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Minireview

Photosynthesis research in Greece: a historical snapshot (1960–2001)

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Abstract

The origin of photosynthesis research in Greece can be traced to the early 1960s, and the first dedicated laboratory was established by George Akoyunoglou in the Nuclear Reseach Center (now National Center for Scientific Research) Demokritos, in Athens. More photosynthesis groups subsequently emerged, in Demokritos and in the universities. Research in Greece benefited greatly from the links of Greek scientists with laboratories and personalities, primarily in the USA and western Europe. The local research output is a proportional part of global research and, more or less, in tune with the shifting priorities of the latter. The list of references provided includes only a sample of publications: it is not inclusive.

Abbreviations: Chl *a*, Chl *b* – chlorophyll *a*, chlorophyll *b*; LHC – light-harvesting complex; PS I, PS II – Photosystem I, Photosystem II

Introduction

Thinking about photosynthesis in Greece, one is tempted to begin by digging into the sayings of the 6th and 5th century BC physical philosophers of Ionia, or at least into what Aristotle (384–322 BC) said. Aristotle, who dismissed the dogmas of his predecessors, was convinced that plants feed on soil only (heterotrophy), that the mission of leaves is to attract moisture and to protect the fruit from the excessive heat of the sun, and that leaves are green because they are more moist than the bark.[1] He and his most prominent pupil and successor, Theophrastus of Eresos (372–287 BC), never thought of light as being indispensible for plant growth. Remarkably, however, Theophrastus, the founder of phytotherapy, thought of the foliage as a vital part of the plant.

The concept of plant photosynthesis is a modern one, and is founded on two pillars, the pillar of autotrophy (Joseph Pristley 1733–1804, Jean Senebier 1742–1809, and Nicolas Theodore de Saussure 1767–1845) and the pillar of phototrophy (Jan Ingenhousz 1730–1799, and Jean Senebier; see Rabinowitch 1945; Gest 1997, 2000). With the advances in physics, chemistry, biology and instrumentation after the 18th century, that concept acquired a more specific content. Today, oxygenic photosynthesis is decribed as a photon-driven process, which plants and cyanobacteria employ to *synthesize* complex carbohydrates from water, carbon dioxide, phosphates, and sometimes from simpler organic molecules. For the history of the definition of *photosynthesis*, see Gest (2002).

There is no record of true photosynthesis research prior to the 1960s in Greece. Elementary knowledge was taught in undergraduate botany, and chlorophylls *a* and *b* (Chl *a*, Chl *b*) were described in undergraduate organic chemistry. For example, when the author graduated from the Chemistry School of the Aristotle University of Thessaloniki, Greece in 1958, he knew the structural formulas of Chl *a* and Chl *b* and of their derivatives, the 1918 work of Richard M. Willstätter (Nobel Prize in Chemistry, 1915) and A. Stoll

on CO_2 uptake by Chl *a*, and its intriguing similarity to the CO_2 uptake by Grignard reagents. On the other hand, he had no idea whatsoever about the work of Robert Emerson, William A. Arnold and Louis N. M. Duysens, about photosystems, photosynthetic units, electron transport chain, and the synergistic and antagonistic effects of different wavelengths of light (for references see Clayton 2002; Myers 2002). He discovered all these unorthodox ideas after he had traveled to the United States in 1963 for graduate education.

I would say, therefore, that the first true photosynthesis research laboratory in Greece was the one that George Akoyunoglou started in 1963 (helped by a CF Kettering grant), when he and his wife Joan returned to Greece after graduate studies in the USA. George obtained a PhD with Melvin Calvin (Nobel Prize in Chemistry, 1961) at the University of California at Berkeley, and then worked for the National Aeronautics and Space Administration (NASA). Joan came back with degrees in Biochemistry from the same university. In Greece, they joined the scientific staff of then young Nuclear Research Center Demokritos. In 1969, I joined the Demokritos group, at George's invitation, having a PhD from the University of Illinois. My mentor in Urbana was Govindjee (see Papageorgiou and Govindjee 1967, 1968a, b, 1971 Papageorgiou 1968). I was his first PhD student; we were of the same age. I came to biophysics from physical chemistry, he from biology. Govindjee was the junior professor, and Eugene Rabinowitch the senior professor in the famous Photosynthesis Laboratory of Robert Emerson in Urbana, Illinois.

For several years, the group in the Department of Biology Demokritos was the only internationally salient photosynthesis research group of Greece. It projected itself through publications, active participation in conferences, research collaborations, and organization of international meetings. Certainly, the peak was the organization of 5th International Photosynthesis Congress in Halkidiki, Greece in 1980. George was the chief organizer, the spirit and the soul of the congress.

The distinction of Demokritos as being the only hub of photosynthesis research in Greece did not last long. In the 1970s and thereafter, more photosynthetic groups emerged in Demokritos and in the universities. As is the norm for nearly all scientific disciplines in Greece, the proliferation of photosynthesis research was not planned centrally. Simply, it reflected interests and aspirations of individual Greek scientists, and admittedly a willingness of the state to provide reasonable support. Undeniably, the local research output benefited greatly from the international links with personalities and laboratories, primarily in the USA and western Europe, but also in Japan, Eastern Europe and Israel.

Photosynthesis research units in Greece

Published proceedings of international congresses are excellent time snapshots of global research in photosynthesis, and of its agonists and protagonists. I used them to identify consistently active research groups in Greece. The criterion was applied, however, in awareness of two *caveats*. First, not everybody travels to the international congresses, especially when they are held overseas. For example, 1040 and 1017 papers were presented at Montpellier (1995) and Budapest (1998), but only 725 at Nagoya (1992) and 578 at Brisbane (2001). For a complete list of International Photosynthesis Congresses, see Govindjee et al. (2002). Second, not all congress papers are about photosynthesis. Many are about techniques, organisms, biotechnology, ecology, etc. Additionally, I sought help in journals that publish only on photosynthesis, such as *Photosynthetica* and *Photosynthesis Research*, or journals that publish a great deal on photosynthesis, such as *Biochimica Biophysica Acta – Bioenergetics*, *Plant Physiology* and *Biochemistry*. Consistently active photosynthesis research units in Greece are grouped below by institute, and are identified by the group leader.

National Center for Scientific Research Demokritos, Athens

George and Joan Akoyunoglou (a husband and wife team at the Institute of Biology): the first true photosynthesis laboratory in Greece, founded by the late George Akoyunoglou. Many scientists worked or began their careers in scientific research there, including: G.C. Papageorgiou, A. Melis, Y. Manetas, J. Isaakidou, E. Anni, S. Tsakiris, M. Tsimilli-Michael, G. Castorinis, K. Triantaphyllopoulos, A. Akoyunoglou, G. Tzinas, P. Antonopoulou, P. Tavladoraki, J. Georgakopoulos, R. Anastasiou, L. Tziveleka, and A. Prombona. Research themes include: RuBP (ribulose biphosphate) carboxylase-oxygenase; thylakoid biogenesis (Chl biosynthesis; photosynthetic unit and LHC (light-harvesting complex) formation and stabilization, particularly under intermittent illumination,

a method discovered in this laboratory); circadian rhythms of Chl biosynthesis; grana stacking and lateral LHC movements; and thylakoid protease against LHC II and core D1/D2 heterodimer. In 2001, Joan was succeeded by Anastasia Prombona, who continues research on the circadian expression of LHC II multigenes of *Phaseolus vulgaris*.

A sample of references on some of the above topics, in chronological order, includes: Argyroudi-Akoyunoglou and Akoyunoglou (1970), Manetas and Akoyunoglou (1976), Akoyunoglou (1977, 1981), Argyroudi-Akoyunoglou et al. (1982), Akoyunoglou and Argyroudi-Akoyunoglou (1986), Tavladoraki et al. (1989), Georgakopoulos and Argyroudi-Akoyunoglou (1994), Argyroudi-Akoyunoglou and Prombona (1996), and Georgakopoulos et al. (2002).

George C. Papageorgiou (Institute of Biology): an offshoot of the Akoyunoglou lab. Among its collaborators were J. Isaakidou, M. Tsimilli-Michael, G. Sotiropoulou, K. Kalosaka, K. Stamatakis and N. Ladas. Research themes include: bioenergetic processes in and across the thylakoid membrane of chlorophytes and cyanobacteria (excitation transfer, photosynthetic electron transport, proton-ion translocation), and across plasma membranes of cyanobacterial cells (osmotic volume changes, water and solute transport); cell defenses against salinity; and stabilization of the photosynthetic activity of cells, chloroplasts, and membranes by matrix immobilization, chemical cross-linking, and presence of compatible osmolytes. In 2001, George was succeeded by Kostas Stamatakis who continues research on cell defenses against salinity, and particularly on Na^+/H^+ anti-port in freshwater *Synechococcus*. A sample of references on some of the above topics, in chronological order, includes: Isaakidou and Papageorgiou (1975), Papageorgiou (1975), Kalosaka et al. (1985), Papageorgiou et al (1989), Papageorgiou and Murata (1995), Papageorgiou et al. (1996), Ladas and Papageorgiou (2000, and Stamatakis and Papageorgiou (2001).

Vassilis Petrouleas (Institute of Materials Science): research in this laboratory has centered on investigating electron and proton transport cofactors in PS II and PS I, particularly through the use of molecular probes (NO, CN^- and carboxylate anions); also on the trapping of metallo-radical intermediates, and H^+/electron exchanges between tyrosine Z and the Mn_4 cluster during S-state transitions of the oxygen evolving complex. Principal methodologies are EPR (electron paramagnetic resonance) and Mössbauer spectroscopies. Its scientifically salient progeny includes Y. Deligiannakis, C. Goussias, N. Ioannides, D. Koulougliotis, Y. Sanakis, and J. Sarrou. A sample of references on some of the above topics, in chronological order, includes: Petrouleas and Diner (1986), Diner and Petrouleas (1990), Deligiannakis et al. (1994a, b), Sanakis et al. (1994), and Ioannides et al. (1998, 2000).

University of Patra, Patra, Peloponnese

Yiannis Manetas (Department of Biology): research interests of this laboratory included (a) the regulation of photosynthetic enzymes by light–dark cycles, and by compatible osmolytes; and (b) the ecophysiology of mediterranean plants, focusing on their responses to climatic periodicity and to biotic and abiotic stresses. Among its research active progeny, I may list K. Stamatakis, G. Grammatikopoulos, A. Kyparissis and E. Levizou. A sample of relevant publications, in chronological order, includes: Manetas and Akoyunoglou (1976), Karabourniotis et al. (1983), Stamatakis et al. (1988), Karavatas and Manetas (1999), Kyparissis et al. (2000), and Levizou et al. (2002).

University of Crete, Herakleion, Crete

Dimitris Ghanotakis (Department of Chemistry): research interests of this group (protein chemistry, enzyme function, biotechnology) go beyond photosynthesis. Within the confines of the latter, research addresses problems on the structure and function of Photosystem (PS) II-core/oxygen evolving complex, including photoinhibition.

George Tsiotis (Department of Chemistry) Applications of electron microscopy and 2D electron crystallography to the structure of reaction center core complexes (PS I, PS II and green sulfur bacteria).

Kyriakos Kotzabasis (Department of Biology). Main interest is the regulation of chloroplast development by natural polyamines.

A sample of references on some of the above topics, in chronological order, includes: Kotzabasis et al. (1993, 1999), Mishra et al. (1994), Andreadakis et al. (1996), Hasler et al. (1997), Lydakis-Simantiris et al. (1998), Tsiotis et al. (1999), Spyridaki et al. (2000), Chroni and Ghanotakis (2001), and Psylinakis et al. (2002).

(A)

(B)

(C)

(D)

(E)

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Figure 1. (A) Photosynthesis personalities photographed at the entrance of the Photosynthesis Laboratory of the Pushchino Research Center, in Pushchino-na-Oke, during the 3rd International Biophysics Congress in Moscow, USSR (1972). *Foreground, from left to right:* Jeanette Brown (USA), Ellen C. Weaver (USA), V.B. Evstigneev (USSR), head of the Photosynthesis Laboratory. *Center:* Laszlo Szalay (Hungary), Elisabeth Szalay (Hungary), Govindjee (USA), George Akoyunoglou (Greece), George C. Papageorgiou (Greece) and Bacon Ke (USA). *Behind and to the left of Jeanette Brown:* Wim Vredenberg (The Netherlands). (B) *Left to right:* Joan Akoyunoglou (Greece), Govindjee and George Akoyunoglou during the 6th International Photosynthesis Congress in Brussels (1983; chaired by Chris Sybesma). (C) *Left to right:* George C. Papageorgiou and Govindjee walking up the Propylaia of Acropolis in Athens, Greece (1976). (D) *Foreground:* Bruce Diner (USA) and Vasili Petrouleas (Greece). Photo by Govindjee at the Gordon Research Conference on Biophysical Aspects of Photosynthesis (Proctor Academy, Andover, New Hampshire, 1991; chaired by Robert Blankenship, USA). (E) Participants of the European Research Conference on Biophysics of Photosynthesis (Sitges, Spain, 1996; photo by Govindjee).

Aristotle University, Thessaloniki, Macedonia

Thomas Lanaras (Department of Biology; collaborator C. M. Cook). *Michael Moustakas* (Department of Biology; collaborator Georgia Ouzounidou). Research of these groups focuses on the effects of heavy metals on photosynthetic activities and pigment content of plants. A sample of publications, in chronological order, includes: Moustakas and Ouzounidou (1994), Moustakas et al. (1995, 1997), Ouzounidou (1996), and Chettria et al. (1998).

Among distinguished Greek plant scientists, who are or were peripherally interested in photosynthesis during the period covered by this account, I may mention G. Karabourniotis at the Agricultural University of Athens, K. Angellakis-Roubelakis at the University of Crete, I. Tsekos at Aristotle University, Thessaloniki, A. Kiparissis at the University of Ioannina, the late K. Mitrakos and K. Anagnostides at the University of Athens, and the late N.A. Gavalas at the University of Patra.

Finally, although I write about photosynthesis research in Greece, and not about Greeks in photosynthesis research, I would like to end by making passing reference to scientists, who were educated in Greece, but who work or worked in the broader domains of photosynthesis and bioenergetics abroad. The list is partial and includes E.M. Moudrianakis (Johns Hopkins), A. Melis (UC Berkeley), M. Tsimilli-Michael (Cyprus), F. Anni (T. Jefferson University), K. Gounaris (Imperial College), K.K. Hatzios (Virginia Tech), P. Tavladoraki (University of Rome) and N.F. Tsinoremas. I am afraid there must be many omissions here, particularly from the younger generation.

I close the account with some photos from the last century (Figure 1).

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Note

[1] '*[φύλλ]* α δη ουκ έχουσιν άλλον σκοπόν ει μή την εφέλκυσιν της υγρότητος, και ίνα ώσι και περικαλύμματα των καρπών από της σφοδρότητος του ηλίου...και απομένει τι εκεί υγρόν, ό φαίνεται έξωθεν και τούτον έοτι η χλοερότης.' Aristotle (4th century BC).

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