Preface: ferredoxin

Guy Hanke¹

Published online: 18 October 2017
© Springer Science+Business Media B.V. 2017

As attention in the field of photosynthesis research turns increasingly toward ways in which its basic reactions can be manipulated for improved agronomy or synthetic biology, it is timely to turn the spotlight on one of its fundamental components—ferredoxin. Originally discovered in the early 1960s as a small, soluble iron-containing electron transfer component in *Clostridium pasteurianum* (Mortenson et al. 1962), work in Dan Arnon's lab rapidly established that this protein was the initial electron acceptor at photosystem I, capable of transferring these electrons either to NADP⁺ photoreduction or returning them to the electron transport chain in a “cyclic” electron flow (Tagawa et al. 1963). As such, ferredoxin occupies a unique position in photosynthesis: it is “of the membrane”, but not “in the membrane”; a mediator and messenger between the thylakoid and stroma. The properties of this simple 10 kDa protein determine how the vast flux of reducing power generated by the intricate machinery of the thylakoid membrane is distributed and consumed.

I began working on ferredoxin in my first Post-Doc, with Toshiharu Hase at the Institute of Protein Research in Osaka University. Work by the Hase laboratory had been fundamental in establishing that photosynthetic organisms contain multiple different kinds of ferredoxin (Hase et al. 1991) and proving that these ferredoxins differed in electron transfer properties (Onda et al. 2000; Yonekura-Sakakibara et al. 2000). In addition to supporting NADP⁺ reduction by the ferredoxin:NADP⁺ reductase (FNR), ferredoxin is capable of donating electrons to multiple other enzymes in a wide range of pathways (Hanke and Mulo 2013). The current list

of ferredoxin dependent enzymes is certainly not exhaustive and, as more chloroplast and cyanobacterial redox enzymes are characterized, it will surely be extended. At this time in the Hase laboratory, enzymatic studies were being combined with structural work to unpick the molecular mechanism of electron transfer between ferredoxin and various enzymes, and to identify the basis of ferredoxin specificity (Kurusu et al. 2001; Saitoh et al. 2006). This special issue contains one such manuscript, with the groups of Yoko Kimata-Arigo and Genji Kurisu collaborating to elucidate the molecular basis for the specific interaction of root type ferredoxin and FNR, which enables efficient electron transfer in the reverse direction to that seen in photosynthesis (Shinohara et al., this issue).

It was at the IPR that I first met David Knaff, former Editor-in-Chief of *Photosynthesis Research*, whose interest in the ferredoxin-dependent enzymes nitrite reductase and glutamine oxoglutarate amidotransferase (Fd-GOGAT) had drawn him into collaboration with the Hase group. Years later he visited me in Osnabrück, Germany, where I was an assistant professor. Over a glass of wine he suggested that I guest edit a special issue of *Photosynthesis Research* on ferredoxin, and even agreed to contribute a manuscript. I am now proud to be writing the introduction of this special issue, and especially proud that it contains a contribution on ferredoxin–GOGAT interaction from the Knaff lab, written by his former co-workers Masa Hirasawa and Richard ‘Max’ Wynn (Hirasawa et al., this issue) after his untimely passing.

Photosynthesis has been classically described as consisting of “light reactions”, which generate energetic components and “dark reactions”, which consume them in order to drive bioassimilation. Just as ferredoxin uniquely shuttles electrons between components of these two great fields of research, scientists who study ferredoxin also find themselves continually shuffling back and forth between “light”

✉ Guy Hanke
g.hanke@qmul.ac.uk

¹ School of Biological and Chemical Sciences, Queen Mary University of London, London, UK

and “dark” sessions at conferences. Understanding how ferredoxins can potentially control the flux of photosynthetic power into different pathways, and even the extent of the proton motive force by driving cyclic electron flow, demands that we solve fundamental research questions in both research areas. This special issue on ferredoxin combines reviews and experimental work in a set of excellent contributions on both the supply of electrons from photosynthesis and their consumption in bioassimilation.

While [Pierella Karlusich and Carrillo](#) (this issue) review evidence that oxygenic photosynthesis necessitated the evolution of oxygen insensitive electron carriers such as ferredoxin and its functional counterpart flavodoxin, [Migné et al.](#) (this issue) present data revealing how the interaction of ferredoxin with photosystem I modulates electron transfer within the photosystem. Recent advances in our understanding of how electron transfer occurs between ferredoxin and its principle partner enzyme, FNR are reviewed by [Mulo and Medina](#) (this issue), who also discuss an ongoing puzzle in the field—how FNR localisation both at the membrane and as a soluble enzyme could impact on electron transfer around photosystem I. Data relating to this problem in the alga *Chlamydomonas reinhardtii* are presented by [Mosebach et al.](#) (this issue), who compare the impact of FNR membrane association on electron transfer with different ferredoxin iso-proteins. *C. reinhardtii* is notorious for its extensive ferredoxin complement (Terauchi et al. 2009), and recent findings on different *C. reinhardtii* ferredoxins are reviewed by [Sawyer and Winkler](#) (this issue), who focus on the longstanding problem of optimizing electron flux away from FNR into alternative pathways, such as bio-hydrogen production. As Synthetic Biology seeks to manipulate chloroplast and cyanobacterial metabolism, to increase flux through specific biosynthetic pathways and drive synthesis of novel products, tuning ferredoxin interactions is increasingly seen as a powerful tool. [Mellor et al.](#) (this issue) review evidence that ferredoxin is capable of electron donation to heterologous enzymes, and outline a vision of how the protein could be used in the future for Synthetic Biology purposes. Finally, [Schreiber](#) (this issue) describes data generated with a recently developed DUAL/KLAS-NIR spectrophotometer, capable of following the redox state of ferredoxin in intact leaf tissue. This equipment could add a new dimension to studies on the acceptor side of photosystem I, and the onus is now on the research community to test the limits of this exciting new tool and to apply it appropriately.

Great thanks are due to the authors for their outstanding contributions and patience in the reviewing process and

issue preparation, and to all the reviewers for their constructive and informative comments. We acknowledge the initial idea for the special issue from David Knaff (former Editor-in-Chief) and the help and encouragement of Terry M. Bricker (current Editor-in-Chief) in continuing this process and realising its eventual production. We are very grateful to Ellen Klink and Jaap van der Linden of Springer for their help during the production of this special issue.

Perhaps the last word should go to David Knaff. When we first met and after I had given a slightly over-enthusiastic explanation of my current research project: “Listen”, he said, “as Dan Arnon’s former Post-Doc, I have no problem with the idea that ferredoxin is the center of the universe”.

References

- Hanke G, Mulo P (2013) Plant type ferredoxins and ferredoxin-dependent metabolism. *Plant Cell Environ* 36(6):1071–1084. doi:[10.1111/pce.12046](#)
- Hase T, Kimata Y, Yonekura K, Matsumura T, Sakakibara H (1991) Molecular cloning and differential expression of the maize ferredoxin gene family. *Plant Physiol* 96(1):77–83
- Kurisu G, Kusunoki M, Katoh E, Yamazaki T, Teshima K, Onda Y, Kimata-Arigo Y, Hase T (2001) Structure of the electron transfer complex between ferredoxin and ferredoxin-NADP(+) reductase. *Nat Struct Biol* 8(2):117–121. doi:[10.1038/84097](#)
- Mortenson LE, Valentine RC, Carnahan JE (1962) An electron transport factor from *Clostridium pasteurianum*. *Biochem Biophys Res Commun* 7:448–452
- Onda Y, Matsumura T, Kimata-Arigo Y, Sakakibara H, Sugiyama T, Hase T (2000) Differential interaction of maize root ferredoxin:NADP(+) oxidoreductase with photosynthetic and non-photosynthetic ferredoxin isoproteins. *Plant Physiol* 123(3):1037–1045
- Saitoh T, Ikegami T, Nakayama M, Teshima K, Akutsu H, Hase T (2006) NMR study of the electron transfer complex of plant ferredoxin and sulfite reductase: mapping the interaction sites of ferredoxin. *J Biol Chem* 281(15):10482–10488. doi:[10.1074/jbc.M510530200](#)
- Tagawa K, Tsujimoto HY, Arnon DI (1963) Role of chloroplast ferredoxin in the energy conversion process of photosynthesis. *Proc Natl Acad Sci U S A* 49:567–572
- Terauchi AM, Lu SF, Zaffagnini M, Tappa S, Hirasawa M, Tripathy JN, Knaff DB, Farmer PJ, Lemaire SD, Hase T, Merchant SS (2009) Pattern of expression and substrate specificity of chloroplast ferredoxins from *Chlamydomonas reinhardtii*. *J Biol Chem* 284(38):25867–25878. doi:[10.1074/jbc.M109.023622](#)
- Yonekura-Sakakibara K, Onda Y, Ashikari T, Tanaka Y, Kusumi T, Hase T (2000) Analysis of reductant supply systems for ferredoxin-dependent sulfite reductase in photosynthetic and nonphotosynthetic organs of maize. *Plant Physiol* 122(3):887–894