

EDITORIAL

Professor Peter J. Lea: The man, the scientist

Professor Peter John Lea (Figure 1), PhD, Emeritus Professor at Lancaster University, passed away on 16 June 2024. Tributes such as the one by Lancaster University (<https://portal.lancaster.ac.uk/intranet/news/article/professor-peter-lea-phd-dsc-liverpool-fibiol>), among others, have been paid to him soon after and an announcement was published on the website of *Annals of Applied Biology* (<https://onlinelibrary.wiley.com/journal/17447348>).

Peter was a highly esteemed colleague, former *Annals* Senior Editor, and a dear friend. He retired as Emeritus Professor of Lancaster University and was renowned not only in his field, but well beyond.

Peter Lea received his BSc, PhD and DSc from the University of Liverpool in the late 1960s. He was a postdoctoral research fellow in the Department of Botany and Microbiology at University College London from 1970 until 1973. Following this he worked for almost 12 years in the Biochemistry Department at Rothamsted Experimental Station, now Rothamsted Research (<https://www.rothamsted.ac.uk/>). In 1985 he moved to Lancaster where he worked at Biological Sciences Department, now Lancaster Environmental Centre (<https://www.lancaster.ac.uk/lec/>—Figure 2), Lancaster University (<https://www.lancaster.ac.uk/>), as Professor of Biology until his retirement over 20 years later. His main research interests have been the pathways and mechanisms by which plants are able to take up nitrogen and convert it to amino acids and proteins that are used as animal and human food.

Peter's work on nitrogen assimilation was extremely relevant to crop improvement and to the work on nitrogen metabolism ever since. The discovery of glutamate synthases (E.C. 1.4.1.13 and E.C. 1.4.7.1) caused a major re-assessment of the way in which ammonium is assimilated in bacteria and higher plants. Two key articles (Lea & Mifflin, 1974; Mifflin & Lea, 1976) published with his colleague Prof. Ben Mifflin are classical citations. He has also contributed with a significant amount of important work to the advancement of plant stress responses to abiotic stresses (Gratão et al., 2005), amino acids metabolism (Azevedo et al., 1997) and photorespiration (Keys et al., 1978).

Peter was also heavily involved in numerous other activities and was a member of the Association of Applied Biologists (<https://www.aab.org.uk/>) as President Elect 2005–2006 and President 2007–2008. He was also an *Annals of Applied Biology* Senior Editor for Crop Improvement for almost 12 years. He was a mentor to many students, scientists and editors.

He published/edited dozens of books and book chapters and over 300 papers. He also left his mark publishing important papers in *Annals* such as “Asparagine in plants” (Lea et al., 2007), which is the 8th most cited paper of the journal in its 110 years.

Peter will be missed. We all worked together with him and although science united us, a true friendship kept us together for decades! A remarkable scientist and man who will be missed.

1 | RICARDO AZEVEDO

Peter was my PhD supervisor in Lancaster (1988–1992). I also spent just over 1 year (1996–1997) working with him as a post-doc in his lab. The PhD was on amino acids metabolism and the post-doc on ozone-induced stress in plants.

Over the last three 3 months I have exchanged so much information about Peter with his colleagues and daughter, Julia Lea. I revisited our work, our trips together, our photographs.

When I first met Peter: I arrived in Lancaster on a Friday sunny early evening, 12 August 1988. I had only exchanged a couple of Fax messages with him (he had accepted me as a PhD student on 12 January 1988, my birthday—what a present!). After a 5-minute talk at the Lancaster University Reception House, Peter got me a room at Furness College and told me to meet him at the department the next day, 12 noon Saturday, when we talked about the idea I had for my PhD project, and he also gave a tour in the department. On Sunday he had me for dinner with his wife Christine and daughter Julia! On Monday 9 am he asked his secretary to help me opening a bank account, with the University's accommodation service office in getting me accommodation for the following four weeks and a flat on campus for my family from September on. That was the beginning of a strong working relationship and also a friendship that only grew over the years.

The PhD: My project was on lysine and threonine metabolism in maize. I managed to complete it, write the papers and also help other students in less than 4 years. One curious thing happened during the thesis defence: it started at 9 am, a very short break of 1 h for lunch, and it was finally over around 5:20 pm. I was told by my co-supervisor, R. John Smith, that Peter was walking about the department wondering what was going on! It should not have lasted more than 2–3 h. But all was fine, no changes to the thesis and both members were very pleased with the work.

Peter was a special man: There were many overseas students and others from Europe and Asia in the department and on the last week of the year, between Christmas and New Year, he would invite all of us to his house one night for a kind of “Christmas Dinner” with his family. He knew that was important especially for us who were literally by ourselves in the UK. I had my wife Jacqueline and my two-



FIGURE 1 Professor Peter John Lea, BSc, PhD and DSc from the University of Liverpool, and Emeritus Professor at Lancaster University.



FIGURE 2 Peter Lea in front of the entrance of the Lancaster Environmental Centre, Lancaster University, 2018.

years-old daughter Juliana, and two years later my son Rogério, and every year we waited anxious for that dinner at his house.

He was always very kind to me and to my family. He kind of looked after us while there and even after we got back to Brazil. He took me under his wing! In 1993 I got my job at the University of São Paulo and just could not be happier. We carried on collaborating on his and my projects, we got grants together in the UK and in Brazil, and we visited each other numerous times in the following years, at least 2–3 times a year. The visits were very special too because most times I would have Jacqueline with me and he would have Christine with him, so we always managed to get work done, but we also had time together with our families. I remember how excited he was on a day trip we did to the Wedgwood Visitor Centre (Figure 3); he was an avid Wedgwood collector! It was common when I was travelling to Europe for a conference or something else, and Peter alone or with Christine, would take the weekend to join me or me and Jacqueline, wherever we were! We met in so many places and some of them were truly special such as the weeks in Vienna and in Paris when we had some free extra days after conferences we were attending. The same was true when we were in Brazil and we managed to travel to a few places, such as the five-day trip to Rio de Janeiro where he insisted on staying in a hotel with a room with a balcony on Copacabana beach; the name of the hotel was Lancaster Othon Palace, and while Christine and Jacqueline would go for long walks on the beach, we

would sit on very comfortable chairs on the balcony, he would light a cigar, lots of coffee, and we would do some work and even have people visiting us to discuss their research, science in general.

The collaboration was prolific. Peter received several of my former PhD students in his lab for periods of 6–18 months as part of their PhD training. We published almost 50 papers together and some book chapters. During my post-doc in Lancaster I worked on ozone stress with the low catalase barley mutant mentioned below by Alf Keys, and only some months later when I was already back in Brazil, while waiting for me at the reception of the hotel in Piracicaba during one of his visits to my lab, he found a local magazine and tried to read it. When I arrived at the hotel's parking lot he got into the car and said before anything else: “you should read this” and gave me the magazine. “I hope they don't mind I took it!”. He said he could not understand the text in full, but it was about heavy metals (Cadmium and Barium) contamination of the Piracicaba river. He was absolutely correct and that was the beginning of our joint work on heavy metals stress in plants.

Peter was also the one that took me to the “editorial world” by suggesting my name to Martin Parry, who was then *Annals* Editor-in-Chief and who was introduced to me by Peter during a conference in Southampton in 2003, as an associate editor for *Annals* in 2006. What a journey and it became my favourite part of science. Working side-by-side with Peter, Martin and so many good editors was, and has been, something to be thankful for.



FIGURE 3 Peter Lea, an avid Wedgwood collector, visiting (and shopping!) at the Wedgwood Visitor Centre.

Working with him was so good! I could go on here with hundreds of stories we have since we met in 1988, but I will wrap this up with two moments that marked me profoundly. I was in Lancaster attending the Nitrogen 2007 Conference (Figure 4), which was organized by Peter and others. A few days after it was over, I was still in Lancaster and on a sunny afternoon, Peter got a call from my daughter Juliana who asked him to let me know that my dad had passed away. He and John Smith did what they could to comfort me over the following two days before I left Lancaster. The other moment was in 1997 when I was a post-doc in Lancaster. I suggested that we had to write a review article on the aspartic acid metabolic pathway, a topic we were working on for 9 years. He agreed and he proposed a way to do it: we divided the work and we would write our parts in our own time, but two times a week, after 9 pm, we would meet and sit side-by-side in his office by the computer and put the text together, literally writing and complementing each other's texts and words, checking the literature, etc. We did it in a few weeks and the last bit was to add the two other parts written by two other colleagues. It was such a great fun and a learning experience. When it was published, he left a hard

copy of the *Phytochemistry* issue on my bench in the lab with a yellow sticker on the first page of our paper saying: "Congratulations, absolutely magnificent." That was Peter! I keep that yellow sticker in a safe place at home.

I apologize if my text is too personal, but Peter was my mentor, my best friend and the model of a true brilliant man and scientist I tell my students to follow. I remember everyone excited in the lab when they knew that "Prof. Peter Lea is coming to Piracicaba to visit the lab"! It is a thank you Peter for making me and my family's lives better and sharing 36 incredible years together with you, Christine and Julia. My admiration and respect for you cannot be measured.

2 | MARTIN PARRY

I first met Peter at Rothamsted when I was a new graduate student and frankly found his knowledge, boundless energy, and enthusiasm a bit intimidating. He was definitely a competitive, larger than life character who always had a finger on the pulse and knew what everyone was doing often even before they did themselves.

Over the years I got to know Peter better, we collaborated on a number of projects and he became a close friend and mentor (Figure 5). Peter was a good strategist and always had a plan so that we ended every meeting or discussion with action points so that everyone was clear with what they were doing, how they were doing it and by when. He was demanding but really cared for and supported his colleagues and ensured that they all got the recognition they deserved.

When I became EIC of *Annals of Applied Biology* Peter was the first person that I co-opted to the editorial board where he continued for many years as a senior editor ensuring the work that was published was of the highest standards and helping authors achieve that quality.

3 | BEN MIFLIN

I first met Peter Lea in 1973. He was then on a Pickering Fellowship of the Royal Society with Leslie Fowden who had recently been appointed Director of Rothamsted Experimental Station. I took up my position as Head of the Biochemistry Department there later that year and Peter joined the Department. Peter had been working on non-protein amino acids and the specificity of tRNA synthases. However, it was not long before Peter and I started a long collaboration on the way plants assimilate nitrogen. Peter had done a PhD on glutamate dehydrogenase with David Thurman in Liverpool and was not enthusiastic about its role in N assimilation in leaves. I had spent a sabbatical in Harry Beevers' lab separating and studying the distribution of enzymes in root and shoot plastids. The results suggested that GDH was not the route for N assimilation but that chloroplasts had plenty of glutamine synthase and the full range of enzymes to convert nitrate to glutamine. Prior to my sabbatical I had worked in Newcastle University and shared equipment with Charlie Brown who had told me of



FIGURE 4 Nitrogen 2007 Conference held at Lancaster University. (a). Peter Lea and Ricardo Azevedo. (b). Ben Mifflin, Ricardo Azevedo and Peter Lea. (c). Ben Mifflin, Bertrand Hirel and Peter Lea. (d). Peter Lea and Bertrand Hirel.

his discovery of Glutamate Synthase (GOGAT). Peter and I became convinced this enzyme could solve the problem if we could demonstrate it in plants and particularly chloroplasts. Attempts to use the previous assays with NADH or NADPH as donors failed. Peter worked out a chromatographic assay for glutamate and we decided to use ferredoxin as a donor. In those days this was not available from chemical suppliers but David Hall of Kings College kindly donated a supply and it worked as a donor to catalyse the production of glutamate from glutamine. Fifty years later the route of nitrogen assimilation in plants that we proposed still holds.

Peter was always interested in surveying and reviewing the literature, which gave him a broad view of the field and was always useful in provoking discussion and suggesting approaches to any problem. He wrote a number of reviews with Rothamsted colleagues during and after his time there; our last joint review was published in 2011.

He was also very open and cooperative which led to many research projects with visiting workers who came to Rothamsted. Many of these focused on his interest in asparagine metabolism, a theme that continued in collaboration with Rothamsted long after he had left for Lancaster.

Peter had a passion for playing sport—virtually any sport that was available in Rothamsted's social domain. We were both members of

the cricket team in which we were joined by Alf Keys which gave us plenty of time for discussions and these led on to the topic of nitrogen reassimilation. Alf and I had both worked with Charles Whittingham on the flow of carbon through glycine and serine in photorespiration. The main concern about this pathway in the literature was over the loss of carbon dioxide. The parallel loss of ammonia was virtually ignored. This led to research that resulted in us proposing the photorespiratory nitrogen cycle.

4 | ALFRED KEYS

Peter reminded me frequently that on his first day of work at Rothamsted in October 1973 he attended a seminar given by me in which I talked about the conversion of glycine to serine with ammonia as one of the products in leaves. Mifflin asked the question: what happens to the ammonia? Much to Peter's delight I said the two of them knew the answer and in fact the GS/GOGAT cycle was shown on the complex slide I used showing how photorespiration was an intimate part of photosynthesis. With colleagues, I had been assaying all the enzymes believed at that time to be involved in glycolate metabolism with special interest in the activities in relation to published rates of



FIGURE 5 Alfred Keys, Peter Lea and Martin Parry at Rothamsted Research in 2003.

photorespiration. They were surprised that this meant ammonia production so fast, certainly faster than activity of glutamic dehydrogenase.

Inter-Department competitions on the Sports field were regular events and Peter was highly competitive in these as in science and took part happily. He also expected the Department team to be strong and it was rumoured that interviews for prospective new staff were conducted on the Sports Field. He also often played in cricket matches with the Rothamsted club in the evenings against various local clubs.

Peter decided that he wanted to look for mutants in the enzymes involved in glycolate metabolism in barley following the example of the selection of mutants by the Somerville's in *Arabidopsis*. Seeds were treated with a mutagen and germinated in the constant environment rooms at high CO₂. On transfer to rooms with lower concentrations, seedlings showing distress were selected and extracts made for assay of enzymes. Peter was rather disappointed to first find a seedling that had low catalase rather than deficiencies in enzymes of the GS/GOGAT cycle but proceeded to investigate the mutants and used tissue from them to produce a spectacular demonstration. Professor Whittingham was not impressed with the work as it used facilities and staff normally regarded as Botany Department. It did fit with interests of the Biochemistry Department where mutation of Barley was already being used.

When Whittingham retired the Botany Department ceased to exist and it was clear that the Bawden Building laboratories occupied by

some of us would become vacant; Peter, ever aware of developments, could be seen walking the corridors deciding where he might find space, highly superior to the rooms occupied by Biochemistry.

5 | BILL DAVIES

After 12 very successful years as a researcher at Rothamsted Research, Peter Lea joined the faculty at Lancaster University. He came with a strong reputation as a plant biochemist and brought new teaching and research strength to the Department. He very quickly established an active research group and Peter's extensive professional collaborations and profile with several professional societies meant that the group quickly broadened and thereby strengthened the reputation of Lancaster as a centre of excellence in Plant Science. Peter was an assiduous research supervisor and he developed many collaborations across the Department, particularly with colleagues in air pollution research. He worked hard and played hard, never more so than in intra-Departmental Cricket matches. Over the years a group in the Department fell into the habit of travelling to Old Trafford (not the football stadium!) and Headingley to watch Test Cricket. At one Ashes Test on a particularly wet, windy and cold Leeds day, one of our joint research students (who hailed from a part of the world where Cricket is not a national preoccupation), asked how long the day's play would last. When told that we would likely be there for another 6–7 h, she

looked as if she was seriously considering a career in something other than plant biochemistry.

In 2007, after several years of discussion, some faculty from Biological Sciences at Lancaster joined with colleagues from the Departments of Environmental Sciences and Geography to form the Lancaster Environment Centre (LEC). Colleagues from NERC-CEH moved onto campus as part of the evolving LEC. The new structure broadened and grew Lancaster's capacity in a range of existing and new disciplinary areas of environmental concern. When the opportunity arose to recruit prominent new staff, Peter was influential in helping to convince Martin Parry and members of his Photosynthesis team to join the Environment Centre. This was a key development for LEC and this group has grown, attracted substantial outside funding and made significant scientific advances as part of a high-profile international team addressing the world's food security crisis.

6 | ADAM PRICE

I was sad to hear of Peter's passing for a number of reasons that centre on the fact that Peter actually gave me my first job. I started as a postdoc on a 12-month contract in 1988 under his supervision in the Biology Department at Lancaster. I was working on the impact of ozone on plant reactive oxygen biochemistry, so a bit outside his core expertise in nitrogen metabolism. He was a very supportive supervisor, allowing me a lot of space to do what I wanted while instilling in me the need to publish, which I tried to hold on to through my career. I have to say though that his interest in H factors was both earlier and

deeper than my own. I have a strong memory of chatting in his freezing cold office while he smoked a cigar, him helping me write my first paper and the only one we were co-authors on. He had infectious enthusiasm and a great sense of humour, and encouraged me to embrace the joys of the SEB annual conference where I had one of my best scientific ideas. I am forever grateful to him for the position, and the opportunity to mix with the great minds that were in the Biology Department in Lancaster at the time that proved influential for me. It turned out I never left the UK university system that Peter inducted me into. All the very best to Peter's family.

7 | BERTRAND HIREL

In 1974, the chloroplast enzyme glutamate synthase (GOGAT) was identified in plant tissues by Lea and Mifflin (1974) at Rothamsted Research Station. Such discovery drastically changed the existing ideas regarding the pathway of nitrogen assimilation in plants, because it was previously considered that the enzyme glutamate dehydrogenase was involved in this metabolic function. Following the discovery of the ammonium assimilatory pathway, also involving another enzyme called glutamine synthetase (GS), it was thought that this was present as a single protein species likely and located in the plastids. Following the demonstration that in higher plants, ammonia is incorporated into organic molecules via the GS/GOGAT pathway, the occurrence of two types of glutamine synthetase isoenzymes, one located in the cytosol (GS1) and the other in the plastids (GS2) was demonstrated.



FIGURE 6 Rank Prize Funds Symposium in Grasmere (2006) “Can we improve nitrogen use efficiency in cereals.” Left to right: Reaching the top of the hill in Grasmere and in plant science: Peter Shewry, Bertrand Hirel, Peter Lea, Keith Goulding and Malcolm Hawkesford.

In 1981 at a meeting of the Society for Experimental Biology in Leicester, during which I gave my first talk in a foreign country, I was arguing about the proposal from the Rothamsted group that photorespiratory ammonium was reassimilated via the cytosolic GS isoenzyme. Our results ruled this out for many species, leaving a role in the photorespiratory N cycle for chloroplastic GS. This marked the beginning of an increasing number of informal and friendly scientific exchanges with Peter and co-workers mostly at meetings and symposia (Figure 6). Much later on, we managed to concretize these scientific exchanges by a very productive period of collaborative research, leading to the publication of more than 20 joint papers and book chapters from 2006 to 2023. Such scientific collaboration also led to the development of a friendship which was no less rewarding-scientifically, gastronomically, and enologically, notably during the co-organization with Peter of the 6th International Symposium on Inorganic Nitrogen assimilation which took place in Reims in 2001.

Among the number of studies performed in collaboration with Peter, the most remarkable was to demonstrate that an increase in grain yield was obtained in maize plants overexpressing GS1 whereas a reduction in yield was observed in mutants deficient for the enzyme (Martin et al., 2006). Such collaboration illustrates how rewarding collaborative science can be, and how Peter was able to put a determining impulse for the development of such a fruitful collaboration and for its achievement.


Interestingly, both Peter and I, at the end of our career, decided trying to elucidate the exact physiological role of GDH, even if it was finally admitted that the enzyme played a marginal role during the ammonia assimilation process. A number of these studies allowed to demonstrate that GDH is rather involved in the recycling of carbon molecules to plant tissues that are carbon limited (Fontaine et al., 2012). We even managed to publish, as he used to say, “a very last paper on GDH” in 2023 (Tercé-Laforgue et al., 2023) in which we evidenced the role of the enzyme in maize productivity, proving again that Peter was, more than ever, keen on studying plant science and nitrogen.


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