

Lloyd Thomas Evans 1927–2015*

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Lloyd Evans, a leading plant scientist, published extensively on the regulation of flowering and on crop production during a lifetime spent in research at CSIRO. His significant achievements included: identification of a gibberellin plant hormone as a flowering regulator in the grass *Lolium temulentum*; discovery of a synthetic gibberellin growth retardant that blocked endogenous gibberellin synthesis; and discovery in *Pharbitis* of a novel biological flowering clock with a 12 h (semidian) period. In crops, he established the impact on yield of photosynthate production and transport to competing sinks. Two of his books, *Crop Evolution: Adaptation and Yield* and *Feeding the Ten Billion* have had a major influence on agricultural research and policy. His ability to define research options led to many years of international advisory work. He was an Officer of the Order of Australia (AO), and was elected a Fellow of the Royal Society (FRS), and of the Australian Academy of Science (FAA) (including a term as president).

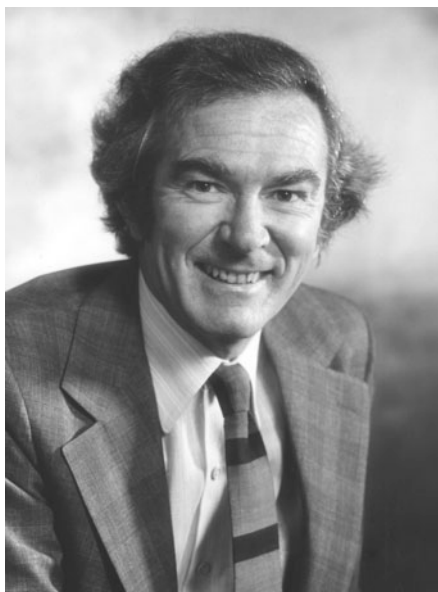
Preamble

In the 2003 volume of the prestigious *Annual Reviews of Plant Biology*, Lloyd Evans wrote a preparatory chapter on his life and scientific career,¹ and together we have summarized our successful search for flowering regulators of the grass, *Lolium temulentum*.² Lloyd shied away from ‘grandstanding’. Here, I have chosen to reveal something of the ‘colour’ of Lloyd’s life from my recollections of events over our long friendship, from the chapter cited above and from extensive private notes that he developed from his diaries.³

Family Background and Early Life

Lloyd was born on 6 August 1927 at Whanganui, New Zealand. His younger brother, Morgan Evans, was born in September 1928. Their father, Claude David Evans, was in charge of wool operations at the meatworks in Whanganui. Lloyd recalled that ‘Claude enjoyed an occasional beer and, late in life, even an occasional whisky, but was never seen even mildly inebriated.’ Along with a strong devotion to his father, Lloyd upheld his father’s moderation but with a shift from beer to sampling his substantial cellar of fine Australian wines.

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Lloyd’s mother, Gwendolyn Lois Maude Evans (née Fraser), contracted tuberculosis and died when Lloyd was ten years old. Neither the early loss of his mother nor the hardship of food and fuel rationing during World War II seem to have affected his childhood experiences. Lloyd’s main chore at this time was supplying enough firewood and, always resourceful, supplementing household supplies with fish caught in the nearby Whanganui River.

Lloyd's secondary education at Whanganui Collegiate (1941–4) was initially a shock. Studying at a level he thought was beyond him, he floundered at the first term exam. Frank Gilligan, the headmaster, read him the riot act. By year's end Lloyd was top of the class.

In addition to academic success, there were two especially notable 'moments' of Lloyd's high school years. Lloyd had a very retentive memory and during a lesson on the Romantic poets, the Head asked if anyone knew Wordsworth's 'Daffodils'. Lloyd recited it verse by verse.

Years later, Lloyd's love of literature and ability to memorize poetry came to the fore in his award in 1951 of a very prestigious New Zealand Rhodes Scholarship to Oxford. Asked what he knew of modern poetry he quoted passages from works of T. S. Eliot and W. H. Auden. In science, these skills of memory were invaluable for recalling and drawing inferences from the scientific literature. Socially, his memory of literature was also a skill he enjoyed when interacting with his nine grandchildren and with a long-time friend and biochemist, Professor Frank Gibson. These two could spend an evening, and many glasses of red wine, reciting slabs of Shakespeare to each other.

His second 'moment' involved farming. Over school vacations, Lloyd joined shearing gangs as 'rouse-about, fleecio' and, often worked as a stand-in wool classer when the regular wool classer had a bad hangover. This early exposure to farming sustained his later interest in agriculture.

University Education

New Zealand

In February 1945, Lloyd began a science degree at Canterbury University College, Christchurch. His memory was of dismal botany lectures, but he then transferred to the nearby affiliate, Lincoln Agricultural College, and completed a BAgrSc. While at Lincoln, he attended several brilliant public lectures on the 'Scientific Method' by the world renowned philosopher, Karl Popper. He also developed his practical outlook on agriculture as the course required a full year of work on farms. Recreation involved hockey, table tennis, and running. However, his greatest love was the outdoors, which

he experienced through 'tramping' and mountaineering in the nearby New Zealand Alps.

His favourite subjects were soils and plant science; both in the context of farm and natural ecosystems. Most significantly for his career, Lloyd also began at Lincoln College what was to be a lifelong interaction with Otto Frankel, who at the time was Director of the nearby Wheat Research Institute. Frankel arranged seminars by renowned international scientists including Theodosius Dobzhansky, Richard Goldschmidt, E. B. Ford and R. A. Silow. These seminars and the chance for face-to-face discussions provided Lloyd with a career-defining richness of scientific exposure.

Awards and a scholarship in 1948, and the award of the University of New Zealand Senior Scholarship in Botany, provided the means for him to complete his BSc in botany. By 1951, with first class honours and a masters' degree he was employed as an assistant lecturer in agricultural botany. By then, he had presented his first conference paper and published three scientific articles.

Oxford University: More than a DPhil

As a 24-year-old who had never travelled overseas, Lloyd arrived at Oxford committed to expanding his scientific horizons and to experiencing all the culture Europe had to offer in literature, art and music. During his three years at Oxford (1951–4) he learnt to love being a part of Brasenose College. There were, however, several challenges including the outdoor sprint across the 'quad' to have a bath at restricted hours in winter. There was also difficult College after-hours access but in his words;

the first stage involved climbing into the garden of the Rector of Lincoln. Then there was a difficult traverse of a high spiked fence (which had claimed at least one life), a traverse along the crest of the uninhabited bathroom followed by a controlled slide down its often-frost covered slate roof to a rotating row of steel spikes and, with luck, a clearing jump to the ground. On one occasion, on a frosty night, I had real problems with those rotating spikes. So I gave up working late in the lab.

Extra curricula student life was filled with sport, including hockey, and travel to Europe. The Poetry Society was particularly appealing because of the range of poets who presented their work including: Cecil Day Lewis, Arthur Waley,

Kathleen Raine, Louis Macneice, Stephen Spender, Roy Campbell and, eventually after several escapes into pubs, Dylan Thomas.

Lloyd's own poetic endeavours were not without merit but were trumped in 1953 by the appearance in his life of Margaret Honor Newell (1927–2014), a fellow New Zealander.⁴ To many people in many countries, Margaret was known as the woman who never went anywhere without her tennis racket, and who was happy to play anywhere and with anyone. To many in Australia, England and California, Margaret was a perceptive, wise and trusted advisor and for many years she was Head Counsellor at the Australian National University (ANU) in Canberra. To yet others she was a resourceful and renowned cook and hostess, able and willing to run something up for unexpected visitors; and always a source of fun. To Lloyd, 'Margaret was the most important influence on his life, his beloved wife, counsellor, gadfly, companion, colleague and co-parent.'

Lloyd's DPhil studies were submitted in 1954 and focussed on aspects of soil chemistry and pasture growth. However, it was the occasional lectures at Oxford that most inspired Lloyd, including: Sir John Russell on modern agriculture, and a rambling lecture by Colin Clark on world food supply. Of more immediacy, Lloyd's imagination was fired by a lecture from Professor Fritz Went on the value for plant physiological research of the environment control facility at the Earhart Laboratory at the California Institute of Technology (Caltech), Pasadena, Los Angeles. Later, after talking with Went, Lloyd applied for and was awarded a prestigious Harkness Foundation postdoctoral fellowship.

Caltech: a Postdoctoral Experience

Armed with his DPhil, and now married to Margaret Newell, these two New Zealanders arrived at Caltech in mid-September 1954. Lloyd already knew of the excellence of the various scientists at Caltech including the plant biochemist and flowering physiologist, James Bonner. Went as Laboratory director was renowned for his work on environmental responses of plants.

Another physiologist at Caltech was Roy Sachs a horticulturalist studying the flowering of *Chrysanthemum*. Roy became a lifelong friend of Lloyd and Margaret. A firm friendship

was also established with W. S. (Bill) Hillman who was a fine scientist and flowering physiologist and in the 1970s, became president of the American Society of Plant Physiologists. Not so far away at Los Angeles (UCLA) was Anton Lang who in 1955 became internationally famous for studies on the regulation of growth and flowering by the gibberellin class of plant hormones.

Despite all that was positive about Caltech, at that time there were strong anti-communist sentiments across the USA. Senator McCarthy and the FBI hounded many staff at Caltech, regarding it as a haven for the politically liberal and no place for the modest. Among these 'liberals' was Linus Pauling. Bloody but unbowed, he was protected by his recent Nobel Prize. However, it was considered a defiant act when Lloyd, Margaret and others went to hear the openly pro-Soviet Paul Robeson sing in the First Unitarian Church in Los Angeles. As a penalty, the authorities charged the church with an additional \$10,000 in 'taxes', with only \$2000 of that sum being raised from that evening's small audience.

The eighteen months Lloyd spent at Caltech had a defining role for his subsequent career. By examining a large collection of the grass, *Lolium*, he isolated a unique *Lolium temulentum* genetic variant, 'Ceres,' that flowered after exposure to a single long day.⁵ This precision in flowering of *L. temulentum* opened up many opportunities for experimentation over the next fifty years. To Lloyd, *Lolium temulentum* was *Lte* after his initials but to Margaret it was '*Lolly*', regarded as Lloyd's first love as it demanded attention over Christmas and during many escapades late at night.

At Caltech, Lloyd learnt much about the design and engineering of controlled environment facilities. As a consequence, and because CSIRO Plant Industry (PI) in Canberra was expanding, in 1955, Otto Frankel, its new Chief, offered Lloyd a research position and, as well, asked him 'to take a role in the design, testing, construction and management of a new state-of-the-art plant growth facility'.

Research at CSIRO: the Start of a Lifetime in Science

In August 1956, the Evans family (now three) began a four-month return to the southern

hemisphere, but to Australia not New Zealand. The Harkness Fellowship required a three-month tour from the Western to Eastern USA. Then, after revisiting England, to see Margaret's parents, there was the long sea voyage to Australia. By November 1956, they arrived in Canberra, the National Capital, then a small, sleepy, dry and dusty country town where the PI research laboratories were being developed.

Lloyd and Margaret soon established their first home for their now three children, Nicholas (born 21 February 1956), and twins John and Catherine (born 5 June 1958). Academically, all three children have been high achievers and Nicholas and John are now Professors at ANU. John, like his father, is a plant scientist and, in 2013, was elected FAA.

The family loved the outdoors and had ready access to bushwalking, and skiing. They spent much time at the coast in the house they built in 1971 at Guerilla Bay, a two-hour drive from Canberra. Many an academic visitor experienced Lloyd and Margaret's hospitality not just in Canberra but also at Guerilla Bay.

CERES The Canberra Phytotron

The Canberra Phytotron was named CERES both because of the Roman goddess of agriculture and because it was an acronym for C-ontrolled E-nvironment RES-earch. By world standards this was one of the larger controlled environment facilities for plant growth and it could mimic natural environments from the tropics to cold, sub-polar extremes.⁶ Its building costs were fully funded by the Australian government (a total of \$1,064,000), an outcome achieved by some forcible argument by Otto Frankel. There was also substantial backing by Sir Ian Clunies-Ross the then Chairman of CSIRO, by Sir Frederick White his successor, by Bert Goodes a senior public servant and by the responsible minister, Bert Casey (later Lord Casey). In April 1958 Casey wrote:

Cabinet tonight. I got the phytotron submission through, for the full \$1,000,000. I aired myself at some length on the potentialities of this piece of equipment—and got no opposition.⁷

Roger Morse, head of the CSIRO Engineering Section, understood the engineering, and Lloyd the biological limitations of other phytotrons, and together they carried out extensive

prototype testing.⁸ The building made a majestic addition to Canberra with its large rounded feature windows and a row of fifteen large controlled environment glasshouses. Its architect, Roy Grounds, had earlier designed the Australian Academy of Science dome that was opened in 1959; although very striking, the Academy building was frivolously referred to by locals as the Fried Egg.

CERES was opened in 1962 and the journalist and author George Johnston writing in the *Australian* newspaper saw it as 'a compelling example of the centralizing forces at work in Canberra ...for the betterment of Australia', and of 'a new adventurous age into which we as Australians were entering'.⁹

At the opening ceremony, the large audience was addressed first by Fred White as Chairman of CSIRO and then, brilliantly, by the Prime Minister Bob Menzies with a superb imitation of an Australian farmer (a 'cocky'); Otto Frankel closed the proceedings with a vote of thanks. The many distinguished scientific invitees from overseas, included Fritz Went, Sterling Hendricks and Pierre Chouard. All were impressed by the speeches and CERES, as well as by the following symposium on 'The Environmental Control of Plant Growth'.

Five years after its opening, CERES and Lloyd were featured in 'The Hungry World' segment of the first live 'One World' TV link-up, watched by 500 million people. Taken for granted these days, this first world link-up on 26 June 1967 was a complex effort, especially when the USSR withdrew its satellite at a late stage. The newspapers made a meal of Lloyd's role. The Brisbane *Courier Mail* ran a headline '700 million will watch the shy scientist,' a label that stuck and resurfaced several years later when Lloyd became president of ANZAAS (Australian and New Zealand Association for the Advancement of Science). In conversation he may have appeared shy but this was not a characteristic of Lloyd. Rather, he was modest both in science and in all his dealings with people. Throughout his life he was always reluctant to use the personal pronoun 'I', an attitude reflected in 2003 in his use of a quote from Claude Bernard 'Art is I, Science is we.'¹⁰ Lloyd did not try to dominate, was prepared to consider all options, master all the facts, draw conclusions and then reach a decision.



Figure 1. (Left) John, Margaret and Lloyd Evans, CERES 50 year anniversary. (Right) Ola Heide (Norway), Lloyd Evans and Rod King (CERES entrance 1985).

CERES provided Lloyd with fixed environmental conditions for his ongoing studies of the flowering of *L. temulentum*, but its huge range of available environments also allowed answers to the question of the adaptive value of particular flowering responses. For example, Lloyd wanted to know if adaptation was seen in the flowering of Kangaroo grass (*Themeda australis*), an Australian species. So, he collected and vegetatively propagated 30 clones from latitude 6°S to 43°S. What he found was that, for flowering, the optimal daylength and temperatures determined in CERES matched conditions at their sites of origin.¹¹ Unfortunately, the selective (that is evolutionary) value of such adaptation has more often remained as speculation but CERES has provided a powerful tool for unravelling flowering-time adaptation, not just for native species but for many domesticated crop and pasture species.¹²

Today (2016), CERES still operates as a valued research facility despite exceeding its originally estimated engineering life of twenty years. Other major facilities closed two or more decades ago including those in France, Canada and the first phytotron, the Caltech facility.

The long life of CERES is testimony to the skill and planning of Lloyd Evans and Roger Morse,¹³ and to the efforts of its four Officers-in-Charge, Lloyd Evans, then Wardlaw, King and Rawson. Its output highlights Lloyd's original vision. From our 1985 review of its first two decades of operation,¹⁴ of the 520 papers published, one quarter were by researchers outside CSIRO, a clear vindication of its conception as a national research facility. Research in CERES

involved a wide range of scientific disciplines from plant pathology and microbiology to ecology, crop physiology and forestry. Fittingly, in 2013, as part of its latest upgrade, Lloyd Evans and family were present (Fig. 1) when he was honoured at a 50 year celebration of CERES by the placing of a plaque on its front entrance which reads, 'Celebrating Five Decades of Controlled Environment Plant Research, Realizing the Founding Vision of Dr Lloyd T Evans of CSIRO'. On the opposite wall sits its original 1962 dedication: 'Cherish the Earth For Man Shall Live By It Forever', an apt creation of Lloyd's scientific mentor, Otto Frankel.

By the 1970s, Lloyd had published groundbreaking papers on flowering of *Lolium* and, with his role in developing CERES, he was elected a Fellow of the Australian Academy of Science (FAA) in 1971 and, then, as a Fellow of the Royal Society (FRS) in 1976.

Management Roles

Chief of CSIRO, Plant Industry (PI): a Reluctant Conscript

When the third chief of PI, Dr John Falk, died in 1970, Lloyd resisted attempts to install him as chief. He wrote in his diary 'I ... preferred to get on with research, and I knew that a colleague and friend Dr John Philip aspired to the position, so I did not apply.' However, apparently at the instigation of Sir Otto Frankel, John Philip had just been appointed the first Chief of the CSIRO Environmental Mechanics group. So, following Lloyd's election as FAA in 1971, his potential as PI Chief was raised again by Sir Otto Frankel. There soon

followed a visit from a Canberra member of the CSIRO Executive who ‘invited’ Lloyd to Head Office and told him to apply. Lloyd noted he ‘still wasn’t keen to do so, but after talking it over with Otto and my Margaret, I sent in my application’.¹⁵ In his application he said:

I would prefer to continue my full time research and that I neither enjoy administration nor am I adept at it. However, I then indicated the four broad areas where I thought the Division’s research should be concentrated: (1) the productive processes of plants; (2) genetic resources and manipulation; (3) evaluation of agricultural systems; (4) the management of natural ecosystems.

His requests were accepted by the Executive, but this body remained less enthusiastic about his request for a fixed term appointment ‘for something like six years, with the right to return to a research position in the Division after that.’

PI at this stage was the largest CSIRO Division. Its staff numbers were close to 400 in a Government Research organization of ~6000 staff spread over Australia, and with research interests ranging from agriculture to land use, radio astronomy, mining and domestic building.

As Chief, Lloyd was able to expand ecological research on fire, water-use and aspects of native vegetation. He established an interdisciplinary group on storage proteins in plants and a molecular biology group under Jim Peacock, who was eventually weaned from *Drosophila* to maize, other crop plants, and the experimental plant species, *Arabidopsis thaliana*. Crop research was given a further boost in 1973 by the transfer to PI of responsibility for cotton research. When Jim Peacock stepped up to the position of Chief in 1978, cotton research was further enhanced.

Up to the 1970s, the economic returns from PI’s research on pastures were very impressive. By 2003, when independently analysed by the Centre for International Economics in Canberra, there were similar outstanding returns for PI’s work on wheat productivity, GrazFeed and cotton breeding (benefit: cost ratios of 19, 79 and 51, respectively). All these programs were begun or under way during Lloyd’s period as Chief.

The Australian Academy of Science

In 1971, as a new FAA, Lloyd had little time to participate in the affairs of the Academy because

he had just begun as PI Chief. However, by 1974 he was chairman of the Academy’s Biology Sectional Committee. In 1976, he was elected to Council and quickly saw how difficult it was to reach a consensus because its Fellows came from diverse backgrounds and were accustomed to others bowing to their unrelenting/forcible argumentation. When in 1977 he was elected Vice-President of the Academy he saw three reasons for his appointment: a shiny new FRS in 1976, he was located in Canberra, and he was one of the few plant scientists on Council. His progression to President in 1978 was not surprising.

His assessment after serving for four years as President was:

The Academy’s 25th jubilee in 1979 went well including the participation of Prince Charles. I broadened our science education activities, reached out to the Australian scientific societies, enhanced our cooperation with the other Academies, and Beauchamp House and its grounds immediately adjacent to the Academy Dome were secured for long term use.

Science

The Physiology of Flowering Lolium

In his first ten years at CSIRO, Lloyd worked alone in his research on *Lolium temulentum* and elegantly established the overall picture of its floral induction. He showed that: it flowered in response to longer summer daylengths; the leaves perceived this light signal; and that a positive, transmitted floral stimulus was produced in leaves.¹⁶ These findings confirmed evidence for several other species.¹⁷ However, in addition, he found evidence of a transmitted inhibitor produced in shorter days and which maintained vegetative development.¹⁸ This latter claim was severely criticized at the time by Anton Lang who was well known for his extensive studies on floral induction.¹⁹ Interestingly, fifteen years later, by using grafting techniques, Lang²⁰ provided elegant confirmation of Lloyd’s claim.

This emerging picture of transmissible regulators of flowering of *Lolium*, led Lloyd to application studies with two plant hormones, the gibberellins as candidates for the floral stimulus (Fig. 2),²¹ and abscisic acid as the inhibitor.²² Then, based on further application studies, but with inhibitors of nucleic acid metabolism, he



Figure 2. Lloyd Evans applying gibberellin to the young leaf of 6-week old plants of *Lolium temulentum*. This single application causes flowering.

reported that the early events of the floral transition at the shoot apex involved the synthesis of new mRNA.²³

The speed with which Lloyd took his experiments to publication was quite phenomenal. His 1966 *Science* paper implicating the plant hormone abscisic acid as the *Lolium* floral inhibitor, was written in one night.²⁴ He did this while repeating the necessary confirmatory study on the effect of applications at different times overnight.

After this early decade of research, Lloyd took great joy in the next decade in collaboration with other scientists from different backgrounds, approaches, interpretations and skills. From his diaries and private notes, his reflections of these collaborations starts with Ian Wardlaw in 1963:

Ian examined the movement of the floral stimulus from leaf to shoot apex;²⁵ then to Bruce Knox for histochemical and autoradiographic studies of the shoot apex;²⁶ Sterling Hendricks and Harry Borthwick (USDA Maryland USA) helped to sort out the spectral light requirements for long day induction of *Lolium* leaves;²⁷ the enthusiastic Toon Rijken provided microchemical analyses of the shoot apices at various stages of floral induction.²⁸ ...Much later (1980–90's),

with Rod King, Dick Pharis (Calgary Canada) and Lew Mander (ANU) we renewed our studies with *Lolium* and established gibberellin structural requirements for flower induction as against its action on stem growth.²⁹ Later, Rod, in collaboration with Tom Moritz at Umea, Sweden, provided ultra-sensitive measurements of the gibberellins in our *Lolium* apices³⁰ and the leaf.³¹ Another very crucial collaboration was between Rod, Carl McDaniel and me; we showed that gibberellin was all that was necessary for flowering of isolated *Lolium* apices in vitro.³² With Carl, as sometimes with other collaborators, we could agree on the results while differing in our interpretations.

True collaboration never denies continued questioning and, within ten years of Lloyd's 1966 *Science* publication,³³ by using GCMS assays, we showed that endogenous abscisic acid was not the daylength-regulated inhibitor of floral induction in *Lolium*.³⁴ By contrast, it took another thirty years, but we did confirm that gibberellins acted as a floral stimulus in *Lolium*.³⁵ For me, fifty years after starting our collaboration on flowering, I still feel some affinity with the sorcerer's apprentice as Lloyd had an encyclopaedic knowledge in this field.

The final saga of work with *Lolium* involved molecular approaches with two of my PhD students; Greg Gocal and Colleen MacMillan. In confirmation of Lloyd's initial suggestion of an early unique role for nucleic acid synthesis in flowering,³⁶ Greg developed beautiful *in situ* molecular information on the earliest changes in expression of specific RNAs at the shoot apex in transition to flowering. Interestingly, the very earliest increase (<6 h) was in expression of a potentially gibberellin-regulated gene, *LtCDKAI*.³⁷

Colleen provided essential gene sequence information that allowed us to show daylength up-regulation of expression in leaves of a critical gibberellin 20-oxidase biosynthetic gene.³⁸ In the leaf there was a large (>10-fold) and rapid (<3 h) increase in its expression with the triggering of flowering. In association with the 20-oxidase increase, the level of its endogenous substrate dropped while there was a matching increase in its bioactive products.³⁹ Then, after some hours to allow for leaf to apex transport,⁴⁰ there was a 2- to 3-fold increase at the shoot apex of the same bioactive gibberellins.⁴¹ Even more rewarding, however, was our evidence in 2008 of how turnover controlled gibberellin levels.⁴² In this final collaboration with Lloyd, we drew a line under all the previous twenty-two years of our studies. Acting like a stop/go traffic light just below the shoot apex, gibberellin-degrading enzymes blocked access by some growth-active gibberellins but not of our florigenic gibberellins.⁴³

To reach this milestone took us 45 years of searching, 555 experiments and the growth of almost 222,000 plants of *Lolium* with each experiment taking 9 weeks to complete. After our compulsory age retirement we both continued working as Honorary Research Fellows: for Lloyd starting in 1992 and in 2008 for me.

In 2003, we summarized our findings and predictions in a major review of gibberellins and flowering of *Lolium*.⁴⁴ It was with some hesitation that we claimed to have sufficient proof that gibberellins were one of the 'florigens' of *Lolium*. Subsequently, in 2006 we had expanded this claim to allow for an additional 'florigen' after we examined the timing of expression of the gene *FT*.⁴⁵ The next year Corbesier and others⁴⁶ showed that the FT protein was a daylength-responsive, transmitted

regulator of the flowering of *Arabidopsis*. It was rankling to us that many scientists were 'reluctant' to acknowledge our gibberellin studies although they were the first and still by far the more comprehensive evidence of the endogenous nature of a 'florigen'.⁴⁷ Although intellectual parentage drives scientific progress, a 'two-handed' approach is often wise. Fortunately, because we looked for both the positive and the contrary answer to any simple question, Lloyd and I had recognized that our 'baby' was at least twins (gibberellins and FT) and not a unique, single 'florigen'.

A Commercial Outcome: a Tale of Curiosity, Informed Minds and Tenacity

This account of work on *Lolium* has omitted our isolation and characterization of an anti-gibberellin growth retardant that reduces the height of cereals and can stop cool-season turf grass growth, a slow-grow, no-mow treatment.⁴⁸ A single spray on wheat led to 14–20% yield increases for 14 sites in Europe over two years. When sprayed on turf, water use and mowing frequency were halved.⁴⁹

Lloyd was pivotal at the start because he persisted in questioning the purity of one of our chemically synthesised, natural gibberellins. To humour Lloyd, various batches of this compound were analysed by Professor Lew Mander at ANU, Research School of Chemistry and he found varying amounts of a contaminant (16,17-dihydro GA₅), which he then synthesized as pure compound.

Using our work-horse, *Lolium*, we saw its powerful action as a growth retardant.⁵⁰ I clearly remember that first result in June 1992 because I was listening to Beethoven's Ode to Joy on the radio while making the measurements of plant growth. One application of dihydro GA₅ blocked growth over three weeks but flowering was normal. Lloyd's meticulous data recording and tenacity led to this discovery.

Subsequently, in collaboration with Professor Olavi Junttila, a frequent Norwegian visitor, we applied molecular/chemical approaches to show that this gibberellin derivative was a competitive inhibitor of GA₂₀ (Fig. 3) the substrate for the enzyme responsible for the last step of gibberellin biosynthesis.⁵¹ Dihydro GA₅ inhibited plant growth by lowering the levels of active gibberellins.

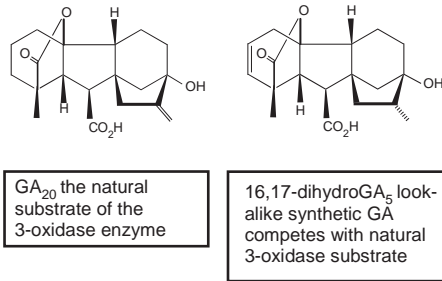


Figure 3. Close structural similarity between GA₂₀ and the synthetic contaminant 16,17-dihydroGA₅.

By serendipity linked with curiosity and informed minds, we had found a plant growth retardant. Then, with patents in hand, we began a five-year collaboration with the German agrochemical company, BASF. Unfortunately this tale has an unhappy ending, in 2002 the lawyers and management at BASF terminated the project because BASF was moving away from its interest in agrochemicals.

The Physiology of Flowering Pharbitis nil a Short Day Species

Despite his love for *Lolium*, Lloyd saw great benefit in ‘running more than one horse in a race if you wanted to succeed.’ Therefore, in 1966 we began parallel studies on the short day plant *Pharbitis nil*. This species kept us occupied for many years of fruitful study and highlighted similarities and differences between flowering processes of short and long day plants.⁵²

A memorable interaction in these studies involved Professor Ola Heide from Norway (Fig. 1) who took a sabbatical leave in Canberra in 1984 and repeated this on two more occasions. In addition to its well characterized twenty-four hour circadian clock for flowering, we found that *Pharbitis* used a unique twelve hour, ‘semi-dian’ biological clock.⁵³ This remains the first ever report of a semidian rhythm in plants or animals although tidal organisms can function on a 12.5 h lunar clock. Because rhythm studies go on day and night, our work became a true test of collegiality with Lloyd arriving daily at 7 a.m. to relieve me after the night shift and Ola starting late in the day until 10 p.m.; of course we also maintained a full daytime cycle of work.

As well as enhancing our studies on *Pharbitis*, over the years, much of our continuing research on flowering of wheat and *Lolium* was

enhanced by often repeated sabbatical visits by no fewer than sixteen international scientists.

Crop Physiology

Despite great success in his studies on flowering, Lloyd recognized the value in having separate fields of research.

Fifty years on in his private notes and diaries he reflected that:

Not only have these two fields, Crop Physiology and Flowering Physiology, cross-fertilized one another, but whenever I came to a road block in one, I could keep moving with the other. For example, after my initially productive burst with *Lolium* in the 1950s/1960s, I got stalled on the role of light⁵⁴ ...It was then that I moved into crop physiology and had an exciting time through the 1970s in spite of many administrative chores. Indeed, it was crop research that kept me sane and switched on through those years, so that I could return productively to flowering physiology and then have a final fling with crops. This duality in my research along with my writing of books undoubtedly broadened my perspectives of plant biology.

As with his studies on flowering, his research program on wheat photosynthesis and evolution involved input of colleagues who included Bob Dunstone, Rod King, Bob Williams, Howard Rawson and Ian Wardlaw.

Cross-fertilization of ideas from flowering to crop responses arose from Ian Wardlaw’s use of radioactive carbon tracers to follow the transport in *Lolium* of photosynthate.⁵⁵ What was clear was that lower more mature leaves did not import carbon from the younger upper leaves of a plant. It was this knowledge that led to debate with a colleague, Jim Davidson, who had published a pioneering quantitative model of pasture growth.⁵⁶ He had assumed that at high values of leaf to ground area the lower, older leaves continued to import and respire carbon as they became more and more shaded in denser crops. Thus he predicted that crop and pasture growth would reach an optimum and then decline. Lloyd disagreed and examined the relationship between leaf density and crop growth by measuring photosynthesis and dark respiration in mini crops of cotton and sunflower grown in artificially illuminated growth chambers. The results were compelling; total crop respiration levelled off at a constant value as the crop grew.⁵⁷

A pivotal step in Lloyd's developing interest in crop physiology involved our 1965 study of feed-back control of the photosynthetic rate of wheat leaves. Lloyd had long wondered if plants could produce too much photosynthetic assimilate and become 'constipated'. Inability of the rest of the plant to rapidly utilize carbon might lead to a reduction in its photosynthetic rate due to carbohydrate accumulation in source leaves. Many previous studies over more than six decades had suggested there were long-term responses to reduction in assimilate demand but cause and effect could not be determined. In our study, the response was clear cut. The photosynthetic rate of a wheat leaf could first be depressed rapidly by 50% in 3–5 h on removing the ear of the wheat plant, its major 'sink' organ for assimilates. Then, by enhancing demand from another sink, its photosynthetic rate could be rapidly restored.⁵⁸

Our conclusion, that crop yields may be limited by the internal demand for assimilates as well as by photosynthetic supply, fashioned much of Lloyd's concepts of reproduction as a potential limit to yield and subsequently he focused on several aspects of assimilate supply and utilization, including:

- (i) the potential for evolutionary differences in the rate of carbon assimilation (CER) by the leaves of ancient and modern wheats.⁵⁹ Surprisingly, CER had fallen not risen, in the course of evolution and domestication but this conundrum was explained by evidence that, as CER declined, individual leaf area had increased in parallel with grain yield.
- (ii) assimilate transported to the wheat grain sink comes from several sources including the leaf, the awns on the ear and from stored stem reserves.⁶⁰ As in the photograph below, these experiments could involve floret sterilization (Fig. 4).
- (iii) competition for assimilates depended on sink size and its distance from the source.⁶¹ For Lloyd the message was clear: 'as in human affairs, it pays to be large, close to the source, and with direct connections to it.'

The crucial test for crop physiology is whether its insights relate to plant breeding and agronomic practice. Along with John Bingham and Roger Austin at The Plant Breeding Institute,



Figure 4. Wheat emasculation.

Cambridge, UK, Lloyd confirmed that change in assimilate partitioning did account for increase in yield potential of twelve British wheats released by breeders since 1900.⁶²

Subsequently Lloyd's appetite for looking at the past and future of agriculture led to one of his favourite and widely cited articles 'Natural History of Crop Yield'.⁶³ Then, in 1999, he concluded this adventure with crops when he and Tony Fischer published a definitive view of the meaning of the term 'yield potential'.⁶⁴

In the intervening years he was not idle. He published fifteen papers with the three Mary's: Lush on grain legumes; Roskams on wheat and; Cook/Bush on wheat, rice and the grasses *Echinochloa* and *Poa*.⁶⁵ Also in 1983 he began his 'big book', *Crop Evolution, Adaptation and Yield*.⁶⁶ At 500 pages, it was 30% smaller than the first version, and its original 2500 references were cut to 1900. To date, more than 2000 copies of the book have been sold and it has received wide acclaim.

An International Agricultural Scientist

The Phytotron and IRRI: a Vignette of Evans' Impact on Agriculture in Developing Countries

At the time of accepting responsibility as Chief of Division, Lloyd was nurturing an additional and

rapidly growing interest in agricultural research in the Philippines. The publicity surrounding the Canberra Phytotron in the 1960s, led to a visit by Robert F. Chandler, the Director of the International Rice Research Institute (IRRI) at Los Banos, the Philippines. Subsequently, with Lloyd's support, he was successful in obtaining Australian funding for the construction of a similar facility at Los Baños. Lloyd's first onsite visit was in 1970 to advise the Australian Department of Foreign Affairs on the need for and design of a phytotron at IRRI. Two years later he returned briefly and then in 1974 was an invited speaker at the symposium to mark the official opening of the phytotron that involved among other luminaries, the Australian Minister for Science. The next year, 1975, he returned for an extremely comprehensive review of IRRI's research as a member of the first Quinquennial Review team commissioned by TAC, the Technical Advisory Committee of the CGIAR (Consultative Group on International Agricultural Research).

Determined to mix scientific studies with his involvement in international research management, and with great admiration for IRRI's work and impact, in 1978 Lloyd spent part of a sabbatical leave there after he stepped down as Chief of PI. At that time, with agronomists and the plant physiologist, S. K. DeDatta, he examined the results of rice trials that exposed for the first time the long-term decline in yields on the intensively cropped areas of the field station. R. F. Chandler had retired and it was with considerable reluctance that the new Director General, Nyle Brady, allowed the results to be published.

Subsequently there followed a six-year term on the TAC committee (1978–84) and later Lloyd was also co-opted for two terms as a Trustee on the IRRI Board (1985–9). Over this period he initiated a most successful Australian Development Project in Kampuchea involving IRRI as a source of much needed rice seed and staff back-up from IRRI agronomists.

In 1989, he left the IRRI board with doubts about his effectiveness as a Trustee and a growing unwillingness to accept some management philosophies. However, in his private notes he relates that others saw a great contribution and asked him to take on the task of the Director General of IRRI. The staff wrote, 'You have encouraged us to engage in good science to

solve production problems' and the then Chairman of the IRRI Board, Wally Forman, wrote: 'There are not many bright, well informed, level-headed, no-axe-to-grind scientists on the Boards of Centers, and you are one of them.' John Flinn, the senior economist, wrote: 'We need more interaction with distinguished scientists such as yourself: people with vision, humour, and who care about people.' Regretfully, Lloyd told the IRRI Board, 'I have ties to CSIRO which I feel are not to be broken.'

Leadership in International Agriculture and Food Production

Over time Lloyd's contribution at IRRI as a scientist with excellent analytical skills, was reproduced in his burgeoning agricultural advisory role in Australia and internationally. In 1975, he led a mission to the USSR to establish exchange visits for agricultural scientists. Two years later he was a member of an Academy delegation to China. At that time Australians knew little of their agriculture so he published accounts of both the Russian and Chinese visits.

In the late 1970s he also began prolonged discussions on Australia's role in international agriculture with Sir John Crawford (ANU economist and Chancellor) and Jim Ingram (Director of the Australian Government Development Assistance Bureau). Then, in 1981, because the Commonwealth Heads of Government were to meet in Australia, the Prime Minister, Malcolm Fraser, wanted 'something dramatic to offer developing countries of the Commonwealth.' Crawford, Lloyd Evans and Ingram had the answer, the Australian Centre for International Agricultural Research (ACIAR). It fitted the bill because Fraser wanted maximum visibility overseas combined with minimum visibility in Australia. The remit for ACIAR was to support Australian agricultural scientists in truly joint research in developing countries. It was not surprising that Lloyd became a founding member of the new ACIAR advisory committee.

As an aside, Sir John Crawford (1910–84) had a major influence on Lloyd. Not only did Lloyd know Sir John as a public figure and friend, but succeeded him in several activities including; Overseas Fellow of Churchill College, Cambridge (UK), President of ANZAAS,

a member of TAC and a member of the ACIAR Board. Lloyd diarized that:

to have observed the arts of chairmanship by which Sir John shaped debate, elicited contributions, formulated conclusions and controlled the members with a mixture of humour, wisdom and open-mindedness, fashioned my approach to committees and decision making.

He also admired his other great scientific mentor, Sir Otto Frankel, for his perceptiveness, eloquence, courage, strategic sense, unwavering belief in the value of ‘basic’ research, and his loyalty to friends in the face of fire.

In 1978, at the same time that Lloyd was pushing for ACIAR to be established, he was appointed for six years to TAC, which provided oversight to CGIAR. Then, as now, CGIAR supported sustainable agriculture in developing countries and focussed on crops, livestock, fisheries, forestry, land, and water. Its 600 public and private sector supporters in the 1980s included the World Bank, FAO, the International Fund for Agricultural Development and UNDP. Over the six years of Lloyd’s appointment, he attended twelve TAC meetings generally in Rome or Washington that were often combined with CGIAR meetings where he attended as an observer. He also fulfilled brief review roles of The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), and the International Food Policy Research Institute (IFPRI). As he put it, ‘I was not of the faith (not an economist) but I thought I would learn a lot from IFPRI’s economists.’

Near the end of his appointment (1984–5) Lloyd was tiring of meetings where he heard:

the same old issues, even the same old speeches by some TAC members and the same old evasions and manipulations by chairmen. They argued a lot about who would do what, and how, and with which, and to whom!

Somewhat tongue in cheek, the French Executive Secretary, Philippe Mahler, summed up Lloyd by describing him as ‘TAC’s Exocet missile; he hit his targets and effected some change.’

Lloyd knew from his reputation that he had spent his time valuably and felt the CGIAR and its research centres were delivering real help to the poor and hungry. Not surprisingly, therefore, completion of his term with TAC did not end his involvement with the international research institutes. Because of his ongoing research

interest in wheat, in 1990 he agreed to serve a six-year period on the Board of Trustees of CIMMYT (the International Wheat and Maize Breeding Institute) located in Mexico.

World Food Production

While still a high school student in New Zealand, Lloyd had read John Boyd Orr’s book *Food, Health and Income*⁶⁷ and this began his interest in world food supply. Later, at Oxford he revisited Malthusian predictions of overpopulation and insufficient food. Later still, his involvement with TAC reviews led to interaction with many able and committed agricultural scientists and economists from around the world who sharpened his thoughts on the agricultural constraints on world food production.

Such was his concern for ‘the hungry world’ and how many people it could hold that in the late 1990s he began his last and perhaps most significant book, *Feeding the Ten Billion*.⁶⁸ Fittingly, this book was published in 1998, the bicentenary of Malthus’ *Essay on Population*.⁶⁹ In his diary, Lloyd recalls that ‘I received the first copy of my book in October 1998, just in time to wave it around at the international symposium on World Food Security in Japan, at which I gave the opening address on ‘Steps towards feeding the ten billion’.’

Two months later, for a study week of the Pontifical Academy of Science at the Vatican, Lloyd gave a similar talk, ‘Food Needs of the Developing World in the Early 21st Century’. For Lloyd, it was a ‘plus’ to sleep in a cardinal’s bed in St Martha’s, but he regretted having no time to visit the Vatican Library or see the Sistine Chapel again. Also, he had brought with him one copy of his book (*Feeding the Ten Billion*), which he left on display only to come back after lunch to find it had disappeared; he tempered his regret with the hope that the thief was too poor to buy a copy of the book. A more welcome response came from the Rockefeller demographer, Joel Cohen in the first review of *Feeding the Ten Billion*: ‘Evans writes with authority, subtlety, accuracy, clarity, a marvellous richness of detail, and a very engaging human touch.’

Further praise for Lloyd’s contribution to international agriculture, world food issues and his crop research came with a successful nomination to the American Society of Plant Biology

for the 2004 Adolph E. Gude Jr Award for Service to Agriculture. For the Gude nomination, several leading international scientists provided me with glowing accounts of their interactions with Lloyd and parts of three letters are detailed below.

Professor Gurdev S. Khush (Former Principal Plant Breeder at IRRI) wrote:

Lloyd has made outstanding contributions to International Agriculture and thus helped produce more food for the world's hungry.

Dr Don Duvick Senior Vice-President Research (retired) Pioneer Hi-Bred International, Inc. wrote:

Dr Lloyd Evans is a scientist who has made great contributions to advancement of the beneficial use of agricultural science in industrialized and (especially) in developing countries around the world. Two of his books⁷⁰ have helped international policy-makers, as well as research scientists in agriculture, in food production as well as environmental protection.

And Dr Tony Fischer Honorary Research Fellow CSIRO Plant Industry:

Lloyd was always fully informed, forthright, tolerant, solicitous and, especially, aware of and concerned about different farming cultures. ...He has always been a strong advocate for continued investment in agricultural research.

Lectures and Books

Lloyd thrived on the sudden understanding that came from research but was also delighted when he could combine insights and set them in a broader, often historical context. For example, on the centenary of Charles Darwin's death, Lloyd celebrated the event by publishing an article in the *Journal of History of Biology*.⁷¹ He used Darwin's analogy between artificial and natural selection as a focus for how he and other plant biologists were approaching plant improvement.

Over his career Lloyd delivered more than 63 prestigious invited public lectures both in Australia and overseas; about half of these were published as articles, the other half as chapters in conference books. The invitations ranged from universities and learned societies to leading international agricultural companies including Monsanto and Du Pont and to international

foundations including a very prestigious CIBA Foundation Lecture in London. There were also several addresses to The Australian Academy of Science and to meetings in the UK organized by the Royal Society.

As the titles of some of these lectures show, they were provocative; 'The Two Agricultures: Renewable or Resourceful,' 'The Plant Physiologist as Midwife' and, 'The Divorce of Science': others were forward-looking for example: 'Variability of Cereal Yields: Sources of Change and Implications for Agricultural Research and Policy'. Overall, with his liking for historical perspective, Lloyd first assembled the facts and then developed answers to his questions; he was a true synthesizer.

Although always heavily committed, he was an author on four prestigious articles in *Annual Review of Plant Physiology/Plant Biology* and one in *Advances in Agronomy*. He edited five books and was sole author of three books; a small university text on flowering and his two major books, *Crop Evolution: Adaptation and Yield*, and *Feeding the Ten Billion*.⁷² These last two books have had major influences on agricultural research and policy and are considered essential reading for students in this field.

Lloyd Evans' influence on Australian plant science was been widely felt through his Presidency of the Australian Society of Plant Physiology, of ANZAAS and of the Australian Academy of Sciences. The many honours conferred on Lloyd included Officer of the Order of Australia in 1979, one of Australia's highest civilian honours and the Centenary Medal of Australia in 2003.

Lloyd was a legendary scientist and a true man of letters. He passed away peacefully in Canberra on 23 March 2015 after his wife, Margaret, had passed away the year before. He had suffered from steadily increasing dementia but was supported magnificently by all his family and friends.

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Only a few of Lloyd Evans' 224 refereed papers are cited in this memoir. For a full list of his publications arranged chronologically see Supplementary Material Number 1 (available online only), and for his CV see Supplementary Material Number 2 (available online only).

Acknowledgements

It has been an honour, a privilege and a very pleasing experience to write about the life and career of Lloyd Evans, my friend and colleague of some fifty years. During the process I drew on many sources and people. For their comments and suggestions I would like to thank Lloyd's three children Nicholas, John and Catherine and, also, Robyn Diamond, Tony Fischer, Elizabeth King John Passioura and Ian Rae. I especially thank Carl Davies and Lew Mander, who provided some of the photographs. The frontispiece photograph was taken in 1978 by Godfrey Argent and is reproduced with permission.

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