CHRONICLE OF RESERARCH in the MELIS LAB

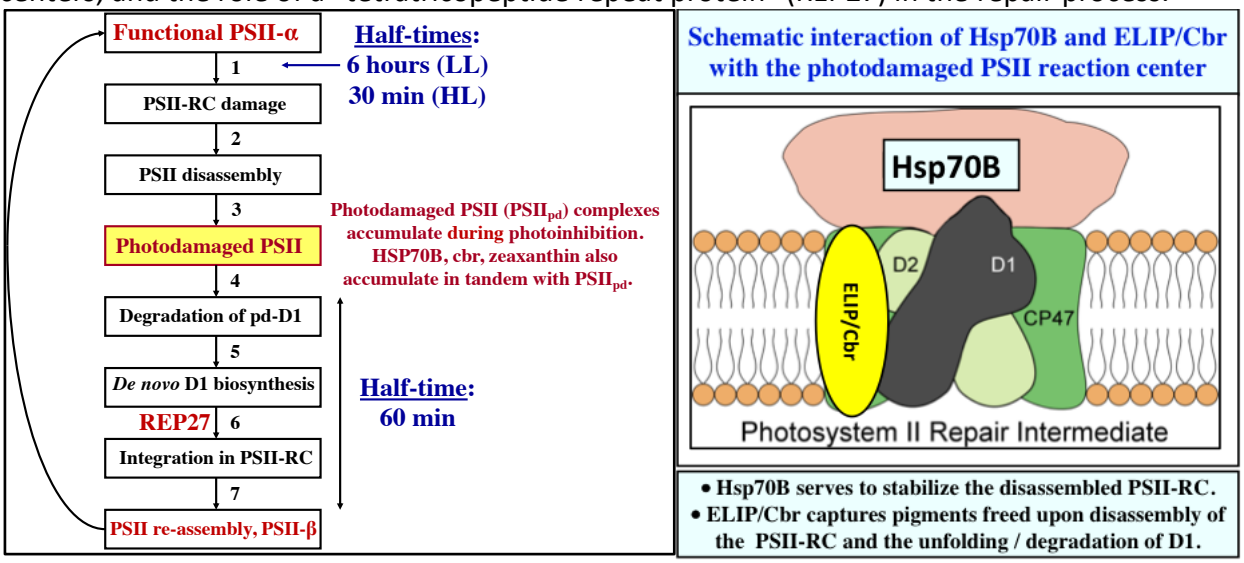
There is a history of pioneering contributions from the Melis lab. Below is a chronological synopsis of major achievements:

Photosystem-II (PSII) heterogeneity and the PSII damage and repair cycle in chloroplasts:

Melis discovered and named the "alpha-beta heterogeneity" of PSII reaction centers in chloroplasts and showed this duality of reaction centers to be a consequence of a unique process, which he termed the "PSII damage and repair cycle". He defined PSII-α centers to be the functional PSII, while PSII-β centers were those in the process of repair.

Photodamage of PSII is a dynamic phenomenon and a daily occurrence in the life of the oxygenic photosynthetic apparatus. The repair process selectively removes and replaces the photo-oxidized D1/32 kD PSII reaction center protein from the massive (>1,000 kD) multi-subunit H_2O-oxidizing and O_2-evolving PSII holocomplex. The repair mechanism is unique in the annals of biology and specific to photosynthetic organisms. Nothing analogous in complexity and specificity has been reported in other biological systems.

Melis and co-workers made several fundamental contributions to elucidating the mechanism of this unique PSII repair process. Included are the molecular mechanism and kinetics of photodamage and repair, the transient conformation and status of photodamaged PSII centers, and the role of a "tetratricopeptide repeat protein" (REP27) in the repair process.



(**Left**) Pathway of the conserved PSII damage and repair cycle in chloroplasts. (**Right**) Stabilization of the photodamaged PSII by the molecular chaperon HSP70B, and a role of zeaxanthin and of the ELIP / Cbr proteins in the PSII repair through photoprotection of the partially disassembled, and presumably vulnerable, PSII core complexes from potentially irreversible photooxidative bleaching.

Selected publications:

Melis A, Homann PH (1976) Heterogeneity of the photochemical centers in system II of chloroplasts. Photochem. Photobiol. 23: 343-350.

Melis A, Duysens LNM (1979) Biphasic energy conversion kinetics and absorbance difference spectra of photosystem II of chloroplasts. Evidence for two different system II reaction centers. Photochem. Photobiol. 29: 373-382.

Melis A (1985) Functional properties of photosystem II-β in spinach chloroplasts. Biochim Biophys Acta 808:334-342

Guenther JE, Melis A (1990) The physiological significance of photosystem II heterogeneity in chloroplasts. Photosynth. Res. 23: 105-109

Vasilikiotis C, Melis A (1994) Photosystem-II reaction center damage and repair cycle - chloroplast acclimation strategy to irradiance stress. Proc. Natl. Acad. Sci. USA 91: 7222-7226

Melis A (1999) Photosystem-II damage and repair cycle in chloroplasts: what modulates the rate of photodamage in vivo? Trends in Plant Sci 4: 130-135

Yokthongwattana K, Chrost B, Behrman S, Casper-Lindley C, Melis A (2001) Photosystem II damage & repair cycle in the green alga *Dunaliella salina:* Involvement of a chloroplast-localized HSP70. Plant Cell Physiol 42:1389-1397

Jin E-S, Polle JEW, Melis A (2001) Involvement of zeaxanthin and of the Cbr protein in the repair of photosystem-II from photoinhibition in the green alga *Dunaliella salina*. Biochim. Biophys. Acta 1506: 244--259

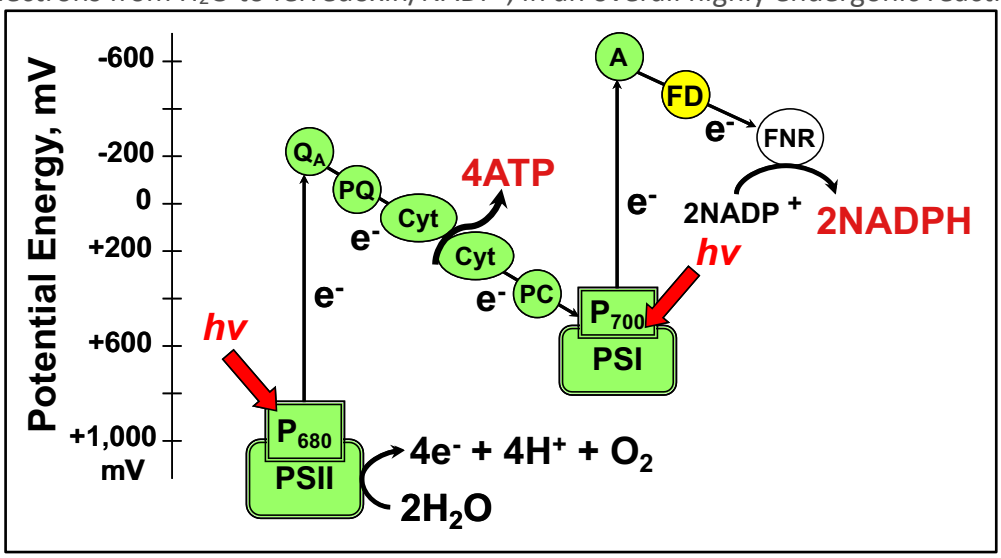
Jin ES, Yokthongwattana K, Polle JEW, Melis A (2003) Role of the reversible xanthophyll cycle in the photosystem-II damage and repair cycle in *Dunaliella salina* (green alga). Plant Physiol. 132: 352-364

Park S, Khamai P, Garcia-Cerdan JG, Melis A (2007) REP27, a tetratricopeptide repeat nuclear-encoded and chloroplast-localized protein functions in the D1/32 kD reaction center protein turnover and PSII repair from photodamage. Plant Physiology 143: 1547-1560

Dewez D, Park S, Garcia-Cerdan JG, Lindberg P, Melis A (2009) Mechanism of the REP27 protein action in the D1 protein turnover and photosystem-II repair from photodamage. Plant Physiol. 151:88-99

Photosystem stoichiometry in oxygenic photosynthesis:

Since the 1960 hypothesis by Hill and Bendall (Function of the two cytochrome components in chloroplasts: a working hypothesis. Nature 186:136-137), and the pioneering research published in 1961 by Duysens, Amesz and Kamp (Two photochemical systems in photosynthesis. Nature 190:510-511) and in 1962 by Duysens and Amesz (Function and identification of two photochemical systems in photosynthesis. Biochim Biophys Acta 64:243-260), the field of photosynthesis research accepted the concept of two photosystems, PSII and PSI, functioning concurrently in the linear electron transport chain, moving electrons from H_2O to ferredoxin/$NADP^+$, in an overall highly endergonic reaction.



The Z-scheme of linear electron transport in oxygenic photosynthesis, depicting the pathway of electron transport and the mechanism of H_2O oxidation, ATP and NADPH generation. Electrons originate at PSII upon the photooxidation of H_2O, their potential energy is elevated upon transfer to plastoquinone (PQ) in a light-mediated endergonic reaction. Electrons from the plastoquinone pool are transported via the cytochrome *b-f* complex (Cyt) to plastocyanin (PC) and PSI, where their potential energy is elevated further upon transfer to ferredoxin (FD) in a second light-mediated endergonic reaction. P_{680}, Reaction center of PSII; Q_A, primary quinone acceptor of PSII; P_{700}, reaction center of PSI; A, primary electron acceptor of PSI; FD, ferredoxin; FNR, ferredoxin-NADP reductase.

Based on the Z-scheme of electron-transport in photosynthesis, and with the advent of time, it became a dogma in the field that stoichiometrically equal numbers of the two photosystems functioned jointly as a supercomplex in the photosynthetic of all oxygenic photosynthesis. The advent of sensitive absorbance difference spectrophotometry and Melis' own and unique laboratory-designed split-beam absorbance difference spectrophotometer, enabled him to quantify, directly and for the first time, the actual concentration of the photosystems in a variety of different photosynthetic membranes. Photosystem I reaction centers were quantified from the light-induced absorbance change at 700 nm (oxidation of the primary electron donor, P700). Photosystem II reaction centers were quantified from the light-induced absorbance change at 325 nm (reduction of the primary quinone electron acceptor, Q_A). Spinach chloroplasts and membrane fractions obtained by French press treatment, mature and developing pea chloroplasts, and blue-green algal membranes were initially investigated. The results showed a large variability in the ratio of system-II to system-I reaction centers (from 0.43:1 to 3.3:1) in different photosynthetic membranes. Thanks to this work, it is now established that phycobilisome-containing cyanobacteria and red algae have a PSII/PSI ratio substantially lower than 1:1, whereas green plants and algae have a PSII/PSI ratio > 1:1. Chlorophyll deficient mutants and chloroplasts in the early stages of development have a PSII/PSI ratio that is substantially greater than that of the corresponding wild type or mature chloroplasts.

Melis provided evidence that plants, algae, and cyanobacteria dynamically adjust and optimize the ratio of their photosystems in response to genetic, developmental, and environmental light conditions for the purpose of maintaining a balanced and efficient electron flow through the electron transport chain. This pioneering discovery comprised a drastic departure from the accepted dogma of the structurally inflexible PSII-PSI-LHC supercomplex organization of the photochemical apparatus of photosynthesis and was, for a period of time, a controversial and highly debated issue. This work was expanded to support the concept of the lateral separation of the photosystems, whereby localization of different photosystems occurs in separate regions of chloroplast membranes.

Selected publications:

Melis A and Brown JS (1980) Stoichiometry of system I and system II reaction centers and of plastoquinone in different photosynthetic membranes. Proc. Natl. Acad. Sci. USA 77: 4712-4716

Melis A and Harvey GW (1981) Regulation of photosystem stoichiometry, chlorophyll *a* and chlorophyll *b* content and relation to chloroplast ultrastructure. Biochim. Biophys. Acta 637: 138-145

Anderson JM, Melis A (1983) Localization of different photosystems in separate regions of chloroplast membranes. Proc. Natl. Acad. Sci. USA 80: 745-749

Manodori A, Melis A (1986) Cyanobacterial acclimation to photosystem I or photosystem II light. Plant Physiol. 82: 185-189

Ghirardi ML, McCauley SW, Melis A (1986) Photochemical apparatus organization in the thylakoid membrane of *Hordeum vulgare* wild type and chlorophyll *b*-less chlorina f2 mutant. Biochim. Biophys. Acta 851: 331-339

Melis A (1989) Spectroscopic methods in photosynthesis: photosystem stoichiometry and chlorophyll antenna size. Phil. Trans. R. Soc. Lond. B 323: 397-409

Chow WS, Melis A and Anderson JM (1990) Adjustments of photosystem stoichiometry in chloroplasts improve the quantum efficiency of photosynthesis. Proc. Natl. Acad. Sci. U.S.A. 87: 7502-7506

Kim JH, Glick RE, Melis A (1993) Dynamics of photosystem stoichiometry adjustment by light-quality in chloroplasts. Plant Physiol. 102: 181-190

Melis A, Murakami A, Nemson JA, Aizawa K, Ohki K and Fujita Y (1996) Chromatic regulation in *Chlamydomonas reinhardtii* alters photosystem stoichiometry and improves the quantum efficiency of photosynthesis. Photosynth. Res. 47: 253-265

Microalgal hydrogen production research:

Following his earlier pioneering work on the "photosystem II damage and repair cycle", a term that he coined, Melis made a 60-year breakthrough in 1998-99, when he found that deprivation of sulfur nutrients causes a sealed culture of green microalgae to switch from evolving oxygen (O_2) to producing hydrogen (H_2) via the microalgal native enzyme hydrogenase.

Upon S-deprivation, the repair of PSII from photodamage is retarded, effectively lowering the number of PSII-α centers and lowering photosynthetic O_2 generation to a level below that of cellular respiration. Melis showed that, under these conditions, the rate of respiration is greater than that of photosynthesis, resulting in the consumption of all cellular oxygen. The ensuing anaerobiosis was necessary and sufficient to induce gene expression and activation of the cellular H_2 metabolism, diverting the natural flow of photosynthetic electrons toward the hydrogenase. A sustained generation of photosynthetic H_2 prevails, instead of the normally evolved O_2.

He showed that the process can be sustained for several days, instead of the 90 seconds previously achieved, or as long as the cellular respiration continues to consume endogenous O_2. Thus, application of know-how from the PSII repair mechanism enabled Melis to bypass the long-known incompatibility in the simultaneous O_2 and H_2 photoproduction by green microalgae and constituted a long-sought breakthrough, tracing back to the initial discovery by Gaffron and his coworkers (1939, 1942) of the ability of unicellular green microalgae to metabolize molecular H_2. Melis' S-deprivation H_2 photoproduction method has been adopted globally and employed by numerous laboratories, serving as a platform for further photosynthetic H_2-production research.

His breakthrough publication in year 2000 attracted widespread interest by the scientific news media, academia, and the public. Melis' primary publications in the field have exceeded 3,000 scientific citations.

A hydrogen-producing *C. reinhardtii* culture. Hydrogen bubbles emanate toward the surface of the liquid medium. The gas is drained through a syringe (inserted in the middle of the silicone stopper) and, through teflon tubing, collected in an inverted burette and measured by the method of water displacement. Photograph courtesy of Michael Barnes, UC Office of the President. From Melis and Happe 2001.

Selected publications:

Melis A, Zhang L, Forestier M, et al. (2000) Sustained photobiological hydrogen gas production upon reversible inactivation of oxygen evolution in the green alga *Chlamydomonas reinhardtii.* Plant Physiol. 122: 127-136

Ghirardi ML, Zhang L, Lee JW, Flynn T, Seibert M, Greenbaum E, Melis A (2000) Microalgae: a green source of renewable H_2. Trends in Biotechnology 18: 506-511

Melis A, Happe T (2001) Hydrogen Production: Green Algae as a Source of Energy. Plant Physiol. 127: 740-748

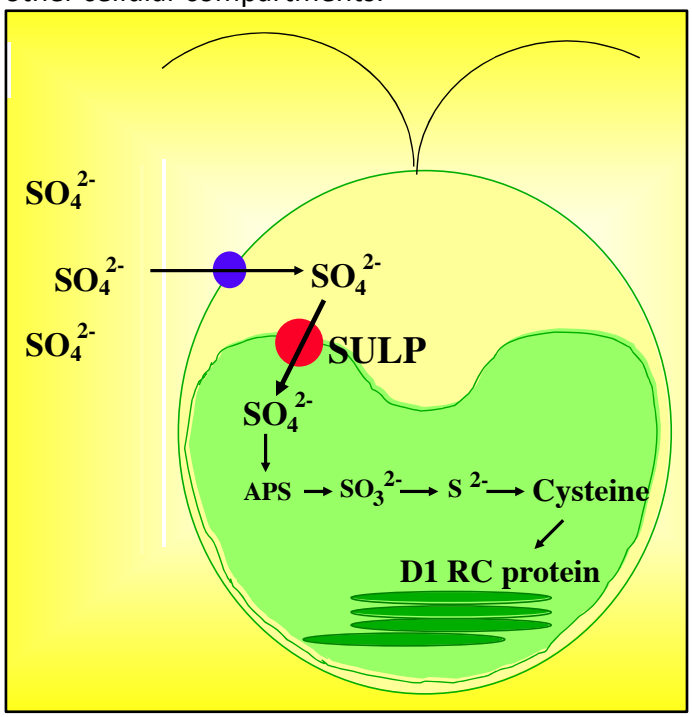
Zhang L, Happe T, Melis A (2002) Biochemical and morphological characterization of sulfur-deprived and H_2-producing *Chlamydomonas reinhardtii* (green alga). Planta 214: 552-561

Melis A (2002) Green alga hydrogen production: progress, challenges and prospects. Intl J Hydrogen Energy 27 (11), 1217-1228

Chloroplast sulfate transport in hydrogen production research:

Melis spearheaded further advances by applying molecular biology approaches to the hydrogen production process, including cloning and engineering of the *Chlamydomonas reinhardtii* chloroplast sulfate permease genes—a first for a photosynthetic eukaryote and a major advance in understanding the link between sulfur deprivation and hydrogen production.

Chlamydomonas reinhardtii strains with attenuated expression of the chloroplast sulfate permease (*SULP*) gene were able to grow photo-heterotrophically under anaerobic conditions in sealed cultures stabilizing the cellular H_2-production and its associated metabolism. Specifically, downregulation in the expression of the *SULP* gene attenuated sulfate uptake by the *Chlamydomonas reinhardtii* chloroplast, without depriving other cellular compartments (e.g. cytosol and nucleus) of sulfate nutrients. This condition enabled a constitutive H_2-production process by the cell, without exerting adverse sulfur deprivation effects on the biochemistry of other cellular compartments.



Sulfate anions are transported from the environment through the cell plasma membrane sulfate transport system to the cytosol. A separate chloroplast sulfate transport system (SULP) is responsible for the subsequent sulfate transport from the cytosol to the chloroplast stroma. Sulfate assimilation occurs exclusively in the chloroplast of the green algae, leading to the biosynthesis of cysteine. Continuous cysteine biosynthesis is required for the D1 reaction center protein turnover, thereby enabling normal photosynthesis, oxygen evolution, and biomass accumulation. A limitation in the supply of sulfate to the chloroplast impedes D1 protein turnover, thereby limiting the capacity of PSII function, and lowering water oxidation and O_2-evolution activity.

The green microalga *Chlamydomonas reinhardtii*

Selected publications:

Chen HC, Yokthongwattana K, Newton AJ, Melis A (2003) *SulP,* a nuclear gene encoding a putative chloroplast-targeted sulfate permease in *Chlamydomonas reinhardtii*. Planta 218: 98-106

Chen H-C, Melis A (2004) Localization and function of SulP, a nuclear-encoded chloroplast sulfate permease in *Chlamydomonas reinhardtii.* Planta 220: 198-210

Chen H-C, Newton AJ, Melis A (2005) Role of *SulP*, a nuclear-encoded chloroplast sulfate permease, in sulfate transport and H_2 evolution in *Chlamydomonas reinhardtii.* Photosynth. Res. 84: 289-296

Melis A, Chen HC (2005) Chloroplast sulfate transport in green algae: genes, proteins and effects. Photosynth. Res. 86: 299–307

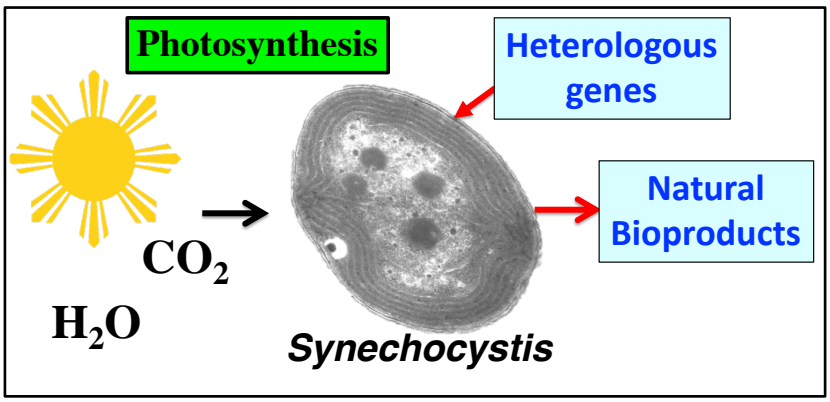
Lindberg P, Melis A (2008) The chloroplast sulfate transport system in the green alga Chlamydomonas reinhardtii Planta 228:951-961

The microalgal H_2-production breakthrough constituted a turning point in the field of Photosynthesis Research, as it was the first experimental approach showing the generation of a useful product directly from photosynthesis. Following this work, Melis originated the concept of "Photosynthetic Bioproducts", entailing the direct application of photosynthesis for the generation of biofuels, useful chemicals, and biopharmaceuticals. According to this concept, a single photosynthetic microorganism operates both as photocatalyst and processor, consuming carbon dioxide (CO_2), synthesizing, and emitting ready-to-use commodity products.

Natural chemicals and biopharmaceuticals:

Melis expanded the concept of "Photosynthetic Bioproducts," when he introduced a platform for the renewable generation of isoprene (C_5H_8) and monoterpene ($C_{10}H_{16}$) hydrocarbons, derived entirely from sunlight, CO_2 and H_2O in cyanobacteria. He correctly predicted that small-sized hydrocarbons (C_5H_8 and $C_{10}H_{16}$), like H_2, would spontaneously diffuse and separate from the cell interior and the liquid culture, enabling easy harvesting of the product.

He applied metabolic engineering approaches to enhance the activity and yield of the terpenoid biosynthetic pathway in microalgae, resulting in notable increases in the yield of heterologous C_5H_8 and $C_{10}H_{16}$. To accomplish this, he installed the genes of the exogenous mevalonic acid (MVA) pathway, along with isoprene and monoterpene synthase genes from plants, in a cyanobacterium (*Synechocystis*) that normally uses the sluggish methylerythritol-phosphate (MEP) pathway. The work employed a novel chromosomal integration and simultaneous expression of three heterologous synthetic gene operons in *Synechocystis* under the control of single promoters. This was the first time when an entire biosynthetic pathway with 12 recombinant enzymes had been expressed in a photosynthetic microorganism. In constituting a major addition to the genetic engineering toolkit, the work serves as a paradigm in the pursuit of approaches using sunlight for the renewable generation of high-impact products.



The Photosynthetic Bioproducts approach utilizes sunlight, CO_2, and water to generate fuel and chemicals in a high capacity process. Cyanobacteria offer an opportunity to develop such technology, with the micro-organism acting as a single-cell factory, capturing carbon dioxide and converting it into natural commodity products.

Selected publications:

Lindberg P, Park S, Melis A (2010) Engineering a platform for photosynthetic isoprene production in cyanobacteria, using *Synechocystis* as the model organism. Metabol Engin 12:70-79

Bentley FK, Melis A (2012) Diffusion-based process for carbon dioxide uptake and isoprene emission in gaseous/aqueous two-phase photobioreactors by photosynthetic microorganisms. Biotech Bioeng 109:100-109

Bentley FK, García-Cerdán JG, Chen H-C, Melis A (2013) Paradigm of monoterpene (β-phellandrene) hydrocarbons production via photosynthesis in cyanobacteria. BioEnergy Res. 6:917–929

Bentley FK, Zurbriggen A, Melis A (2014) Heterologous expression of the mevalonic acid pathway in cyanobacteria enhances endogenous carbon partitioning to isoprene. Molecular Plant 7:71-86

Formighieri C, Melis A (2015) A phycocyanin•phellandrene synthase fusion enhances recombinant protein expression and β-phellandrene (monoterpene) hydrocarbons production in *Synechocystis* (cyanobacteria). Metab Eng 32:116–124

Formighieri C, Melis A (2016) Sustainable heterologous production of terpene hydrocarbons in cyanobacteria. Photosynth Res 130:123-135

Chaves JE, Rueda-Romero P, Kirst H, Melis A (2017) Engineering isoprene synthase expression and activity in cyanobacteria. ACS Synth Biol 6:2281-2292

Chaves JE, Melis A (2018) Biotechnology of cyanobacterial isoprene production. Appl Microbiol Biotechnol 102(15):6451-6458

Betterle N, Melis A (2019) Photosynthetic generation of heterologous terpenoids in cyanobacteria. Biotechnology and Bioengineering Epub DOI: 10.1002/bit.26988

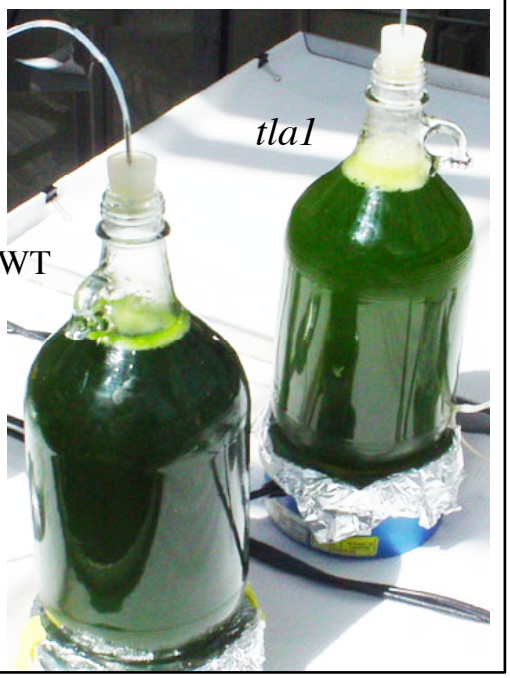
Efficiency and productivity of photosynthesis in microalgae, cyanobacteria, and crop plants:

Melis conceived, designed and pioneered, and currently leads an international effort to improve, theoretically, by up to 3-fold the efficiency and productivity of photosynthesis under direct and bright sunlight conditions. Inefficient sunlight utilization in cultivated microalgae and crop canopies occurs widely because of a genetic tendency of all photosynthetic organisms to assemble large arrays of light-absorbing chlorophyll and other antenna molecules in their photosystems. This is a survival strategy and a competitive advantage in the wild, where light is often limiting. Maximum competition in the wild requires capturing more light for self, even if wasted, and preventing light capture by competing neighbors. Obviously, such over-absorption and wasteful dissipation of excess sunlight is detrimental to the yield and productivity in high density cultivated monocultures, including microalgae and crop canopies under bright sunlight conditions.

He correctly predicted that genetically minimizing the size of the array of chlorophyll molecules that serve as antennae to harvest sunlight for the photosynthetic apparatus could minimize overabsorption of sunlight and the ensuing wasteful dissipation. He coined the term **T**runcated **L**ight-harvesting **A**ntenna (TLA) and showed that the TLA concept brings about enhancement in the photosynthetic productivity of microalgal cultures and, more recently, of a model crop plant, tobacco, cultivated in high density under direct sunlight. In this ground-breaking work, Melis noted that TLA cultivars show promise of increased yields, while minimizing field space needed for cultivation. Higher density planting of crop plants, in addition to greater yields per canopy, offer ancillary benefits, such as lower fertilizer and herbicide use.

(Above) Visual appearance of a pair of *Nicotiana tabacum* wild type and TLA canopies, shown at the end of their growth period and immediately prior to harvesting of the plants. The wild type leaves had a dark green coloration and the TLA tobacco a lighter green coloration. The overall foliage density was greater in the TLA canopy, compared to the wild type. Canopy characteristics: TLA / WT total biomass ratio = 1.25:1; TLA / WT leaf biomass ratio = 1.35:1; TLA / WT stem biomass ratio = 1.05:1

Cultures in the Greenhouse



High-density-cultures of *Chlamydomonas reinhardtii* for measurement of photosynthetic productivity under direct sunlight conditions. The wild type (WT) and the ***tla1*** antenna mutant were grown in 2.5-L size bottles having an internal diameter of about 15 cm. Photosynthetic O_2 was collected through a syringe (inserted in the middle of the silicone stopper) and Teflon tubing and the volume and rate of oxygen gas produced was measured. Note the higher cell density (biomass) and the lighter green coloration attained by the ***tla1*** culture, as compared to the wild type.
Culture Characteristics at the time of test:
WT: 6.4×10^6 cells/mL, 25.6 µM Chl concentration, rate of oxygen evolution 22 mL/h.
tla1: 10×10^6 cells/mL, 15.4 µM Chl, concentration, rate of oxygen evolution 31 mL/h.

The 40% greater photosynthetic productivity of the ***tla1*** over WT culture is attributed to better sunlight penetration and less wasteful energy dissipation.

Selected publications:

Melis A, Neidhardt J, Benemann JR (1999) *Dunaliella salina* (Chlorophyta) with small chlorophyll antenna sizes exhibit higher photosynthetic productivities and photon use efficiencies than normally pigmented cells. J. Appl. Phycol. 10: 515-525

Polle JEW, Kanakagiri S, Melis A (2003) *tla1,* a DNA insertional transformant of the green alga *Chlamydomonas reinhardtii* with a truncated light-harvesting chlorophyll antenna size. Planta 217: 49-59

Melis A (2009) Solar energy conversion efficiencies in photosynthesis: minimizing the chlorophyll antennae to maximize efficiency. Plant Science 177: 272-280

Kirst H, Garcia-Cerdan JG, Zurbriggen A, Melis A (2012) Assembly of the light-harvesting chlorophyll antenna in the green alga *Chlamydomonas reinhardtii* requires expression of the *TLA2-CpFTSY* gene. Plant Physiol 158: 930–945

Kirst H, Garcia-Cerdan JG, Zurbriggen A, Ruehle T, Melis A (2012) Truncated photosystem chlorophyll antenna size in the green microalga *Chlamydomonas reinhardtii* upon deletion of the *TLA3-CpSRP43* gene. Plant Physiol. 160(4):2251-2260

Kirst H, Formighieri C, Melis A (2014) Maximizing photosynthetic efficiency and culture productivity in cyanobacteria upon minimizing the phycobilisome light-harvesting antenna size. Biochim Biophys Acta - Bioenergetics 1837(10):1653-1664

Kirst H, Gabilly, ST, Niyogi KK, Lemaux PG, Melis A (2017) Photosynthetic antenna engineering to improve crop yields. Planta 245:1009–1020

Patents: Ten patents, with Melis and former and current postdocs as co-inventors, have been issued to the University of California, derived from the above described research.

Publications: Melis has published more than 280 peer-reviewed Original Research Articles, Reviews, and Book Chapters.

Invited seminars and lectures: Owing to his research contributions, Melis has been invited as a speaker and has delivered more than 180 international and national invited lectures and seminars at academic, conference, government, and industry settings in (alphabetically) Brazil, Canada, Europe (multiple countries), India, Israel, Japan, Korea, Turkey, and the US (multiple states).

Awards and honors: Melis has received many honors, including prestigious fellowships enabling him to do research in Europe (Universities of Leiden, Lund, Leeds and Hamburg), Australia (CSIRO in Canberra) and Japan (National Institute for Basic Biology in Okazaki). He has been honored by awards from the US Department of Energy (Research Achievement Award), Daimler-Chrysler Corporation (University Research Award), and UC Berkeley (Distinguished Teaching Award). He has also been elected a Fellow of the American Association for the Advancement of Science (AAAS). These honors attest both to the excellence of Melis' research and his dedication to teaching.

Service to the scientific community: Melis' contributions extend to professional service. He gives admirably of his time as an organizer and convener of conferences and workshops, as a peer-expert reviewer of manuscripts, member of grant review panels, and as a scientific journal editor. In the latter capacity, he has served as a *Plant Physiology* (ASPB) Editorial Board member, *Plant and Cell Physiology* Overseas Editor, and Associate Editor of both *Photosynthesis Research* and *Bioenergy Research*. Furthermore, he has served on the Editorial Board (since 1995) and as Editor-in-Chief (since 2002) of the prestigious international plant biology journal *Planta*.