European Science Foundation
Standing Committee for Life, Environmental and Earth Sciences (LESC)

ESF LESC EXPLORATORY WORKSHOP

Flavin-based sensorial photoreceptors: from bacteria to plants

Centro Santa Elisabetta, Università degli Studi di Parma
Parma, Italy, 25-27 March 2004

Convened by:

Aba Losi

Dipartimento di Fisica, Università degli studi di Parma

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with co-funding from

Università degli Studi di Parma

SCIENTIFIC REPORT

Content

Summary of the workshop topic : Flavin-based blue light sensorial receptors (cryptochromes, phototropins and blue-light driven cyclases) regulate many light-driven processes in plants and they were recently discovered in lower organisms,e.g. bacteria and fungi. A first aim of this workshop was to design a strategy to figure out the physiological role of these photoreceptors in lower organisms, to characterize their molecular properties and to elucidate common mechanisms of blue-light-to-signal transduction in distant taxa. A second, similarly important aspect of this workshop was the aim to create a stronger cooperation at an European dimension in this fast developing field, by bringing together the expertise of diverse research groups.

1. EXECUTIVE SUMMARY

The ESF-LESC exploratory workshop "**Flavin-based sensorial photoreceptors: from bacteria to plants"** took place in Parma (Italy) in the Centro Santa Elisabetta of the University of Parma, on March 25-27th. Funding was provided by ESF, co-funding by the University of Parma (details are given in the financial report). The workshop was convened by Dr. Aba Losi. Local organization was coordinated by Roberta Bedotti (Department of Physics, University of Parma). The 23 invited participants came from 5 different European countries. Another four participants (PhD or PostDoc students) took part, financed by home projects, and presented posters.

The workshop was organized in four discussion forums, introduced and led by discussion leaders, including presentations of ca. 20 minutes each (20 presentations in total). On March 26th the ESF representative, Salvatore Cannistraro, opened the meeting by giving a thorough representation of ESF and LESC activities and aims. The convenor, Aba Losi, gave then an introductory lecture, an overview on known and putative flavin-based photosensors. The first day of the meeting (March 26) was devoted to biophysical aspects and molecular mechanisms. Forum 1, Light-induced reactions mechanisms and structural studies, led by Silvia E. Braslavsky, hosted the largest number of presentations (8). In Forum 2, Light-to-signal transduction mechanisms, led by Wolfgang Gärtner, 3 speakers presented their recent results. Poster viewing closed the day, with 3 contributions. The second day of the meeting (March 27) was dedicated to biological and biochemical aspects. During Forum 3 (discussion leader) Alfred Batschauer, with the aid of 3 presentations, the audience discussed about the more recent progress/problems in Protein chemistry, expression and purification. Finally Forum 4, with 5 presentations, chaired by Francesco Lenci, was dedicated to the present knowledge about the Physiological role of flavin-based photoreceptors and to the many perspectives still opened in this field.

After the conclusion of the 4 forums, it was discussed about the possibility of building a European scientific cooperation on the workshop topic, in the framework of ESF activities. A committee representing the 5 participating countries was established, in order to undergo/perform the required activities (see also point 3). The workshop closed on Saturday, March 27 at 16:00.

2. SCIENTIFIC CONTENT OF THE WORKSHOP

Background: Blue-light regulates a broad variety of developmental and physiological responses in plants, e.g. photoperiodism, phototropism, flowering and circadian rhythms. Blue-light-sensitive photoreceptors from plants, the **cryptochromes** and the **phototropins**, have only recently been identified and have demonstrated the importance and spreading of **flavin-based blue light** perception. The **cryptochromes** are related to the photolyases, enzymes for light-repair of DNA lesions. They actually consist of a two-chromophore system with a Deazaflavin/pterin, acting as an antenna pigment and a flavin-adenin-dinucleotide chromophore (FAD). Their light-induced reactions have up to now been only partially elucidated. The **phototropins** are light-driven kinases that contain in the N-terminal part two specialized chromophoric domains, **LOV1** and **LOV2** (from Light Oxygen and Voltage), which function as binding sites for flavin mononucleotide (FMN). The **LOV domains** undergo a photocycle, involving, from the decay of a primarily formed triplet state, the formation of a covalent adduct between the thiol group of a conserved active site cysteine and FMN at the -C4a position. This mechanism has established a **new paradigm** in the field of biological photoreceptors, in contrast with chromophore photoisomerization, as it occurs e.g. in retinal proteins or phytochromes. A third type of flavin-based photoreceptors is represented by **AppA**, that binds FAD in its **BLUF** (sensor of Blue-Light Using Fad) domain and is, as is known up to now, involved in regulation of photosynthesis gene expression in the purple bacterium *Rhodobacter sphaeroides*.

Flavin-based blue-light perception has rapidly crossed the borders of **life domains** in which the specific photoreceptors have been first identified. **Cryptochromes** and phototropin related proteins (referred to as **LOV-proteins**) have been found in the genome sequences of phototrophic and heterotrophic bacteria. In some cases protein expression and functional analysis have demonstrated that these putative photoreceptors bind the predicted chromophores and undergo a photocycle, but their light-driven role in vivo is unknown. Conversely, **BLUF domains** have been recently described in an algal light activated adenylyl cyclase that mediates a phototactic response to blue light .

The research in the field of blue-light perception has experienced an exceptional blooming in the recent few years and is likely to give us in the near future a more comprehensive understanding on the common mechanisms by which phylogenetically **distant organisms** “see” their world. This research field requires a **multidisciplinary approach,** in that molecular biology, bioinformatics, physiology, spectroscoy and physical-chemistry can be integrated to obtain detailed information on these biological systems. Yet, many questions are still open and they have been discussed within the 4 **discussion Forums** of the workshop.

For review see: Briggs, W. R. & Christie, J.M. **Phototropins 1 and 2: versatile plant blue-light receptors** *Trends Plant Sci.* **2002**, 7, 204-210; Cashmore, A. **Cryptochromes: enabling plants and animals to determine circadian time** *Cell* **2003**,114: 537-543; M. Gomelsky & G. Klug, **BLUF: a novel FAD-binding domain involved in sensory transduction in microorganisms**, *Trends Biochem. Sci.*, **2002,** 27: 497-500. Iseki, M., S. Matsunaga, A. Murakami, K.

Ohno, K. Shiga, K. Yoshida, M. Sugai, T. Takahashi, T. Hori, and M. Watanabe A blue-light-activated adenylyl cyclase mediates photoavoidance in Euglena gracilis. *Nature*, **2002**, 415:1047-1051. A. Losi, **The bacterial counterparts of plant phototropins,** *Photochem. Photobiol. Sci.*, **2004**, 6, in press, DOI: 10.1039/b400728j

In the following the speakers are indicated in red. Links connect this section to the final programme and from there to the abstracts.

Forum 1, Light-induced reactions mechanisms and structural studies, discussion leader: Silvia E. Braslavsky. The majority of the talks and of the accompanying discussion were devoted to the reaction mechanism of the phototropin LOV domains. The formation of the covalent FMN-cysteine adduct occurs via the decay of the FMN triplet state. The covalent adduct formation has been elegantly demonstrated by NMR spectroscopy (Gerald Richter) and by X-ray crystallography (Astrid Jung). One of the major questions concerns the non-bonding character of the triplet state, so that other intermediates have to be postulated, albeit they have not been detected in the photocycle. UV-visible spectroscopy with LOV domains, mutated in the reactive cysteine, point to a reaction mechanism where the FMN triplet decays into a neutral radical after hydrogen extraction from the cysteine, with subsequent fast recombination of the radical pair and adduct formation (Peter Hegemann). X-ray crystallography (Astrid Jung) and Electron Paramagnetic Resonance (EPR) studies (Robert Bittl and Stephan Weber) also suggest that a radical pair is involved in the reaction mechanism. Ultrafast UV-visible spectroscopy nevertheless failed to detect a transient species beyond the FMN triplet, and a mechanism involving ultrafast proton transfer as rate limiting step has been proposed (John Kennis).

A new aspect of LOV domains photochemistry has been highlighted by femtosecond spectroscopy studies, showing that the photoadduct can be re-converted into the dark parent state not only thermally, but also in a light-driven way during a two-photon photocycle, rendering LOV domains reversible photochromic switches (John Kennis). Advanced vibrational spectroscopy coupled with site-specific mutagenesis can provide important details about the structural changes accompanying photoadduct formation, e.g. by identification of light-induced conformational changes on diverse LOV proteins (Joachim Heberle).

Long sought light-driven electron transfer reactions have been characterized in plant cryptochromes (Margaret Ahmad). A chain of tryptophan residues can donate an electron to the excited flavin, thus forming a flavin radical. Mutagenesis studies have furthermore shown that these reactions are important for cryptochrome function *in vivo.*

The light-driven reactions on BLUF-carrying proteins are presently being thoroughly investigated by means of ultrafast transient absorption experiments (John Kennis). The data point to a new kind of photocycle, in which the photoexcited flavin chromophore undergoes no chemical changes but induces subtle alterations in the surrounding protein moiety. X-ray structural studies are likely to provide a substantial contribution to the understanding of the novel BLUF paradigm in the near future (Astrid Jung).

Forum 2, Light-to-signal transduction mechanisms, discussion leader: Wolfgang Gärtner In phototropin an α–helix linking the LOV2 core to the C-terminal kinase domain, has been recently proposed to play a central role in interdomain communication and in the light-to-signal transduction mechanism. John Christie presented data showing that mutations in this region indeed attenuate the light-induced kinase activity of phototropins, producing the first evidence that the light-driven destabilization of the α–helix linker has a functional role.

Mutations of a conserved salt bridge, located at the surface of the LOV core, also impair the kinase activity. Work is in progress to elucidate the functional roles of these two protein regions in phototropin signalling.

In the paradigmatic organism *Neurospora crassa,* a fungus, sensorial responses to blue-light (e.g. carotenoid synthesis, circadian regulation) are mediated by the flavin-binding LOV protein WC-1 (white collar-1) that regulates the expression of specific genes within the so-called WC-1 complex. New experiments show that also chromatin modifications are necessary for light control of gene expression, highlighting a fundamental mechanism of light-to-signal transduction (Paola Ballario). Furthermore, WC-1 physically interacts with *Neurospora* protein kinase C that phosphorylates the DNA binding domains of WC-1 and regulates its cellular level in a light-dependent way (Lisa Franchi)

Forum 3, Protein chemistry, discussion leader: Alfred Batschauer One of the most critical points in the field of flavin-based photoreceptors is the challenge to obtain reproducible biological samples, with reasonable yield and definite chromophore composition for biophysical studies. This has been instructively been shown for the plant cryptochromes, where only recently it was possible to obtain soluble material carrying the flavin chromophore in high percentage, by expressing them in insect cells (Alfred Batschauer).

The expression and purification of bacterial LOV-proteins, has been successful for *Bacillus subtilis* YtvA, readily soluble as a full-length protein (different from plant phototropins) for which the blue-light driven photocycle has been characterized (Wolfgang Gaertner). Other systems, e.g. a LOV kinase from *Caulobacter crescentus*, appear to be expressed in a misfolded form in heterologous systems, only partially recovered by adding external chromophore (Wolfgang Gaertner).

The BLUF domain of AppA from *Rhodobacter sphaeroides* can be expressed in *E. coli*, but in this case it is able to accommodate different flavin chromophores, depending on the growing conditions. It is also possible to reconstitute the BLUF domain with a specific flavin, by adding excess of the desired chromophore to a protein solution, an interesting approach for biophysical studies (Klaas Hellingwerf).

Forum 4, Physiological role of flavin-based photoreceptors, discussion leader: Francesco Lenci

Whereas all known bacterial and fungal LOV proteins contain a single LOV domain, plant phototropins carry two conserved photosensing units, LOV1 and LOV2 in a tandem arrangement. John Christie has investigated the role of the two domains, and found that only LOV2 is essential for the light-driven effects of phototropins. Furthermore, in a tandem construct without the C-terminal kinase, it could be demonstrated that the two LOV domains interact.

In the unicellular algae *Euglena gracilis* photomovements are mediated by a BLUF containing protein that acts as a blue-light dependent adenylyl cyclase. The synthesis of cAMP modulates the flagellar beat and thus causes light-dependent responses. This BLUF protein is also active in relatives of *Euglena gracilis* and in mutants that show limited photomovements (Donat Häder). In bacteria, the BLUF photoresponsive motif is represented in the *Rhodobacter sphaeroides* protein AppA, a blue-light driven regulator of photosynthesis gene expression. It is the first known protein that can sense blue light via a bound flavin and in parallel the redox state via a multicysteine motif (Stephan Braatsch).

Quite surprisingly, the hypogeous fungus *Tuber borchii* responds to blue light that regulates mycelial growth. *Tuber borchi* contains a gene (tbwc-1) homologous to the blue-light photoreceptor of *Neurospora crassa,* WC-1*,* it is however unlikely that this protein acts as a transcriptional regulator. The photochemical properties of tbwc-1 have been presented during this section (Benedetto Grimaldi).

Although cyanobacteria constitute the most diverse group of microorganisms performing oxygenic photosynthesis (like plants), very little is known on blue light perception in these bacteria. A considerable number of cyanobacterial putative flavin-binding photosensors are being found in public databases, but only one of them has been characterized: a blue light sensor in *Synechocystis* PCC 6803, similar to eukaryotic cryptochromes (Nicole Tandeau). The cyanobacterial LOV proteins sharing similarities with plant phototropins are still fully uncharacterized and their role is unknown.

3. ASSESSMENT OF THE RESULTS, CONTRIBUTIONS TO FUTURE DIRECTION OF THE FIELD, OUTCOME

The topic of the workshop has demonstrated to be timely and the object of active investigation from many research groups. In fact, during the last year, more than 60 new papers related to this subject appeared on international scientific journals. The average quality of the talks presented during the workshop was definitely high, demonstrating that European research in this field is characterized by accurate scientific work and critical evaluation of the results. A positive note was added by the work of the four chairpersons, who managed to keep the discussion very alive and in the same time friendly, therefore extremely productive.

Assessment of the results.

The convenor let the speakers a free choice among the 4 Forums for their presentation, from which a clear picture emerged of the state- of- the- art. The characterization of the molecular mechanisms of flavin-based photosensors has received the largest attention from the participants to the meeting, with the support of very modern biophysical facilities optimized in various European labs. The discussion during Forum 1 and Forum 2 was accordingly very alive, a common language could be employed and understood and the formulation of the sections (short talks + extended open discussion) appeared fully proper. Forum 3 and Forum 4, dealing with more biological aspects, were instead more similar to conventional congress sections and the different talks less integrated with each other, albeit of high individual level. Partially this may be due to the fact that the preparation of biological samples is very specific for each case studied and among flavin-based photosensors few protocols have been optimized and normally cannot be extended even to strictly related systems (Forum 3).The physiological significance of flavin-based photoreceptors in unicellular organisms has been elucidated just in few cases, excellently highlighted during Forum 4, whereas we still don't have hints of their role in bacteria.

Contributions to future direction of the field

The **biophysical characterization** of flavin-based photoreceptors is entering a new phase, that requires a broader range of expertises. As an example, in phototropins and related proteins, LOV domains exhibit a large sequential, structural and functional similarity but an astonishing broad range of lifetimes for the overall kinetics of the photocycle (from few seconds to hours). The kinetics is also influenced by the presence of extra protein domains or fragments or by the occurrence of mutations. The molecular basis of the observed broad range of lifetimes can be understood only if a larger number of full-length proteins and

extended constructs will become available, thus requiring optimization of biochemical protocols.

It became clear during the meeting that it is necessary to obtain more information on the **light-to-signal transduction pathways**. This is still, in many cases, a major missing link between the chromophore-centered, light-triggered reactions and the observed photoresponses *in vivo*. The reason for this partially relies on the lack of structural information on photosensor domain in complex with their partners. X-ray crystallography cannot be always successfully employed, therefore alternative techniques (e.g. NMR, modelling, vibrational spectroscopy) must be more exploited. Details on the mechanism of the **light-triggered reactions** are likely to come from advancend time-resolved techniques, together with the design of mutated proteins and **chemically modified chromophores**. Again this requires that samples preparation is optimized in order to control, for example, the chromophore identity and incorporation.

The **physiological significance** of flavin-based photosensing proteins in lower organisms for which light-driven responses are not known (e.g. non-phototactic or non-photosynthetic bacteria), remains unknown. It is clear that this aspect demands more engagement and is conversely prone to future developments. As an encouraging starting point, many of the presenters have been shown to be familiar with bioinformatics tools, surely of great help in the discovery of new photoreceptor systems and in obtaining hints on their function. An important contribution would come from photophysiology studies in this field, not yet undertaken, and from advanced genomics and proteomics techniques

Outcome

At the workshop end a committee was constituted, formed by representatives of the 5 participant countries. The committee is composed by Aba Losi (Italy), Klaas Hellingwerf (The Netherlands), Nicole Tandeau (France), John Christie (United Kingdom) and Peter Hegemann (Germany). They should explore the possibility of building a scientific European network or programme, in the frame of ESF activities. A first step in this direction will be an attempt to involve research groups operating in a larger number of European countries (research groups likely to be interested have been already identified by the convenor in Spain, Switzerland and Sweden). Francesco Lenci, president-elect of the European Society for Photobiology (ESP), has offered the support of the society during the developing phase of this activity.

4. FINAL PROGRAMME

Thursday 25 March 2004

17:00-21:30 *Arrival and Registration at the Hotel*

19:00-21:30 Dinner at the Hotel

Friday 26 March 2004

08:45 Wellcome from the organizers and outline of the workshop

09:00 **Presentation of the European Science Foundation (ESF)**
Salvatore Cannistraro LESC (Standing Committee for the Life, Environmental and Earth Sciences)

09:15 Introductory lecture
Aba Losi
I1. Flavin based photoreceptors: ubiquitous "eyes for the blue"?

09:40 **Forum 1**
Light-induced reactions mechanisms and structural studies
Discussion leader: **Silvia E. Braslavsky**
e-mail: braslavskys@mpi-muelheim.mpg.de

F1A. **Peter Hegemann**
The photoreaction mechanism of LOV-type blue light receptors

F1B. **Margaret Ahmad**
Mechanism of action of cryptochrome photoreceptors

F1C. **Robert Bittl**
Cofactors of blue-light photoreceptors studied by EPR spectroscopy

30 minutes Coffee Break

F1D. **Joachim Heberle**
Vibrational spectroscopy explores the mechanism of blue-light photoreceptors

F1E. **John T.M. Kennis**
Primary reactions of flavin-based photoreceptors

F1F. **Gerald Richter**
NMR Investigations on LOV domains from the photoreceptor phototropin

F1G. **Astrid Jung**
Structural characterization of flavin-based photoreceptors

F1H. **Stefan Weber**
EPR-Studies on the Reaction Mechanism of Blue-Light Photoreceptors

Open Discussion (to be continued in the afternoon)

13:00 *Lunch at the workshop site*

14:00 **Forum 1**
open discussion (continued)

15:00 **Forum 2**
Light-to-signal transduction mechanisms
Discussion leader: **Wolfgang Gärtner**
e-mail: gaertner@mpi-muelheim.mpg.de

F2A. **Paola Ballario**
Light induction of transcription is mediated by histone tails modifications

30 minutes Coffee Break

F2B. **Lisa Franchi**
Role of Neurospora PKC in the regulation of light signal transduction and circadian rhythm.

F2C. **John Christie**
Phototropin receptor signalling.

Open discussion

Poster viewing

Posters presented (for co-authorship see the abstract section)

P1. Maria Ntefidou **Photoactivated adenylyl cyclase in *Euglena gracilis, Astasia longa,* and mutant strains**

P2. Tilman Kottke **Irreversible Photoreduction of Flavin in the Mutant C57M of a Phot-LOV1 Domain**

P3. Aba Losi **Tryptophan fluorescence in the *Bacillus subtilis* phototropin-related protein YtvA as a marker of interdomain interaction**

20:30 *Dinner at the restaurant "Al Mulino", Torrechiara (PR)*

Saturday 27 March 2004

09:15 **Forum 3**
Protein chemistry

Discussion leader: **Alfred Batschauer**
e-mail: batschau@mailer.uni-marburg.de

F3A. **Alfred Batschauer**
Progress in expression and purification of plant cryptochromes for structural and spectroscopic studies

F3B. **Wolfgang Gaertner**
Progress and problems in the expression of bacterial phototropin-related proteins

F3C. **Klaas Hellingwerf**

Structural characterization of flavin-based photoreceptors

11:30 **Forum 4**
Physiological role of flavin-based photoreceptors
Discussion leader: **Francesco Lenci**
e-mail: francesco.lenci@ib.pi.cnr.it

F4A. **John Christie**
Structure and function of plant phototropins

F4B. **Donat Häder**
The photoreceptor for phototaxis in the flagellate *Euglena gracilis*.

F4C. **Stephan Braatsch**
Blue light photoreceptors in *Rhodobacte*r

13:00 *Lunch at the workshop site*

F4D. **Benedetto Grimaldi**
The hypogeous fungus *Tuber borchii* responds to blue light and contains a gene (tbwc-1) homologous to the blue-light photoreceptor of *Neurospora crassa.*

F4E. **Nicole Tandeau**
Blue-light photoreceptors in cyanobacteria

Open discussion

15:00 **Concluding remarks**

16:00 *Departure*

5. LIST OF PARTICIPANTS

1. Convenor:
Dr. Aba Losi
University of Parma
Department of Physics, Biophysics Unit
Parco area delle Scienze 7/A
43100 Parma, **Italy**
Tel:+39-0521-905293
Fax:+39-0521-905223
e-mail: losia@fis.unipr.it

2. ESF Representative:
Prof. **Salvatore Cannistraro**
Università della Tuscia
Dipartimento di Scienze Ambientali
Unità di Ricerca di Viterbo
1100 Viterbo, **Italy**
Tel: +39 076 135 71 36
Fax:+39 076 135 71 36
e-mail: cannistr@unitus.it

Invited Participants
3. Dr. **Margaret Ahmad**
Physiologie Cellulaire et Moléculaire des Plantes, Université Pierre et Marie Curie 4, Place Jussieu - Tour 53 E5 - Casier 154 - 75252 Paris Cedex 05 - **France**
Tel:+ 33 -1 44 27 59 04;
Fax: + 33-1 44 27 62 32,
e-mail:ahmad@ccr.jussieu.fr
margaretahmad@hotmail.com

4. Dr. **Paola Ballario**
Dipartimento di Genetica e Biologia Cellulare, Università "La Sapienza" P.le A. Moro 5, 00185 Roma, **Italy**
Tel. +39-06-49912318 / 12238
Fax: +39-06-4440812
e-mail: paola.ballario@uniroma1.it

5. Prof. **Alfred Batschauer**
FB Biologie/Botanik, Philipps-Universität, Karl-von-Frisch-Str. D-35032 Marburg, **Germany**,
Tel: +49-(0)6421-28-27064
Fax: +49-(0) 6421-28-21545
e-mail: batschau@mailer.uni-marburg.de

6. Prof. **Robert Bittl**
Freie Universität Berlin; Fachbereich Physik (WE 1) D-14195 Berlin; **Germany**
Tel: +49-30 838-56049
fax: +49-30 838-56046;
e-mail: Robert.Bittl@Physik.FU-Berlin.DE

7. Dr. Stephan Braatsch
Institut für Mikrobiologie und Molekularbiologie, Universität Giessen, D35392, Giessen, **Germany**
Tel: 49-641-99-35542
Fax : 49-641-99-35549,
e-mail: Stephan.Braatsch@mikro.bio.uni-giessen.de

8. Prof. **Silvia E. Braslavsky**
Max-Planck-Institut für Bioanorganische Chemie, Postfach 10 13 65D 45413 Mülheim an der Ruhr,**Germany**
Tel:+49-208-306-3681
Fax: +49-208-306-3951
e-mail: braslavskys@mpi-muelheim.mpg.de

9. Dr. **John Christie**
Royal Society University Research Fellow,Plant Science Group,Bower Office Suite University of Glasgow,University Avenue, Glasgow, G12 8QQ ,UK,
Tel: (+44) 0141 330 2392/6989
Fax: (+44) 0141 330 6342
e-mail: J.Christie@bio.gla.ac.uk

10. Dr. **Lisa Franchi**
Dipartimento di Biotecnologie Cellulari ed Ematologia Sezione di Genetica Molecolare, Policlinico Umberto I° Viale Regina Elena 324, 00161 Roma **Italy**
Tel: +39-06-445 2806
Fax : +39-06-446 2891
e-mail: Franchi@bce.uniroma1.it

11. Prof. **Wolfgang Gärtner**
Max-Planck-Institut für Bioanorganische Chemie, Stiftstr. 34-36, D-45470 Mülheim and der Ruhr, **Germany**
Tel.: +49-208-306 3693
Fax: +49-208-306 3951
e-mail: gaertner@mpi-muelheim.mpg.de

12. Benedetto Grimaldi PhD student
Dipartimento di Genetica e Biologia Cellulare, Università "La Sapienza" P.le A. Moro 5, 00185 Roma, **Italy**
Tel. +39-06-49912318 / 12238
Fax: +39-06-4440812
benedetto.grimaldi@uniroma1.it

13. Prof. **Donat-P. Häder**
Friedrich-Alexander Universität, Institut für Botanik und Pharmazeutische Biologie, Lehrstuhl für Ökophysiologie der Pflanzen, Staudtstr. 5-91058 Erlangen, **Germany**,
Tel. +49 9131 852 8216
Fax +49 9131 852 8215
e-mail : dphaeder@biologie.uni-erlangen.de

14. Prof. **Joachim Heberle**
Forschungszentrum Juelich,IBI-2: Biolog. Strukturforschung, 52425 Juelich, **Germany**
Tel.: +49-2461-61-2024
Fax: +49-2461-61-2020
e-mail: j.heberle@fz-juelich.de

15. Prof. **Peter Hegemann**
Institut für Biochemie, Universität Regensburg, Universitätsstr. 31, 93040 Regensburg, **Germany**
Tel.: 0941-9432814
FAX: 0941-9432936
e-mail: peter.hegemann@biologie.uni-regensburg.de

16. Prof**. Klaas Hellingwerf**
Laboratory for Microbiology, Swammerdam Institute for Life Science, Nieuwe Achtergracht 166, 1018 WV Amsterdam, **The Netherlands**
Tel: +31-20-5257055
Fax: +31-20-5257056
e-mail: K.Hellingwerf@science.uva.nl

17. Astrid Jung PhD Student
Max Planck Institute for Medical Research, Department of Biomolecular Mechanisms,Jahnstrasse 29 D 69120 Heidelberg, **Germany**
Tel: + 49 6221 486 512
Fax: + 49 6221 486 273,
Astrid.Jung@mpimf-heidelberg.mpg.de

18. Dr. **John T.M. Kennis**
Department of Biophysics,Faculty of Sciences,Vrije Universiteit, De Boelelaan 1081,Amsterdam, 1081HV,
The Netherlands
Tel: +31204447937
Fax: +31204447999,
e-mail: john@nat.vu.nl

19. Prof. **Francesco Lenci**
Istituto di BioFisica, Consiglio Nazionale delle Ricerche,Via G. Moruzzi 1, 56100 PISA **Italy**
Tel: +39 - 50 - 315 - 2765/3020
Fax:+39 - 50 - 315 - 2760
e-mail: francesco.lenci@ib.pi.cnr.it

20. Prof. **Monique Martin**
Directeur de recherche au CNRS- UMR ENS CNRS 8640, P.A.S.T.E.U.R., Departement de Chimie, Ecole Normale Superieure, 24 rue Lhomond, 75231 Paris Cedex 05- **France**
Tel: +33 144322412
Fax: +33 144323325,
email: Monique.Martin@ens.fr

21. Dr. **Pascal Plaza**
Chargé de recherche au CNRS- UMR ENS CNRS 8640, P.A.S.T.E.U.R. Departement de Chimie, Ecole Normale Superieure, 24 rue Lhomond- 75231 Paris Cedex 05 **France,**
Tel: +33 144322414
Fax: +33 144323325
email: Pascal.Plaza@ens.fr

22. Prof. **Gerald Richter**
Institute of Organic Chemistry and Biochemistry, Technical University Munich, Lichtenbergstrasse 4, 85747 Garching, **Germany**
Tel: +49-89-289-13336
Fax: +49-89-289-13363
e-mail: gerald.richter@ch.tum.de

23. Prof. **Nicole Tandeau de Marsac**
Unite des Cyanobactéries, Département de Microbiologie Fondamentale et Médicale,Institut Pasteur, 28 rue du Docteur Roux, 75728 Paris Cedex 15 **France**,
Tel: +33 1 45 68 84 15
Fax: +33 1 40 61 30 42,
e-mail: ntmarsac@pasteur.fr

24. Dr. **Maurice van Gastel**
Max-Planck-Institut fuer Bio-Anorganische Chemie,Stiftstr. 34-36, D-45470 Mülheim, **Germany**
Tel: +49-208-306-3865
FAX: +49-208-306 3951, e-mail: vgastel@mpi-muelheim.mpg.de

25. Prof. Stefan Weber

Free University Berlin - Physics Department , Arnimallee 14, 14195 Berlin, **Germany,**Phone: +49 (30) 838-56139; FAX: +49 (30) 838-56046,e-Mail: Stefan.Weber@physik.fu-berlin.de

Extra Participants

26. Maxime Alexandre PhD student
Department of Biophysics,Faculty of Sciences,Vrije Universiteit, De Boelelaan 1081,Amsterdam, 1081HV,
The Netherlands
Tel: +31204447932
Fax: +31204447999,
MIA.Alexandre@few.vu.nl

27. Dr. Tilman Kottke Institut fuer Physikalische und Theoretische Chemie Universitaet Regensburg, **Germany**,
Tel. (+49) 941 / 943-4470
Fax (+49) 941 / 943-4488 e-mail: tilman.kottke@chemie.uni-regensburg.de

28. Yinghong Lu PhD student Institut für Biochemie, Universität Regensburg, Universitätsstr. 31, 93040 Regensburg, **Germany**
Tel.: (+49) 941 / 9432814
Fax:(+49) 941 / 9432936
e-mail: yinghong.lu@vkl.uni-regensburg.de

29. Maria Ntefidou PhD student
Department of Plant Ecophysiology, University of Erlangen-Nuernberg, Staudtstr. 5, 91058 Erlangen, **Germany**;
Tel.: +49-9131-8525095
Fax: +49-9131-852 8215
e-mail: ntefidou@biologie.uni-erlangen.de

6. Statistical information on the participants (ESF representative is omitted)

Invited participants

Age	Male	Female
Under 35	**4**	**2**
35-50	**7**	**2**
50+	**5**	**4**
Total	16	8

Nationality*	Male	Female	Total
France	1	3	4
Germany	10	2	15
Italy	2	3	5
The Netherlands	2	-	3
United Kingdom	1	-	1

Total Participants (Invited + Extra)

Age	Male	Female
Under 35	**7**	**3**
35-50	**7**	**2**
50+	**5**	**4**
Total	19	9

Nationality*	Male	Female	Total
France	1	3	4
Germany	12	3	15
Italy	2	3	5
The Netherlands	3	-	3
United Kingdom	1	-	1

*: Institutional addresses.