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PERSPECTIVE

Light and plant development: the discovery of phototropins by Winslow R. Briggs (1928–2019)

Ulrich Kutschera and Zhi-Yong Wang

Department of Plant Biology, Carnegie Institution for Science, Stanford, CA, USA

ABSTRACT
The American biologist Winslow Russel Briggs (1928–2019) was a global leader in plant physiology, genetics and photobiology. In this contribution, we try to share our knowledge of the remarkable career of this outstanding scientist. After earning his PhD at Harvard (Cambridge, Massachusetts), he started his independent research program at Stanford University (California). Among many major contributions was his elegant experiment that conclusively demonstrated the role of auxin transport in the phototropic bending response of grass coleoptiles. During subsequent years as Professor of biology at Harvard University, Briggs focused on phytochrome and photomorphogenesis. In 1973, he re-located to Stanford to become Director of the Department of Plant Biology, Carnegie Institution for Science, and faculty member in the Biology Department at Stanford University. After his retirement (1993), he continued his research on "light and plant development" as an emeritus at Carnegie until the day of his death on February 11, 2019. Through his long research career, Briggs stayed at the cutting edge by re-inventing himself from a plant physiologist, to biochemist, geneticist, and molecular biologist. He made numerous discoveries, including the LOV-domain photoreceptor phototropin. Winslow Briggs, who was also a naturalist and gifted pianist, inspired and promoted the work of generations of young scientists – as mentor, colleague and friend.

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Introduction

In their 1882 book *The Power of Movements in Plants*, Charles and Francis Darwin analyzed the bending reaction of dark-grown grass seedlings toward unilateral light.[1] Based on their results, the Darwins postulated that a substance, later discovered and called auxin, may mediate this rapid phototropic growth response of the coleoptile. Seventy-five years later, Winslow R. Briggs (Figure 1), at that time an assistant professor in the Department of Biological Sciences at Stanford University in California, published a paper in *Science* wherein he provided solid evidence for the auxin-phototropism-hypothesis that originated with the work of the Darwins.[2] However, it took 41 additional years of hard work until the Briggs-laboratory, in collaboration with an international team of plant biologists, finally identified the blue-light receptor for phototropism, later named phototropin, as described in two key reports published in *Science* by Huala et al. (1997) and Christie et al. (1998).[3,4] The discovery of phototropin opened up a broad field of inquiry, as this family of photoreceptors, containing the LOV-domain, turns out to be present in a wide range of organisms, including bacteria and all plants, with broad functions ranging from pathogenesis to symbiosis, in addition to phototropic responses in plants.

Here, we summarize the life and scientific work of this eminent plant biologist from a personal perspective.

Botany – music – plant development

Winslow Russell Briggs was born on April 29, 1928 in Saint Paul, Minnesota, USA. His father was a schoolmaster and shared, together with his mother (a professional pianist and teacher), a strong interest in wildflowers. Accordingly, Winslow learned to play piano at the age of six, and became a naturalist, with a focus on botany, at an early age. Winslow studied biology and music at Harvard University in Cambridge/Massachusetts. At the age of 25, he published his first floristic paper on "Some plants of Mount McKinley National Park" (Briggs 1953),[5] but thereafter left taxonomy to focus on "auxins in ferns". Under the supervision of Harvard-Professor Ralph H. Wetmore (1892–1989), Briggs earned his PhD with a thesis on the role of auxin during leaf development in the fern *Osmunda cinnamomea*. This first scientific project yielded three research papers published in the journal *Phytomorphology*, and his first article in *Plant Physiology* (Briggs et al. 1955).[6]

In the year this paper was published, Briggs was offered to take a position at Stanford University in Palo Alto, California. After his move to the "Golden State", he focussed his new research agenda on the auxin-light-relationships, using etiolated maize (*Zea mays*) and oat (*Avena sativa*)-seedlings as experimental systems. The Briggs-team at Stanford University employed sophisticated techniques (such as placing a coverslip barrier vertically through the upper part of the coleoptile) to explore the validity of the Cholotny-Went-theory of lateral auxin-redistribution as a cause for the blue-

CONTACT Ulrich Kutschera kut@uni-kassel.de; Zhi-Yong Wang zwang@carnegiescience.edu

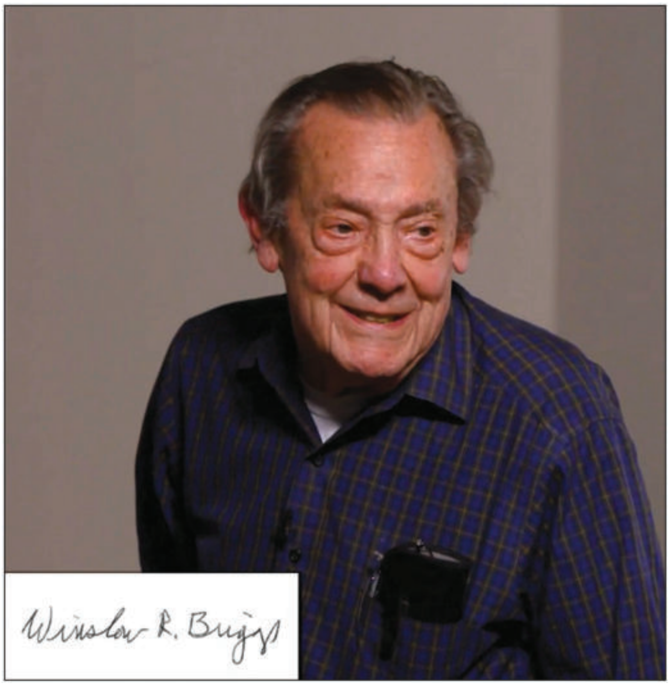

Figure 1. The American biologist Professor Dr. Dr. h. c. Winslow R. Briggs (1928–-2019), Director Emeritus of the Plant Biology Department, Carnegie Institution for Science, Stanford, California (USA). (Screenshot: video – My Journey with Tony/ Encounters with an Artist Explorer. The Foster Watercolor Exhibitions of Wilderness Journeys, CA-USA, 30.04.2018). The signature was reproduced from a Letter of Invitation of W. R. B. to U. K., dated November 13, 2018.

light mediated phototropic bending response (Figure 2). The resulting *Science*-paper[2] was of special importance in the early career of Winslow as a team leader and innovative plant researcher. From 1957 onwards, Briggs pursued (among many other projects) the identification of the photoreceptor responsible for phototropic responses in plants.[7,8] Remarkably, almost fourty years later, his team achieved this goal, using molecular genetics in *Arabidopsis* (Huala et al. 1997).[3] Two more decades later, Briggs (2016) published another article in *Science*, dealing with the questions raised by him (and his colleagues) during the mid-1950s.[9]

A life-long focus on phototropism and photomorphogenesis

As detailed in his autobiography published in 2010,[10] he scientific questions Winslow Briggs and coworkers investigated were broad. They reached from the role of red light in the development of the water fern *Marsilea vestitia* via auxin (IAA)-transport into membrane vesicles isolated from etiolated *Curcubita pepo*-epicotyls, to the biomechanical basis of IAA-mediated growth in pea (*Pisum sativum*) stem segments.[10–12] This spectrum of research activities was one key feature of Winslow Briggs that contributed to his success as a world-wide leader in the plant sciences. In his own words, "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".[10]

In 1967, Briggs was offered a position at Harvard as Professor of Biology, where he established, together with Lawrence Bogorad (1921–2003), an innovative plant biology group. At Harvard University, the Briggs lab focussed on phytochrome and photomorphogenesis research, and established the connection to Hans Mohr's (1930–2016) group at the University of Freiburg i. Br. (Germany). Only six years

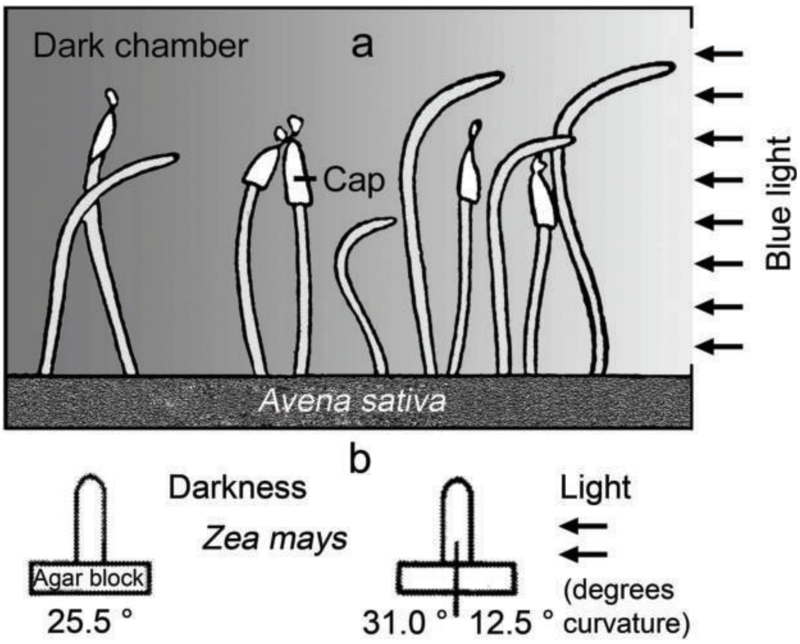

Figure 2. Phototropism of etiolated grass seedlings in response to unilateral blue light-treatment. (a) When the tip of the coleoptile is darkened by a cap, no bending occurs. The classical experiment by W. R. Briggs revealed that in the tip of the organ an auxin-redistribution occurs in response to unilateral light-treatment. (b) The numbers indicate the amount of auxin recovered by diffusion into agar-blocks, and expressed in the units "degrees curvature" (adapted from Briggs, W. R. et al, 1957, ref. 2).

after his move from California to Cambridge/Massachusetts (1973), Briggs accepted the position as Director of the Department of Plant Biology in the Carnegie Institution of Washington (later re-named "of Science") on the campus of Stanford University, where he also became Full Professor in the Biology Department at Stanford University (Figure 3). During the subsequent two decades, he not only expanded his Department by adding new research facilities, but also hired new faculty members, so that numerous graduate students, postdocs and visiting scientists from Europe, Asia, and America were invited to conduct a variety of research projects at Carnegie. By establishing a strong research agenda in plant development, Winslow Briggs connected ecophysiology and photosynthesis research, areas that were well established in the department when he took over the position as Director. As a result, the Department of Plant Biology of Carnegie Institution developed into a world-class research institute that covered all major topics in the plant sciences – from classical physiology (biomechanics etc.) to molecular biology and genetics.

After his retirement in 1993, Briggs continued to work as an Emeritus in the Carnegie Institution until the very last hours before his death. It was during these 26 years as leader of a small, but very productive team of first-class plant scientists that Briggs and coworkers discovered the blue-light (BL) photoreceptors responsible for the initiation of phototropic bending in grass coleoptiles (Figure 2) and other plant organs. The history of this major discovery is summarized below.

After a failed attempt to characterize the BL photoreceptor in maize coleoptiles[11] during the 1970s, in 1988, a "pea stem-auxin-project" yielded unexpected results. During the early 1960s, Scott and Briggs[12] had studied the "auxin-growth-relationships" in light vs. dark-grown seedlings of "Alaska peas" (*Pisum sativum*). As a result, the first author of this article (U. K.) analyzed, as a Postdoc during this time in the Briggs lab, the effects of IAA on growth, tissue tension, the role of the epidermis, and on the patterns of soluble and wall-associated proteins in pea stem segments.[13,14] This search for the elusive auxin-dependent "growth-limiting proteins" was carried out in cooperation with a Postdoc (Sean Gallagher) in the Biology Department at Stanford University (laboratory of Peter M. Ray). One- and 2-D-Gels were run to check whether IAA changes the abundance of proteins in sections cut from the upper internode of the stem. Using entire epicotyl sections, Kutschera and Briggs failed to detect any reproducible effect (Figure 4(a,b)). To our disappointment, we likewise did not find IAA-induced proteomic changes, using the then-popular O'Farrell-technique (2-D-Gels).

Our colleague S. Gallagher in the Ray-lab used the same "Scott and Briggs"-system[12] as we did (i.e. etiolated pea seedlings). Unfortunately, Gallagher and Ray were unable to detect IAA-effects on protein phosphorylation of hormone-treated stem segments. However, when they placed dark-grown pea seedlings into white light, an unexpected effect emerged: light activated the phosphorylation of a specific protein in the upper (growing) region of the pea stem (see Figure 4(a), inset). As a result of this "discovery by chance", in March 1988, Winslow Briggs and his colleague Peter Ray decided to switch projects: the light effect was from now on studied by Tim Short in the Briggs-lab, whereas the search for the hypothetical, IAA-dependent "growth-limiting proteins" was continued in the Ray-lab by U. K., with a focus on the expansion-limiting epidermal cell layer.

As a result, in 1990, two major "Carnegie & Dept. of Biological Sciences"-Stanford-papers were published in *Plant Physiology*, wherein the authors used the same Alaska pea-test system[12] to analyze two entirely different problems. The first article described a "Rapid, blue light-mediated change in detectable phosphorylation of a plasma membrane protein from etiolated pea (*Pisum sativum* L.) seedlings" (Short and Briggs 1990),[15] whereas the second report dealt with "Auxin enhancement of mRNAs in epidermis and internal tissues of the pea stem and its significance for control of elongation" (Dietz, Kutschera and Ray 1990).[16]

This episode documents the enormous creativity and flexibility of Winslow Briggs when he had to handle and manage research projects. In all of these arrangements, he was a fair, open-minded and unselfish science advisor who used to play down his impact when it came to the presentation of the results generated by members of his international research

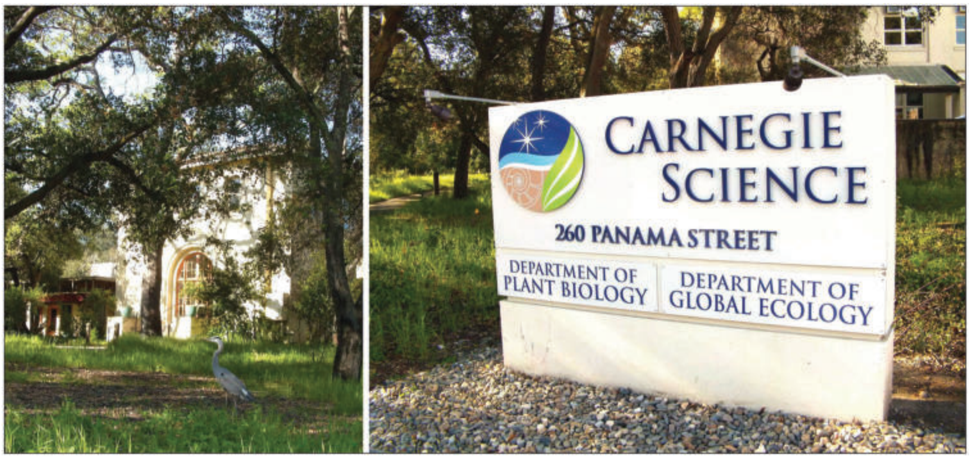

Figure 3. Main building of the Department of Plant Biology (Carnegie Institution for Science), with seminar room (left) and the new stone monument with the logo for Carnegie Science (right) (photo: U. Kutschera, Stanford/California, March 16, 2019).

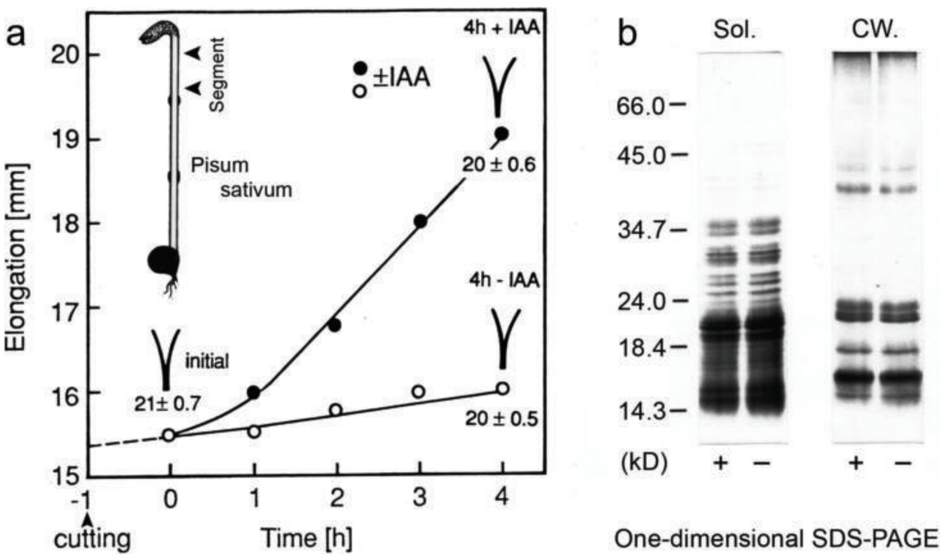

Figure 4. Effects of auxin on the elongation response of excised 15 mm-segments cut from the upper internode of 7-day-old red light-grown pea (*Pisum sativum*) seedlings (inset). (a) During IAA (10 μmol/l)-mediated growth, tissue tension, measured as spontaneous outward bending of split internode sections (bending angles in degrees), is maintained. Despite these large differences in the rate of IAA-dependent stem elongation, the patterns of soluble (Sol.) and cell wall-associated (CW.) proteins, extracted 2 h after hormone-application, are indistinguishable (silver-stained 1 D-gels) (b) (U. Kutschera and W. R. Briggs, unpublished Carnegie-data, 1987).

team. In his autobiography, Briggs[10] concluded that the "pea-BL-studies" yielded the insight that light-activated phosphorylation (a biochemical response) was associated with phototropism (a physiological process). However, his team failed to purify the protein; moreover, the photoreceptor was unidentifiable, using the "materials and methods" of the time.[17] As detailed in the Briggs-account of 2010,[10] it was the use of mutants of *Arabidopsis thaliana* (Figure 5) that finally led to the discovery of the protein and photoreceptor (a flavin).

In 1995, Liscum and Briggs[18] isolated an *Arabidopsis* mutant designated non-phototropic hypocotyl1 (*nph1*) that failed to respond to unilateral light in the hypocotyl curvature and lacked the light-activated phosphorylation reaction. In 1997, the NPH1-gene was cloned encoding the protein that contained two

Figure 5. Flowering sporophytes of the model plant "mouse-ear cress" (*Arabidopsis thaliana*), raised in the Green House of the research facilities at the Carnegie Institution, Department of Plant Biology. Mutants of this small angiosperm were used by Winslow Briggs and colleagues to elucidate the structure and function of phototropins (photo: U. Kutschera, Stanford/California, September 27, 2011).

N-terminal LOV domains (as they were similar to domains in other proteins that were sensitive to light, oxygen, or voltage), and a downstream protein kinase domain.[3] One year later, Christie et al. (1998)[4] demonstrated that NPH1 bound a flavin, and that light induced its phosphorylation in the absence of any other plant proteins; NPH1 was named phototropin1. These major results, published four years after Briggs' retirement as Department Director (and four decades after the publication of the classical "Briggs et al. *Zea mays*-article" mentioned in the Introduction)[2] (see Figure 2) led to the reconstruction of the mechanism of photoreceptor-mediated phototropism.

Three years later, and after extensive discussions with members of the scientific community, these new blue light-photoreceptors were finally named phototropin 1 and 2 (phot 1/2) (Figure 6). The elucidation of their structure and function was based on intensive international cooperations of Briggs with scientists all over the world. It soon turned out that phototropins not only mediate phototropic bending movements – stomata opening, leaf expansion, solar tracking, intracellular chloroplast re-location, and the irradiation-dependent modulation of stem elongation are likewise mediated via phot 1 and 2 (Figure 6). The results of these experimental studies were summarized by Briggs and Christie[18] in their classical 2002-review entitled "Phototropins 1 and 2: two versatile plant blue-light receptors".

Doctor honoris causa – University of Freiburg, Germany

In recognition of his outstanding achievements, the Faculty of Biology of the University of Freiburg i. Br. (where Winslow Briggs had spent three sabbatical years), awarded him on July 5, 2002 a "Doctor honoris causa". In the *Laudatio*, written and read by Peter Schopfer (Figure 7), the discovery of the phototropins by Briggs and coworkers

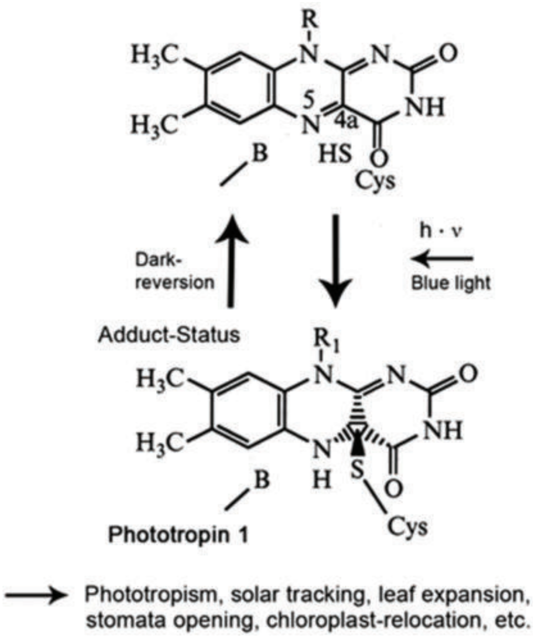

Figure 6. Structure and photoconversion of phototropin 1 (flavin-light receptor) in response to a blue light-pulse. The LOV-domains (protein component) is not shown (adapted from ref. 25).

was recounted in detail.[19] Some quotes, translated into English, read as follows:

"The scientific work of Winslow Briggs is remarkable in several respects. First, he has continued over almost five decades to analyze one central topic, i.e. the elucidation of those regulatory mechanisms that are involved in the orientation of growth of plant organs, notably under the influence of light. This basic phenomenon, i.e. phototropism, which Darwin had already investigated, was analyzed by Briggs and collaborators using numerous experimental tools and methods. As a result, he was able to elaborate basic rules to understand this physiological process. Winslow Briggs started with classical physiological and photobiological methods; later, when the corresponding tools became available, he employed with great success the techniques of biochemistry and molecular genetics. Remarkably, he achieved his greatest success after he became Director Emeritus: Briggs and collaborators discovered the elusive photoreceptor involved in phototropism and characterized the 'phototropins' as autophosphorylating flavoproteins. Today, the facts and theories published by Briggs et al. are already classical topics in textbook chapters dealing with the physiology of plants (for instance, the role of auxin during phototropic bending, characterization of photoreceptors etc.). …

Winslow Briggs maintained a long-term cooperation with his colleagues of the *Faculty of Biology* in Freiburg. In 1973/74, he spent his first sabbatical year in Rainer Hertel's laboratory, where they were searching for the elusive blue light photoreceptor, using maize seedlings. One decade later, Winslow Briggs came back to Freiburg to work, as the recipient of a Humboldt-Research Award, in Eberhard Schäfer's lab to study light-mediated gene expression patterns in seedlings of *Avena sativa*.

During his two stays in Freiburg, Winslow Briggs was working daily in the laboratory and was performing basic tasks, for instance harvesting large quantities of *Avena*-shoots for the analysis of light-induced transcription patterns, using his private knife. In addition to his practical work in the laboratory, Winslow Briggs was an inspiring, creative partner in discussions on all aspects of biology, so that the entire Schäfer-research group profited enormously from the presence of this outstanding American Visiting Scientist. Remarkably, Winslow Briggs rapidly learned the German language and used these newly acquired linguistic skills whenever possible. As a result of his activities in the *Biological Institute* in Freiburg, numerous young scientists (such as the first author of this article) where invited by him to work as postdocs or visiting scientists in the Briggs-lab in Stanford, California. This intensive Stanford-Freiburg-cooperation developed into a mutual relationship with bilateral benefits: it was a kind of 'symbiosis', driven by joint scientific interest, but not sponsored via formal programs.

Figure 7. Winslow Briggs (right) during a discussion with Ulrich Kutschera (middle) and Peter Schopfer (left) in the Institute of Biology, University of Freiburg i. Br., Germany. The conversation took place after Prof. Briggs was awarded a Dr. h. c. in recognition of his discovery of the phototropins, and his long-term support of research programs in Freiburg. Prof. Peter Schopfer wrote and read the Laudatio (photo by W. Thien, Freiburg, July 5, 2002).

In summary, it should be pointed out that Winslow Briggs supported and promoted numerous research projects and individual scientists located in our Faculty. In recognition of this ongoing support, and as a big 'Thank You' for his continuous, constructive impact on research and education in Freiburg, the *Faculty of Biology* of the Albert-Ludwigs-University awards to Winslow Briggs a *Doctor honoris causa*" (Peter Schopfer, July 5, 2002).[19]

The text was translated from the original *Laudatio* that was read in German. Winslow Briggs was 74 years old when he received his Dr. h. c. from Freiburg University (Figure 7). His ongoing activities over the subsequent seven years are summarized by Briggs in detail.[10]

Sunflower and peas: back to the roots

The autobiography by Winslow Briggs[10] was published in advance *online* on December 8, 2009, so that, in his *Epilog*, the author referred to his then timely 2007-*Science*-paper, wherein he described that phototropins (i.e. LOV-domain sequences) also occur in bacteria. Surprisingly, light activation in these microbes increased bacterial virulence up to ten-fold. According to Briggs, "This finding represents a highly unexpected outcome for research on higher-plant blue-light receptors. It also provides a powerful argument for basic research".[10] Based on this sentence, we have to conclude that Briggs' discovery of the phototropins inaugurated a new research agenda that may be labeled "bacterial photophysiology".

In this section we will summarize his work during the last ten years of his career, with a focus on sunflower, pea plants and bacteria. In February 2007, the first author, who had spent two productive years as a postdoc in the Briggs-lab (1985 to 1987) that yielded a number of Carnegie-articles,[13,14,20–23] was invited by the Director Emeritus to give a lecture on plant-associated methylobacteria. This Carnegie seminar led to a long-term cooperation between U. Kutschera and W. R. Briggs that yielded another series of publications.[24–28] The final one, on photomorphogenesis of the root system in sunflower seedlings (Figure 8), was published in 2019, a few weeks after the death of Winslow

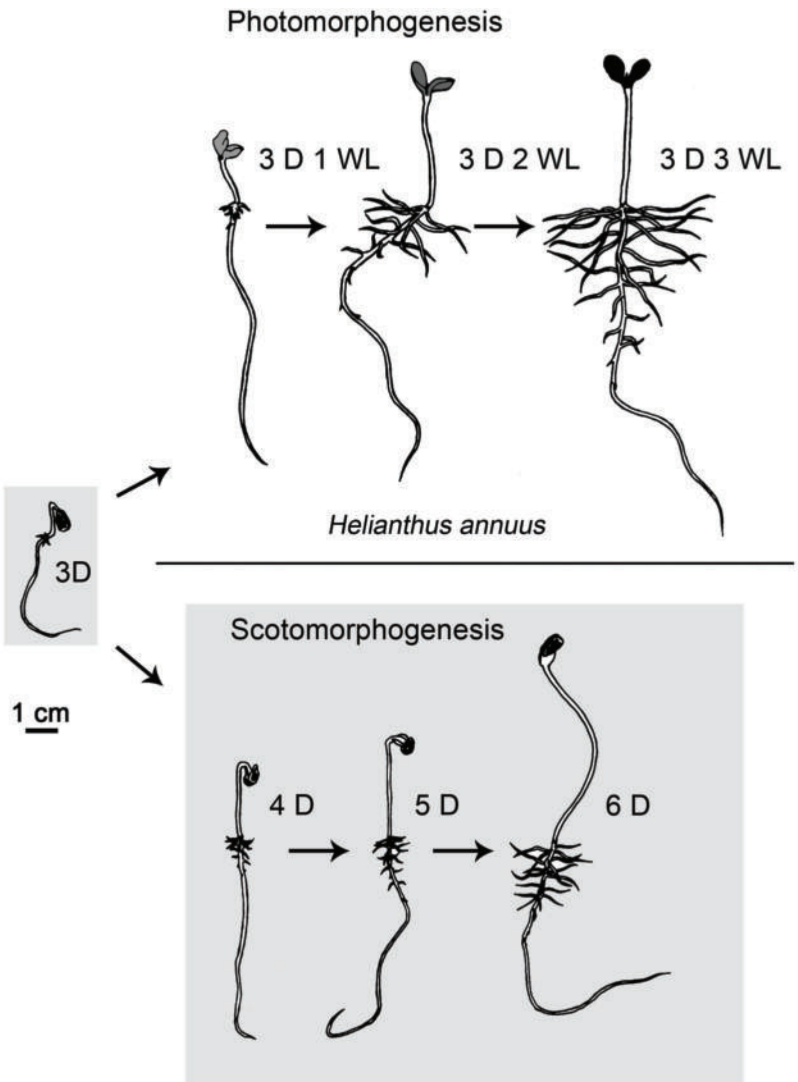

Figure 8. Photomorphogenesis in juvenile sunflower plants, showing the development of the shoot and the root system of seedlings that were raised in moist (non-sterile) vermiculite. Note that, in white light-grown seedlings, the root system expands, whereas hypocotyl elongation is reduced. D = darkness, WL = white light (U. Kutschera and W. R. Briggs 2019, unpublished results; suppl. data to ref. 28).

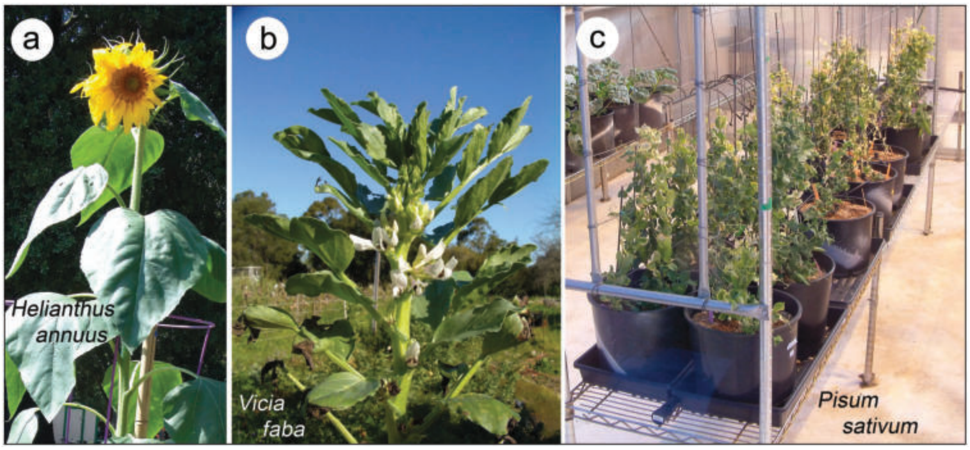

Figure 9. Three crop species that were used by W. R. Briggs and coworkers for the study of fundamental processes in flowering plants. Sunflower (a), Fava bean (b), and Pea (c). In addition to his work on *A. thaliana* (see Figure 5), Briggs and coworkers elucidated the mechanism of phototropic solar tracking and light-activation of rhizobia during nodulation of the roots of the two legume species depicted here (photos: U. Kutschera, Carnegie Institution/Stanford, California; September 10, 2013 [a], and March 16, 2019 [b, c]).

R. Briggs.[28] In addition, the authors of this article initiated a productive Carnegie-cooperation (supported by the Alexander von Humboldt-Foundation, Germany) that resulted in five articles on hormone- and light action in grass seedlings,[29–33] plus a joint publication on BL-induced proteomic changes in *Arabidopsis*, coauthored by W. R. Briggs (Deng et al. 2014).[34]

In a discussion on phototropic solar tracking in developing sunflower plants between Kutschera and Briggs that took place in 2012, it was decided that, when it comes to a causal explanation of this well-known phenomenon, there are so many open questions that a re-investigation of this process is necessary. As a result, sunflower plants (which were studied by Garrison and Briggs in 1975 with reference to phytochrome action and shading)[35] were raised in the open spaces of the *Department of Plant Biology* and analyzed using classical methods (Figure 9(a)). Contrary to what had been proposed before, Kutschera and Briggs[27] documented that maximization of leaf photosynthesis during daytime hours is not the key factor of BL-mediated solar tracking. Rather, in dense populations, a shade avoidance-response may be involved in this unique plant behavior. In 2016, Winslow Briggs published the above-mentioned *Perspectives*-article in *Science*, wherein he summarized the pertinent work on phototropic solar tracking in sunflower, beginning with his 1957-paper to the present.[9]

However, of much more importance and significance for progress in basic plant research and agriculture was a discovery of Winslow Briggs that he made when he was ca. 85 years old. Based on his earlier work on blue light-induced promotion of virulence in pathogenic bacteria,[10] he now focussed his attention on root nodules in *Pisum sativum* and related plants.[36] The senior scientist 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. Figure 9(b, c), shows the pertinent experimental system of the "W. R. Briggs et al. Carnegie-team". This project, which was summarized by the PI W. R. B. during the last days of his life,[37] will be finished posthumously by his collaborators.

Concluding remarks

Winslow Briggs was a unique personality with a broad interest in science, music, art and philosophy. He started his active years as field biologist, collecting plants in nature, and developed an interest in systematic botany. In addition, he began to play piano at an early age, and gave one of his last private piano recitals in the presence of the first author (U. K.) and his collaborators Rajnish Khanna and Tong-Seung Tseng at home when he was 89 years old (Winslow played the *Phantasy in d minor* KV 397 of W. A. Mozart). As summarized in an Obituary[38] authored by the "Friends and Colleagues of Winslow Briggs", he was the President of the *American Society of Plant Biologists* (ASPB) from 1975 to 1976, President of the *American Institute of Biological Sciences* (1981), and a member of the *US National Academy of Sciences*, the *American Academy of Arts and Sciences*, the *California Academy of Sciences*, and the *Deutsche Akademie der Naturforscher Leopoldina*. Briggs was a member of the Board of Directors of *Annual Reviews*, Inc. (Palo Alto, CA), and Editor of the *Annual Review of Plant Biology* for more than four decades. In recognition of his achievements, Briggs won many awards, including the *Alexander von Humboldt* U.S. Senior Scientist Award, the ASPB Stephen Hales Prize, the Sterling Hendricks Medal from the *United States Department of Agriculture* (USDA), and the *American Chemical Society/Adolph E. Gude, Jr.*-Award from ASPB for his "outstanding service to the plant science community". Moreover, in 2009, Briggs was awarded the *International Prize for Biology* (in the field of "Biology and Sensing") from the *Japan Society for the Promotion of Science* for his "outstanding contributions to the advancement of basic research".[38] In two articles dedicated to Winslow Briggs on the occasion of his 90th birthday, the authors argued that "Briggs serves as a role model to what every biologist should aspire".[39,40]

Together with his wife, Ann, the lab-scientist Briggs was a volunteer at the Henry W. Coe State Park close to San José, California, so that his early interest in the study of plants and animals in natural ecosystems continued until the end of his life [41] Winslow Briggs died on Feb. 11 at Stanford University Medical Center at the age of 90 years and 10 months. He is survived by his wife of 63 years, whom he met while they were students at Harvard University in Cambridge/Massachusetts, and by his daughters Marion, Lucia and Caroline, as well as four grandchildren and one great-grandchild.[42]

Acknowledgments

This article is to a large extent based on personal recollections of the authors. We apologize to all of our colleagues and friends who were closely associated with Winslow Briggs, but are not mentioned in the text. We again refer to the Briggs-autobiography (2010) [10] wherein his international network of collaborators is described in many details. The cooperation of the authors is supported by the Alexander von Humboldt-Foundation (AvH, Bonn, Germany; Stanford-Fellowships to U. Kutschera, Institute of Biology, University of Kassel, Germany, and a Humboldt Research Award to Z.-Y. Wang).

ORCID

Zhi-Yong Wang http://orcid.org/0000-0003-4602-3390

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