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"Listen to the trees!" A tribute to the father of modern cavitation research, Professor John Milburn, on the 20th anniversary of his untimely death

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Abstract

Over the last 35 years, the study of cavitation in plants has become an accepted and important component of the water stress studies performed by plant physiologists. Although the existence of cavitation had been known since Berthelot's (1850) pioneering work on the tensile strength of water in glass tubes, the tensions at which it occurred in such systems were far more negative than were considered likely to occur in plants. It is to the late Professor John Milburn's sharp observational powers, lateral thinking and problem-solving approach — illustrated by his pioneering detection of cavitation in plants — that we owe today's field of cavitation research. John Milburn was constantly thinking of new ways to approach and solve plant physiological problems. In 1966, Milburn and Johnson published their seminal work on the occurrence of cavitation in plants, using data collected via a record player needle and an amplifier. After the invention of the Scholander pressure chamber (Scholander et al., 1965), it became possible to measure easily the xylem pressures at which plants cavitated. Milburn and McLaughlin (1974) found that such pressures were within the physiological ranges that plants experienced and so the phenomenon of cavitation in plants under stress became a fruitful field of research.

Professor John Milburn was tragically killed in a flying accident in 1997. The premature loss of such a great scientist, aged only 60, was felt keenly in the Botany Department of the University of New England, Armidale, Australia, where he had been a Professor for 16 years, and also around the world. This article is a tribute to Professor John Milburn, encompassing several of his key discoveries (a rare recording of the sound of cavitation occurring in the audible range is included in this tribute), as well as some of the many aspects of the man. It is timely, on the 20th anniversary of his death, to remind ourselves that today's experimental water stress research would be the poorer without John Milburn's pioneering work.

Introduction

"The man o' independent mind, he looks an' laughs a' all that",
from "A man's a man for a' that" – Robert Burns (1759–1796)

The above quotes were used in two of the late Professor John Milburn's works. "Listen to the trees!" was the title of a lecture he regularly gave to first year biology students at the University of New England, Armidale, Australia; the Robert Burns quote was one that he chose to begin a commissioned, and nearly completed, work for the *New Phytologist*

Tansley Lecture (unpublished). These two quotes, particularly when taken together, encapsulate the phenomenon that was John Anthony Milburn.

Part of the aim of this tribute, on the 20th anniversary of Professor John Milburn's tragic death in 1997, is to focus anew on the many discoveries that he made which have furthered our understanding of plant physiology. It is important to remind ourselves, as well as educate those new to the area of xylem research, that without his original and lateral thinking, we would not have the required depth of knowledge that enables us to delve into the many mysteries that remain in understanding xylem function and how plants adjust to water stress. The other aspect that this tribute will cover is some of the many facets of the man, to give readers who did not have the privilege of knowing Professor Milburn an insight into his personality and character.

Undoubtedly, John Milburn's greatest discovery was to provide direct, acoustic evidence of cavitation in plants. An example of the sounds, which he termed 'clicks', is provided herein. His seminal work was published in 1966, but the acoustic signals were first heard by John Milburn on 6 February, 1963 and were based on observations and hypotheses made over the previous months of his PhD studies. He had noticed differences in the water uptake patterns of water-stressed petiolar leaves compared with leaf discs, the latter not requiring water transport via key xylem conducting elements. Thus, he inferred, and set about testing, that cavitation had occurred in the petioles, which constrained the whole leaves' ability to take up water via the xylem conduits compared with across the mesophyll of the leaf discs. Previously, cavitation was considered to occur only at exceedingly negative water potentials, as shown by physicists' studies (for example, Briggs, 1950), suggesting extreme and unlikely conditions of water stress in plants. However, John Milburn's ingenious technique for detecting cavitation acoustically showed that it was of a much more common occurrence and could take place at the physiological pressures experienced by plants. The frequency of sap flow disruption was encapsulated in one of the chapter titles of John Milburn's book, *Water Flow in Plants* (1979): "Xylem – the vulnerable pipeline". Monitoring the incidence, frequency and repair of water flow disruption in the xylem by using John Milburn's cavitation detection methods only added to the robustness of Dixon and Joly's (1894) Cohesion Theory and their discussion of air bubble dissolution.

It is this author's belief that one cannot truly compartmentalise any life, particularly that of someone such as Professor John Milburn. Nevertheless, for clarity, this tribute is divided into sections in which I hope to provide some insights into the many aspects of the man. What follows is a combination of facts and memories from the author's personal experiences of having studied and worked under the tutelage of Professor Milburn (known as "Prof." to his students) for the last 13 years of his life and the many conversations that we shared during that time.

Education and PhD Studies

John Anthony Milburn was born in Carlisle, Cumbria, UK on 7 August, 1936 and attended Carlisle Grammar School. He was enrolled at King's College, University of Durham from 1955–1958, where he graduated with a BSc (Hons) in Botany. After his graduation, he worked as an agronomist on sugar cane in British Guiana from 1958–1960. It was during this time that, as a new science graduate, John Milburn took with him a German-English dictionary, intending to both learn German and translate Ernst Münch's book on the pressure-flow hypothesis (1930). He often quipped that "everyone cites Münch, but no-one's ever read it because it's in German". He quickly realised that such a translation was overly ambitious at the time, but never forgot his desire to showcase Münch's genius[1] to the English-speaking world, so he returned to this work in the later years of his life with the help of Prof. Dr Karl Kreeb (University of Bremen). Together, they completed the translation of Münch's book, which was published in 2003, after Prof. Milburn's death.

[1] This was a term that John Milburn used to describe Ernst Münch. John Milburn spoke the following words about Münch in his invited talk (see Fig. 1) in 1996 for the "75 years of Münch's Pressure Flow Theory" celebration at Dresden's Technical University, "What is the meaning of the term 'genius'? It is certainly not a term I am prepared to bestow lightly. I believe it involves an appreciation of key discoveries which become the foundation of virtually all future work over the course of time. Such discoveries have also the benefit of simplifying a mass of otherwise incomprehensible observations. In my view, Münch, like other great men, such as Harvey, Malpighi, Hooke, Leeuwenhoek, Newton, Faraday and Mendel, has now exhibited these qualities through his work on phloem transport" (Milburn, 1996).

John Milburn's fascination with transport mechanisms in plants led to the continuation of his studies. From 1961–64, he undertook his PhD on The Uptake of Water and Solutes by Plant Tissues at the University of Aberdeen under the supervision of Professor P.E. Weatherley, FRS. While observing the different patterns of water uptake in *Ricinus communis* L. leaf discs compared with water-stressed leaves attached to petioles during his PhD, John Milburn proposed, and set about demonstrating, that the leaves with petioles attached underwent cavitation. The usefulness of his discovery did not become apparent until after 1975, when the ecophysiological implications of plants' vulnerability to cavitation were recognised – implications which are still as relevant today for tree survival in a changing climate.

Career Post-PhD

Following the completion of his PhD in 1964, John Milburn worked at the University of Glasgow for several years in the following increasingly senior positions, interspersed with an overseas posting at Harvard University: Lecturer (1964–1975), Senior Lecturer (1975–1980) and then Reader (1980–1981). In 1981, he moved to Australia when he was appointed Professor in the Botany Department at the University of New England (UNE), a position he held until his death in 1997.

When John Milburn succeeded Professor Noel C.W. Beadle as Professor and Head of Botany at UNE in 1981, he soon realised that the shoes he had to fill were very different from his own. Professor Beadle was the Foundation Professor of Botany at UNE, appointed in 1954, and remained Head until his retirement in 1979. UNE had become an independent university in 1954 when it relinquished its inaugural 1938 status as a College of the University of Sydney. Professor Beadle's expertise revolved around taxonomy, plant morphology and ecology. Although Prof. Beadle retired in 1979, these areas of teaching and research remain strong to this day at UNE, as represented by several distinguished alumni from the Botany Department in taxonomic (e.g. Gwen Harden: Botanist, National Herbarium of New South Wales and Dr Gordon Guymer: Director, Queensland Herbarium) and other fields (Professor C. 'Barry' Osmond, FRS: plant physiology, photosynthesis).

The appointment of a plant physiologist, Professor John Milburn as the successor to Prof. Beadle was not without some controversy, therefore, within the ecologically and taxonomically focused Botany Department. However, Prof. Milburn did not outwardly react to working among Antipodean botanists, some of whom held fixed research ideas and were not interested in collaboration in fields outside their own. Instead, John Milburn continued on with his research, developed links with other departments at UNE (e.g. Physics, Chemistry), as well as overseas, and frequently worked with visiting scientists, often brought to the Department by his colleagues in Botany. The collaboration on the translation of Münch's book with Prof. Dr Karl Kreeb was one such fruitful example: Karl initially came to UNE in 1963 to work with Professor Beadle for eight months; he later collaborated with Associate Professor R.D.B. 'Wal' Whalley (Botany Department, UNE), before joining forces with Professor Milburn. Prof. Milburn ultimately developed some successful collaborations with scientists in the Botany Department and published several excellent international journal articles with Dr Jose Kallarackal on the water relations of banana, a plant in which latex flow complicates traditional water potential measurements.

John Milburn held many administrative positions at UNE: in addition to being active on numerous committees, he was Head of Department (Botany) from 1981 to 1988 and Dean of the Faculty of Science from 1982–1984. Outside UNE, he was the external botany examiner at the University of Hong Kong from 1990 to 1993. During these appointments, he continued with his undergraduate teaching load, supervised several Honours, Master and PhD students, as well as published approximately 40 international journal articles in those years.

Figure 1: Professor John Milburn, giving an invited presentation about Ernst Münch in 1996 for the "75 years of Münch's Pressure Flow Theory" celebration at Dresden's Technical University, Germany.
He is holding an original copy of Münch's book, *Die Stoffbewegungen in der Pflanze.* This was a typical teaching pose of John Milburn. (Photo courtesy of Prof. Dr Manfred Tesche.)

Table 1: Key research findings of Professor John Milburn

Year	Finding	Published
1966	Acoustic detection of cavitation in vascular plants	Planta 69: 43–52
1970	Discovery of phloem exudation from *Ricinus* plants	Planta 95: 272–276
1971	Analysis of conduit lengths by india ink injection	New Phytologist 70: 427–434
1971	Recognition of the importance of growth in relative water content assays	New Phytologist 70: 929–938
1974	Analysis of embolisation reversal in isolated vascular bundles	New Phytologist 73: 861–871
1974	Demonstration of the role of osmotic water in phloem transport	Planta 117: 303–319
1980	Measurement of turgor pressure in sieve tubes	Berichte der Deutschen Botanischen Gesellschaft 93: 153–166
1983	Discovery of the freezing sap mechanism of sap exudation in maples	Canadian Journal of Botany 61: 3100–3106
1988	Comparison of ultrasonic and audible acoustic emissions	Journal of Experimental Botany 39: 1237–1248
1990	First measurements of banana water potentials: utilised laticifer exudation	Australian Journal of Plant Physiology 17: 57–68
1996	Refutation of cohesion theory challengers	Annals of Botany 78: 399–407

Key Research

Some of Prof. Milburn's key research findings are shown in Table 1. John Milburn published well over 100 journal articles in numerous prestigious journals, as well as several books and book chapters. His aim was to publish in every area of botany and he was well on the way to achieving that goal. For example, in addition to the body of work he produced on both xylem and phloem transport, he published work on marine algae in 1972 and in plant pathology (cavitation in ascospores) in 1970. He also extended his plant water relations work to that of root hemiparasites (Pate et al., 1990). John Milburn believed "very strongly that from a functional point of view the plant must be regarded holistically" (Milburn, 1997, unpubl. Australian Research Council grant application). In this way, he believed that the controversial cohesion theory challenge of the 1990s could have been avoided.

The corner stone of his life's work, John Milburn's research on cavitation detection (Fig. 2), cemented his international reputation, so much so that Sir David Attenborough wrote to him in the 1990s, showing interest in his cavitation material as part of the BBC documentary series, *The Private Life of Plants*.

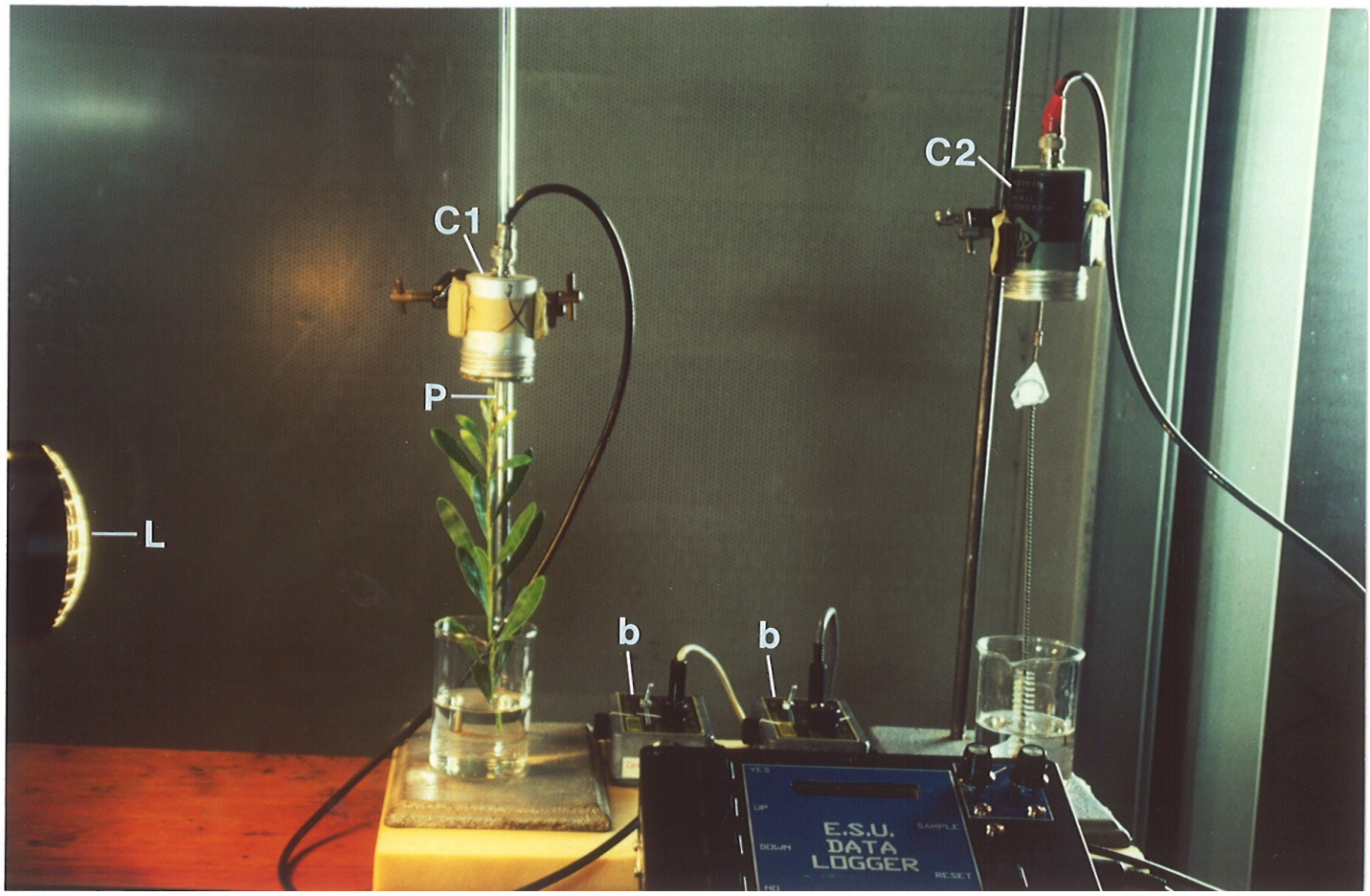

Figure 2: Apparatus used for acoustic detection of cavitation.

This apparatus was a refined version of the original used in John Milburn's original (1966) publications. A wire probe (P) was inserted into the xylem of a plant stem and the cavitation events (or Audible Acoustic Emissions, AAE) were recorded on Channel 1 (C1). Channel 2 (C2) was a coincidence counter to detect any extraneous noise that occurred, which was then subtracted from counts occurring on C1. Electromagnetic transducers are located in the two metal jars in C1 and C2. The transducers convert the audio signals from the plant into electronic signals. The signals are amplified and converted into digital signals (located in the small black boxes, b) and recorded on a data logger. (Photo: Williamson, 1996).

International recognition also came from the late, and similarly great, Professor Martin Zimmermann, who also died prematurely, aged 57. Prof. Milburn recounted to me his first meeting with this eminent plant physiologist. They were at the same conference and, at the end of the day's sessions, John Milburn walked past a group of plant physiologists, one of whom was Martin Zimmermann. The group were doing backflips in the snow and trying to work out the physics of the action, when Martin Zimmermann called out to Prof. to ask him what he thought. From such an unusual beginning, a fruitful research partnership was born that was to result in the publication of an edited volume in 1975 on phloem

transport (Fig. 3), as well as book chapters and several journal articles on phloem and xylem transport. The two men worked together at Harvard between 1973–75 after Prof. Milburn was awarded a Charles Bullard Research Fellowship and a Fulbright Fellowship. When Martin Zimmermann completed his eminently readable book in 1983, shortly before he died, he sent John Milburn a signed copy (Fig. 4). It was fitting that the memorial tree which was planted in the Botany Department garden at UNE following Prof. Milburn's death was a Sugar Maple (*Acer saccharum* Marsh.), a plant that both John Milburn and Martin Zimmermann had worked on together and published several journal articles about over the years. (The other plant candidate, Prof's 'guinea pig', *Ricinus communi*s, was quickly discounted as being an unsuitable memorial plant because of its notorious toxic properties.)

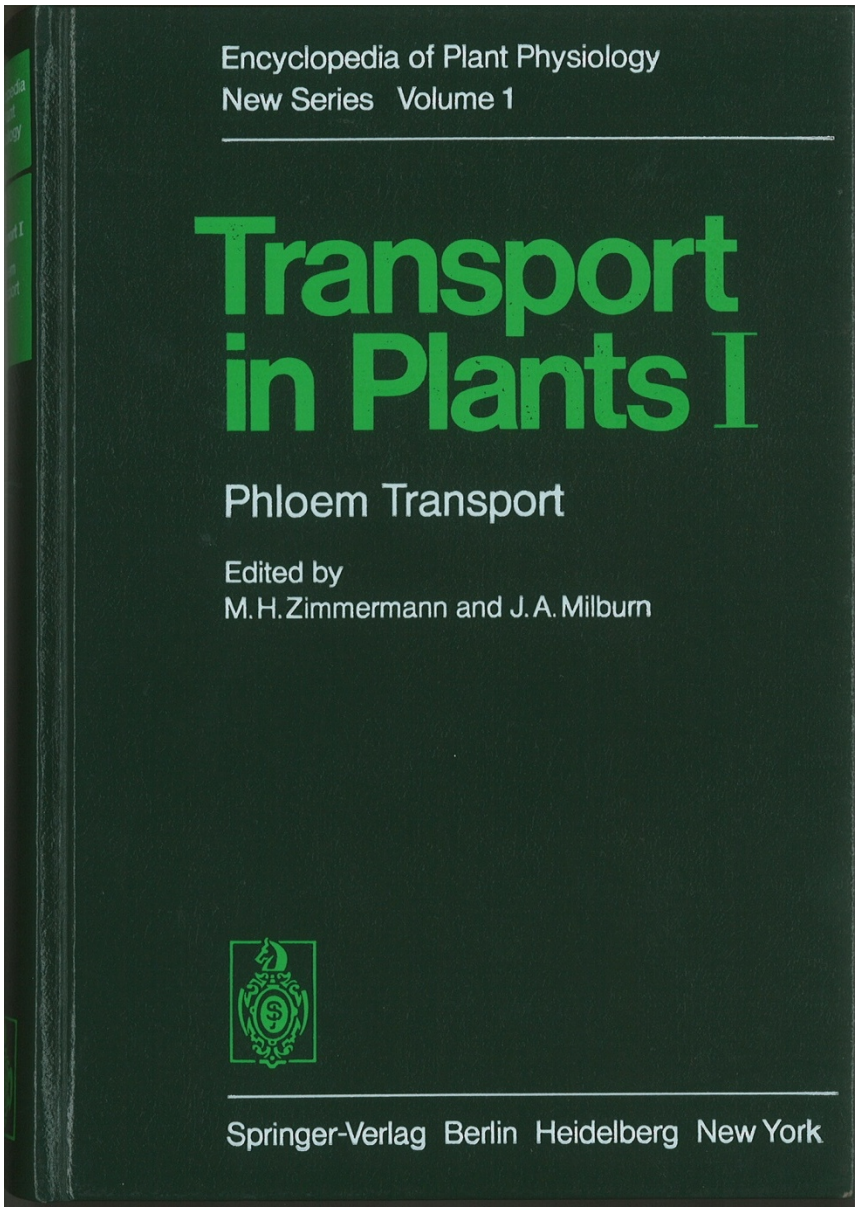

Figure 3: Edited volume of phloem transport in plants (1975), one of several collaborations between John Milburn and Martin Zimmermann.

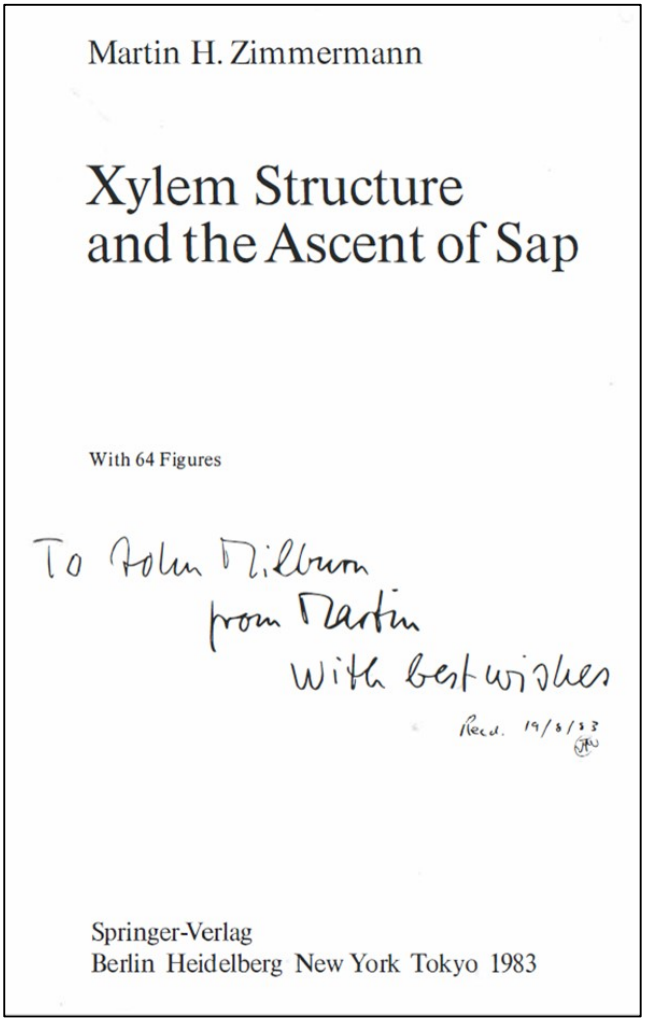

Figure 4: The frontispiece of Professor Martin Zimmermann's book, signed by him and received by John Milburn on 19 August, 1983, approximately six months before Martin Zimmermann's untimely death.

The Family Man

John Milburn met his future wife, Anita, at a fancy dress party during the first year of his PhD. I can't exactly recall what he told me that either of them went dressed as, but I do remember him saying that it was an instant attraction. He also added that from Anita's costume (did she go as a plant?), he thought that she was unusual enough to hopefully understand him! They married during the second year of his PhD, in 1962. Theirs was a lifelong partnership and he always spoke very fondly of Anita. They had three children, Dirk, Erik and Hazel. John and Anita Milburn had recently become grandparents shortly before his death. The sound of the crying grandchild during Prof's funeral was a source of some comfort through my tears: it brought the hope that John Milburn's 'greatness genes' had been passed on to further generations.

John and Anita lived on a small farm approximately 5 km from the centre of Armidale. He built an additional room on the home himself and was also a keen gardener. Once he was a little late picking me up to drive interstate to a conference because he'd been busy planting poplars as a windbreak on his farm prior to our departure. He apologised and said that he thought that by the time he returned from the conference, the spring weather may have warmed too much and the plants would not have transplanted well.

He held end-of-semester parties at his home for his third-year plant physiology students and I have fond memories of the time he encouraged us to catch yabbies (*Cherax* sp.) in the dam on his property and of our excitement and surprise when we caught some. He also hosted an end-of-year party at his home for staff and postgraduate students of the Botany Department, even after he was no longer Head of Department. He'd even set up a badminton net for people to play the

sport (including himself). John and Anita had an old, small dog, Mozzie, of whom he was very fond. 'Moz' would excitedly race around us at such gatherings. Prof. was privately, deeply saddened when Moz died several years later and wrote a wonderful, clever and moving tribute poem for her, which he shared with his close friends. He was a man who not only thought deeply, but also cared deeply, about so many things.

The Man

"The humane scientist" was the title of a tribute written by Associate Professor John Ryan, School of Arts, in the University of New England's *Smith's Weekly* publication, following Prof's sudden death. Although A/Prof. Ryan's title related to John Milburn's (1997) publication in the humanities on the term "a blue moon", it was also apt for the man: he was humane in the full sense of the word. Prof. Milburn was kind to everyone, even to those who showed some irritation towards him. He was a man who was very generous with his time, helped when he could, and was always fair and honest, reflecting his high moral standards. He knew what it was like to be an 'outsider' – to think differently from others – and so he offered, for example, a retired chemist, work with him on small technical projects. He gave a home to such people in his lab and fruitful collaborations resulted.

His interests and knowledge lay beyond science and he was constantly reading and furthering his knowledge in many areas of the arts and history. Some of this history came into his lectures, for example, students learned of John Snow's epidemiological discoveries around the spread of the water-borne disease, cholera, from the Broad Street pump. This was also to give students an example of how careful thought and observation could eventually triumph over established (and erroneous) ways of thinking, aided by a dash of reasoning outside of accepted norms.

John Milburn's musical interests were eclectic, to say the least. On entering his office, one never knew whether to expect to see Prof. calmly working to the strains of Enya, Donna Summer or classical music. He was particularly fond of the symphonies of Sibelius, and Vivaldi's Four Seasons was often heard. He made life interesting because one learned to expect the unexpected in so many areas.

John Milburn had a strong sense of community. He volunteered his time to give free lectures to the Armidale branch of the University of the Third Age (U3A) shortly after it began in Armidale in 1992. He introduced the 'over 55s' to his world of plants and cells that clicked, moved and jumped. By all accounts, both he and the participants enjoyed the classes he gave.

The inclusion of Prof. Milburn's biographical details in the Australian edition of *Who's Who* a few years before he was killed were particularly pleasing to him. His satisfaction at the entry did not come from an egotistical motive, but rather a contentment that his research had been recognised on the wider stage. After years of having his work seen as being on the periphery, he felt valued and accepted.

The *Who's Who* entry listed John Milburn's recreational interests as squash, photography and landscaping. To that list could be added virtually any sport – he would try most sports to which he was newly exposed, including volleyball, archery, badminton, swimming and windsurfing – and do well at them. He was a regular and key participant in the Botany Department's inter-departmental sports teams at lunchtimes. Squash was a particular passion, and he played several times a week, regularly punishing younger and unwary quarries! He believed that a healthy mind required a fit body. His photographic interests resulted in one of his photographs being published in an English magazine a couple of years before his death. He was very pleased at his non-science publication and showed me the photo, which he had entitled 'Ghost Bird' because it was a perfect outline of a bird, left after it had flown against a glass window at his mother's home in England. He was a constant student of nature in all its forms.

Because Prof. Milburn thought differently from other people, he was also unfazed by what could be considered unusual behaviour. Once, as a second-year biology student, I was hitchhiking home from university and he stopped to give me a lift, although he didn't know or remember me from his large first-year class the year before. He didn't bat an eyelid when I said I only wanted to go two blocks and, I suspect, he was too polite to say he recalled the incident when I brought it up with him years later. Similarly, when I told him at the beginning of my Honours year that I was going to

sleep in the lab one weekend so that I could "understand my plant" by measuring its diurnal water potential cycle every three hours, he said it was a good idea. No judgement was passed on either of these occasions.

The Teacher

John Milburn was a keen student of history and early scientific discoveries, which were evident in so many of his publications as well as his lectures to students. He thought it important to imbue in his students the necessity of understanding and respecting how our current knowledge is built upon that of the early pioneers in a particular field. His fascination with the work of early researchers meant that students were regularly regaled with examples of Leonardo da Vinci's genius. Perhaps da Vinci's notes and drawings influenced Prof. Milburn to keep meticulous notes and sketches of his own research ideas, all catalogued in his notebooks.

He introduced undergraduate students to the pioneering work of Berthelot (1850) when he described early experiments that demonstrated the cohesion of water and the occurrence of cavitation. From there followed descriptions of Briggs' (1950) 'spinning Z-tube' to induce cavitation. These experimental descriptions led on to information about Hagen (1839) and Poiseuille's (1840a; b) independent work on hydraulic flow that gave us the Hagen-Poiseuille equation that we still use today. Into the mix were descriptions of Askenasy's (1895) porous pot model to exhibit capillarity and how that was integral to Dixon and Joly's (1894) Cohesion Theory. Of course, all this made studying for exams rather nebulous and I now wonder how today's generation of students, with their clearly defined expectations for content and exams, would manage. The importance of these historical works was lost on me as an undergraduate student and their relevance and significance only became evident during my postgraduate studies. How exciting it was when, during my PhD, he showed me his copy of Henry H. Dixon's and John Joly's (1895) seminal publication, The Path of the Transpiration-Current, that had been signed by Dixon (Fig. 5)!

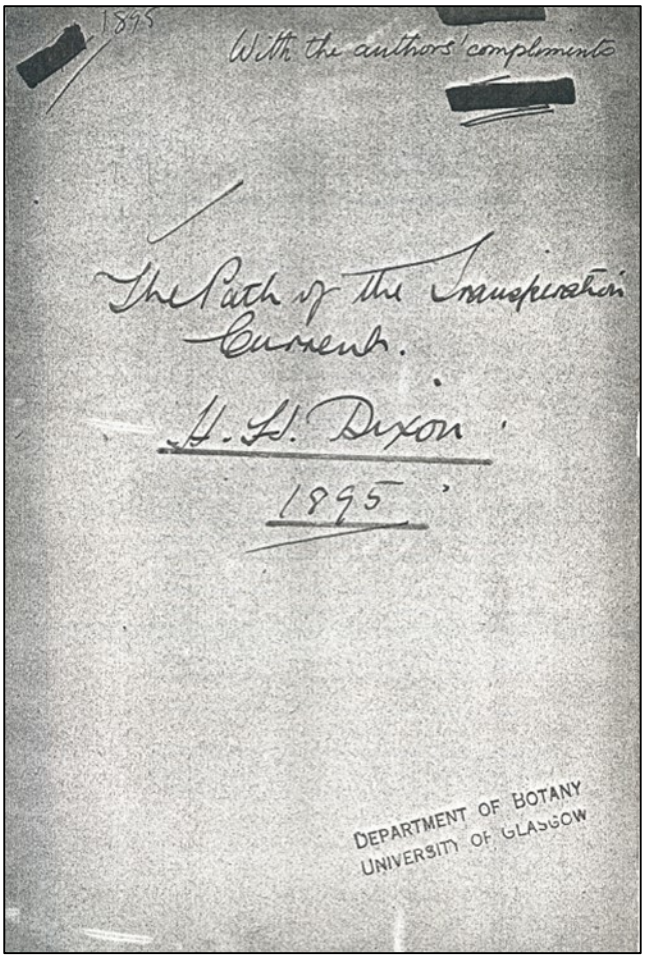

Figure 5: A copy of Dixon and Joly's (1895) article, signed by Henry H. Dixon.
(From John Milburn's personal collection.)

Prof. Milburn was always available to discuss results or problem solve and often chose to draw diagrams on a notepad in order to explain anatomical or physiological concepts using visual methods. As a PhD student once trying to explain a result to him, I was given a valuable lesson about William of Occam: the simplest explanation is often the best. Making appointments to see Prof. was unnecessary because he always had an 'open door' policy. Only once during all my years of working in his lab did he say that he could not see me at that time and that was because he was literally about to walk out the door to give a lecture. His laboratory equipment and excellent photographic microscopes were available for his students to use, even as undergraduates doing third-year plant physiology projects with him.

John Milburn was an innovator in every sense. Apart from devising a way to detect cavitation in plants using an amplifier and a record player needle, and the continuous design of equipment for the next piece of research, Prof. Milburn also recorded videos to show aspects of plant anatomy and physiology long before it was common to use such a medium in teaching. His lectures to first-year biology students were variously interspersed with: plant physiology videos that he had made; Martin Zimmermann's ciné film on xylem vessel lengths; several demonstrations, such as a Büchner filter manometer; a "porous pot" model to showcase Askenasy's (1895) system; large perspex models of bordered pits; and, of course, recordings of cavitation detection in the audible range, which students loved. No other lecturer was quite like him! Selection of subjects by distance education students was often purely based on the fact that John Milburn would be teaching them in the lectures and practical classes.

The Tragic Accident

John Milburn chose a calm, clear winter's day to undertake the maiden flight of his custom-built ultralight single-seater aircraft. He had been flying ultralight aircraft for four years and had obtained his pilot's licence a few years earlier. His flying instructor had described John Milburn as a cautious flyer. Single-seater aircraft have an inherent risk, but Prof. Milburn had told his instructor that he would only take off if he felt comfortable doing so. He had been practising taxiing and picking up speed on the runway for a while prior to taking off on the day of the accident. It is believed that about one hour after take-off, the engine stalled and the aircraft went into a spin before crashing in a paddock approximately 3 km from Armidale airport. John Milburn was killed instantly. His ubiquitous brief case was found at the airport hangar. Inside was one of his detailed research notebooks. He had been working in the Botany Department that morning (a public holiday), preparing for a subject that he was about to teach to distance education students.

When a close-knit rural university community loses a Professor of such international stature, tributes and obituaries abound. One of the obituaries for John Milburn that was in *The Sydney Morning Herald* newspaper appeared opposite that of musician Jeff Buckley, who had also died in tragic circumstances days earlier. This brought a rare smile amongst all the gloom because I thought how chuffed Prof. would have been to be in such good musical company.

In one of the eulogies at Prof. Milburn's funeral, Associate Professor Prakash (Head of Botany, UNE, at the time), recounted that Prof. had a 'Snake Tales' cartoon on his office door which said, "I have been lost for over a week and I bet no-one even missed me. Except perhaps my squash partner". How often over the years since have so many people, myself included, lamented that this is just not so.

Conclusion

John Milburn wrote the following words when describing the genius of Ernst Münch at the 1996 celebration conference in Dresden, Germany on the 50th anniversary of Münch's death: "The critical test of any great discovery is that it can withstand the test of time. I have tried to show how Münch's theory has achieved this, which is indeed a great tribute to this hitherto largely unsung genius" (Milburn, 1996). John Milburn, your discovery of cavitation and its detection in plants has withstood the test of time. It has opened up numerous avenues of water stress research since then, many of which were presented at the 3rd Xylem International Meeting in Bordeaux, France, 2017. John Anthony Milburn, you, too, are in the category of genius.

As John Milburn once wrote, "I can only say I did my best" – what a best it was. Thank you, John Milburn. Your work lives on.

About the Author

Dr Virginia Williamson was fortunate to be a PhD and Honours student of Prof. Milburn's. His influence is still felt and he remains keenly missed. Figure 6 shows what may be the last known photograph of Professor John Milburn, taken six weeks before his death at the author's PhD graduation ceremony. It has pride of place on the author's work desk.

Figure 6: Professor John Milburn with the author at her PhD graduation ceremony, University of New England, Armidale, Australia. The photo was taken approximately six weeks before he was killed.
(From the author's personal collection.)

Acknowledgements

Dr Kim Ritman is gratefully acknowledged for provision of the audio recording of cavitation in a *Ricinus communis* leaf.

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