CONJECTURES, REFUTATIONS, AND EXTRAPOLATIONS

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INTRODUCTION

One reason why I have enjoyed reading earlier prefatory chapters is for the glimpses one gets of how the perception of problems, and insights into their nature, have grown from chance readings, comments by colleagues, or unexpected results. There is also the broader perspective on the evolution of our discipline and on the interactions among scientists. In short, they reveal the human face of science. But writing such a prefatory chapter is a different matter, as earlier authors have indicated. Scientists of my generation were trained to avoid the personal pronoun. “Art is I, Science is we,” as Claude Bernard stated.

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EARLY YEARS

I was born in 1927 in Wanganui, New Zealand, and grew up in Gonville, described by the novelist Janet Frame as “the quietest suburb in the world.” My father’s occupation, like his father’s, was wool, one of New Zealand’s major exports in those days, and it was expected that I would continue in that tradition. In fact, I could “class” wool quite accurately from an early age and was later able to supplement my income as a university student by wool classing. However, my mother’s parents had both been school teachers, and my mother wanted my brother and me to have as extended an education as we could get. We inherited our maternal grandparents’ library of English literature and history, from which I memorized a great deal of poetry and still remember it with pleasure, even though I may now forget your name within a few minutes.

However, my greatest delight as a boy was “messing about in boats” on the Wanganui River, which passed directly in front of our home. We became such competent rowers that, after our mother died, when I was ten, my father allowed me to row up-river with school friends during holidays, camping on its banks near the properties of farmers we knew. On one occasion this Tom Sawyer–like existence meant returning downstream with the river in full flood, dodging the uprooted trees and the legs-up, bloated carcasses of cattle.

My secondary schooling coincided with World War II, i.e., with blackouts, food rationing, anxious listening to the radio news, scarcity of imported goods, and military training. I went on a scholarship to Wanganui Collegiate School, which was modeled on British public schools for boys only, with a strong emphasis on “character,” discipline, and sport. This meant compulsory cricket in summer and rugby football in winter, with hockey (which I liked best) and tennis only if you could find the time. Our headmaster, Frank Gilligan, was an outstanding cricketer but also enjoyed hockey and played with us when he could. Our French and mathematics master, on the other hand, was a keen golfer and occasionally used the hickory handle of his mashy-niblick to discipline our backsides.

Because the teaching of science was weak, with absolutely no biology, I gravitated toward English and history in my university entrance exams. My father thought I should become a forester, but I had enjoyed working on a variety of farms during school holidays and preferred to study agricultural science. Wanganui being far too small to have a university, I left home in 1945 for Christchurch, where I could stay with my father’s parents for the first year of “pure” science at Canterbury University College and then transfer to Lincoln Agricultural College, a few miles away in the country, for my agricultural training.
UNIVERSITY IN NEW ZEALAND

I wish I could report that my first contacts with botany at university converted me to plant physiology, but it was not so. Far more effective in that respect was my involvement in what was called tramping (i.e., bushwalking) and in mountaineering. These became consuming hobbies, and several of my climbing companions went on to excel in the Himalayas as a consequence of the ice skills they developed on the southern alps of New Zealand. But I also became fascinated by the ecology of New Zealand’s alpine flora, so I was at last converted to botany, despite the greatest of all New Zealand scientists, the physicist Lord Rutherford, equating botany with stamp collecting.

However, in the genesis of my wanting to become a scientist, the greatest influence was a series of Friday evening lectures on the scientific method given by Karl Popper, the great Viennese-born philosopher of science, in 1945. Attended by packed audiences of staff, students, and the public, Popper’s lectures brought the history and practice of science alive for me before he moved to London later that year, hence my title for this paper.

Having done some preliminary military training, I was liable to be called up for service after my 18th birthday on August 6, 1945, but the first atomic bomb was dropped that day, sparing me from any further experience with military camps. Nevertheless, my grandfather’s anxious comment on the bomb was “You scientists, you will ruin the world.”

My newly minted enthusiasm for research barely survived the next three years of agricultural coursework at Lincoln College, however. Plant breeding and ecology were emphasized, whereas plant physiology was hardly mentioned. I therefore decided to take an additional course in plant physiology at Canterbury College while completing my agricultural degree at Lincoln, commuting by car between the two campuses and earning a scholarship that allowed me also to complete a degree in science.

In those days one could not get a Ph.D. in New Zealand, so there developed a tradition of substantial theses for a Master’s degree. There being no facilities or supervisor for a thesis in plant physiology, I did mine on the ecology of some salt marshes at a nearby lake, which involved a great deal of soil analysis and of kneeling in the mud with a point quadrat.

OXFORD

In the 1950s, most of the New Zealand students wishing to do a doctorate sailed to England. I had planned to go to Cambridge to continue my ecological research. However, the unexpected award of a Rhodes Scholarship took me to Oxford instead. Having been advised—wrongly, it turned out—that neither plant physiology nor ecology was strong in Oxford, I elected to do my doctoral research with E.W. Russell in soil science.
In the eight-month gap between graduation and sailing for Europe, I worked for the New Zealand Department of Scientific and Industrial Research on a highly educational roving commission, which included a period in the Grasslands Division. There I was able to put the soil analysis techniques used in my thesis to good effect at the end of a long-term experiment by Peter Sears that examined the buildup of soil fertility under various pasture regimes. The results were quite striking and interested Walter Russell, so my Oxford thesis research was on the interactions between soil organic matter and clay particles.

Because Oxford University did not formally recognize degrees from the University of New Zealand, I was in statu pupillari, living in Brasenose College, whose heavy gates, like those of other colleges, closed at 11 P.M. So, like other scientists who worked late in the lab, or played late elsewhere, I learned to climb over or through its medieval walls, adding to the skills and hazards of my doctorate. I also played a lot of hockey, attended a great range of stimulating lectures, and read widely.

One book, *Crop Production and Environment* by R.O. Whyte, fired my ambition to become a plant physiologist. Although not a particularly good book, when I open it now, it did three things for me then. I was enthralled by the phenomena of photoperiodism, of time measurement by plants, and by the apparent role of hormones in the flowering process. I was fascinated by the truly international perspective of the field that Whyte presented, thanks to his familiarity with research in the USSR and India as well as in Europe and America, and I fell in love with the shoot apex of grasses and cereals from his illustrations. My coeval New Zealand colleague, Ian Sussex, has admitted to the same infatuation in his prefatory chapter (12): “Anyone who has dissected the bud of a vascular plant under a stereomicroscope must surely have been thrilled by the translucent, glistening beauty of the apical meristem,” to which I would add, especially of the grasses during their transition to flowering.

My opportunity to do research on the flowering of grasses came toward the end of my three-year scholarship at Oxford. Frits Went gave a lecture on the climatic control of plant growth, mostly about early research in the world’s first phytotron, the Earhart Laboratory at CalTech. Here was my chance to work on photoperiodism, and Frits said I’d be welcome if I could find the requisite support. So I applied for a Commonwealth Fund Fellowship, which, after a memorable interview, took me and my newlywed wife Margaret—in those days Rhodes scholars weren’t allowed to marry until the final payment was in the bank—to California for 21 months, 3 of which had to be spent in travel around the United States, allowing us to visit a lot of universities and laboratories.

**CALTECH**

As we disembarked from the SS Queen Elizabeth in New York in September 1954, I was asked if I had a gun. “No, do I need one?” I replied. My first visit to CalTech made me wonder because the campus cops liked to pat their holsters and many
of the students also seemed to have holsters at their hips. I soon found out these were for slide rules, not guns. Slide rules ruled at CalTech in those days. The first seminar I attended there was also a shock: 8 A.M. on Monday morning! Not only was the timing surprising, after Oxford’s leisurely ways, but I was also surprised by the egalitarian atmosphere in which postdocs might challenge an assertion by one of the galaxy of biological stars in the plant physiology group: Frits Went, James Bonner, Art Galston, George Laties, and occasionally that agent-provocateur from UCLA, Sam Wildman.

During my two years at CalTech, I witnessed a dramatic extension of the known plant hormones from the auxins that Frits Went had discovered and that still preoccupied James Bonner’s group when I arrived. The isolation of gibberellic acid (GA\textsubscript{3}) in 1954, and of kinetin in 1956, extended the reach of plant hormones, and before I left, Bernie Phinney had shown our seminar group his first experiments with GA\textsubscript{3} on dwarf maize, while Folke Skoog had, warily, told us about kinetin.

Within the phytotron, which he had created, Frits Went was the unchallenged authority. Ralph Erickson, in his prefatory chapter (1), records that he “was incarcerated daily with Lloyd T. Evans, Harry R. Highkin, William S. Hillman, Margareta G. Mes, Paul E. Pilet, Roy Sachs, and (Frits) Went when he was not travelling!” I would add Taco van den Honert, Paul Kramer, Fausto Lona, Bill Hiesey, and others. We were, indeed, a refreshingly diverse and disputatious group, and the variety of their problems and approaches was, for me, highly educational.

The control of flowering by daylength and temperature had been examined in the Earhart phytotron for a wide variety of species, to which I added several more. I was so impressed by the analytical opportunities that Frank Salisbury and James Bonner gained in their experiments with \textit{Xanthium}, because it required exposure to only one inductive short day (SD) for flowering to occur, that many of my experiments focused on finding a plant that needed only one long day (LD) for floral induction. Dissections on my last day in the Earhart made it clear that I had found such a plant in the grass \textit{Lolium temulentum} and that its flowering response was elegantly quantitative. Fifty years later I am still at work on its flowering behavior. It has been a deep well of insight and refreshment. We share the initials L.T., and I have a sense of identity with it, as many scientists do with their experimental systems.

My 18 months in the Earhart made me enthusiastic about the potential of phytotrons for analyzing climatic limitations on plant growth and development; and I transmitted my enthusiasm to Otto Frankel when he visited there in 1955. He was thinking of building a phytotron at the Commonwealth Scientific Industrial Research Organisation (CSIRO) Division of Plant Industry in Canberra, of which he was Chief. The Division had research groups scattered all over Australia, and as we talked about the great variety of plants and experiments in the Earhart, he decided to begin his campaign in earnest and, as part of that, to recruit me. He also arranged for Roger Morse, the officer-in-charge of the CSIRO Engineering Section, to visit the Earhart before I left so that we could discuss possible alternative designs. This we did, and after a fruitful couple of days one began to emerge.
Just before I left CalTech in 1956, I visited Anton Lang at UCLA to see his first experiment with the application of GA$_3$ to the LD plant *Hyoscyamus* in SD. At that time his treated plants had bolted but not yet flowered. Anton knew his plant well enough to send an excited letter to *Naturwissenschaften*, received on May 2, followed by another on May 30 to announce their flowering. The mythical florigen seemed within reach. In England a few months later, Percy Brian gave me a sample of GA$_3$ to test its effect on the flowering of *Lolium* when I got to Canberra. And so began a long and still-evolving series of experiments, discussed elsewhere in this volume (8).

**THE CANBERRA PHYTOTRON**

As our small airplane from Sydney circled over Canberra before landing, we recognized why it was mockingly called the bush capital. Since that time, when there were only 35,000 people, its population has increased almost tenfold; the facilities have also increased. Small though its population was in 1956, Canberra was, nevertheless, host to a range of research laboratories, including those of several Divisions of CSIRO. The largest of these was Plant Industry, which Otto Frankel, as Chief, was in the process of transforming into a better-equipped and more lively research center. Acquiring a wide range of controlled environment facilities was central to Otto’s plans.

Because of the relatively high solar radiation, even in winter, because much of the work would relate to field problems, and because artificial lighting was still improving rapidly, much of the controlled growing space was, initially, to be in large glasshouses (i.e., greenhouses) with square-wave temperature control to ±1.5°C in 3° steps from 15/10°C to 36/31°C, not unlike the Earhart. Within these glasshouses, however, more than half of the space would be occupied by cabinets with automatic shutters for daylength control and with closer and more flexible control of day and night temperatures. The highest level of environment control, including irradiance and humidity, was to be in artificially lit cabinets. It was at this level that most space for future expansion and improvement was left, and that is where *Arabidopsis* now reigns supreme.

My responsibility was to subject all components of the design to biological testing. The rate and direction of air circulation was central in this, so we built a series of wind tunnels for preliminary tests. To get the specified level of temperature control, the engineers wanted air speeds across the cabinets of 3 m s$^{-1}$, but I showed that these were detrimental to plant growth. Reducing them gave unacceptable gradients in temperature across the cabinets, so we finally settled on vertical air movement at 0.5 m s$^{-1}$, downward, which gave better uniformity and only a small vertical gradient. Natural plant communities are exposed to frequent fluctuations in their profiles of irradiance, temperature, air movement, etc., so I also investigated some of the effects that these might have on experimental plants, which I reported to our phytotron-launching symposium.

After much other testing, Roger and I then prepared overall plans for the building and services, which were approved by the CSIRO Executive and passed on for
consideration by the Australian government. The CSIRO Division of Radiophysics had a competing claim for a similar sum to build the Parkes radiotelescope, and we were warned that, because they were “reaching for the stars,” we didn’t have much chance. In any event, both projects were fully funded, and for once the plant sciences were a match for radioastronomy, which moved Otto to adorn the entrance to our phytotron with the words “Cherish the earth for man will live by it forever” as a reminder of the responsibility of the plant sciences. The phytotron, by the way, was called CERES after the Roman goddess of agriculture, while also standing for Controlled Environment Research.

The paper that Roger Morse and I wrote describing the design of CERES (11a) became one of Eugene Garfield’s Citation Classics simply because it was referred to by so many of its users in their papers as an easy way of describing the facilities. CERES was officially opened by Prime Minister R.G. Menzies on August 29, 1962, during an international symposium, The Environmental Control of Plant Growth, an event as opportune for the graduate students who attended as it was for the burgeoning practitioners of what Pierre Chouard called phytotronics.

Five years later, on June 26, 1967, CERES was included in the first live “One World” TV link up, along with the Parkes radiotelescope, partly because we both happened to have things to do in the middle of our Australian night, conveniently timed for mass viewing in the United States and Europe. After 20 years of operation, Ian Wardlaw, Rod King, and I reviewed all the work done in CERES (7). And now, 40 years old and with a face lift, it is still full of a great variety of plants, many of them crops in the process of being genetically engineered, but still in the company of Arabidopsis, Lolium, etc.

**PHYSIOLOGY OF FLOWERING**

*Lolium temulentum*

Darnel, the “tares” of the Bible, can be a serious weed in cereal crops. However, its sensitive and quantitative flowering responses make it a model system for the analysis of LD induction in grasses and cereals, but until the Canberra phytotron was built I wasn’t able to do many experiments with my Canadian strain of *L. temulentum*. I was, however, able to calibrate its flowering response to one LD in terms of plant and leaf age and to show that only a few square centimeters of one leaf blade exposed to one LD sufficed for the floral induction of plants 5 weeks old. So I was able to proceed to my first, and then topical, question, Did a leaf in LD produce a mobile stimulus to flowering, or did those in SD export an inhibitor of flowering, as several German and British physiologists had suggested? The symmetry will be recognized by admirers of M.C. Escher’s graphic works, especially “Day and Night.”

My results suggested that the LD leaves exported a floral stimulus and that the SD leaves exported a mobile inhibitor of flowering in *Lolium*, which interacted quantitatively at the shoot apex. In his comprehensive review of the physiology of flowering in 1952 Anton Lang (9) had concluded that there was no mobile SD
inhibitor exported by leaves of LD plants in SD, and both he and Jan Zeevaart offered alternative explanations of my results at the symposium for the opening of CERES in 1962. But by then I had found another condition, namely, anaerobic atmosphere, that differentially affected the LD promotive and the SD inhibitory processes in *Lolium*. You can imagine how delighted I was when, 15 years later, Anton and Mikhail Chailakhyan announced that their grafting experiments with tobacco indicated the presence in the LD plant *Nicotiana silvestris* in SD of a “potent flower-inhibiting and growth-regulating material that can also be transmitted (10).” Anton kindly annotated the reprint he sent to me “who believed in flower inhibitors much sooner than I did.”

In 1966 Fred Addicott shared his small sample of abscisic acid (ABA) with me, and I found that it inhibited flower induction in *Lolium*, particularly when applied late on the LD. Rod King and I subsequently found that water stress during the LD, which greatly raised the ABA level of both leaves and shoot apices, was very inhibitory to floral induction, but we have been unable to show a consistent effect of daylength on ABA levels, so it remains an open question whether ABA is the putative SD inhibitor.

As for the LD stimulus in *Lolium*, Rod, Cheryl Blundell, and I have shown that, although the flowering response increases with high sucrose concentration in the shoot apex, high sucrose alone does not replace the LD for shoot apices in vitro. Moreover, we found that our standard effective LD treatment, with 16 hours of low-intensity incandescent light, does not raise the concentration of sucrose in the shoot apex significantly above that in darkness, so sucrose cannot be the LD stimulus in *Lolium*. In this we part company with Georges Bernier, whose experimental plants have a much less rigorous LD requirement for flowering than that for *Lolium*. But whereas sucrose in the medium does not induce flowering in excised apices of *Lolium*, several gibberellins (GAs) can do so. This work is discussed at length later in this volume (8), so here I shall note only that it led to a fruitful collaboration with that master of gibberellin chemistry, Lew Mander, and also to commercial interest in the use of related compounds in formulations for the dwarfing of cereals.

Another major step forward in our *Lolium* experiments was pioneered by Carl McDaniel, during sabbatical leave in Canberra, when he succeeded with in vitro culture of excised shoot apices of *Lolium*. This technique has been invaluable to us in many ways, but we have not yet succeeded in using it, as we had hoped, to identify florigenic components either exuded or pressed from *Lolium* leaves during or after the LD.

What in vitro apex culture has allowed us to do, however, is to determine exactly when the shoot apex undergoes floral evocation after the LD, something not known with such precision in any other plant. In the 1960s, Ian Wardlaw and I had devised a way of measuring the speed of translocation of the LD stimulus to flowering in *Lolium* leaves. At 1–2 cm h$^{-1}$, it was clearly not in mass flow with $^{14}$C-labeled photosynthate, which moved simultaneously at 77–105 cm h$^{-1}$. We estimated that the LD stimulus begins to arrive at the shoot apex early on the morning after the LD.
This agreed with the time when applications of 5-fluoro-uracil and actinomycin D near the shoot apex were most inhibitory to flowering, so we assumed that was when floral evocation occurred, and the excised apices concurred: Evocation was complete by the end of the daylight period after the LD.

In the mid-1960s, my colleague Toon Rijven was honing his microchemical skills, and we analyzed a lot of Lolium shoot apices for changes in protein and nucleic acid contents at and after floral evocation. Although coarse by today's standards, these analyses gave us valuable insights into changes in the shoot apex during early inflorescence development, as did the histochemical changes that Bruce Knox and I examined. Not much was evident during floral evocation, but Bruce and I did find a rise in $^{32}$P and $^{35}$S incorporation on the day after the LD in the sites where future spikelets would develop, as well as at the apical dome. By the next day, RNA accumulation in these cells was histochemically evident in plants exposed to the LD, whereas in SD these cells would, only weeks later, begin to form tillers. In this and other grasses, therefore, the induction of flowering can be viewed as precocious branching, first to form spikelets instead of leafy tillers and then to form florets after a couple of leafy glumes.

Given the probable role of GAs in the floral evocation of Lolium, Rod and I began a collaboration with Dick Pharis of Calgary to examine changes in the GA content of Lolium leaves and shoot apices during and after the LD, which initially required up to a thousand shoot apices per sample. But as physical assays of GAs have replaced bioassays, the number of apices required has been greatly reduced. In our recent collaboration with Thomas Moritz of Umea, only 40 apices per sample were required for replicated measurements of many GAs, and progress has been rapid (8).

The grasses are one of the great success stories of the plant kingdom, surviving in a great range of environments and dominating a quarter of the land area of the world. Among the characteristics contributing to their success is the adaptive range in their flowering behavior, some of which I have sampled. Soon after arriving in Australia, I asked our taxonomist Nancy Burbidge if there was any grass species that occurred throughout the country and got an immediate reply, Kangaroo grass, Themeda australis. With the help of colleagues, I established a collection of 30 clonal populations, both diploid and tetraploid, from all over Australia, ranging from latitude $6^\circ$S to $43^\circ$S and from the east to the west coast via the central deserts. Several of the low-latitude populations were strict short day plants (SDP), whereas the southerly populations were long day plants (LDP), including those from colder areas that also required vernalization. By contrast, those from the drier areas were indifferent to daylength: They flowered following rain. Bruce Knox found their breeding systems to be versatile, i.e., both sexual and aposporous, so here was an excellent example of the adaptive role of photoperiodism in nature, which my ecological colleague Richard Groves extended to the effects of temperature on growth and seed dormancy.

Most temperate grasses are LDP, but they ring many variations on that theme, especially at high latitudes. One that I worked with, crested dogstail (Cynosurus...
cristatus) needed only 3 LD, after vernalization, to initiate inflorescences, but it needed two weeks in LD to form perfect inflorescences. With fewer LD their inflorescences were proliferous, their spikelets forming plantlets. As my Norwegian colleague Ola Heide of Ås has shown with several high-latitude grasses, this can be a valuable survival strategy in the short cool summers, but it also illustrates the quantitative nature of floral induction in the grasses with the initiation first of spikelets, then of florets, and finally of anthers requiring a nudge by LDs, 1 LD sufficing in *Lolium temulentum*, whereas 14 are needed to complete the process in crested dogstail.

Ola and I worked together on some high-latitude accessions of Kentucky bluegrass (*Poa pratensis*) in which exposure to LD causes flowering only when preceded by prolonged exposure to either low temperatures or SDs. I had earlier found the same requirement in some British wheats, work which subsequently proved useful in the breeding of dual purpose winter wheats.

In my hunt for a grass requiring only one SD, I came across the serious tropical weed, itchgrass (*Rottboellia exaltata* L.f then, now *R. cochin-chinensis* Lour), which turned out to need a minimum of 6 SD. But before discarding it I asked the question, “Where are those 6 SD summed up, in the leaf or at the shoot apex?” The answer was clear: at the shoot apex, because the SD could be given singly to different leaves. Years later, in Papua New Guinea, I collected seed of what proved to be a day-neutral ecotype of itchgrass, which has the potential to become a serious weed of summer crops at higher latitudes.

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I have probably spent too long on my flowering research, although there is much I haven’t mentioned, such as all that with Rod King and Ola Heide on phytochrome transformations in *Pharbitis* and our semidian rhythm hypothesis. But questions on how plants sense and respond to daylength, the nature of the message(s) sent from the leaves that perceive it to the shoot apex that reacts to it, and how the apex shifts from leaf to flower formation have dominated my life in science.

Given the variety of environmental conditions to which plants, both wild and cultivated, must adapt, it is inevitable that their responses will, like Cleopatra, be of infinite variety. This is not a field for physiologists in search of universalities, but it is one of great significance to evolutionary studies, to ecology, and to the adaptation and modification of crops and pasture plants and of their accompanying weeds.

Research is surely one of the most involving, frustrating, exhilarating, and unending games in the world. After 50 years of it I am still, and just as impatiently, awaiting the answer to a question in our flowering work raised by a recent paper from Japan (11c), which could explain much of our structural work with GAs.

**CROP PHYSIOLOGY**

The case for building the Canberra phytotron encompassed its use to resolve problems in the adaptation of crops and pastures to Australian climatic conditions, and many examples of such analyses were considered in our review of the first two decades of its operation (7).
As well as this trouble-shooting research, however, I thought we should explore some physiological aspects of the limits to crop yields. In the early 1960s, crop photosynthesis and respiration were widely considered to be the primary targets for improvement. Much emphasis was placed on the geometry of light penetration into the canopy of leaves and on the profiles of photosynthesis and respiration in determining an optimum leaf area index (LAI). This was no easy matter with the grasses and cereals, but the work that Ian Wardlaw and I had done on the translocation of $^{14}$C-labeled assimilates out of the various leaves of *Lolium* in our flowering experiments suggested that lower older leaves were not “parasitic.” They survived on their own photosynthesis or senesced. If that were so, we should find that the net CO$_2$ exchange rate (CER) of the crop canopy maintained a plateau at high LAI, rather than undergoing a sharp fall when it passed the optimum, as crowding experiments and a model by our agrophysical colleagues suggested.

So, in collaboration with Toshiro Saeki of Japan and John Ludwig, we adapted an artificially lit phytotron cabinet to function as an assimilation chamber for a cotton crop grown in situ until it reached a high LAI. We then measured the photosynthesis and dark respiration of the crop as we progressively removed layers of leaves from below. The answer was clear, not only for cotton but also for sunflowers and several other crops: There was no sharp optimum LAI, a conclusion that Keith McCree in New Zealand soon confirmed.

Models of crop photosynthesis at that time also assumed that growth and yield were largely determined by the net photosynthesis rate. However, Frits Went and others had suggested that there might often be conditions in which photosynthesis was limited, instead, by the capacity of the plant to grow. The removal of “sink” organs had often been shown to reduce the photosynthetic rate of leaves, but it had not been shown that the rate could then rise again in response to restored demand. Thanks to our earlier flowering experiments, Ian Wardlaw and I knew that whereas the upper leaves largely supported grain growth, the lower leaves largely supported root and tiller growth. So, by combining continuous measurement of the photosynthetic rate of the flag leaf of wheat in constant conditions with measurements of the distribution patterns of $^{14}$C-labeled assimilates from the lower leaves, with our new colleague Rod King, we were able to show not only that removal of the ear led to a sharp fall in the CER of the flag leaf, as others had done, but also that this could then be reversed by removing the lower leaves, thereby restoring demands on the flag leaf to take over the supply of assimilates to the roots and young tillers. The paper in *Planta* became a Citation Classic (8a).

**PHYSIOLOGY OF CROP EVOLUTION**

At about this time I was asked to review the book *Crop Plant Evolution*, edited by Sir Joseph Hutchinson. What particularly struck me as I read the various crop chapters was how much insight into the cytology and genetics of crops had been gained by comparing the wild progenitors with the domesticated crops. By contrast, we physiologists had sometimes compared old and new varieties but had largely
neglected the wild progenitor species. So I gathered together seed samples of several species, races, and varieties from each stage in the evolution of wheat, both wild and cultivated diploids, tetraploids, and hexaploids. Bob Dunstone, and then Roger Gifford, later joined me in this work, from which I mention just one counterintuitive finding, which Ralph Riley labeled the Evans paradox. In our comparisons of the CER per unit area of the flag leaves, we found that it had fallen, not risen, in the course of evolution and improvement. However, flag leaf area had increased progressively, more than compensating for the lower CER, so photosynthesis per flag leaf had increased. Selecting for high CER without reference to leaf size could, therefore, be counterproductive. This may be why this paper (5a) also became a Citation Classic, an endorsement that seems to impress the bureausaurs of science more than it should, reflecting as it does the size of the readership as much as the significance of the paper.

In some later experiments with Ola Heide and Mary (Cook) Bush on Poa pratensis, in which leaf length was varied over a twofold range by either daylength or GA application, we obtained a very similar relation between CER and leaf area. Consequently, I suspect that the striking differences in flag leaf CER among the wheats largely reflect the adaptation of leaf size to their usual growing conditions. Having collected seed of the wild diploid species with Danny Zohary near the sea of Galilee in hot dry conditions, I could see the advantage in water conservation of small flag leaves with high CER. Likewise, having followed modern wheat crops through a cloudy, cool, and wet summer in Cambridge, the advantage of larger flag leaves with lower CER was also apparent.

I should also mention that, unknown to me, M.A. Khan and Shigeru Tsunoda had also been comparing the photosynthetic rates of wild and cultivated wheats and likewise found much higher rates in the wild species. Their paper (7a) was received only three weeks after ours.

With various colleagues I subsequently extended such physiological comparisons of wild progenitors and their domesticated counterparts to other crops, such as rice, barley, barnyard millet, and, to the delight of Jack Harlan, cowpeas with Mary Lush. But wheat remained the focus of my experiments, many of them in collaboration with Howard Rawson.

**Sink Size and Strength**

Crop physiologists often speak of sink organ “strength,” as distinct from the photosynthetic “source,” in the determination of crop yield, but those who venture to define “sink strength” encounter a minefield. The problem is that all growing organs are sinks for assimilates, that sinks like young leaves later become sources, and that they differ in size, and in distance from, or vascular connection to, the sources. I had long wondered how to approach the problem in relation to cereal yields until I read a paper by Peel and Ho (11b) in which small and large colonies of aphids, equidistant from a 14CO2-labeled source, competed for assimilates. They had used willow, but I adapted their system to wheat by having the flag leaf of the main stem as the only source of 14C-labeled assimilates, with the ears of the first two
defoliated tillers as equidistant competing sinks. With this system Mary Cook and I also found that the larger sink always got more than its proportional share of assimilates.

However, I wanted to be able to vary not only the relative size of the two competing sinks, but also the effect of their distance from, and vascular connection to, the source. Some earlier work with John Bingham at Cambridge had shown me how photosynthetically active the awns of wheat can be, so Mary and I set up a system with a central awn as the only source of labeled assimilate, while the two competing sinks were other spikelets with differing numbers of grains at different distances above and below the source spikelet, or even on the other side of the ear with a less direct phloem connection to the source. The results were clear: The share of labeled assimilate increased in proportion to the square of the relative size of the sink, decreased in proportion to the relative square of the distance, and was 10–30-fold greater for the sink on the same side of the ear as the source than for that on the opposite side. As in human affairs, it pays to be large, close to the source, and have good connections.

So far as I know, these experiments have failed to spawn any successors, so our frequent use of the phrase sink strength is likely to remain conveniently vague in spite of the significance of the concept in crop physiology. Of course, sink strength is also determined by many factors other than size, position, and vascular connections. It is, for example, greatly influenced by the interplay of plant hormones, with auxins, GAs, cytokinins, and abscisic acid all involved. Perhaps it is this very complexity that discourages research on it.

**Yield Potential**

An equally much-used but vague term in crop physiology is that of the “yield potential” of a variety. In my 1993 book *Crop Evolution, Adaptation and Yield*, in which I tried to summarize what was known of the physiology of crop yield, I defined yield potential as “the yield of a cultivar when grown in environments to which it is adapted, with nutrients and water non-limiting, and with pests, diseases, weeds, lodging and other stresses effectively controlled.” Defined in this way, yield potential may seem to be rather remote from actual yields, but as agriculture becomes more intensive, this definition becomes more relevant to practice. My ever-challenging colleague Tony Fischer and I added several glosses to this definition for a meeting on the subject in 1999 (6) because higher yield potential remains an important objective in plant breeding programs.

During a sabbatical leave in Cambridge in 1969, I had discussed with John Bingham how we might assess progress in the yield potential of British winter wheat varieties. We decided that disease control procedures were not good enough at that time, but on my next sabbatical there in 1978 we joined forces with Roger Austin and his colleagues in such a trial. The results suggested that the yield potential of recent cultivars was approximately 40% more than that of early twentieth century ones, although the modern cultivars did not grow any faster than the older ones. Rather, they mobilized a higher proportion of their resources into the grain.
Some Lessons

Great progress in plant physiology has come from research at ever smaller scales of analysis, but when it comes to the performance of crops in the field, it is important to set these findings in the context of the whole crop and of the whole plant breeding process, where they may have counterintuitive effects, as we have seen for leaf photosynthetic rate.

Also, agronomic progress may shift the physiological analysis of yield profoundly. In the 1920s, before nitrogenous fertilizers were widely used, E.S. Beaven concluded that grain yield in barley depended closely on the extent of “uplift” of reserves from the stems and leaves to the ear after anthesis, when the flag leaves began to senesce. By the 1940s, when Helen Archbold began her $^{14}$C-labeling experiments, and when the level of crop protection and agronomy was improving, she found that photosynthesis after anthesis was contributing significantly to grain growth. Nowadays, with more comprehensive and longer-continued crop protection and fertilizer application, photosynthesis throughout the grain growth period, including that by the ear, contributes most of the carbohydrate stored in the grain. The duration of photosynthesis by the upper leaves has become a major yield-limiting factor. Also, with the rise of crop modeling, there is a far more comprehensive appreciation of the variety of developmental pathways to high yield.

Crop physiology can, therefore, aid the plant breeder, but it also assists the agronomist through the diversification and improvement of inputs such as adjuvants, fertilizers, protectants, herbicides, and irrigation water use. Equally, of course, plant breeders and agronomists have many insights to offer plant physiologists, and I have profited greatly from those of John Bingham, Don Duvick, Gurdev Khush, and others.

By doing research in crop physiology as well as in the physiology of flowering, I could be accused of dilettantism. But having two separate fields of research has, in my experience, been helpful. Not only have they cross-fertilized one another, but also whenever I came to a road block in one, I could keep moving with the other. For example, after an initially productive period with *Lolium* in the 1950s and 1960s, I got stalled on the role of phytochrome and not even a sabbatical year with the redoubtable Sterling Hendricks at Beltsville solved that problem. It was then that I moved into crop physiology and had an exciting time there through the 1970s before returning, more productively, to the role of GAs in the flowering of *Lolium*.

ADMINISTRATIVE INTERLUDE

In his preface to Ronald Clark’s biography of J.B.S Haldane, Peter Medawar includes “perhaps a manly grappling with administration” in his list of phases in the lives of academics. When John Falk, Otto Frankel’s successor as Chief of the CSIRO Division of Plant Industry, died in 1970, I did not apply to succeed him.
because I wanted to get on with my research, and CSIRO Chiefs up to that time were appointed until retirement, still 22 years away for me then.

When invited by the CSIRO Executive to be Chief, I eventually agreed but said I would do the job for seven years only, with the right to return to full-time research within the Division after that. No head of an American university department would see anything unusual in that, but other CSIRO Chiefs and would-be Chiefs saw this stipulation as threatening. I suspect it was accepted only because the Executive thought I would become so hooked on the joys of administration that I would soon change my mind. They were too far removed from the delights of research, from what Victor Weisskopf has called the joy of insight.

The Executive also agreed in advance to my proposals for some restructuring of our Division’s research, which was still focused on pastures because of constraints imposed by an agreement with the State Departments of Agriculture 40 years earlier, which left the improvement of major crops to them. Given the way Australian agriculture was developing, I thought it essential that our Division should have the freedom to expand its research on crops other than apples, citrus, and tobacco. Also, there was a growing appreciation of the diversity and roles of our flora and natural vegetation and of the need for its conservation, which justified an increase in our taxonomic and ecological research. Given the emphasis by the new Labour government, elected in 1972, on the National Estate, I was able to use the sharp reduction in wool-funded pasture research to build up these other areas. These included a major effort, led by Don Spencer, on seed protein biology, the first interdisciplinary, process-focused group in the Division, which had previously been organized by discipline. Also established before my term ended was a group on the molecular genetics of cereals, under the leadership of Jim Peacock. In all this I was greatly helped by my deputy, Don Spencer, another plant physiologist.

As the end of my term approached, I reminded the Chairman of CSIRO that I still wished to be replaced by the end of 1977. Nothing succeeds like a successor, and mine, Jim Peacock, has now been Chief of the Division for 25 years, while I have had another 25 years immersed in the great game.

While Chief of the Division, I accumulated a variety of other diversions from research, such as being involved in the gestation of the *Australian Journal of Plant Physiology* as well as serving as President of the Australian Society of Plant Physiologists (1971–1973), Chairman of the Board of Standards for the Australian Journals of Science (1977–1982), President of the Australian and New Zealand Association for the Advancement of Science (1976–1977), and President of the Australian Academy of Science (1978–1982), during which period we celebrated our 25th anniversary in some style.

My wife Margaret, a student counsellor, has always regretted that I have had only occasional contacts with students and have never taught a university course except when I was still a student in 1950. Quite apart from the fact that I would not have been a good teacher, I would not have handled well the combined demands of teaching and research. Being able to focus wholly on research, as I could in CSIRO, was the right life for me.
THE INTERNATIONAL AGRICULTURAL RESEARCH CENTERS

The lives of scientists can be divided into three phases: becoming, being, and representing. In the third phase you find yourself on too many committees and are often asked to introduce meetings or provide a closing summary. Memorial lectures are another hazard, but given my liking for historical perspective, I mostly enjoyed these. My first, in 1975, was for my predecessor as Chief, John Falk. In recognition of the world population reaching four billion that year, I spoke on “Crop plants, an international heritage and opportunity” (2).

I had visited the International Rice Research Institute (IRRI) in the Philippines in 1970 and the International Center for Wheat and Maize Research (CIMMYT) in Mexico in 1974, and the main purpose of my lecture was to emphasize the very real help that the International Agricultural Research Centers (IARCs), supported by the Consultative Group on International Agricultural Research (CGIAR), were giving to the less developed countries of the world in their efforts to reduce chronic malnutrition and to promote development.

One of the founding fathers of the CGIAR, Sir John Crawford, was in the audience and arranged for me to participate in the first five-year review of IRRI, the oldest center in this forest of acronyms, which I had previously helped to get its own phytotron, as acknowledged in a wall plaque of a kangaroo leaping over the rice paddies. Sir John then arranged for me to follow him as a member of the CGIAR’s Technical Advisory Committee (TAC), beginning in 1978 when I stepped down as Chief. The role of TAC was to advise the CGIAR donors on the overall priorities for agricultural research on behalf of all the developing countries and to evaluate the research programs of its various centers, which totaled 11 when I joined TAC, 13 when I left, and is 16 today. Half of the members of TAC came from the developing countries, two from each of the three developing regions. Among us we covered most areas of agricultural research, so our meetings were a wonderful opportunity to get a comprehensive perspective on world agriculture. Our debates could be vigorous at times, and much homework was needed, but our field trips were often the most educational and provided many insights into the great variety of agricultures and their problems, as presented by local farmers and their advisors. After my six years on TAC, I served another six on the IRRI Board of Trustees, followed by six more on the CIMMYT Board, which included many more field trips in developing countries.

For all their faults, the CGIAR and its international centers have been an attractively informal and highly effective way of enhancing food production in many developing countries. I count myself lucky to have been so involved with them in the early years before their procedures became more formal and to have been able to savor the wisdom and foresight of the founding fathers such as George Harrar, Frosty Hill, David Bell, and Sir John Crawford.

The IARCs still have an important role to play as long as the population of the developing world continues to increase. It is projected to increase by another two
billion by 2025, and by a further 1.4 billion by 2050, so although the developed world no longer needs to produce more food for itself, the developing countries must increase their food production by more than 70% by the year 2050 if they are to be largely self-sufficient.

Unfortunately, the rapid development of biotechnology and the growing importance of intellectual property rights has led to such a strong expansion of agricultural research in the private sector—where it now exceeds public sector agricultural research in the developed countries—that funding for public sector research is declining. In recent years there have also been reductions in the funding of the CGIAR centers and in that of agricultural research in the less developed countries by USAID and the World Bank, presumably on the assumption that it can safely be left to the private sector, whereas I believe we should be enhancing their capacity to collaborate with the private sector.

**BOOKS AND MEMORIAL LECTURES**

Had I written only research papers, but no books, I suspect that my path in research might have been rather different. It is the evolution of ideas and insights in a field, and the broader perspective that engages me and has induced me to edit five books and to write three, leading one of my colleagues to say, rather dismissively, “Oh, Evans, he writes books.” Despite the outstanding example of Charles Darwin who wrote many books, including several that could be called plant physiological, scientists who write books are often viewed as suspect.

Some years after I became immersed in the physiology of flowering, I found myself struggling to identify what processes were common to photoperiodic species in the way that metabolic processes are. James Bonner, tongue in cheek, liked to summarize the flowering behavior of plants as “different plants differ in different ways.” Given the importance of flowering behavior to the survival of species, and the great variety of environments to which plants have adapted, Bonner’s crisp summary is bound to hold, but it was the more general processes, like the dark reversion of phytochrome discovered by the Beltsville group, that needed more emphasis.

I therefore planned a book, *The Induction of Flowering* (1969), containing case histories of the 20 main experimental species written by acknowledged experts, with an historical introduction and an attempt at integration in the final chapter. This last chapter is still quoted not only because it provides a convenient summary of early work, but also because I introduced the term evocation for the processes at the shoot apex that commit the plant to flower, as distinct from the photoperiodic processes of induction in the leaves. Subsequently, I was asked to write a small book, entitled *Daylength and the Flowering of Plants* (1975), covering similar ground but in a way more accessible for students.

Because the structure of *The Induction of Flowering* seemed to work well, especially the final attempt at integration, I subsequently edited a similarly structured
book entitled *Crop Physiology* (1975), later translated into Spanish, Arabic, and other languages. During a visit to China in 1977, I was asked to autograph many copies of an unauthorized Chinese translation of that book. My friends at Cambridge University Press, the authorized publishers, turned quite green when they heard an estimate of its sales in China, and this experience brought home to me how useful and influential books can be compared with research papers, particularly in developing countries with limited access to scientific journals.

One consequence of this realization was that I decided to write a book with crop physiology as its core, entitled *Crop Evolution, Adaptation and Yield* (1993). It cost me a huge effort, over many years, but I have no regrets at having tried to expound the relevance of crop physiology for the evolution of agriculture, especially in the delightful ambience of the Rockefeller Foundation’s Villa Serbelloni in Bellagio for one memorable month.

As part of that process I was led to consider the current world food-supply situation and the ways it could be enhanced to meet the needs of future populations. In his *Essay on the Principle of Population* (1798), Malthus emphasized the miseries of populations always increasing to the current limits of food supply. By contrast, in her book *The Conditions of Agricultural Growth* (1965), the Danish economist Ester Boserup turned that around to argue that it was population pressure that drove the further development of agriculture. So, in my last book, *Feeding the Ten Billion: Plants and Population Growth* (1998), also completed at Bellagio on a later visit and published exactly 200 years after Malthus’ *Essay*, I explored the interrelations between the human population of the world and the evolution of agriculture, with emphasis on the role of science. I happened to be born in the year when the world population may have reached two billion and was writing this book as it approached six billion, which gave me the idea of dividing the text by steps in population growth rather than by time. The structure worked well and made me rethink many aspects of the story. But it also led me to a clearer appreciation of the problems ahead for the less developed countries, where they already have to support more than four times as many people as the developed countries do on the same amount of arable land and will have to support six times as many within the next 50 years, and to do so in the context of changes in climate that are likely to disadvantage them far more than they will the temperate developed countries. The less developed countries need all the help in plant research that can be given to achieve the requisite increase in their food supply, and there will be no shortage of challenging problems for the next generation of crop physiologists, who will probably face the same ethical dilemmas that I discuss toward the end of my book, and which led me to declare myself, like Rene Dubos, a despairing optimist.

For me, as no doubt for many others, the writing of books is a great learning experience, from which one emerges with changed perspectives and fresh insights, just as one does from experiments and from reviewing books and papers by others. Likewise, the preparation of memorial lectures, of which I have given quite a few. It was in preparing the first of these that I began to understand how improvements in agronomy have allowed plant breeders to select for higher yield potential.
In my memorial lecture for Professor J.G. Wood, entitled, “The Plant Physiologist as Midwife” (3), I explored a statement by Stephen Hales, who is usually granted paternity of the discipline of plant physiology, that “a farther insight into the vegetable economy must needs proportionally improve our skill in Agriculture and Gardening.” In that lecture I included an imaginary interview by a hard-headed review panel of a rather esoteric research proposal by a young Dutch plant physiologist, Frits Went, on the potential usefulness of his proposed research. Frits was delighted with the interview, commenting that “today’s scientists are under too much pressure to provide a framework of relevance for their work.”

Another memorial lecture (5) was for the feisty Australian essayist, Walter Murdoch, who waged war against what he called the suburban spirit, i.e., submission to authority. In it I explored the “suburbanization” of science, i.e., its taming by governments and bureaucrats ever in search of relevance and wanting more of what Francis Bacon called experiments of fruit rather than his experiments of light. I argued that it is the lateral thinking and the bringing together of disparate elements that has made science so useful. But I also argued that “applied” science has often been of great value to “pure” science, giving the outstanding example of how Charles Darwin’s remarkably comprehensive investigations of artificial selection in plant and animal breeding were central to his recognition of the power of natural selection in evolution. This was a subject I had researched at some length for the centenary of Darwin’s death (4), including an examination of the marginal markings and comments in Darwin’s reprint collection in the Cambridge University Library.

FAMILY AND COLLEAGUES

My wife Margaret has had to endure my preoccupation with research probably more than I realize, as have our three children, Nicholas (a linguist specializing in aboriginal languages) and twins John (also a plant physiologist) and Catherine (an artist). Our family recreations have been mostly on the tennis court and on or in the sea near our coast house, Witjweri, known to many plant physiologists.

As I hope this account of my life in research makes clear, a wonderfully able, diverse, and dedicated array of colleagues, from many countries, has worked with me in Canberra on a wide variety of experiments. They have brought different approaches, new techniques, alternative interpretations, and healthy scepticism. They have shared in the labor, especially welcome in all-night experiments for our photoperiodic studies. They have persuaded us to work on their problems, their plants, and their theories. They have enriched our understanding of other countries and other cultures and of the problems faced by scientists in developing countries.

Such opportunities for real collaboration are one of the most rewarding features of a life in science. As Peter Medawar (11) put it, “In no other form of serious creative activity is there anything equivalent to a collaboration between scientists.” I have enjoyed and learned from all of these, but one collaboration in
particular I must acknowledge here, namely, that with Rod King, which began almost 40 years ago with photosynthesis and has been central to all my flowering work for many years now. Like many other scientists, I believe I have been incredibly lucky in my career, in my mentors—especially Otto Frankel, Frits Went and Sterling Hendricks—and in being recruited by such an enlightened research organization as CSIRO has been. Looking ahead, what concerns me most is that my young colleagues may not have the opportunities we had to follow our own hunches as to what might prove significant or useful and to learn for ourselves from those hunches that didn’t prove to be either. Although I was reluctant to prepare this account of my life because of the personal pronoun problem, I am grateful for the invitation because, as Kierkegaard put it, “Life must be lived forwards, but can only be understood backwards.”

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