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OBITUARY

László Mustárdy (1945–2022)

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László Mustárdy, the former scientific adviser of the Biological Research Centre (BRC), Szeged, Hungary, died of cancer at the age of 77 on 20 April 2022. After graduating in Biology and Geography at the Attila József University (JATE, today, the University of Szeged) in 1969, he started as an assistant research fellow, recruited for the Institute of Plant Physiology (later Plant Biology) of the BRC, which officially opened in 1971. Laci (alias László) joined the Photosynthesis Laboratory of Ágnes Faludi-Dániel (1929–1986), a team of young researchers – physicists and biologists – all in the early years of their scientific careers. Except during his visits abroad, Laci remained an employee of the BRC (Fig. 1), from where he retired in 2010; between 2000 and 2007, he also served as a professor and chair of the Department of Plant Physiology at the Eszterházy Károly College, Eger, Hungary.

In photosynthesis research, in the early 1970s, one of the main problems was to understand the structure and functions of the thylakoid membranes (TMs) of chloroplasts of vascular plants. Laci, with his great skill and legendary patience, took care excellently of the tasks of electron microscopic ultrastructure (Mustárdy *et al.* 1976, Bialek *et al.* 1977, Horváth *et al.* 1978). Being puzzled by the numerous – often contradictory – models, he set his sights on the organization of granal chloroplasts, the assembly of granum and stroma thylakoid membranes, the most abundant membrane system in the biosphere. He had the ambitious goal to explore the 3D ultrastructure of grana. This dream came true in the Laboratory of Judy Brangeon (Université Paris-Sud XI, Orsay, France), where he performed a full serial thin-sectioning electron microscopy (EM) of a pair of granum–stroma TMs of a *Lolium multiflorum* chloroplast and constructed a 3D model of grana (Mustárdy and Brangeon 1978, Brangeon and Mustárdy 1979). Their model confirmed the basic claims of the helical models of Heslop-Harrison (1963), Wehrmeyer (1964), and Paolillo (1970) but it substantially refined them. In particular, it was shown that the stroma TMs cannot be envisioned as large sheets interconnecting the grana but are instead strips wounding around each granum disc. It also became clear that the granum and stroma TMs are jointed together *via* slits around the rims of the granum and that adjacent granum–stroma TM assemblies are joined merely *via* narrow fusion of the helices. Most remarkably, Laci constructed a palm-size 3D model, carefully glued together from proportionally tailored thin polyfoam-textile 'membranes' – a fascinating model that one could hold and look at from all angles (*see* Fig. 5 in Mustárdy *et al.* 1996). The computerized version of this model showed that this highly organized membrane structure can be easily constructed from relatively simple, overlapping elements of TMs (*see* Fig. 4 in Mustárdy and Garab 2003). The same helical array was excellently visualized by scanning EM (Mustárdy and Jánossy 1979) and freeze-fracture EM (Staehelin 1986). Later works of electron tomography revealed fine details about the 3D ultrastructure of this membrane system (Mustárdy *et al.* 2008, Daum *et al.* 2010, Austin and Staehelin 2011, Bussi *et al.* 2019). The spectroscopic and

Fig. 1. László Mustárdy. Photograph taken in 2000 for his BRC ID card; provided by BRC.

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Fig. 2. László Mustárdy at the *Zeiss CEM 902* electron microscope of the BRC. The photo was taken by the author in 2003.

photophysical properties and their remarkable structural plasticity of grana are still puzzling many scientists (Lambrev and Akhtar 2019, Staehelin and Paolillo 2020, Ünnep *et al.* 2020).

Regarding the correlation between the ultrastructure and the spectroscopic and functional properties of grana, Laci was particularly interested in the origin of the giant circular dichroism (CD) (Rózsa *et al.* 1980, Faludi-Dániel and Mustárdy 1983). His works significantly contributed to the recognition that the ('giant') psi-type CD, following the theory of Keller and Bustamante (1986) on psi-type aggregates, is associated with the 3D, multilamellar organization of TMs and the lamellar aggregates of purified light-harvesting complex II (Barzda *et al.* 1994, Simidjiev *et al.* 1997, 2000; Garab and Mustárdy 1999, Garab *et al.* 2002, Szabó *et al.* 2008). He also established interesting correlations between the development of granal ultrastructure and some other spectroscopic features as well as the energization of membranes (Faludi-Dániel *et al.* 1986) and revealed ultrastructural changes due to saturation of double bonds of TM lipids (Horváth *et al.* 1986).

Another major area of research where all his talents and skills were needed was immuno-EM, which he elaborated on in the Laboratory of Elizabeth Gantt (University of Maryland, College Park, MD, USA). He was the first to determine the localization of seven different chloroplast proteins in one organism, *Porphyridium cruentum* (Mustárdy *et al.* 1990); he also developed the technique of quantitative *in situ* immunolabeling of photosystems I and II (Mustárdy *et al.* 1992). Later, in the Laboratory of Norio Murata (National Institute for Basic Biology, Okazaki, Japan), his immunocytochemical work led to the localization of acyl-lipid desaturases in cyanobacterial cells (Mustárdy *et al.* 1996) and the choline oxidase in *Arabidopsis thaliana* (Hayashi *et al.* 1997).

Besides these seminal works, Laci participated in many projects in the BRC and abroad – in each, he contributed significantly to the essence of the works, mainly with his high-quality EM images (Fig. 2). However, he also participated in discovering the alternative pathways of hexose metabolism (Black *et al.* 1987) (in the Laboratory of Clanton Black, University of Georgia, Athens, GA, USA) and chlororespiration in higher plants (Garab *et al.* 1989) (in the BRC). He was also deeply involved in exploring the origin of the non-random orientation of the pigment dipoles in prothylakoids and mature TMs (Garab *et al.* 1980, 1981; Szitó *et al.* 1984). In a series of works, he investigated the effects of chilling – focusing on the stomatal behaviour of chilling-exposed maize and grapevine leaves (Vigh *et al.* 1981, Bálo *et al.* 1986), and encountered a mechanism of protection against chilling injury of plants – by low doses of diuron (Mustárdy *et al.* 1982, 1984). His EM works helped elucidate the role of compatible solutes, such as proline and betaine, in salt tolerance and proper division of cyanobacterial cells (Ferjani *et al.* 2003) and salt tolerance of plants (Sulpice *et al.* 2003). In his last work, in a project with Dima Los, his friend and colleague from Okazaki, they proved that the AqpZ aquaporin of *Synechocystis* participates in the regulation of the photosynthetic activity of the two photosystems under salt and high-light stress and that this water-channel protein might be necessary for their repair mechanisms (Sinetova *et al.* 2015).

The scientific community of photosynthesis research will remember for a long time the achievements of László Mustárdy. Those who had the privilege to work with Laci, and/or to spend leisure time with him, will cherish memories of his friendly and modest personality and good humour. We all sense a deep loss.

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