry Blinks with tie and sweater. To his right is Alexander Müller. John Olson is sitting third from the right.



Figure 7. Left to right: Stacy French, Bessel Kok and David Fork.

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