BIOGRAPHICAL MEMOIRS

Winslow Russell Briggs

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A Biographical Memoir Edited by Gary Gardner, Elaine Tobin, and Zhi-Yong Wang

Introuction

Over the course of his long career, Winslow Russell Briggs made many seminal contributions to our understanding of the physiological, biochemical, and molecular mechanisms underlying plant growth and responses to the environment. He was one of the most admired plant scientists of modern times, known for his fearlessness, stamina, and love of a well-designed experiment. He reinvented himself several times from physiologist, to biochemist, to geneticist, to molecular biologist, while he remained at the cutting edge until the end of his life.

Briggs was born in 1928 in St. Paul, Minnesota, although he came from Boston aristocracy. Both he and his wife Ann were descendants of passengers on the *Mayflower*. He attended Harvard University as both an undergraduate and a graduate student and considered a music major, but after taking some science courses he became a biology major.

After receiving his Ph.D. in 1956, he accepted a position at Stanford University, where he began his work on phototropism, the subject which remained a primary interest throughout his career. He returned to Harvard in 1967 as a professor in the Biology Department. There he pursued research primarily on phytochrome, the plant photoreceptor that affects many aspects of plant development. However, the opportunity to lead the Department of Plant Biology at the Carnegie Institution on the Stanford campus brought him back west, where he spent the rest of his career.

At the Carnegie Institution his research interests expanded and actively continued until his death in 2019. His lab led the field of plant photobiology for decades. It was inspiring to watch him achieve his goal of understanding the molecular mechanism of phototropism when his lab spearheaded the molecular cloning of the blue light receptor phototropins during the first few years after his official retirement from administration. His recognition that the LOV-domain present

in phototropins was also present in a number of other blue light receptors, including ones outside the plant kingdom, led him to explore their roles as well.

In addition to his laboratory research, he and Ann became involved for nearly 40 years as volunteers in what eventually became the Henry W. Coe State Park. Winslow actually created a detailed map of the trails in the park. He was awarded the 2013 Philanthropist of the Year by the California State Assembly for his work in helping to save the park from imminent closure and, furthermore, in having it declared a State Park.

Briggs' scientific contributions were widely recognized. His many honors include election to the National Academy of Sciences in 1974, the American Academy of Arts and Sciences in 1975, and the German National Academy of Natural Scientists Leopoldina in 1986. In 1994 he received the Steven Hales Prize from the American Society of Plant Physiologists, in 1995 the Sterling Hendricks medal from the U.S. Dept. of Agriculture and the American Chemical Society, and in 2000 the Finsen Medal from the Association Internationale de Photobiologie. He received the 2007 Adolph E. Gude, Jr., Award from the American Society of Plant Biologists for his "outstanding service to the plant science community." He was awarded doctoral degrees *honoris causa* by the University of Freiberg, Germany (2002) and the Hebrew University of Jerusalem (2016). An award about which he was especially proud was the International Prize for Biology from the Japan Society of the Promotion of Science for his "outstanding contributions to the advancement of basic research." This was awarded in Tokyo in 2009 in a ceremony attended by Emperor Showa and that included Winslow's family.

Briggs was a leading figure in the plant science community and served it in many important ways. He was the President of the American Society of Plant Physiologists (now American Society of Plant Biologists) in 1975–1976 and President of the American Institute of Biological Sciences in 1981, and he was also a member of many other groups that served plant science, including the Botanical Society of America, the American Society of Photobiology, the American Association for the Advancement of Science, and the California Academy of Sciences. He was an active member of the Board of Directors of Annual Reviews, an editor of *Annual Reviews of Plant Biology* for more than four decades, and the founding Honorary Editor-in-Chief of *Molecular Plant*.

In editing this Biographical Memoir, as Winslow's colleague during the last part of his life, Zhi-Yong Wang has given us a clear picture of his continual scientific pursuits up until the day of his death. And as Winslow Briggs' students from over 50 years ago, Gary Gardner and Elaine Tobin are honored to be a part of helping to provide a full view of his life and many talents. As a mentor, he gave us incredible freedom to make our own mistakes, but he also provided rigorous criticism, always with a sense of humor.

In undertaking this effort, we decided that the many articles written by and about him tell the tale of his career more fully than we can do in a short space.[1] His own description of his career published in the *Annual Review of Plant Biology* in 2010[2] provides exactly what a Biographical Memoir is supposed to do. In addition, Annual Reviews also conducted an interview with Winslow by Sabeeha S. Merchant, Editor of the *Annual Review of Plant Biology*, and Elaine Tobin.[3] However, Briggs had another decade of research productivity in his career. Therefore, with the permission of Annual Reviews,[4] we are reproducing his 2010 review in its entirety, and we are supplementing it with two brief sections written by his collaborators in that last decade. In addition, we have solicited comments from many of Winslow's students, postdocs, and collaborators, and we have annotated the review with those comments.[5] We appreciate these contributions, and, in addition, we thank Winslow's daughters, Caroline, Marion, and, especially, Lucia for their advice and insights in the preparation of this Memoir.

We hope that these comments and additions, along with Winslow's own reflections, demonstrate the wide-ranging influence he has had on research in plant biology. More importantly, we hope that these words illustrate, although the word is often over-used, that Winslow Briggs was truly a mensch.

References

1 See, for example, *Molecular Plant* 12, 461–463, April 2019, https://doi.org/10.1016/j.molp.2019.02.007 and *Plant Signaling and Behavior* 14, 10, e1652521, 2019, https://doi.org/10.1080/15592324.2019.1652521.

2 *Annu. Rev. Plant Biol.* 61: 1-20, https://doi-org.ezp2.lib.umn.edu/10.1146/annurev-arplant-042809-112326.

3 Interviews with Winslow by Annual Reviews (2011): https://www.youtube.com/watch?v=T55JqEBSaq8.

4 Republished and modified with permission from the *Annual Review of Plant Biology*, Volume 61, © 2010 by Annual Reviews, http://www.annualreviews.org.

5 Comments are denoted with lettered footnotes in the text and can be found at the end of the document. Because of space considerations, we have edited these comments for presentation here. However, the full text of each comment can be found on the Carnegie Department of Plant Biology website (https://carnegiescience.edu/NASBriggs).

A Wandering Pathway in Plant Biology: From Wildflowers to Phototropins to Bacterial Virulence

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Key Words

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Abstract

The author describes the somewhat convoluted pathway he followed from amateur taxonomy of Minnesota wildflowers to identification of the phototropin family of blue-light receptors. He also mentions individuals who were important in moving his career first into plant taxonomy, then plant development, and finally plant photobiology (and out of music). He emphasizes the many twists and turns a research career can take, including a few that lead to blind ends. He also emphasizes the oscillatory nature of his career—back and forth between the Atlantic and Pacific oceans (with occasional forays to Freiburg, Germany) and back and forth between red-light receptors and blue-light receptors. There is a short intermission in which he describes his longtime relationship with California's Henry W. Coe State Park. Finally, he relates how he followed the unlikely pathway from plant blue-light receptors to a blue-light receptor required to maximize virulence of a bacterial animal pathogen.

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Minnesota Wildflowers

The man with the shotgun under his arm was wearing a plaid lumberjack shirt and a matching plaid cap with the earflaps down. He did not look one bit pleased. My father, sitting awkwardly on the ground behind a small tripod, was photographing a lovely flowering specimen of the terrestrial orchid *Orchis spectabilis*. He was hardly situated to offer even a lame excuse for trespassing in the man's woodlot. (In being there in the first place, my father was, of course, setting a splendid precedent for his teenage son). After a bit of stammering and apologizing, he got up awkwardly (he stood over six feet tall) and apologized again. We left hastily, the man with the shotgun following closely behind.

Neither my father nor I said very much for the next hour or so.

The location of this minor drama was not far from the village of Savage, Minnesota, along the south bank of the Minnesota River, some 20 miles upstream from the Twin Cities and its confluence with the Mississippi. The woodlot was adjacent to a large swampy area that sloped down to the river and harbored the most remarkable collection of terrestrial orchid species: four different lady slipper species (*Cypripedium candidum* [**Figure 1**], *C. reginae*, *C. parviflorum*, and *C. parviflorun* var. *pubescens*) and the rare prairie-fringed orchid, *Habenaria leucophea*. There were many other botanically interesting plants in that location, but it was the orchids that attracted my attention and whetted my appetite for studying plants. My father, recently retired as a schoolmaster, was trying to document in Kodachrome every Minnesota wildflower he could find. I don't remember exactly how he learned about this particular treasure of a wetland, but we were to make many other visits there over the next few years.[A] (Unfortunately, there was no Nature Conservancy to purchase this remarkable botanical resource. Eventually, the Cargill company bought it, drained it, and put ugly buildings on it. Opposition by botanists at the University of Minnesota was to no avail.)

Those teen years saw visits to many other botanically fascinating areas. Once we headed far south along the Mississippi River to photograph a rare dogtooth violet, *Erythronium propullans*, likely an endangered species. I recall driving up to the Boundary Waters in the Superior National Forest and then up the Sawbill Trail to make a canoe trip many miles up Sawbill, Alton, Kelso, and Lujenida lakes (the last, a Native American name but hardly romantic; a Native American had named the lake after his three daughters: Lulu, Jenny, and Ida) to collect a rare plant we had seen for a Minnesota botany professor named Ernst Abbe. Abbe was writing a flora of Cook County Minnesota and needed herbarium specimens for documentation. As most of the county and its many beautiful lakes are on spectacular Laurentian shield granite, our task was not unpleasant. We had canoed through this country many times.

Figure 1 *Cypripedium candidum* Muhlenb. Ex. Willd., small white lady slipper. Photograph by John DeQ. Briggs.

A Gruff Mentor

By the time I left for Harvard for my freshman year, my father and mother (who shared his intense interest in wildflowers) had become close friends with Abbe and his wife, Lucy. The Abbes took us to Minnesota's Lake Itasca State Park one spring to photograph *C. arietinum* (**Figure 2**), the rare ram's head lady slipper (and step across the Mississippi River at its source). It was Abbe's conviction that I should major in biology with an emphasis in botany. He had obtained his doctorate under the guidance of Ralph Wetmore, a well-known botanist at Harvard. He also knew the other distinguished plant scientists there. However, although I was interested in science, my interest focused on physics and chemistry. I had been inspired by an extraordinary high school science teacher,

Figure 2 *Cypripedium arietinum* R. Br., ram's head lady slipper. Photograph by John DeQ. Briggs.

Russell Varney, and the school I attended, the St. Paul Academy, did not teach any biology at the time. Nevertheless, Abbe refused to give up. Every time I came home from Harvard, we would almost always see Abbe and his wife socially if not botanically and he would always ask the same brusque question: "Have you taken a botany course yet?" There invariably followed a meek "not yet."

A Truly Mediocre Pianist and a Double Major

There was another obstacle to becoming a botanist: I wanted to major in music. My mother was a professional pianist and teacher, my sister Mary was well on her way to becoming a successful pianist and teacher, and I had been studying piano (with a couple of years out to study cello) since about age six. I had great aspirations—fantasy dreams of playing Beethoven concerti with great symphony orchestras. As my sister was majoring in music at Radcliffe, I promptly signed up to major in music as well. I also sang in the Harvard Glee Club. (I had the rare privilege of singing in the Brahms *Requiem* under Serge Koussevitsky and in the Berlioz *Damnation of Faust* under Charles Muench.) Having nothing else to do, I participated on both the freshman and varsity swimming teams in the one- and three-meter dive. As my interest in science hadn't waned, I also took physics, calculus, inorganic chemistry, and (ugh) organic chemistry. (My advisor in the Music Department, Irving Fine, undoubtedly thought I was crazy. It was a while before I told him about the swimming team.)

A bout with rheumatic fever (following a disastrous academic performance—almost failing grades in second-year calculus and second-year harmony—that I naturally blamed on the rheumatic fever) temporarily terminated my studies. I was whisked back home to St. Paul to recover. When I reappeared at Harvard the next fall, I finally took Biology 1a, the introductory botany course—at least partially to silence Abbe. (I also rejoined the swimming team.) To my delight, I found the course fascinating. There was much, much more to botany than just identifying plants.

That course was followed by Biology 1b, introductory zoology, and many other courses, largely botanical, and I was completely hooked. I even took comparative vertebrate anatomy taught by Alfred S. Romer. (Despite his brilliant teaching, I thoroughly disliked the course. That was partially because it was filled with aggressive premed students and partially because I disliked the smell of formaldehyde.) I suddenly discovered that because I had the math and physical sciences behind me I could complete a major in biology but not lose the major in music if I stayed an extra semester. Hence I was able to graduate with honors in biology (plus a music major: two years of harmony, two years of counterpoint, a year of music history, and a year of orchestration). It never occurred to me not to stay at Harvard for both master's and doctoral degrees in biology. (I was spurred away from music as I finally rejected the comfort of denial and admitted that my future as a pianist was not bright. Certain faculty in the Music Department had already made that suggestion.)

From Plant Taxonomy To Auxin In Ferns

I spent my first graduate year, 1951–1952, becoming a taxonomist. In 1952, I took a summer course in tropical botany in Cuba and Honduras that resulted in publication of two floristics papers.[38,39] (We were in Cuba shortly before Fidel Castro emerged from the mountains of central Cuba and took over the island. We had been warned to stay out of those mountains to avoid a gang of "banditos." Most likely, the leader of those "banditos" was Castro.) The following summer (1953), I collected plants in Mt. McKinley National Park (as the unconvincing justification for mountain

climbing in the Alaska Range—including first ascents of Mt. Brooks and Mt. Mather) and wrote a third floristics paper.[5]

Figure 3 *Osmunda cinnamomea* L., cinnamon fern. Central cinnamon-colored fertile fronds give the species its name. Photograph by Janet Novak.

However, Ralph Wetmore's course in plant morphogenesis (with emphasis on ferns) lured me away from the herbarium. A loquacious and brilliant senior postdoc in the Wetmore lab, Taylor Steeves, drove the transition to completion. I started a thesis project with Wetmore, with Taylor as my informal mentor. I promptly fell in love with auxin in ferns. I left taxonomy behind, moved into the growing research area of morphogenesis, and did a thesis on the role of auxin in leaf development—especially leaf unrolling—in the cinnamon fern *Osmunda cinnamomea* (**Figure 3**). Kenneth Thimann, a giant in the auxin field, was on my thesis committee and I had the run of his wonderful facilities. (He was a real gentleman. When I inadvertently flooded his lab and office one evening, he forgave me immediately. His graduate students didn't.)

I was still in "Ask the professor what to do" mode when I took a course from Irving W. Bailey. A brilliant anatomist (he used polarized light to work out the structure of the plant secondary cell wall at least 10 years before the electron microscopists were able to confirm his model), he steadfastly refused to give students any advice in either choosing a laboratory project or carrying it out. He would help generously with techniques and equipment, but for anything else he would say self-deprecatingly, "Well, you really know your system far better than I do. What do you think?" We were on our own. For the first time, I learned that I didn't have to "ask the professor." For my project, I described an anomalous structure in the ovary of a member of the Sapotaceae. Although it really was anomalous, Bailey didn't encourage me to publish it. (I have now completely forgotten why it was anomalous.) Nevertheless, from this experience I learned that I could design my own investigations and could believe that my results might be of some scientific interest.

During and following the completion of my doctorate with Wetmore, I parlayed the thesis into several papers on leaf development in *O. cinnamomea*—all written jointly with Taylor. He was also working on *Osmunda* at the time and our papers included much of his data so we alternated first authorships. Inexplicably, we published three of these in a seldom-read journal.[15,16,68] To my knowledge they have never been cited (with the exception that the later ones cited the earlier ones). The fourth of these[17] was published in *Plant Physiology* despite a scathing review from Folke Skoog (who chose to identify himself). Every time I saw Folke thereafter, he would mutter, "I STILL think it was a lousy paper." Many years later I saw him at a national meeting and confessed that the paper wasn't really super. I believe his comment was, "It's about time."

The First Faculty Position — Phototropism I

In the winter of 1955, Victor Twitty, chair of the Department of Biological Sciences at Stanford University, telephoned Wetmore, an old friend, to ask whether he had any graduate students about to finish their doctorate. Twitty needed somebody to teach a course in mosses and ferns and a course in plant physiology. Since my thesis was on the developmental physiology of ferns, Wetmore asked me whether I was interested. Naturally, I said, "Yes." There were no advertisements in *Science*, no inquiring letters to colleagues, no joblisting web sites, no search committees, and no concerns about affirmative action: only one casual telephone call. Twitty immediately invited me for a seminar and interview. Prior to the trip to California, there was one dismaying incident: I was sleeping late one morning when Wetmore telephoned to tell me that Lawrence Blinks, from the Stanford Department of Biological Sciences (Hopkins Marine Station), was sitting patiently in my office. I hastily dressed and bicycled

frantically to the lab to meet Blinks. To my puzzlement, he began by asking me what I needed to get my lab started. It was suddenly obvious that he thought I had already been offered the position. I haltingly explained the situation and he immediately proceeded to give me a grilling. One of his questions: "What would you be expected to teach?" I replied that Twitty had mentioned a course on mosses and ferns and a course on introductory plant physiology. Blinks snorted, "*I've* been teaching plant physiology at Stanford 20 years." Oops. What would he say to Twitty? The first day at Stanford (my first visit to California), I gave my seminar. The second day I met seriatum with almost all the department faculty members. At the end of the second afternoon, I met with Twitty for an "exit interview." I fully expected him to tell me that he would be getting in touch in a few weeks, after the department had interviewed all of the other candidates. To my astonishment, he offered me the position. Apparently, (*a*) there had been a revolving faculty meeting following me as I went from one faculty member to the next, (*b*) Twitty either hadn't heard back from Blinks or Blinks was relieved that he wouldn't have to teach plant physiology again, and (*c*) there were no other candidates. I immediately accepted his offer. I didn't tell him how little I knew about mosses and liverworts. Needless to say, other plant biology graduate students at Harvard (some considerably brighter than I) were not delighted that I had been offered the Stanford position. (A small detail: I had promised Ann Morrill that if I got the job at Stanford, I'd ask her to marry me—I did and we were married in June 1955. After 54 years, I am still occasionally reminded of that little promise.)

I arrived at Stanford in the fall of 1955 and set up operations in a somewhat primitive basement lab in Jordan Hall (no hot water and far down a convoluted basement corridor from the nearest distilled water source) but with funding for an essential constant-temperature humidified darkroom for auxin bioassays—assays that had been a mainstay of my thesis research. Almost immediately I had graduate students and the lab became productive. National Science Foundation support soon followed. I also managed to learn enough about mosses and liverworts to teach that course the first winter. Unfortunately, nobody thought to list the course in the Stanford course catalog, so at the first lecture I faced a single undergraduate student. A sympathetic graduate student offered to audit and I doggedly taught the course—lecture and lab. Surprisingly, it turned out to be much more of a struggle to put together a broad introductory plant physiology course with lab (I had to teach photosynthesis) but somehow I managed. Note: Although I was proud of having three degrees from Harvard, there were disadvantages. Edward Tatum was still at Stanford and he and George Beadle had just received the Nobel Prize for their one gene–one enzyme work with the pink bread mold *Neurospora crassa*. During my undergraduate and early graduate days, Harvard did not have a geneticist and therefore didn't offer a course in genetics. Wandering dreamily among the *Osmunda* fronds, I didn't have a clue what Tatum did. I don't entirely blame Harvard for this failing—I should have looked beyond those fronds occasionally—but the experience shows the danger of remaining at the same institution through all three degrees.

The second time I gave plant physiology, something occurred that would permanently change my research objectives. I had just completed the section on phototropism, when a hand went up in the back row. James Wilson, a graduate student with Ed Tatum, questioned a classic result by Frits Went[73]: An oat (*Avena sativa*) coleoptile irradiated from one side showed an increase in the growth hormone auxin flowing down the shaded side and a decrease on the irradiated side. Light induction of an auxin differential by light-induced lateral transport of auxin away from the light source had became known as the Cholodny–Went hypothesis. However, because the total auxin from illuminated and shaded sides didn't add up to the amount of auxin emerging from dark controls, the experiment didn't eliminate differential light-activated auxin photodestruction as a mechanism. Jim asked why no one had ever simply placed a coverslip barrier vertically through the entire coleoptile tip to separate the illuminated and shaded sides physically without interfering with the light gradient. If the auxin differential persisted, differential auxin destruction (or inhibition of synthesis) could be at least a part of the mechanism for causing curvature. However, if the differential was eliminated by the barrier, the result would eliminate both auxin destruction and inhibition of synthesis and provide powerful support for the Cholodny–Went hypothesis.

A senior, Richard Tocher, wanted to do an honors project in my lab. Since doctoral student Tom Scott and I were doing literally hundreds of *Avena* coleoptile curvature tests (following the hundreds that had gone into my thesis), we were set up to follow Jim's suggestion. Tocher caught on to the assay right away. We did the experiment, the barrier eliminated the auxin differential, and voila! A paper in *Science*![18] (I can't believe that we gave the light measurements in meter-candles and *Science* let us get away with it.) This work on phototropism over 50 years ago first caused me to entertain the thought of identifying and characterizing the responsible blue-light receptor.

Many more phototropism experiments followed in the next few years. Phototropism is induced by blue light, something first noted in 1817,[55] so we developed a variety of blue-light sources and used red lights as our safelights (standard safelights those days for auxin assays). We switched from 60 W incandescent bulbs to tungsten-halogen lamps

or mercury or xenon arcs and various combinations of filters to produce nearly monochromatic blue light. We acquired a meter that actually measured light intensity and dose in micromoles of photons—a considerable increase in photobiological sophistication over meter candles. We measured light-driven auxin redistribution as a function of pretreatments, e.g., red light,[7] and with respect to parameters such as light intensity and irradiation time.[6] My interests were no longer in morphogenesis: They became permanently transmuted into photomorphogenesis.

I have always expected both graduate students and postdocs first to learn about a lab's interests, capabilities, and limitations and then select their own problem (Bailey's influence, mind you, certainly not my lack of ideas). Thus over the years I have had students working on problems often somewhat distant from my own immediate interests—e.g., the role of red light in the development of a water fern, in this case, *Marsilea vestita*[44]; flowering in the duckweed *Lemna gibba*[27,B]; a mathematical model to describe the complex phototropic responses of *Avena* coleoptiles[74,C]; auxin relations in light and dark-grown pea seedlings[63,64,D]; circadian rhythms both of conidiation in *Neurospora crassa*[62] and of chloroplast movement in the marine green alga *Ulva lactuca*[20]; long-distance photosynthate transport in the giant kelp *Nereocystis luetkeana*[52]; auxin transport into membrane vesicles from etiolated *Cucurbita pepo* epicotyls[37]; light piping through etiolated seedling tissues[49,E]; the exquisite red-light sensitivity of coleoptiles and mesocotyls of oat seedlings grown in "reagent-grade darkness" (Dina Mandoli's terminology[48]); the role of actin in chloroplast movement in the freshwater golden alga *Vaucheria sessilis*[2,3,F]; and other related studies. Although phototropism and photomorphogenesis have dominated my laboratory, I found the breadth of projects incredibly instructive—not just for the students but for me as well.

Late in 1959, Leonard Machlis asked whether I would serve as Associate Editor for *Annual Review of Plant Physiology*. I accepted with some trepidation and thus began an association with Annual Reviews that continues to this day. I succeeded Machlis as Editor in 1973 and finally resigned in 1993 at the same time I became emeritus (although I remained on the Annual Reviews board somewhat longer). In 2004, the Editor-in-Chief, Sam Gubins, talked me back into serving as Associate Editor, a position I still hold. Over the years this association has been a wonderful way to keep abreast of plant biology in areas far from photomorphogenesis and plant development. It also served as a wonderful excuse to decline any other editorial duties.

I won't forget my first meetings with the Editorial Committee. Among other members were Anton Lang, Sterling Hendricks, Kenneth Thimann, Lawrence Bogorad, Harry Beevers, and Folke Skoog, all distinguished senior plant biologists. Machlis instructed me to listen carefully but to let these senior giants in the field battle it out to assemble a list of possible topics and authors for the next volume. (He didn't exactly say, "Keep your mouth shut!" but that was the way I interpreted it.) I had no trouble listening transfixed. It was a real circus. The combined scientific knowledge and wisdom in the room was overwhelming, the arguments intense, and the repartee almost nonstop (Skoog was an active participant as you might imagine). I didn't dare open my mouth. Afterwards Machlis asked me why I had been so quiet.

The Red Shift

A sabbatical in 1963 took me to the United States Department of Agriculture laboratories in Beltsville, Maryland. This was an opportunity to work with Sterling Hendricks, Harry Borthwick, Bill Siegelman, Karl Norris, and Warren Butler, all familiar names throughout plant biology. In 1959, they had published the exciting first spectroscopic evidence for the long-sought red-, far-red-reversible plant phototoreceptor,[22] later designated phytochrome. Under Bill Siegelman's guidance, I first learned about phytochrome spectroscopy by measuring the distribution of phytochrome in etiolated seedlings in an instrument designed for the purpose (called a ratiospect). This work produced a potboiler of a paper,[14] and one that likely resulted in more citations than all previous papers that my students and I had published—including the one in *Science*. (In those days nobody counted citations as the basis for hiring and promotion decisions—perhaps only because there was no conveniently accessible citation data available. The quality and quantity of research plus teaching evaluations were the old-fashioned criteria. Citation frequency is a great way to make the unquantifiable quantifiable. Unfortunately, deans seem to love it almost as much as number of publications.)

I also joined Bill's efforts to purify phytochrome and study its biochemistry and photochemistry. From the phytochrome distribution study, we had learned that oat (*Avena sativa*) was a much richer source of phytochrome than barley (*Hordeum vulgare*), and Bill and most others after him subsequently used etiolated oat seedlings as their source. I was finally exposed to real biochemistry firsthand. I also learned fascinating spectroscopy from Warren Butler—e.g., how to take the absorption spectrum of a one-inch pine plank (or more usefully, of a cuvette loaded with etiolated tissue segments). I then used their special instrumentation to take absorption spectra of bean leaves in a study with Warren on protochlorophyll phototransformation.[21]

Although Warren had a stainless steel forearm and leg (he had stepped on a mine on the Anzio beachhead in Italy toward the end of World War II and lost both), he hadn't lost his

sense of humor. I well remember coming into the darkroom, illuminated mostly with dim red light, that housed the fancy spectrophotometer. There was a green light flashing on another instrument somewhere in the background and the lab definitely looked strange. Warren looked over at me and grinned, raising one famously bushy eyebrow, with his arm nearly elbow deep in a Dewar vessel filled with liquid nitrogen. The combination of the weirdly illuminated cloud arising from the Dewar vessel, the red and green lights both on at once, the flashing white lights on the spectrophotometer, the immersed forearm, and Warren's slightly ghostly grinning face as seen through the cloud was unforgettable.

I carried the phytochrome studies back to Stanford postsabbatical and my lab continued both characterization studies and purification efforts. The shift in our interests from blue light to red light was almost complete. We learned that phytochrome was more labile in its far-red-absorbing form (Pfr) than its red-absorbing form (Pr).[19] Hence, red safelights were a no-no and we (and many others) switched to dim green safelights. These latter aren't really safe either, as the ratio of extinction coefficients between Pr and Pfr is about the same at 530 nm (green) as at 665 nm (red). The absolute values for the extinction coefficients are approximately tenfold lower but are certainly not zero. As a consequence, green light will take phytochrome to the same photoequilibrium between Pr and Pfr as red—it just takes 10 times as much green light as red.[56] We also learned that some systems—e.g., phototropism in maize coleoptiles—are exquisitely sensitive to red light: One second of red light almost too dim to detect by eye altered subsequent phototropic sensitivity to blue light.[23] (I recall once visiting an unnamed newcomer to phytochrome research and he proudly showed off his brand new green-light-equipped facility. Apparently, he thought that if a little green light was safe, a whole lot more green light was safer. The place was dazzling.)

Stanford's Department of Biological Sciences finally qualified for a new building and in 1965–1966 we feverishly designed our own labs. Mine would have real hot water, piped in deionized water, vacuum lines, climate-controlled growth chambers, cold rooms, a superb light-, temperature-, and humidity-controlled dark facility, and generous lab space. Wow! We were scheduled to move into the new labs during the summer of 1967. (The building is not exactly an architectural gem; its style might best be described as late Wagnerian. A colleague, Paul Ehrlich, described it as architecturally defensible only in the military sense of the word).

First Change of Venue: Stanford to Harvard

I never occupied the laboratory I had so carefully designed. As my Stanford colleagues started moving in, I was supervising the transfer of our belongings into a huge moving truck. Ann and I plus our two daughters then climbed into a station wagon and headed east. I had been offered a position at Harvard as Professor of Biology. John Torrey, who had moved from Berkeley to Harvard some years earlier, was already there. Thimann was leaving Harvard to join the faculty at the University of California, Santa Cruz, and Harvard apparently thought it would take at least two people to replace him. (They were probably right.) I was one of them and Lawrence Bogorad was the other. There was the prospect of developing a strong plant biology group—something that Stanford sadly lacked at the time and the Harvard offer was simply too good to turn down.[G] (The Department of Plant Biology of the Carnegie Institution of Washington at Stanford supported an exciting group of plant biologists and they had always welcomed me cordially. However, the Carnegie scientists of that era did not teach and were not interested in mentoring graduate students.)

For the second time, I designed a lab and accumulated a group of able graduate students. However, unlike the years at Stanford, the lab was now highly focused. Siegelman was no longer attempting to purify phytochrome and we jumped in full time. We discovered quickly that phytochrome wasn't a 60-kD protein as published elsewhere[51] but was at least twice that large.[33] One also had to keep everything cold and absolutely minimize light exposure. We had learned well from Bill Siegelman how to scale up biochemical procedures: He had introduced us to cafeteria tray racks and garbage cans. First, we grew multiple cafeteria trays of oat and rye seedlings (Siegelman style) in a controlled-temperature darkroom, sliding the trays into a rack normally provided for used trays. We then harvested the shoots into a garbage can with an electric hedge trimmer (up to 8 kg of etiolated tissue). (Bill grew massive cultures of cyanobacteria in garbage cans and stirred them with carefully encased fluorescent lamps.) Harvest and subsequent extraction in a huge Waring blender started on Monday morning. There followed (*a*) size-exclusion chromatography, (*b*) ion exchange chromatography (on a calcium phosphate form called brushite—also made in a garbage can), (*c*) more ion exchange chromotagraphy, and finally (*d*) a second size-exclusion step. We collected the final samples early Wednesday morning.

Obviously, it had to be a team effort. I left our house in Lexington at 4:00 am on Tuesday to run the third column. Somebody else would then take over and run the last column. However, it didn't always work. Once a fatigued graduate student set up the fraction collector but failed to put tubes in it. Another graduate student offered to take over that step (an offer gratefully accepted). He carefully loaded the fraction collector with tubes but neglected to turn it on. The lab was unnaturally quiet for the next two weeks.

Another time, the DEAE (diethylamino-ethyl) cellulose column was being cantankerous and I was not getting the purification that we had come to expect from it. While I was in Israel giving a series of lectures, somebody else had to run that step. Just before I gave my first talk in Jerusalem, I received a telegram: "The DEAE column works. Stay in Israel." (They were an irreverent bunch. When Ann and I unexpectedly discovered that she was expecting a third child—some 11 years after the second—a sign appeared on my office door: "Planned Parenthood Requires Practice.")

Dividing the spoils (at most one or two milligrams of purified phytochrome) proved delicate, especially when the final yield was low. After a run, Harbert Rice and I wanted some for analytical purposes[60]; Elaine Tobin wanted some for biophysical studies[72]; John Mackenzie and Harbert both wanted ALL of it to make antibodies[47,59]; Gary Gardner wanted it to characterize the degradation of "large" phytochrome[33] or to study protein conformational changes on phototransformation[34,H]; and Carl Pike wanted some as substrate for the protease he was studying.[53,I] Although we learned a great deal about phytochrome using this protocol, we still didn't have the native protein. An amino-terminal end-group analysis gave us four different amino acids. It took the youthful field of plant molecular biology to gain the full sequence.[36]

Futile Effort I

While I was at Harvard, William Purves came from the University of California at Santa Barbara for a half-sabbatical. Bill quickly entered the phytochrome production line and began to study phytochrome phototransformation kinetics both in vivo and in vitro. To our surprise, he detected two distinct components, one fast and one slow (by this time we had our own ratiospect). Were we dealing with two kinetically distinct populations of phytochrome? We ultimately published a paper on his exciting findings.[57] Either the two forms differed in quantum efficiency or extinction coefficient or both and we were anxious to characterize them separately.

At the annual meeting of the American Society of Plant Physiologists, I met Robert Decker, the man who had built our ratiospect. He asked me how things were going and I reported Bill's results. That report generated a frown and a long and ominous silence. Apparently, the instrument *itself* had an abrupt change in sensitivity at about its midrange. Was it possible that we were studying instrument kinetics rather than phytochrome kinetics? Marylee Everett repeated the kinetic studies with a different spectrophotometer. All four phototransformation curves (Pr to Pfr and Pfr to Pr, both in vivo and in vitro) were strictly log-linear. Questions: (*a*) When you publish a retraction,[31] should you add the retraction to your publication list or subtract it? (*b*) Did anybody ever subtract a retraction?

The Freiburg Connection

There were many people throughout Europe, especially in Freiburg, Germany, who were doing exciting research on the physiology and biochemistry of phytochrome. I had met a couple of those from Germany at meetings in the United States, but the others were simply names. However, the North Atlantic Treaty Organization and the University of Athens sponsored an Advanced Study Institute in Greece in 1971. It would last two weeks and included a meeting called the European Symposium on Photomorphogenesis (ESOP). That ESOP had already taken place annually for several years was a good indication of the strength of phytochrome research in Europe. I quickly accepted an invitation to present our work on phytochrome purification. Finally, I would have a chance to meet the European scientists.

That 1971 meeting with its internal symposium was truly seminal: It initiated a series of cross-Atlantic collaborations that continues to this day, some 39 years later.[J] Ultimately, scientists from Japan, Australia, and other countries were warmly welcomed into these exchange pathways and phytochrome researchers became a truly international family.

The meeting was not entirely scientific: It was held on a Greek island on the Aegean Sea at a coastal resort with a wide beach. A single taverna in the only village close by saw a huge surge in clientele. We also convinced ourselves that the two arrogant waiters at the hotel were secret police (a possibility at the time). An enterprising speedboat owner offered waterskiing for a fee. As I was then a waterskiing fanatic, I welcomed the opportunity. (I also basked in the attention and admiration I attracted.)

In those days, photomorphogenesis was focused on phytochrome. Mention a blue-light response and the response was usually, "Oh, *that*." There was not one single report on blue-light effects on plants either in the Advanced Study Institute or in ESOP. Without a blue-light receptor, there was no biochemistry, leaving only confusing physiology and endless arguments (in which we participated) as to whether the photoreceptor chromophore was a flavin or a carotenoid. Such "blue-light" nonsense had no place in a serious conference on photomorphogenesis.

I had another sabbatical coming up for the academic year 1973–1974 and had landed a Guggenheim fellowship to go to Freiburg for a year to work with Rainer Hertel's group.[K] This was the first of three extended stays in Freiburg, and the beginning of close and long-lasting interactions with Hertel, Eberhard Schäfer, Hans Mohr, and others there. Pretty soon I was fractionating and characterizing organelles from etio-

lated maize coleoptiles and learning about nonmitochondrial cytochromes.[41,L]

When I arrived in Freiburg, Rainer and I agreed that when my two older girls entered a German school, we would restrict all lab conversation to German. Despite complaining, the girls made excellent progress with the language. However, by the end of the first week, I was a wreck, fully prepared to abrogate the agreement. Right away. However, Rainer, who spoke excellent English, absolutely refused to use it. There was no escape. It was a miracle that I accomplished any science at all.[M]

Second Change in Venue: Harvard to Carnegie

Before we left for Freiburg, I had a visitor. Our summer place near Plymouth, Massachusetts was on Halfway Pond, an isolated paradise far from Cambridge. Stacy French, then director of the Department of Plant Biology, Carnegie Institution of Washington, paid me a visit. As we were walking slowly around Halfway Pond, he asked me whether I might be induced to return to California. He was about to retire and Carnegie would be looking for a new director. I replied that the answer might be "Yes." However, I thought to myself how unlikely I was to be asked. I had none of that kind of administrative experience.

That fall Philip Abelson, Carnegie president, called me to Washington to discuss the Department of Plant Biology. Shortly thereafter, I was invited to present a seminar at Carnegie's Department of Embryology in Baltimore. To my surprise, Abelson came to the seminar and remained for the postseminar dinner. He spent most of the dinner asking all sorts of questions—about plant biology (research future), Plant Biology (Department), my own research, and my future research plans. Neither of us had much to eat. (By this time I had guessed what was going on.)

Then came a second invitation to go to Washington. This time Abelson asked me what I might recommend for the Department of Plant Biology. The famous department was woefully short of what it took to do most biochemistry (although it was absolutely amazing what they accomplished without it) and the rapidly developing field of plant molecular biology was unrepresented. Hence my reply was blunt: "Either close it down or double the annual budget and invest $1M in capital improvement and equipment." He broke into a grin and said, "That's what we have in mind. Would you be interested in leading the effort?" For the second time in my career, I accepted a position immediately. I didn't even ask Ann. I'd be back on the Stanford campus, now with excellent plant biology colleagues, hard-money support for research, and an absolute minimum of bureaucracy.[N] What a switch! (Several family members questioned my sanity and wondered loudly how I could possibly leave a full professorship at Harvard to move to an institution they had never heard of.)

The aforementioned Freiburg sabbatical was a potential stumbling block (I had no intention of giving up the Guggenheim). However, I agreed to return from Freiburg for a week four times during the sabbatical to touch base and chart progress with renovation, building plans, equipment purchase and upgrade, and to develop a budget. Abelson agreed immediately. (I neglected to tell him that I suffered severe jet lag and would be worthless for at least the first four and a half days of each seven-day visit.)

The summer of 1973 found us packing once again. Ann and I dashed off to Brazil where I had a meeting in Rio as the moving truck drove off to California. We flew from Rio to San Francisco just in time to meet the truck and maybe buy a house. I was all for banking the proceeds from our Lexington, Massachusetts house, storing our belongings in Palo Alto, and buying a house on our return. However, a real estate agent warned somberly that housing prices were soon going to soar. Neither of us believed a word she said. Nevertheless, we did find a house we really wanted. Somewhat relieved, we closed the deal. After renting it out, our family of five (there were now three daughters) headed for Freiburg.

Futile Effort II

With Stanford biology in close proximity and a cordial Stanford–Carnegie relationship, I quickly acquired another able group of graduate students shortly after arriving at Carnegie. Like their predecessors at Harvard, they were (*a*) extremely able, and (*b*) predictably irreverent.[O] For some reason I seem to attract a certain mischievous cadre each time I put a lab together and this group was no different. Once again we dashed off in several directions at once as we had two decades earlier at Stanford. The diversity was challenging but exhilarating.[P]

One finding in particular intrigued us. Some years earlier, a graduate student, Malcolm Sargent, had discovered a circadian rhythm of conidiation in a *Neurospora* strain that was blue-light-sensitive.[62] Stanford undergraduate student Robert Brain wanted a senior honors project. Given that blue-light-induced reduction of a *b*-type cytochrome had been reported in fungal membrane preparations[54] and membranes from etiolated maize coleoptiles,[12] we decided to chase the blue-light receptor in both systems. Bob soon obtained enough spectral and kinetic data for a solid paper in *Plant Physiology*,[4] and we were on our way. The reaction was designated light-induced absorbance change, or LIAC. Nine papers later, we were *still* on our way (and not much farther along). Nevertheless, in a 1983 review, Moritoshi Iino and I wrote optimistically about

the system's promise[13] (although Horst Senger and I had already shared some doubts in 1981).[65]

We applied a number of tests to the system. As red light altered phototropic sensitivity,[7] it might do so by altering the properties of this interesting membrane-associated photoreaction. It didn't. Bright light blinds coleoptiles to subsequent phototropic stimulation, a blindness from which they recover over a matter of minutes. Hence bright light might somehow change the properties of the reaction. It didn't. Other tests were equally negative and we finally admitted defeat. In 1994, Tim Short and I wrote, "Thus, the LIAC remains an enigmatic membrane-associated reaction in search of a physiological role."[67] Nevertheless, these studies provided a generous increase in our list of publications.[Q] (There are publication-counting deans who should know this story.)

Gels

A third sabbatical (1983–1984) took us once again to Freiburg with generous support from the Alexander von Humboldt Foundation.[R] There in Eberhard Schäfer's laboratory, I learned how to do run-on transcription from isolated nuclei and took my first foray into plant molecular biology with Schäfer. We obtained results suggesting that truly minute amounts of red light could alter transcription patterns,[50] and I took some serious molecular biology back to Carnegie.

For several years I had rather mercilessly teased people who relied heavily on running gels for their research. (At a meeting in England, as posters were being set up, I distinctly heard, "I'll trade you this western for those two southerns," over the poster stand behind me.) I once complimented a speaker at the end of his seminar at Carnegie for presenting some superb research results without relying on a single gel. My day of reckoning came soon after I returned from that sabbatical. Presenting a seminar on my accomplishments in Freiburg, I proudly showed a slide of a gel. Instant "Get even" time: Several (nameless) people offered appropriate comments. Here was irreverence I might well have anticipated!

Intermission: Henry W. Coe State Park

Shortly after arriving in California, Ann and I started exploring the many parks within an hour and a half's drive from Palo Alto.[S] One of these was Henry W. Coe State Park, a wild and rugged area south and east of San Jose. Our middle daughter, Lucia, babysat with Marion and many weekends saw us putting on hiking boots early in the morning. On our first visit to Coe, the ranger suggested we take either a five- or a fifteen-mile hike and we opted for the longer one. However, there were two things the ranger didn't mention: First, the route involved just over 4000 feet of elevation change—something like going from the south rim of the Grand Canyon to the Colorado River and back. Second, he didn't mention that the Department of Fish and Game had recently released a half-grown male deer into the park's back country. Somebody had been illegally raising him as a pet.

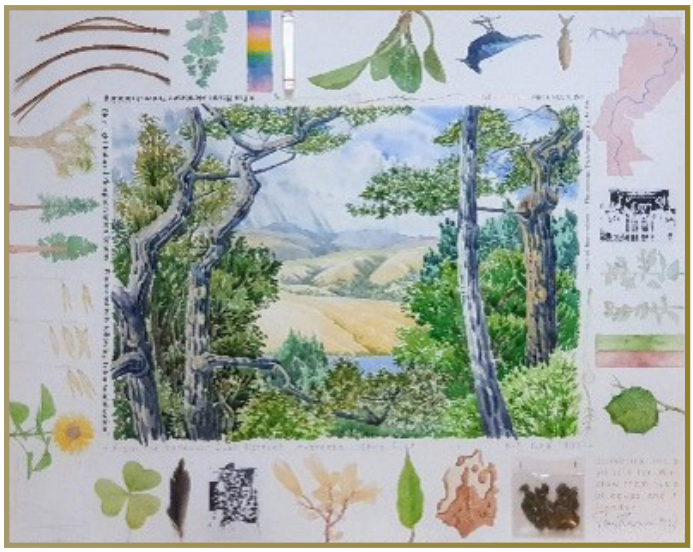

Figure 4 From the Vannevar Bush Retreat Inverness looking East 6-7 June 1993 / Souvenirs for Winslow from his colleagues and friends. *Painting by Tony Foster, ©Copyright Tony Foster all rights reserved.*

We headed off jauntily on a gorgeous day and before long we had some company: a half-grown male deer. He was obviously thoroughly acclimatized to humans. At lunch time he had the gall to stick his nose into my open pack in search of food. He followed just a few feet behind us for the entire hike (including a really brutal elevation gain of just over 1400 foot in little more than a mile). Only when we approached park headquarters (completely exhausted) did he fade off into the forest—most likely awaiting other unsuspecting hikers. Naturally, we reported this peculiar behavior (the deer's behavior, not ours) to the ranger. He reassured us that the deer was not simply a hallucination brought on by 4000 feet of climbing. (He also apologized, saying that he had just plain forgotten to mention the animal.)

Thoroughly intrigued, we returned to the park two weeks later to do another hike. And then another. The park was growing rapidly as a consequence of land purchases, and the next thing we knew we were volunteering and laying out trails for the new land acquisitions. We even wrote a successful grant proposal to the state for $250,000 in bond issue funds to build them. We have now been volunteering there for over 30 years.[T]

Most recently we organized a group of volunteers to monitor the recovery of vegetation in the many park ecosystems—oak savannah, pine forest, chaparral, meadow, and closed-canopy hardwood forest—following a large wildfire. With the blessings of the California Department of Parks and Recreation, we were off and running. At publication time,

the project will have been going for two and a half years.[U] (It has taken me almost that long to revive my limited taxonomy skills from deep dormancy.)

Futile Effort III, or a Glimmer of Hope?

Sean Gallagher, a postdoc at Stanford with Peter Ray, was investigating auxin-induced changes in the pattern of protein phosphorylation in membrane preparations from sections of the growing regions of etiolated peas. He would treat the sections with auxin, prepare a microsomal fraction, and add radiolabeled ATP. A number of proteins would become phosphorylated. By scanning autoradiograms of his high-resolution gels and comparing them with similar gels from control sections, he hoped to identify proteins that showed auxin-induced phosphorylation changes. There was one striking band near 120 kDa that stood out much more strongly than the others, but auxin didn't change its intensity or indeed that of any other bands. Before abandoning the project, he moved some etiolated plants into the light and then performed the same membrane phosphorylation experiment. He compared the results with those from dark controls. To his astonishment, the light treatment had caused that strong band near 120 kD in the control to disappear completely. That region of the autoradiogram was now empty.

Sean showed the autoradiograms to Peter, and Peter immediately suggested that he show them to me. The difference was indeed spectacular. Meanwhile, Timothy W. Short, a new graduate student, was doing a rotation in my laboratory and was looking for a thesis problem.[V] With Peter's blessing, I suggested Tim investigate the phenomenon. By 1988, we had our first publication describing the system.[32] Shortly thereafter Tim discovered that one could drive the phosphorylation reaction by irradiating isolated membrane preparations from dark-grown seedlings.[66] Thus we were suddenly in a position to carry out extensive biochemical characterization of blue-light-activated protein phosphorylation.[11] Might it have something to do with phototropism?

In 1992, a postdoc from Lausanne, Philippe Reymond, took a first look at *Arabidopsis* membranes.[W] Kenneth Poff's laboratory had described an *Arabidosis* mutant, JK224, with impaired phototropism.[43] Hence Philippe compared light-activated phosphorylation in microsomal membranes from wild-type and mutant seedlings. The entire lab was at a dim sum restaurant in San Francisco, and I tried to ban any scientific discussion. Rather timidly Philippe pulled out an autorad and asked me whether he could at least show it to me. There was scarcely a trace of light-activated phosphorylation at 120 kD in the mutant. For the first time we could associate light-activated phosphorylation with phototropism! Voila (again)! A paper in PNAS![58]

Despite years of biochemical and photochemical studies (see 11 for summary), we made no progress in purifying the protein. Once solubilized, it became extremely unstable. Nor did we make progress in identifying the photoreceptor chromophore. We needed a kinase and a photoreceptor to carry out light-activated phosphorylation of the substrate protein but had no idea whether it required a single protein (photoreceptor, kinase, and kinase substrate all in one) or two or three independent proteins. Thus I had to retire as director of the Department of Plant Biology in 1993 without achieving the objective I set for myself in 1957.[X] Bummer! (Fortunately, I was allowed to keep—and still keep—a completely functioning lab with Carnegie support.)

When Chris Somerville became my successor as director, I went again to the Schäfer lab (partially to keep well out of Chris's way), again with support from the Alexander von Humboldt Foundation. Freiburg was almost a second home by this time with many friends within and without the university there. This time the nest was empty and Ann and I went alone. Also by this time, my earlier exposure to German started to pay off. As long as people used *very* simple declarative sentences, I could get along. The science went well (investigating UV-induced changes in gene transcription) but sadly did not produce a publication. However, I was awarded a gilded pipette for breaking some sort of pipetting record.

The End of a Long Road: Phototropism II

A new postdoc, Emmanuel (Mannie) Liscum, arrived in 1994 and insisted that the road to phototropic salvation led through *Arabidopsis* mutants. I should have remembered the gel fiasco and kept my mouth shut. However, I had often declared forcefully that I could get along just fine without that weed. Imagine trying to study the biochemistry of the elongating region from an *Arabidopsis* hypocotyl! We were still struggling to purify the phosphoprotein from pea stem sections, and I had to date successfully avoided jumping onto the *Arabidopsis* bandwagon. Meanwhile, Mannie quietly screened for mutants with impaired phototropism. He soon showed me evidence for five different phototropic mutant classes (*nph1* through *nph5* for non-phototropic hypocotyl.[45,46] I capitulated. Maybe there was something to *Arabidopsis* genetics after all. I was promptly and gleefully reminded by several people of my anti-*Arabidopsis* intransigence.

Mannie and postdoc Paul Oeller then tackled the mutants using a technique called amplified fragment-length polymorphism, or AFLP. (Space limitations preclude presenting a simple two-page explanation of AFLP. Ask Mannie.) They quickly identified an anomalous DNA fragment from *nph1–5*. Postdoc Eva Huala then used the fragment to fish out and sequence that region of the *Arabidopsis* genome. (Although I

personally did most of the sequencing, any intelligent eight-year-old could have done it—it was strictly cookbook.) Eva soon uncovered a kinase with two almost identical upstream domains (we both thought at first that there must be some mistake—or at least I did). We designated these domains LOV domains (they resembled domains in other proteins that mediated response to light, oxygen, or voltage). Thus substrate and kinase were one and the same protein. Voila (third time)! Another paper in *Science*![40] But where was the photoreceptor?

By this time, John Christie had joined the lab. He had written me in the fall of 1996 inquiring about the possibility of a postdoc position, and I stupidly misplaced his letter. Miraculously, he wrote again in the spring! Given his credentials, I immediately offered him a fellowship. I was surprised (and pretty lucky) that he hadn't long since gone elsewhere.[Y] He quickly mastered expressing the *NPH1* gene in insect cells and produced very small amounts of full-length NPH1 protein. He then induced the cells to make the protein in the dark, extracted it under red light, and tested it for blue-light- activated phosphorylation. It worked. Light-activated phosphorylation was occurring in the absence of any other plant protein! What's more, the protein bound a flavin. Voila (fourth time)! Another paper in *Science*![26] We at long last had the photoreceptor for phototropism (the first of a family of two). (It had taken us only 41 years. Some people are slow.)

After considerable international discussion, we named these two photoreceptors phototropin 1 and phototropin 2 (phot1 and phot2 for short; 9). (For some unknown reason, we all agreed to my suggested names.) Successful identification of the photoreceptor for phototropism came a full five years after I had retired. (The phototropins were not the first blue-light receptors identified: Ahmad and Cashmore had already described cryptochrome 1—CRY1—in 1993; 1.) LOV domains aren't just involved in phototropism. Soon, several labs demonstrated that the phototropins also mediated blue-light-activated rapid growth inhibition, chloroplast movements, stomatal opening, leaf expansion, and solar tracking (see 10, 24). Phototropins had become mainstream plant photoreceptors.

Michael Salomon, a senior visitor from Germany, joined the lab, and he and John expressed the LOV domains in *Escherichia coli*. We quickly discovered that they were light sensitive. Spectral studies showed that blue light induced a fully dark-reversible bleaching of the flavin absorption bands and appearance of a single peak near 385 nm. I presented this result at a flavin conference in Konstanz, Germany, and Vincent Massey, a giant among flavoprotein biochemists, pointed out, "You likely have light-activated formation of a cystenyl adduct with the C(4a) carbon of the flavin." I nodded wisely although I didn't have the slightest idea what he was talking about. Careful (and private) scrutiny of a paper from his lab indicated that it was the formation of a covalent bond between a sulfur atom somewhere in the protein and the C(4a) carbon of the flavin. Mutating away a highly conserved cysteine completely eliminated the reaction (61), verifying Massey's hypothesis. (I could now talk authoritatively about flavin-cysteinyl adducts.) In addition, here was some brand-new photochemistry.

In 1998, I began collaboration (still ongoing) with biophysicist Roberto Bogomolni from the University of California, Santa Cruz, and his former student Trevor Swartz joined the lab as a postdoc.[Z] (Good thing! My own competence in matters biophysical is highly questionable.) We quickly carried out the first photochemical studies of the LOV domains.[28,69,71] and provided the first evidence for a light-activated loss of α-helicity. At the same time, postdoc Tong-Seung Tseng uncovered two proteins that interact directly with phot2 and demonstrated that they played important roles in phot2 signal transduction.

Since the LOV-domain photochemistry was completely new, biophysicists from all over the world rushed to study the reaction. (They all had sophisticated and expensive instrumentation, often homemade, and had been waiting hungrily for a new photoreceptor system. They had already beaten to death the retinylidene proteins, photoactive yellow protein, phytochromes, and even cryptochromes, and the LOV domain was definitely new and different.) Electron microscopists and NMR specialists carried out detailed studies of different LOV domains, giving us elegant structural information about both the LOV domain in its dark state and its conformational changes on photoactivation.[29,30,35] From two labs in the world working on phototropins in 1998 (ours and Mannie Liscum's), the number had swelled to over 40 by 2007, producing an explosion of papers (see 8, 24, 25, 42).

Epilogue/Prologue

Once the LOV-domain sequence was published, people started finding it in proteins everywhere—ferns, mosses, green algae, golden algae, fungi, and all manner of bacteria. It occurred in a wide range of otherwise entirely different proteins—from histidine kinases to transcription factors. The animal pathogen *Brucella* sp. contains a LOV-histidine kinase. With colleagues of Roberto's in Buenos Aires who were working on the animal disease brucellosis, we demonstrated that its activation by light caused bacterial virulence to increase an astonishing tenfold in a macrophage assay.[70] This finding represents a highly unexpected outcome for research on higher-plant blue-light receptors. It also provides a powerful argument for basic research.

DNA sequencing tells us that there are now over 100 bacterial proteins with putative LOV domains (Aba Losi, personal communication), representing some 13–14% of all bacteria sequenced to date. Included are plant and animal pathogens, marine photosynthetic bacteria, soil bacteria, cyanobacteria, and even archaea. The discovery of phototropins has opened a huge new area of bacterial photophysiology. Are all of these proteins photoreceptors? If so, what do they do? How do they affect virulence in other animal pathogens and in plant pathogens? What competitive advantage do they provide the many different kinds of bacteria? How did the LOV domain with its unique photochemistry find its way into fungi, algae, lower green plants, and finally into the angiosperms? The future of LOV-domain studies with bacteria is both challenging and fascinating. It will be a thrill to join these studies (even though we haven't forgotten phototropins and their LOV domains!).

Figure 5 *Triteleia laxa* (Ithuriel's spear). Photograph by Winslow Briggs.

The Last Fire (*David Nelson*)

In the wake of the Lick Fire of 2007, Winslow became a fascinated witness to the regeneration of Coe State Park. After giving a talk on the topic at a summer ASPB meeting in Hawaii, in which he noted (with memorable arm demonstrations) the movement of a dead tree's limbs after rain, he and Ann were approached on the banks of the Ala Wai canal by Dave Nelson, a postdoc who was studying perception of karrikins, a recently discovered class of chemicals found in smoke that stimulate seed germination. (Coincidentally, Dave had gotten his start in research discovering a LOV-domain protein that regulated the developmental transition to flowering.) Despite Dave's insensible choice of launching a scientific discussion outside the climate-controlled convention center, and his penchant for genetic methods, Winslow later graciously offered him the opportunity to continue his studies at the Carnegie Institution.[AA] At the time, an F-box protein that was required for karrikin signaling had been identified, but its downstream target was unknown. Over an eventful year, a genetic suppressor of the F-box mutant was mapped, revealing a downstream target that did not conform to any of their expectations, SMAX1.[80] This launched the intensive characterization of a new gene family. SMAX1 and its several homologs, which are distantly related to a heat-shock protein, are now known to comprise a family of developmental regulators that are involved in responses to the plant hormone strigolactone, as well as karrikins.

It is often said that danger lurks whenever a PI returns to the bench. Not to be outdone, Winslow began investigating how fire stimulates the growth of *Triteleia laxa* (Ithuriel's spear), which bloomed in abundance after the Lick Fire. Although *Triteleia* grows from fleshy, bulb-like structures called corms, he hypothesized that chemicals in smoke might wake them up similarly to seeds. Many precious corms later, karrikin treatments turned out be a dead-end ("brilliantly negative" in Winslow's words). However, a cyanide-releasing compound in smoke, glyceronitrile, and other cyanohydrins had been found to stimulate germination of some fire-followers that did not respond to karrikins. This implied that cyanide could be an important cue in the post-fire environment for some plants. Sure enough, Winslow discovered that glycosyl nitrile, which can very slowly break down into cyanide, induced an explosion of roots from *Triteleia* corms. To further the point, Winslow converted plastic sandwich boxes into cyanide gas chambers (what could go wrong?) and was able to replicate the dramatic root response.[75,BB]

LOV Is All You Need (*Rajnish Khanna*)

In Spring of 2012, there were three projects underway in Winslow's Carnegie basement laboratory; (*a*) Winslow was testing karrikin treatments on *Triteleia* corms grown in pots in the greenhouse, working by himself with only occasional help, (*b*) Tong-Seung Tseng was mapping ubiquitination and phosphorylation sites on phot1 and phot2 in collaboration with Zhi-Yong Wang,[76] (*c*) William (Bill) Eisinger, in collaboration with David Ehrhardt, had shown microtubules play an essential role in guard cell function,[77,78] and Bill had recently moved out of state.

It was a sunny March afternoon, when Rajnish Khanna found Winslow at his usual lunch spot (picnic tables by the Carnegie Seminar room). Rajnish Khanna had come to seek career advice from Winslow. Rajnish had decided against

pursuing employment tracks in industry and academia but wanted to continue with basic research. Winslow generously offered one year of funding to continue Bill's project to image GFP-TUBULIN in guard cells, even though Rajnish had no experience with fluorescence microscopy, let alone a spinning-disk confocal equipped with argon ion lasers. David and his laboratory members were graciously helpful, and along with Julian Schroeder, they found that CONSTITUTIVELY PHOTOMORPHOGENIC 1 is involved in coordinating cytoskeletal and electrophysiological activities required for guard cell dynamics.[79] Winslow titled all his presentations of this work, "Mind the gap between guard cells."

Bringing LOV to field trials

Based on his earlier work discussed above on blue light-induced promotion of virulence in pathogenic bacteria, Briggs now focused his attention on root nodules in *Pisum sativum* and related plants. Khanna provided data indicating that crop yield in legumes, such as fava bean (*Vicia faba*) and garden pea (*P. sativum*), is enhanced when the soil microbes (rhizobia) were irradiated with blue light before inoculation of the seeds that are prepared for planting in moist substrate. Rajnish continued as a visiting scientist working part-time, and he, along with Roberto Bogomolni, became involved in filing a joint U. S. Patent between UC Santa Cruz and Carnegie (filed in 2018, unpublished).[CC] Winslow arranged some Carnegie funds for field trials. The first commercial test of this natural system was performed on a field in Washington State. Rajnish traveled to the field, performed some necessary treatments in a make-shift lab in his hotel room, prior to application on hundreds of field-germinated legume plants, before sunrise to minimize photodamage. An important lesson was learnt, even after lengthy discussions, the grower decided to apply standard fertilizers (old habits die hard) and negated the expected outcomes. This triggered a new plan; Roberto quickly found a grower with large commercial acreage in Half Moon Bay, CA. The small team was ready to test the newfound technology on a donated acre of land near a pond with a new hydraulic pump installed for irrigation. This time, there was encouraging data, slated to be repeated in the coming years on Carnegie's backyard fields (halted during the pandemic), now moderately funded through a no-strings attached, Bayer Grant for "Novel solutions to increase crop productivity."

Disclosure Statement

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this chapter.

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Comments

A Winslow had the great fortune to come from a long line of dedicated educators – his father, John DeQuedville Briggs, was the headmaster of St. Paul Academy from 1914 until 1948, and his grandfather, LeBaron Russell Briggs, was the Dean of Harvard College, then the Dean of the Harvard Faculty of Arts and Sciences and the second President of Radcliffe College (from 1903-1923). Winslow's love of nature and his dedication to his favorite local wildlands – Henry Coe State Park – may have been influenced by the Dean's own love for the family compound he built in the backwoods of Massachusetts, on Halfway Pond (a place Winslow's father spent his retirement, and a place that is still loved and visited by numerous family members each year). He was certainly inspired by the canoe trips taken with his father and mother into the Boundary Waters of northern Minnesota.

Times change, but Winslow shared many enduring traits with his father and grandfather. He had that same enthusiasm towards new endeavors, that same endless curiosity, the drive to listen, to ask questions, and to learn more about it, whatever it was. Like his dad and grandad before him, when it came to education, he had the priceless gift of encouraging that which was good, redirecting that which was not a profitable direction for further inquiry, and doing both with kindness, intellectual rigor, and a brilliantly nutty sense of humor–all the qualities of a good mentor and teacher.

Caroline Briggs, Daughter

B Win was an excellent teacher of subjects ranging from a class on mosses and ferns to the most advanced plant physiology courses. In the advanced plant physiology course that he taught at Stanford there were no tests; instead students had to pick a subject of interest and then write a major review article as if it was being submitted for publication. He would evaluate these papers very critically and students learned some valuable lessons, such as to avoid split infinitives and dangling participles.

In my case I decided to write a paper on some aspect of flowering and Win suggested I focus on some recent papers by William Hillman on flowering in *Lemna*. A few months later when I decided I wanted to pursue my Ph.D thesis research with him, he asked me what I wanted to work on. At that point the subject I knew the most about was flowering in *Lemna* and that is how I started my work on *Lemna*.

Charles F. Cleland, Graduate Student, Stanford University, 1962-1966
SBIR National Program Leader, USDA/NIFA, Retired
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C Winslow and I became close friends from the beginning of my graduate studies (1959), which soon extended into many dimensions beyond science. Hiking with Winslow in the wilderness, one was sure to experience a fascinating tutorial on the marvels of the local flora and fauna. His knowledge of all life forms was vast, and I was especially intrigued by his recent studies of how seeds germinated following a wildfire after being dormant for decades.

Burke Zimmerman, Graduate Student, Stanford University, 1959-1962
Expert, National Defense University, 2007-2012
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D One October day in 2007, I was in California on business. I made the usual connection with Winslow at Stanford. As usual I had dinner with Win and Ann. Win brought up the idea of doing a very steep hike to see the condors in the mountains south of San Jose. The very next day we were off to see the condors. We climbed up pretty high on the mountain for about three hours and had our packed lunch on an open area. We had barely taken a bite when a single condor flew over our heads at a close range. WOW! We were not thinking about it or prepared to see the bird and what came after. We saw another go by as we were groping for our cameras. Very few minutes, single and double condors kept flying by. We just had time to grab our cameras and shoot the remaining birds flying over our heads. In all, we must a have seen 10-12 condors flying above us.

What a thrill. What an unexpected thrill!

Tom Scott, Graduate Student, Stanford University, 1956-1960
Professor Emeritus, Dept. of Biology, Univ. of North Carolina, Chapel Hill
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E Winslow covered my first manuscript in so much red ink that it looked like the paper was bleeding. He said "It's a good start" and made me rewrite it. 10 times. "Arggh." At the end of this ordeal, I needed a title, but he was traveling and harried. So I wrote a checklist titled "Pick one:…" followed by serious titles, but mostly inane and stupid options, and stuffed it into his overflowing inbox. After deciphering my tiny handwriting, he came upstairs to my office (shared with Peter Quail), and chortled "Goofball!" Thereafter, I cracked his Boston Brahmin shell unremittingly with pointed statements and my weird and irreverent sense of humor.

Winslow's relentless pursuit of science was joyous in part because it was shared. Science shared was his way of expressing love – for someone's mind, ideas, and thought processes.

English has only one word for love. Winslow 'loved' his friends, colleagues and students in all the myriad ways no single word can adequately express. I cannot speak for anyone else, but I can imagine the look on his face if he were here; his look whenever I said something so blunt, frank or irreverent as to crack the dam of his emotions. He would suddenly relax and quietly say, "You're right". I hope that I am for that is true nobility and Winslow was truly noble.

Dina Mandoli Russell, Graduate Student, Stanford University, 1978-1982
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F Clearly, there is a good reason why the Germans refer to one's thesis advisor as the 'doctor-father'. A good advisor does take on a role of a surrogate father in some ways…. I recall many snippets of my interactions with Winslow over the years that feed into this sense of a father-figure as well as (later) of a colleague. My favourites, though, are of our mutual pleasure in playing word games and the sheer delight that showed on Winslow's face whenever he found a moment to jest. The jokes were often vaguely political but never personal … well, unless directed to himself. I recall his pleasure in pointing out the omission of scale labels on a plot in one of his Annual Review articles to which he had carefully pencilled into the Carnegie library copy 'beers consumed' on the x axis and 'inebriation' on the y axis.

My time as a PhD student overlapped with the reign of Idi Amin in Uganda. No connection, of course, except that Winslow determined that the despot was THE primary amin(e). And on the occasion that the Bay Area Rapid Transport finally opened connections southward on the peninsula side of the bay – and then failed to do more than move passengers more than haltingly – Winslow noted of the experience that "his BART was worse than his bike". I am certain that Winslow was entirely conscious of the many 'typos' in my thesis (including measurements that surpassed the "reverence level") but he let these pass without comment for over thirty years until, on submitting his Founder's Review to me for publication in the January

2014 issue of Plant Physiology, he asked explicitly that I not alter his acknowledgement and reference to the "motive farce" behind the article. Payback!

Michael R. Blatt, Graduate Student, Stanford University, 1975-1980
Regius Professor of Botany, University of Glasgow
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G The Briggs Rule is very important for anybody who is on a faculty that has committee meetings. While I was at Harvard I kept getting asked to be on this committee or that committee so I finally decided the way to handle this is "yes, I'll serve on the committee but I won't stay at any one meeting longer than 50 minutes" (that's the academic hour). So, at the end of 50 minutes I'm going to say "Briggs Rule" and get up and leave and I stuck to it and by gosh- you know the meetings got more and more compact and more and more productive and it really worked.

Winslow R. Briggs, Interview with Sabeeha Merchant and Elaine Tobin, April 1, 2011

H What I remember most about working with Winslow is that it was fun. Winslow was one of those rare individuals who could be a thoroughly nice guy, fun loving, enthusiastic, and generous to a fault, but somehow still be at the cutting edge of modern science. His sense of humor was infectious, and his puns atrocious. There are a million stories of practical jokes, humorous accidents, and just plain hilarity, all side-splittingly funny.

The thing is, chemistry happened. All that fun was intertwined with great science. The tradition continued at Carnegie, where Winslow showed by example how great science and great humanity go together, how great science is always a team effort, and how joyful it can be. I think that's the secret – take joy in what you do, and joy in those who do it with you. That, together with the fact that he was just plain brilliant, is why I think Winslow Briggs was such an extraordinarily successful contributor to the science and community of Plant Biology.

William F. Thompson, Postdoc, Harvard, 1970-1972
Staff Member, Carnegie, 1976-1986
Distinguished University Professor, Plant and Microbial Biology, NC State, Raleigh, NC
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I Winslow Briggs was an exceptional teacher and mentor to me as both an undergraduate and graduate student, and to many others as well.

One story about Winslow as a teacher is well-known among his graduate students who attended his introductory plant biology class. Hearing his lucid and well-organized lectures, we fully expected that his notes would have all the details, experimental data, etc. carefully laid out. So, when we had an opportunity to sneak a look at the notes, imagine our surprise to find that they were minimal – just a few words about the topic, and then "Yak." Winslow excelled at "Yakking."

Winslow encouraged my interest in a position at a research-oriented undergraduate college, and I joined the faculty at Franklin and Marshall College directly after graduate school. Whenever my students presented posters at national meetings, Winslow made it a point to engage them in conversation about their research. They truly valued his encouragement and enthusiasm.

Carl S. Pike, Graduate Student, Harvard University, 1967-1971
Huffnagle Professor of Botany, Emeritus, Franklin and Marshall College
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J I first met Winslow at a photobiology meeting (the Annual European Symposium on Photomorphogenesis) in Eretria, Greece, in September 1971. I had just joined Hans Mohr's lab, as a postdoc, in Freiburg, Germany, excited about plunging into the field of phytochrome photobiology, a new direction for me. Being able to join the other members of the Mohr group in attending this premier meeting in the field so early, was an unparalleled opportunity and a formative experience. I was taken by Winslow's thoughtful questions and constructive comments during the discussions, and was mesmerized by his presentation there. Winslow's talk triggered a desire in me to use my biochemical experience to pursue the open question of phytochrome's molecular mechanism of action, a path that I followed for the remainder of my research career.

During the course of that journey, I came to appreciate Winslow as a wonderful mentor, colleague, friend and human being, always ready to provide wise counsel and help for others. The most pivotal and personal example of that came later for me, when he offered to take me into his lab for a transitional period, while I looked (successfully) for a faculty appointment in the U.S., following a period back in my native Australia. Winslow's thoughtful guidance during that period was invaluable, and I was able to learn both the art of phytochrome purification, and the procedures for antibody production (during a short intervening time in Lee Pratt's lab in Nashville). Both these skills were critical in the subsequent development of my independent research program.

Peter Quail, Senior Fellow, Carnegie, 1977-1979
Professor Emeritus, Plant & Microbial Biology, University of California, Berkeley
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K In 1973/74 Winslow decided to spent a Guggenheim-Sabbatical in my Freiburg lab where — in collaboration with Al Jesaitis, Pat Heners-Reau and Ulrike Dohrmann — we characterized a plasma-membrane cytochrome *b* (*Plant Physiol* 1977 59:941) and a flavin binding site on membrane vesicles (*Planta* 1980 147:312).

1981/82 I had a wonderful, exciting sabbatical in the Briggs-lab at the Carnegie Institution Department of Plant Biology on the Stanford Campus. Together with Terri Lomax we discovered and analyzed an *in-vitro* auxin transport in *Cucurbita* membrane vesicles (*Planta* 1983 157:193). My wife and myself will never forget the hospitality of Winslow and Ann and the splendid natural environment – experienced through their expert guidance.

Rainer Hertel, Collaborator, 1973-1984
Professor Emeritus, Faculty of Biology, Albert-Ludwigs-Universität, Freiburg, Germany
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L At the famous 1971 phytochrome meeting in Greece I met Winslow for the first time. Then came his first sabbatical in 1973\74 in Freiburg where we had almost daily contact because he used the new spectrophotometer in my laboratory for his measurements of light induced absorbance changes. From there on we met every year at least once at conferences, at Carnegie, or at Freiburg. I had a wonderful sabbatical at Carnegie working together with Moritoshi Iino as a slave and stayed at Hale Street for three weeks to look after the Briggs animals, during the time Winslow, Ann, and Marion were hiking in the Sierra.

Winslow then stayed twice for a full year in my lab on Sabbatical – or working as a postdoc for me! It had been wonderful experiences for me, my family, and also my laboratory members.

But it was not only science and cooking which connected us — we both loved science and good eating — but it was also the respect for other people, animals, and plants. So the Schäfer family made two backpacking trips with parts of the Briggs family to the Sierra and we spent also a week hiking in the Alps together. So it's not too surprising that this established a long lasting friendship between us, including our wives and the Briggs daughters and my son Andreas.

Eberhard Schäfer, Collaborator, 1973-1984
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M I got a call from the Frankfurt airport by somebody who wanted to know whether I had any knowledge of a person who was bringing me anything. Well this went on a bit and ultimately he said "well we have in our custody a man named Cornelius Rhee" — who actually had done his degree with me "and he has three pounds of hashish that he said he's bringing to you" and I said "what?!" and there was this long silence and he said "Win, this is Hans" [laughing] — And about a month later after that silly telephone call, the phone rang and I wasn't home but one of our daughters answered the phone and it was Stacy French who called up to tell me that I had been elected to the National Academy. So I got home from the lab in Freiburg and she came and said "what's the National Academy?" I said, "well it's the National Academy of Sciences' and she said, "well somebody that says he was Stacy French called up and said that you've been elected to the National Academy" and I thought "Aha! Hans Kende strikes again!" I remember that very vividly, and I had to wait for a couple of weeks before I got some kind of an official notice to realize that in fact it wasn't Hans Kende.

Winslow R. Briggs, Interview with Sabeeha Merchant and Elaine Tobin, April 1, 2011

N Winslow hired me in 1982 as a Staff Member in the Carnegie Institution's Department of Plant Biology…. We had a joint lab meeting for many years and in discussing my inclination to make wayward excursions into a number of different scientific fields, he would always say 'I have absolute faith in your scientific intuitions… and this is exactly what staff members at the Institution are expected to do.' After a while I began to imagine my wayward orientation to be a positive attribute and not just the attitude of a dilettante (which some others may have thought). But this wasn't a one-sided interaction and there were many times when I would walk by Winslow's office to say hello, and he would say 'Do you have a minute. I have something to show you.' And he would take out his latest experiments (on phytochrome responses, the mechanism of phototropin, the function of smoke in the succession of forests after a fire) and two hours later we would still be looking at the data and debating its meaning. These discussions were spontaneous, generous, uninhibited and provoked both of us to shape, dismiss and remold the findings recorded on loose sheets of paper, spread sheets and computer images into potential pathways and mechanisms.

Arthur Grossman, Senior Staff Scientist, Carnegie, 1982-Present
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O Picture the solid wooden table in the Carnegie seminar room, admire the gnarly live-oaks through the wide windows, and smell the burnt coffee. There I was, sitting around that table with my Ph.D. Committee, clutching a folder of homemade graphs, starting to cough up my progress. I'd hardly have begun when Paul Green's eyes would twinkle, his finger would rise, and he'd proffer a terrible pun. I'd smile, tentatively, and keep going. Well, Winslow, not to be un-punned would tilt his head a little to the side, peer seriously at me, and crack another, even more atrocious, pun. Paul would never let that rest, and so it would go, back and forth, for an hour, at which point the Briggs rule would terminate the meeting. At the time, I felt relieved about escaping criticism and also worried that criticism was just what I needed. But now, I realize that all this banter had the salutary effect of putting me at ease. In between their wordplay, I probably explained my work sufficiently, without even noticing.

For Winslow, humor was every bit as important as the proper control. I still remember his delight when I submitted a Ph.D. paper on phototropism in pea with the running title: Phototro*Pisum*. I can also remember, when Anton Lang (the editor-in-chief of *Planta*) refused to print the joke, Winslow was dismayed, being certain that *Planta* had missed a needed opportunity to lighten its heavy pages. He believed that humor should be taken seriously.

Tobias I. Baskin, Graduate Student, Stanford University, 1980-1986
Professor of Biology, University of Massachusetts Amherst
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P Winslow was an awesome scientist and a fantastic mentor who had a real talent for walking the line between training and support. He was detailed where it mattered, bringing incredible care to experiments, to the wording of conclusions and the manner of presentation. His wisdom made me a better scientist and communicator.

Winslow was an early feminist. He brought many female graduate students and postdocs into his lab, and supported and championed all of us so well that I never once thought that my identity as a woman was an issue. When my first faculty position turned out to be less welcoming, Winslow came out to visit. He was visibly angry, on my behalf, and helped me find my way to a new position at Oberlin College, which has been a great fit and provided me with an opportunity to enjoy both research and teaching. I have come to think of Winslow as a second father and it is a real joy to celebrate his memory.

Marta Laskowski, Graduate Student, Stanford University, 1985-1990
Professor of Biology, Oberlin College
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Q I was in frequent contact with Winslow from the last year of my PhD, during my tenure as a Carnegie Fellow in his lab studying blue-light induced phosphorylation, and while I worked in Europe. Upon return to the US in 2002, we saw each other more often and whenever at a Conference, we would meet for dinner. If I was in the Bay Area, he insisted I stayed at his house and with his wife Ann, had lively conversation. We would go hiking and discuss experiments, and he and my son would speak Japanese and play piano together. Winslow was always supportive of my work and asked good questions and provided new perspectives. One thing I miss are his written letters—we would write each other approximately every two months, 2-3 page letters. Of course, with my letter I always included black licorice, "the liver of the candy world" as he was fond of saying.

Katherine (Kate) Warpeha, Postdoc, Carnegie, 1991-1992
Assoc. Professor, Dept. of Biological Sciences, University of Illinois at Chicago
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R Winslow gave credit to Dina Mandoli for the phrase "reagent grade darkness" but he was an enthusiastic advocate of the principle and practice. Some where along the way, a member of the Freiburg group (I can't track down who) began referring to Winslow as the "Dunkelverwalter" (dark administrator). Winslow enjoyed the joke. The title resurfaced at Winslow's send off for his von Humboldt sabbatical. He was presented with a blindfold with "Dunkelverwalter" emblazoned

across it. By Winslow's telling, and he was a consummate storyteller, he maintained his strict standards while doing experiments in Germany. That is, all but once. A labmate opened the growth room door while Winslow was harvesting dark-control tissue. The results came back showing deviations from Winslow's usual dark control values. Winslow declared that this magnitude of difference from true dark controls should be called one Egon after Egon Mösinger, the colleague who opened the door. The Dunkelverwalter had the last laugh.

Jim Shinkle, Graduate Student, Stanford University, 1980-1985
Professor, Department of Biology, Trinity University, San Antonio, TX
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S I first met my dear friend Winslow on the John Muir Trail in 1986 – I was hiking the 215 miles from Yosemite to Lone Pine to make a series of paintings. He, with Ann and teenage daughter Marion, was doing the trail with a pack llama.

I stopped to paint at frequent intervals. Winslow's party was equally slow – their pack llama refused to go further than 8 miles a day.

In this way we leap-frogged each other along the trail, and became firm friends in the process.

Since that time Winslow and I shard many adventures—hikes in remote areas of Grand Canyon's North Rim, some with middle daughter Lucia; a ten-day hike across Joshua Tree National Monument in spring bloom; a clifftop hike along Cornwall's rugged North Coast.

Winslow was the ideal back country companion—reliable, knowledgeable, patient, self-reliant. Except for one fierce argument—about the division of our last shreds of beef jerky, we were entirely compatible.

All my memories of Winslow make me smile – his unique hiking gear – red felt pixie hat, shapeless oversized shorts, and, even on our desert adventures, his lucky ice axe; his unfailing hospitality – in the kitchen like a mad apothecary, surrounded by mysterious bowls and dishes, creating a Chinese feast; his eagerness to get involved; his love of music and conversation. He was always fizzing with excitement about his science. I seldom understood his explanations, but his enthusiasm was absolutely infectious.

I have a last poignant memory of Winslow: He had contrived for Anne, myself and my wife Ann, to stay in the Carnegie retreat on Point Reyes so that I could do a painting. In the late afternoon sunshine Winslow and I strolled down a narrow path to a deserted beach. Accompanied by the sounds of surf and the cries of gulls we sat on a log together and caught up on the gossip. I fired up my MSR stove and brewed the last of the many wonderful tea breaks in beautiful places we had enjoyed together.

Tony Foster, Artist and Friend
Cornwall, England

T Winslow and Ann volunteered at Henry W. Coe Park for many years and one way Winslow shared his love of the park with interpretive programs. The Wonders of Coe Park was one such program he would give as an evening slide program.

Wonders of Coe Park allowed Winslow to guide your mind to a broader vision of where you were. Slide one shows a common sight at Coe, a lofty ridge with pine trees called Blue Ridge. The Ponderosa trees atop the ridge were likely remnants of a much larger population from a cooler era in history. Now isolated to high ridges.

Next, a slide of Middle Ridge, showing several plant communities including Oak Savannah, Chamise stands, and other chaparral plants. Winslow identified what was what and the water needs for each group of plants. Suddenly I could imagine where there is water on a slope at the park. Perhaps even where there might be a fissure just below ground directing the water downward and supporting a California Bay tree forest.

Next slide, we see a shot of the northeast side of Cordoza Ridge. This slope has a dense forest of leafy trees. This side of the ridge has more water due to its geography. What stuck with me was when Winslow pointed out the red color cast that was in the photo. The red was from the new Oak leaves that were capturing extra sun and had not turned green yet to do their main task.

In just three slides, Winslow profoundly changed the way I see a small portion of Coe Park. What I can see now goes beyond the easily observable and allows my imagination to experience not only how Winslow saw the world, but elegant processes that are happening all around us. Thank you Winslow.

John Verhoeveen, Park Ranger and Friend, Henry Coe State Park
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U It was as if I knew Winslow before I ever met him. I had read his papers in graduate school and then as a postdoc at Stanford in 1970 I found myself working in the lab he had designed for himself. Peter Ray, my mentor, had inherited the lab after Winslow's unexpected departure for Harvard in the late 1960s. A few years later I met Winslow at a Carnegie seminar; he was warm and welcoming to me as a new assistant professor at nearby Santa Clara University.

About 2000, Winslow invited me to tour the Henry Coe State Park about 50 miles south of Stanford. In his old 4 x 4 we explored the majestic and remote back country. Winslow was just as comfortable clearing brush from the road ahead as he was editing manuscripts with me in his lab. Winslow was horrified in 2007 when a raging forest fire destroyed half the park that he and Ann loved so well. However, in the months that followed, Winslow's spirits rose as each new seedling grew in the scorched soil. Within the next year, many of the trees recovered and there was a bounty of wildflowers not seen in generations. This was a personal victory for Winslow.

William Eisinger, Collaborator, 1988-2019
Professor Emeritus, Department of Biology, Santa Clara University
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V It is hard to imagine a more perfect mentor for a naïve Stanford graduate student than Winslow Briggs. His brilliance as a scientist is undeniable, yet he remained uniquely humble and inspiring as a teacher with seemingly limitless kindness, patience, and humor. Winslow's rarity was exemplified by his eagerness to join me in harvesting seedlings for phosphorylation assays of what turned out to be the phototropin photoreceptor. He frequently chose to set aside his duties as Director of the Carnegie Department of Plant Biology, editor of Annual Reviews of Plant Biology, recipient of a continuous stream of correspondence and speaking invitations, and a thousand other draws on his time, just to spend hours standing in a cold room under "reagent grade darkness" cutting pea epicotyls with me, a mere pre-doctoral mentee. Apart from exchanging outrageous puns during these harvesting marathons, we also discussed my latest experiments and approaches to exploring this new putative blue light receptor, recently published manuscripts, and upcoming conferences. Often, our discussions would continue into our three-times-a-day tea breaks. He gave me free rein to try new experiments – and to fail. At every conference he would remind me that one could always find value in another's experiments, even while evaluating the work

critically. The lesson Winslow was teaching me was that I was a colleague rather than an underling.

Timothy Short, Graduate Student, Stanford University, 1986-1991
Associate Professor of Biology, Queens College of CUNY
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W It is no secret that Winslow loved to cook- and to eat. On my first day as a postdoctoral fellow joining the Briggs lab in January 1991, I was invited to a party Winslow organized at his house for lab members and friends. The abrupt transition from a cold and snowy Switzerland to the postcard-like sunny and palm-tree decorated California was amplified by the long journey and excitation to meet my new mentor. A warm and friendly welcome dissipated my anxiety, which completely vanished when I was offered cheese fondue, an annual tradition which Winslow was proud of! Needless to say, as a Swiss citizen I was particularly scrutinized by the whole group, waiting for a comment that would set Winslow's position on the scale of Swiss cuisine. Full of misconceptions about the New World's junk food and lack of culture for "real" food, I had to humbly acknowledge that this cheese fondue was excellent! A cheerful Winslow got relieved and my introduction to his world was completed. I should have known that Winslow excelled in all he was cooking, as I experienced later during many joyful dinners at his place where he treated us with superb dishes from all over the world, with a preference for Asian delights. This passion and curiosity for cuisine was paralleled by the same attitude towards science.

Philippe Reymond, Post-Doc, Carnegie, 1990-1992
Professor, Dept. of Plant Molecular Biology,
University of Lausanne, Switzerland
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X I cannot do justice to Winslow and his impact on others by just talking about his interactions with me. He led the Department of Plant Biology with a soft and yet a determined hand. He always tried to generate consensus, he never let faculty meetings go for more than an hour (the Briggs' rule), he never dominated discussions, he considered scientific quality and innovation of primary importance and he always protected the faculty from administrative burdens. While the Carnegie Institution itself has a hierarchical structure, that structure was diffuse in the capable hands of Winslow. The number of students, postdocs, collaborators and visitors that passed through Winslow's sphere of influence and who were profoundly impacted by his intellect, enthusiasm, support and generosity of spirit was enormous.

Arthur Grossman, Staff Member, Carnegie, 1982-Present
agrossman@carnegiescience.edu

Y I feel very privileged to have worked with Winslow at Stanford for my postdoctoral studies from 1997-2002 and fondly remember that time as the most enjoyable part of my scientific career. I hadn't met Winslow in person before that, so I was quite nervous to meet him for breakfast at the Briggs residence in Hale St (Ann picked me up at SFO the night before and they had both insisted I stay with them until I found a place to stay). We cycled to Carnegie that morning and I remember struggling to keep up with Winslow as he speedily manoeuvred around the streets of Palo Alto. I was 26 years of age then and Winslow would have been approaching 70. I remember thinking "who is this guy?!". That first impression still continues to this day and I will never forget how his enthusiasm for science and life in general was infectious and uplifting to everyone around him. A brilliant mind and mentor, yet one of the most humble and modest people I have met. He had a great sense of humour. I remember the first time I gave a practice talk for a conference in the Carnegie seminar room. Winslow sat as the back with a cheeky grin and held up a "no um" sign when I struggled for words, which made it all the harder for me to continue for laughing.

John Christie, Post-Doc, Carnegie, 1997-2002
Professor, Institute of Molecular, Cell, & Systems Biology,
University of Glasgow
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Z I had the pleasure to have known Winslow Briggs for the past 46 years and to share my science with him for the last 20 years of his life. I met Winslow Briggs in 1973 during his visit to the Carnegie Institution at Stanford in preparation for taking the directorship of its Department of Plant Biology. We kept in touch since until the opportunity to join in research showed up in 1998 after his discovery of the long sought plant blue light receptor for phototropism, phototropin, a protein that contained a light sensing flavin-binding domain called a LOV domain that he had only partially characterized at the time. He asked me to undertake the biophysical characterization of phototropin. After carrying out some preliminary work we submitted jointly a proposal to NSF that was funded in 2000 and successfully renewed for the following 17 years.

We both originally bet that additional light activation would not improve legume agriculture over what should occur naturally in daylight, as it probably happened during centuries of legume agriculture. Clearly, after we both lost the bet on the potential lack of success of our approach, without having anybody raising the opposite view, Winslow asked me who we had to pay for the lost bet. His humorous suggestion was for us to make a joint donation to the Henry J Coe state park he had been supporting for so many years, as punishment for having such poor judgment on the outcome of our science.

Roberto Bogomolni, Collaborator, 1998-2019
Professor Emeritus, Dept.of Chemistry and Biochemistry, UC Santa Cruz
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AA Winslow loved nature. Whether mountaineering in Alaska, backpacking the high Sierras with family, or volunteering at Coe State Park with Ann, Winslow was in his element outdoors. In 2007, disaster struck as half of Winslow's beloved Coe State Park burned in the Lick Fire. But in its aftermath, nature rebounded and Winslow became fascinated with the regeneration process. As long-dormant species sprouted and burst into bloom, Winslow was there, documenting the transformation. Two years later (after the fire in Coe State Park), I met Winslow on the bank of the Ala Wai Canal in Honolulu, having just heard his talk about post-fire recovery of plants. Despite the sweltering heat and humidity, we had an inspiring conversation about our mutual interest. Winslow later invited me to continue my research on smoke-induced seed germination in his lab. That year was a formative experience, as Winslow set a standard as a scientist and a mentor to which I continue to aspire.

Belying his formidable accomplishments, Winslow was approachable and humble. Rank or experience did not matter – a curious mind was all that was needed for a seat at the table. At conferences, Winslow could reliably be found among the posters, talking to students about their work and sharing advice. At Carnegie, he would issue a near daily invitation to the lab, and his friends Bill Eisinger and Roberto Bogomolni, to meet for lunch. Having convened at the splintering table in the courtyard, we would discuss our research, but Winslow would also share stories about his past adventures, travels, and career. He was a master storyteller, who particularly loved a good joke. Winslow taught me the importance of slowing down and enjoying the human

connections we make in science, which are sometimes overshadowed by the relentless drive to accomplish more. He also showed me how to offer encouragement, criticism, and the space trainees need to grow. Despite his keen-eyed editing, however, he failed to successfully cure my split-infinitive habit.

David C. Nelson, Post-Doc, Carnegie, 2011-2012
Associate Professor of Genetics, Dept. of Botany and Plant Sciences, UC Riverside
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BB Winslow was and will continue to be the role model for scientists and a role model for all humankind. Due to his exceptional empathy and intellect, he was always humble, smiling, friendly, supportive and altruistic. He loved nature and his talks always showed images of his ascent of Denali. He and his wife Ann were responsible for the family atmosphere at Carnegie's Plant Science department. When I joined the team in 2003, he officially translated my German documents and supported my green card and citizenship applications. He was always excited to show me his latest results, e.g., the discovery that bacteria also have blue light receptors. After a destructive wild fire in his park, he became excited about the new life that came up after the fire. Shortly after he showed me that he had convinced a chemist to produce several grams of the 'fire hormone' karrikin. His latest work at over ninety on the effect of light on root nodulating bacteria will likely have a major effect on agricultural practice and soybean yields. He always helped me with critical decisions when I ran the department. We miss him so much….

Wolf B Frommer, Staff Member, 2003-2020, and Director, 2007-2016, Carnegie
Alexander von Humboldt Professor, Heinrich Heine University, Dusseldorft, Germany
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CC I will forever be grateful for the opportunity to work with Winslow R. Briggs on several different projects from the very start of my scientific career. Winslow's enthusiasm for scientific discovery, including in adventurous directions, was contagious. He taught me never to leave any stone unturned. I felt very comfortable discussing the farthest of ideas with him. He was a patient listener with a witty sense of humor. Working directly with Winslow in the last seven years, we started several new projects, which are all currently ongoing. These projects included the commercial development of a LOV-protein related product for application in legume production. Winslow had become an entrepreneur and in 2018 we started field trials in a collaboration with Roberto A. Bogomolni. Winslow's guidance in developing treatment protocols was critical in the success of these field tests. I would look forward (at least twice a week) to having lunch together on the wooden benches at Carnegie to discuss science, life, the universe, art and recipes for spicy sauces and dishes. This is forever accessible in my memory to uplift me at any time.

Rajnish Khanna, Carnegie Fellow Scientist, 2012-2019
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