

# Gustav Senn (1875–1945): The pioneer of chloroplast movement research

Hironao Kataoka\*

Botanical Gardens, Tohoku University, 12-2, Kawauchi Aoba-ku, Sendai 980-0862, Japan.

History



**Hironao Kataoka**

\*Correspondence: [hironao.kataoka@gmail.com](mailto:hironao.kataoka@gmail.com)

**Abstract** Gustav Senn analyzed for the first time light-induced movement and arrangement of chloroplasts. Using many plant species he performed physiological analyses of chloroplast migration in response to external stimuli, with emphasis on light. He determined light paths within a cell by measuring refractive indices and optical thickness of cellular compartments and confirmed that chloroplasts migrate towards the region where the light intensity is optimum. After 6 to 7 years' concentrated study, Senn published the famous monograph “*Die Gestalts- und Lageveränderung der Pflanzen-Chromatophoren*” (*The Changes in Shape and Position of Plant Chloroplasts*) in 1908. This book has stimulated many plant

physiologists and photobiologists, because Senn not only thoroughly classified and defined various types of light-induced chloroplast migration but also already described possible interaction of different photoreceptor systems in *Mougeotia* more than 50 years before the discovery of phytochrome. This book also contains still useful experimental hints and overlooked findings on the interaction between light and other factors, such as temperature, water content, and nourishment. After publishing this book, Senn retreated from the study of chloroplasts and became a researcher of the Greek philosopher, Theophrastus. In this review, I introduce his biographical background and then summarize some of his key research accomplishment.

**Keywords:** Chloroplast; Gustav Senn; *Mougeotia*; photomovement; *Vaucheria*

**Citation:** Kataoka H (2015) Gustav Senn (1875–1945): The pioneer of chloroplast movement research. *J Integr Plant Biol* 57: 4–13. doi: 10.1111/jipb.12311

**Edited by:** Tobias Baskin, University of Massachusetts Amherst, USA

**Received** Sept. 11, 2014; **Accepted** Nov. 13, 2014

Available online on Nov. 18, 2014 at [www.wileyonlinelibrary.com/journal/jipb](http://www.wileyonlinelibrary.com/journal/jipb)

© 2014 Institute of Botany, Chinese Academy of Sciences

## INTRODUCTION

As chloroplasts are the most conspicuous structures in plant cells, their diverse shapes and intracellular orientations have long attracted researchers. However, the first person to analyze the arrangement of chloroplasts systematically and experimentally was Gustav Senn (Britz 1979). He concluded that chloroplast orientation and distribution is determined by the intracellular distribution of light. From the time of publication, his monograph, “*Die Gestalts- und Lageveränderung der Pflanzen-Chromatophoren*” (*The Changes in Shape and Position of Plant Chloroplasts*) (Senn 1908) has been the bible for all chloroplast researchers.

In 1971, I was given a photocopy of this book by Professor N. Kamiya when I was given a sample of *Vaucheria* as research material for my Doctoral research. Along with Senn's book, there were the more recent papers of Wolfgang Haupt on the involvement of phytochrome in rotational movement of the *Mougeotia* chloroplast (Haupt 1959, 1977; Haupt and Schönbohm 1970; Haupt and Wagner 1984). Most of these papers were written in German and although German was necessary for the entrance examination to graduate school in Japan, my knowledge for reading German scientific papers was far from practical. Nevertheless, the beautiful drawings

and summaries of Senn's book stunned me. Also, I soon realized that many of Professor Haupt's studies on chloroplast movement were based on Senn's findings. As early as in 1908 Senn described that the *Mougeotia* chloroplast rotated until its surface became perpendicular to weak blue or red light, while it turned to parallel to strong blue light but not to strong red light. Namely, the *Mougeotia* chloroplast maintained a perpendicular orientation as far as red light was concerned. Reading this as a student, I was shocked by the fact that such an important result was described more than 70 years ago.

Therefore, when I obtained an original copy of Senn's book in 2007, I resolved to translate it into Japanese, because German is known to a diminishing number of scientists, particularly the formal language used for academic work in the 19<sup>th</sup> and early 20<sup>th</sup> centuries, and only a few people know the contents of this important book.

Here, I would like to introduce this book to young photobiologists dealing with chloroplast movement, and perhaps to anyone interested generally in motility. There remain untapped observations and ideas in Senn's monograph and those wishing to learn more will have to consult the original, my soon to be published translation (Kataoka 2015), or await a translation into their own language.

Free Access

## BIOGRAPHY OF GUSTAV SENN

According to the record of the *Bibliothek des Botanischen Instituts der Universität Basel* (Library of the Botanical Institute of Basel University), Gustav Senn was born on 9<sup>th</sup> November 1875 in Basel, Switzerland, the son of Louise Simmoth (birth name) and Gustav Senn (Sr.), a merchant. Gustav Jr. studied natural sciences, especially botany, at the Academy of Neuenburg from 1894, entered Basel University in 1895, and took his Ph.D. there in algal taxonomy in 1898. Still at Basel, he finished his “Habilitation” (Qualification as a university professor) in 1901 and became Associate Professor in 1908. He married Sophie Bernoulli in 1901. She was a member of the famous Bernoulli clan. Her paternal ancestor in the 6<sup>th</sup> generation, Hieronymus (1669–1760), was a brother of Johann Bernoulli (1669–1748), the farther of the famous physicist, Daniel Bernoulli (1700–1782).

Senn was a student of Georg Klebs at Basel University from 1895 to 1898. Klebs, a famous algal taxonomist, studying Chrysophyceae flagellates and for whom the prokaryotic genus *Klebsiella* is named. Senn started his professional studies in the field of algal taxonomy and earned his degree of Ph.D. in 1898 with his prominent achievement in classifying Chrysophyceae flagellates. A contemporary historian has noted Senn contributed a chapter on these flagellates to a seminal monograph on plant taxonomy (Engler and Prantl 1900), and marveled that at the time Senn was only 25 years old (Kristiansen 1995). It is surprising that such a young researcher was able to study huge numbers of flagellates and classify them plausibly into several families, on the basis of reproductive morphology.

After this bravura achievement, Senn completely changed his study to chloroplast movement. He may have looked for analytical or experimental research on plant cells and wanted to work with Professor Wilhelm Pfeffer, because Pfeffer was then a leader on physiological problems, as described in his popular textbook, *Plant Physiology* (Pfeffer 1881). Senn visited Pfeffer’s laboratory in Leipzig, Germany in 1900, and was given the research subject by Pfeffer.

Pfeffer, the uncle if not the father of modern plant physiology, was born in 1845, took his Ph.D. in chemistry at Göttingen and became a professor at Basel in 1877. But he moved to Tübingen only after one year (1878) and nine years later to Leipzig in 1887. When Senn first visited Leipzig, Pfeffer was already a 54-year-old, world-famous unapproachable professor. But I suppose that Pfeffer might have also a sense of closeness to this young scientist coming from Basel. Senn immediately started his experiments on chloroplast movement in Pfeffer’s laboratory. After a short stay in Leipzig (December of 1900 to February of 1901), he returned to Basel and continued the experiments mainly in Basel, although he stayed for a while in the marine station at Helgoland to study chloroplast movement of marine diatoms. However short the stay in Leipzig, Senn had been continuously stimulated by Pfeffer and he thoroughly absorbed Pfeffer’s knowledge and passion for science. During the subsequent 5 to 6 years in Basel, Senn studied morphological changes and movements of chloroplasts in relation to physical stimuli to a greater extent. Senn performed Pfeffer’s teachings with fidelity in his research of chloroplast migration. So, for example, Senn looked at numerous plant species and stimuli, which certainly would

seem to exemplify Pfeffer’s motto: *Die Ausdehnung des Gesichtskreises auf eine möglichst große Mannigfaltigkeit der Erscheinungen ist stets eines der wichtigsten Wergzeuge, um tiefer und tiefer einzudringen* (Expanding your horizon to encompass the largest possible variety of phenomena is always one of the most important strategies to penetrate deeper and deeper) (Pfeffer 1893).

Perhaps indicating the influence of Pfeffer –a man who liked to climb in the Alps (Bünning 1975), Senn wrote a useful illustrated book of alpine flora (Senn 1906) besides his principal studies with chloroplast movement and published a number of papers on the special physiology of alpine plants (Thompson 1945). He was indeed strongly interested in the physiology of alpine plants in relation to light and low temperature.

After publishing his monumental monograph in 1908, Senn changed his study again, this time even more radically, taking up the Greek philosopher and botanist, Theophrastus. As with Chrysophyte taxonomy and chloroplast movement, Senn’s work on the Greek botanist was also highly regarded. No less a scholar than D’Arcy Thompson wrote: “But Senn was chiefly remarkable for his admirable knowledge of Greek, and for his devotion to Theophrastus and other lesser sources of Greek botany; he was the legitimate successor to the last of our own scholar-botanists, Sir William Thiselton-Dyer.” (Thompson 1945).

At 37 years old (1912), Senn became a full professor of botany at Basel University, and subsequently served twice as the president of that University. He also served important roles in academic societies, such as president of the Swiss Society of Botany, between 1921 and 1924, and as both a founding member and president of the Swiss Society for the History of Medicine and Natural Sciences, between 1921 and 1935. Considering that he was swamped with administrative work and that Europe entered a chaotic and dangerous period thereafter, Senn’s shift from physiology to Greek philosophy could be seen as both practical and psychologically stabilizing.

Gustav Senn died on 10<sup>th</sup> July 1945 in Basel. His sudden death was shortly after his retirement from the University and immediately before his 70<sup>th</sup> birthday, when his students were preparing a celebratory symposium (Thompson 1945).

## SENN’S RESEARCH ON CHLOROPLAST MOVEMENT

Senn (1908) wrote in the introduction of his monograph that the relationship between chloroplast distribution and the direction of light penetrating the cells was brought to general interest by the work of Böhm (1856; cited by Senn). Böhm described the intracellular distribution of chloroplasts in Crassulacean leaves and described how they depended strongly on external factors, in particular on the intensity of light. During the following 20 years, various types of chloroplast orientation and distribution were tabulated, with plants of different taxonomic rank in the works of Lüders, Famintzin, Borodin and others (citations in Senn). Senn also noted in the Introduction that although past researchers, like Stahl (1889) and Oltmanns (1892), performed careful studies about the effect of light intensity on orientation and movement of chloroplasts, using *Mougeotia*, and concluded that chloroplasts are moved passively by protoplasm, most

other reports were derived from either a single observation or otherwise inadequate experiments.

Among them, however, Senn highly regarded the studies of Frank (1871; cited by Senn), as the first researcher to have studied this phenomenon to any great extent, and to question why chloroplast positioning in light was different from that in darkness. In addition to light, Frank also studied other external influences, such as temperature, gravity, water content, and injury (Senn 1908). Above all, Senn appreciated Frank because he rejected the then prevalent view that changes in chloroplast positioning resulted from injury. That is, Frank rejected the view that chloroplast movement either to line the anticlinal cell wall or to surround nucleus results from a weakened state of the cell. Instead, Frank concluded that chloroplast migration in the light was the result of a phototactic response.

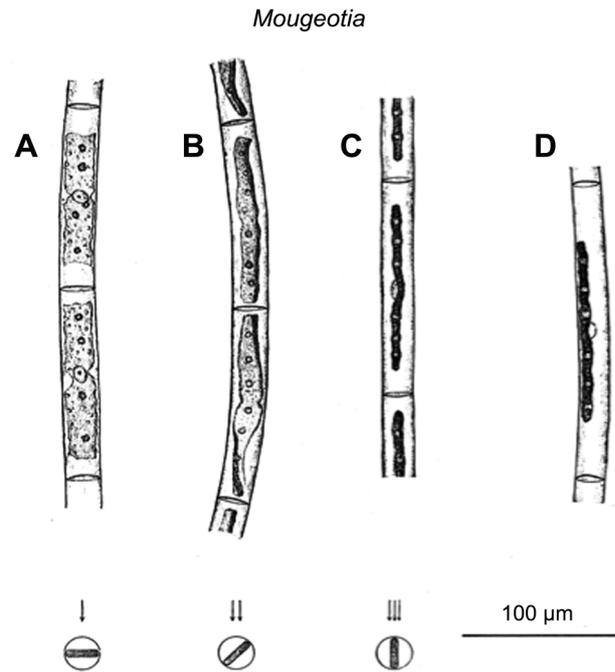
After Frank, the powerful effect of light on chloroplast movement became the focus of attention and had been studied extensively by the end of 19<sup>th</sup> century, in various plant species, ranging from algae, mosses and ferns to seed plants. Although phycologists and botanists whose names remain well known, such as Sachs, Pfeffer, Stahl, Haberlandt, Oltmanns, Küsters, and Molisch, made many of these studies, in contrast their findings are today almost completely forgotten.

Now, let me begin by overviewing the scope of Senn's research on chloroplast movements. He collected and grew many plant species and analyzed the shapes and movement of chloroplasts. In so doing, he developed various apparatus to irradiate a specimen submerged in water or in humid air, an aqueous filter to get blue or red light, as well as an optical wedge filled with India ink to continuously reduce light intensity. To study chloroplast shape and position in multi-layered leaves, he used embedded and sectioned material.

His book comprises five parts, I: Morphological changes of chloroplasts, II: Translocation of chloroplasts, III: Effects of the shapes and distribution of chloroplasts on the color of plants, IV: Biological meanings of the shapes and translocation of chloroplasts, V: General discussion. There are also several appendices, in one of which he gives a mathematical treatment for determining refractive indices of a cell and reconstructs optical paths and the light distribution within a cell. The book contains 83 figures and nine plates of sketches and drawings.

Although not obvious from the table of contents, Senn focused mainly on chloroplast translocation induced by light, although he also treated certain other stimuli, such as temperature, nourishment, and gas. For modern readers, an interesting point is likely to be Senn's classification of light-dependent chloroplast accumulation patterns. He classified them into the following seven types on the basis of cell- or tissue morphology: (i) *Mougeotia*; (ii) *Vaucheria*; (iii) *Chromulina*; (iv) *Elmosphaera*; (v) *Funaria*; (vi) Parenchyma, spongy; and (vii) Parenchyma, palisade. The main differences are outlined here.

(i) ***Mougeotia* type.** One single chloroplast plate rotates around the longitudinal axis of the cylindrical cell (Figure 1). Found in the Conjugatophyta (Streptophyta) *Mougeotia*, but also found in the single-celled desmids, *Mesotaenium* and *Gonatozygon*. Because the *Mougeotia* filament is composed of interconnected cylindrical cells and sways in the water, every cell will receive light from a different direction. Thus, the chloroplast plate of a long



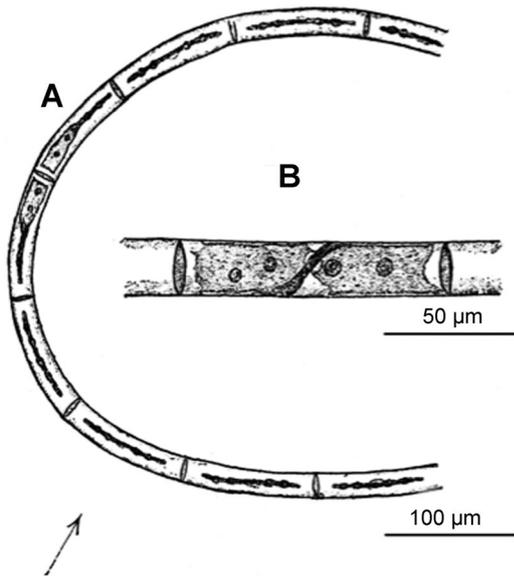
**Figure 1. Axial chloroplast plate of *Mougeotia*. Slightly modified from Senn (1908, Plate I)**

(A) Face position induced by low-intensity light. (B) Intermediate position induced by middle-intensity light. (C) Profile position induced by high-intensity-light. (D) Parietal chloroplast, but not in profile position. Cross sections with direction and intensities of light (arrows) are shown in the bottom.

cell is often twisted but seldom torn off into two pieces (Figure 2).

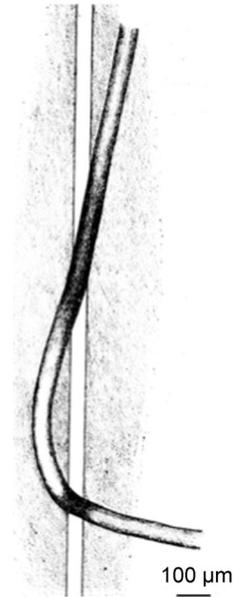
(ii) ***Vaucheria* type.** Within a free-living cylindrical cell, many chloroplasts reside and move in a cortical cytoplasmic layer. When the intensity of incident light is moderate, chloroplasts accumulate in regions of the cell facing the light (i.e., forming a plane of chloroplasts more or less perpendicular to the light direction), but when the light intensity is too high, they move towards shaded area (Figure 3). This type is observed in many algal genera, including *Vaucheria* (Xanthophyceae, Ochrophyta), *Bryopsis*, *Acetabularia* (Chlorophyceae) and *Chantransia* (Rhodophyceae); and it also occurs in moss protonemata and fern prothalia. As experimental material, *Vaucheria*, *Bryopsis*, and *Acetabularia* have been favorites because of their simple shape and large size. Despite not being recognized as such by Senn, they are coenocytes, i.e., they contain numerous nuclei within a non-septated cell. Chloroplasts (and nuclei) can therefore migrate not only transversely but also longitudinally in long distance to the optimum intensity light (Figure 4, Kataoka 1975; Takahashi et al. 2001).

*Vaucheria* sometimes grows on wet soil. When fallen leaves shade a part of such *Vaucheria* mat, chloroplasts escape from the dark region to moderately illuminated region and the cell produces branches emerging from



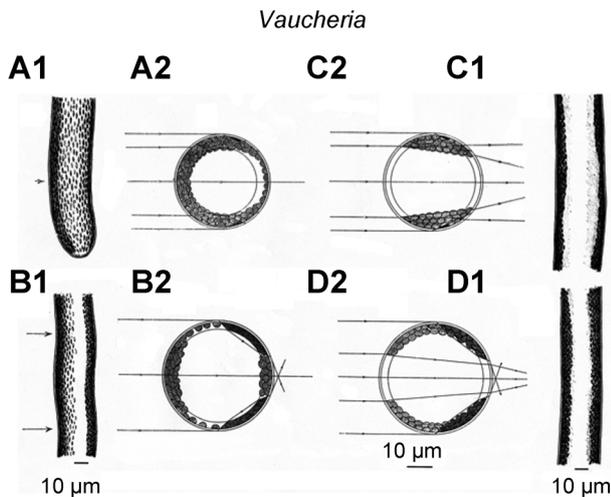
**Figure 2. Torsion of the *Mougeotia* chloroplast plate. Slightly modified from Senn (1908, Figure 15)**

(A) *Mougeotia* filament twisted up to 90° at the curved position. Arrow: direction of almost horizontal incident light. Bar: 100 μm. (B) Magnified cell in which the chloroplast plate is twisted up to 180°. Bar: 50 μm.



**Figure 4. Partially irradiated cell of *Vaucheria*. Slightly modified from Senn (1908, Figure 15)**

When the coenocytic cell of *Vaucheria* is placed under a slit, chloroplasts move towards the lighted regions. Bar: 100 μm.

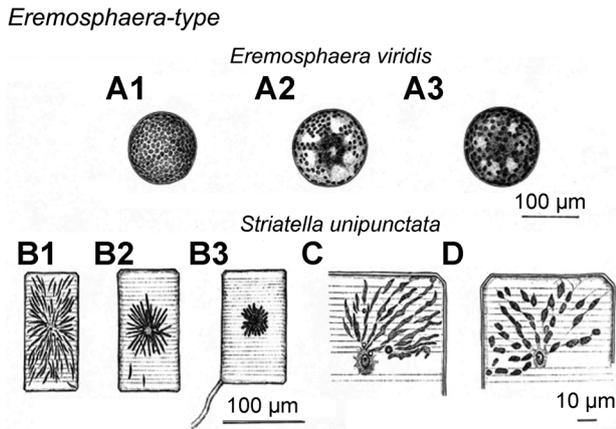


**Figure 3. Distribution of *Vaucheria* chloroplasts under unilateral light beams of middle- and high-intensity-light. Modified from Senn (1908, Plate II)**

(A, B) Light of middle intensity. (C, D) Direct sunlight with constant direction. (A, C) Submerged in the water. (B, D) Exposed in the air. Unilateral Light beams (from left, arrows) run through the cylindrical cell, being refracted at the interfaces between water/cell wall (A and C) and air/cell wall (B and D). In C1 and D1 light comes from below. Note that light beams are refracted greater in the cell exposed in the air than that submerged in the water and that chloroplasts migrate towards the site of optimal light intensity.

the lighted region. Takahashi et al. (2007) recently discovered that this light-induced branching response in *Vaucheria* is mediated by novel blue light receptor, aureochrome.

- (iii) **Chromulina type.** In a free-living spherical or cylindrical cell, single or multiple chloroplasts move in a cortical cytoplasmic layer towards either the near or far side of the cell; in case of multiple chloroplasts, they are accumulated, differently from the *Vaucheria* type, strictly at either the near- or far-side of the cell (with respect to the direction of incident light). Beside *Chromulina* (Ochrophyta), this type of movement occurs in various green algae (e.g., *Ulothrix zonata*, *Rosenvingiella radicans*, and *Ulva*) as well as in the leaves of mosses, ferns and seed plants (e.g., *Adoxa*, *Helleborus*, *Delphinium*, *Pellionia*, *Begonia*, and *Rhynchosglossum*).
- (iv) **Elemosphaera type.** In mostly free-living, spherical cells, chloroplasts reside and move not only within cortical cytoplasmic layer, but also within cytoplasmic strands that run towards the nucleus. This type of movement is observed in *Elemosphaera* (Chlorophyceae) and diatoms (Bacillariophyta; e.g., *Striatella*, *Corethlon*, *Thalassiosira*, *Nitzschia*, *Biddulphia*, *Melosira*, etc.), Dinoflagellates (*Dinophysis*), a moss (*Leptobryum pyriforme*), and in some seed plants (*Adoxa*, *Cucurbita pepo*). In Figure 5 two examples of this type are shown with the chlorophycean unicellular alga, *Eremosphaera*, and the diatom, *Striatella*. Because the strands typically converge around the nucleus, this type of movement often results with the chloroplasts surrounding that organelle, a clustering that is called systrophe. Using systrophe as a



**Figure 5. Eremosphaera-type. Modified from Senn (1908, Plate IV)**

The green alga, *Eremosphaera viridis* and the diatom, *Striatella unipunctata* exhibit Eremosphaera-type chloroplast distribution. (A) *Eremosphaera* cell in diffuse light of middle intensity (A1), 75 min after exposure to diffuse sunlight (A2), and 10 days in darkness (A3). Bar for A: 100  $\mu\text{m}$ . (B) *Striatella* cell showing peristrophe (B1), spreading systrophe (B2), and contracted systrophe (B3); (C, D) Chloroplasts of *Striatella* in higher magnification, showing spreading peristrophe (C) and contracted peristrophe (D). Bar for B: 100  $\mu\text{m}$ ; bar for C and D: 10  $\mu\text{m}$ .

defense response to strong light is a typical characteristic of Eremosphaera-type chloroplast motility.

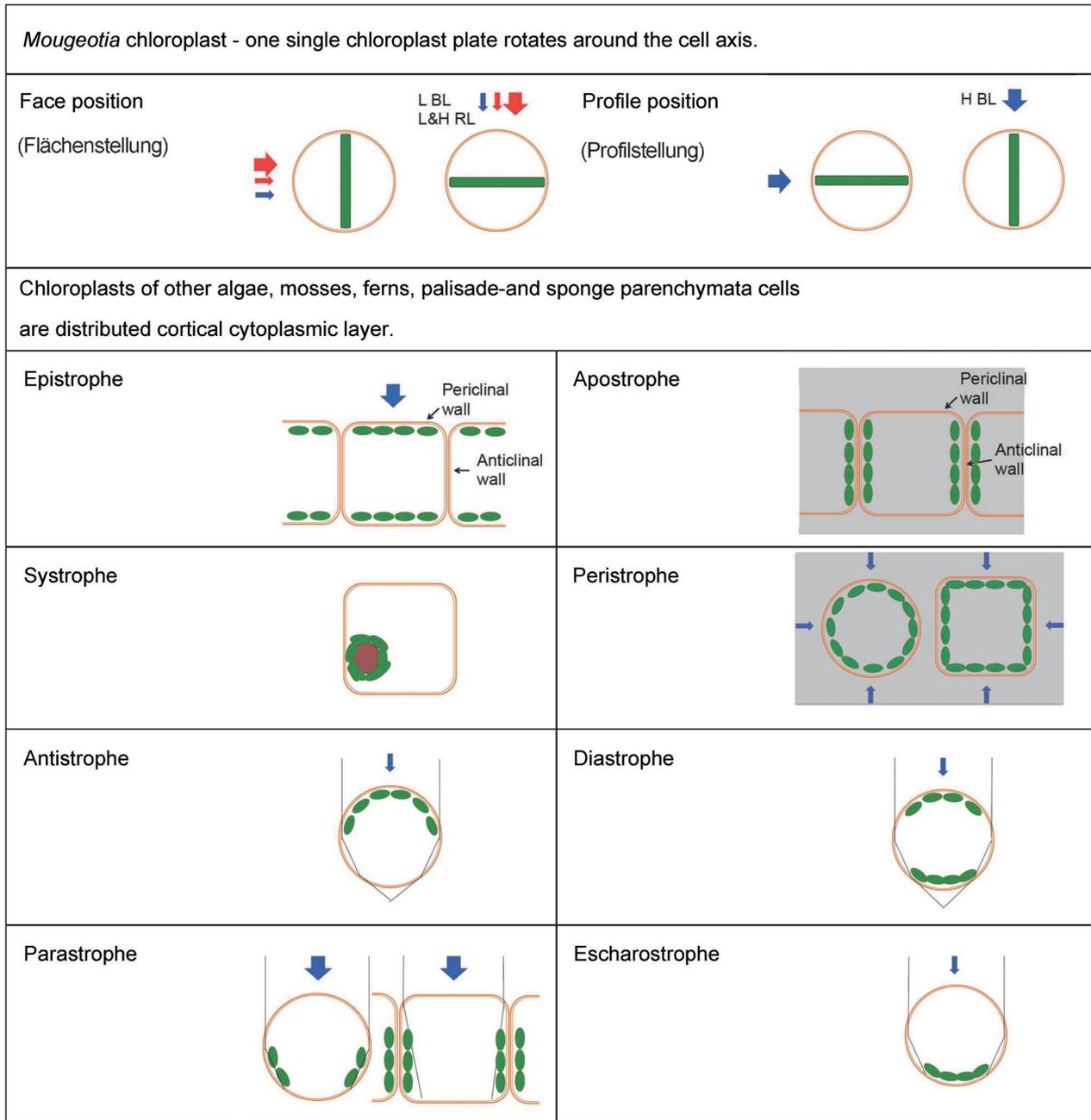
- (v) **Funaria type.** Differing from the Eremosphaera-type, many chloroplasts move within the cortical cytoplasmic layer of a single-layered, brick-shaped, parenchymatous cell. Besides the moss, *Funaria*, this type of movement is observed in many single-layered tissues of Hepatophytes (*Lophocolea*, *Bazzania*, *Marchantia*, *Pellia*, etc.), Bryophytes (*Mnium*, *Schistostegia*, *Fisidens*, etc.), and fern prothallia (*Thlipteris spinulosa*, *Pteris sagittata*, *Aneimia phyllitis* and *Osmunda regalis*).
- (vi) **Parenchyma, spongy.** In multi-layered, parenchyma whose long axes are more or less parallel to the surface of the organ (leaf), many chloroplasts move within the cortical cytoplasmic layer. This type of movement is widely observed in fronds of marine Rhodophyta, such as *Cyclocladia verticillata*, in marine Phaeophyta, such as *Padina pavonia* and *Dictyota dichotoma*, in fern leaves (*Pteris cretica*, *Equisetum arvense*), and in the leaves of seed plants (e.g., *Elodea canadensis*, *Sagittaria sagittariofolia*, *Lemna trisulca*, *Oxalis*, *Fuchsia*, *Asarum*, *Phyteuma*, *Liliodendron*, *Tulipa*, *Manyanthus trifoliata*, *Tradescantia zebrina*, *Aspidistra*, *Chlorophytum*, *Viola*, *Phaseolus vulgaris*, *Vicia faba*, *Zea mays*, and *Sambucus*).
- (vii) **Parenchyma, palisade.** In palisade parenchyma whose long axes are perpendicular to the surface of the organ (leaf), many chloroplasts move within the cortical cytoplasmic layer. Besides many broad leaf plants, a similar type of chloroplast distribution occurs in vertically oriented cells of *Marchantia polymorpha*, the moss,

*Polytrichum*, and in histologically highly organized palisade-like parenchymatous cells of certain red- and brown algae.

Senn next moved from classifications based on species to more analytical classification based on the type of movement that occurs in terms of intensity, quality (wavelength), and intracellular distribution of light. He classified and named 10 different patterns of chloroplast orientation and localization within a cell. These 10 chloroplast orientations are listed in Figure 6, in which I schematically redrew Senn's sketches for the modern reader. Since rotational movement of a chloroplast-plate in a *Mougeotia* cell is very different from others, Senn specifically used the term position (*Stellung*), i.e., he named the orientation of the chloroplast surface perpendicular to the incident light as face position (*Flächenstellung*), and that parallel to the light as profile position (*Profilstellung*). The profile position was later called by Haupt (1977) as *Kantenstellung* (edge position). Face position occurs to low-intensity light irrespective of the light quality. If the intensity of blue light exceeds a certain level, the chloroplast plate rotates and orients parallel to the incident light. However, even when bright red light illuminates the cell, face position is unchanged. This indicates that two different photoreception systems are working in *Mougeotia*, and that the intensity-dependent switchover system for chloroplast rotation works only with blue light. Recently blue light and red light absorbing chimeric photoreceptor, neochrome, was identified in *Mougeotia* and its possible role in Chloroplast rotation is suggested (Suetsugu et al. 2005).

In other plant groups, migration of a single or many chloroplasts is induced only by blue light, and the movement usually occurs in the cortical cytoplasmic layer. Following are the names of chloroplast orientations and their definitions as summarized by Senn. Some of the terminology was invented by Senn while others were derived from earlier sources.

- (i) **Epistrophe:** with middle and low intensity light, chloroplasts gather at the periclinal walls that are not in touch with other cells.
- (ii) **Apostrophe:** chloroplasts accumulate under dim light or in darkness at the inner surface of anticlinal walls that are in touch with adjacent cells (note that it is different from parastrophe).
- (iii) **Systrophe:** chloroplasts enclose the nucleus. Often observed in leucoplasts and diatoms.
- (iv) **Peristrophe:** under dim light or in darkness, chloroplasts are equally distributed in the whole cortical cytoplasmic layer.
- (v) **Antistrophe:** all or most chloroplasts gather in the cortical cytoplasmic layer closest to where light shines. Observed frequently in spongy parenchyma in which the palisade parenchyma already attenuate light intensity.
- (vi) **Diastrophe:** chloroplasts accumulate at both near and far sides from light source. Observed frequently in leaf epidermal cells of floating aquatic plants.
- (vii) **Parastrophe:** under strong light, chloroplasts escape from upper and lower periclinal walls and migrate towards the shaded region of the anticlinal walls.



**Figure 6. Terms and definition of chloroplast orientations/distributions. Originally drawn diagram**  
Schematic diagrams of the chloroplast orientations in cross-sectioned cells are shown in the right sides.

(viii) **Escharostrophe:** chloroplasts accumulate at the locus where the light beams converge on the far side (away from irradiation). In the case of protonematal cells of the cave moss, *Schistostega*, chloroplasts in escharostrophe reflect sparkling green light to the viewer. A similarly beautiful golden glitter is observed with *Chromulina* (Chrysophyceae) cells. The spherical cell of *Chromulina* has a single cup-shaped chloroplast and the cell floats on the surface of calm water, anchored by a specific stalk. As the colony of *Chromulina* forms a thin

layer on the surface of a cave pond, their yellow-colored chloroplasts exhibiting escharostrophe reflect strong golden glitter horizontally to the viewer. Senn had frequently encountered these beautiful golden glitters in Schwarzwald (Black Forest) as a taxonomist of Chrysophyceae; perhaps it was this phenomenon that stimulated his interest in chloroplast positioning.

Any given cell type generally is able to adopt only two or three of the above positions, and that which appears is

generally a function of light intensity. For example, in *Vaucheria*, chloroplasts show peristrophe in darkness or in dim diffuse light, diastrophe to parallel low intensity light, and parastrophe in high intensity light.

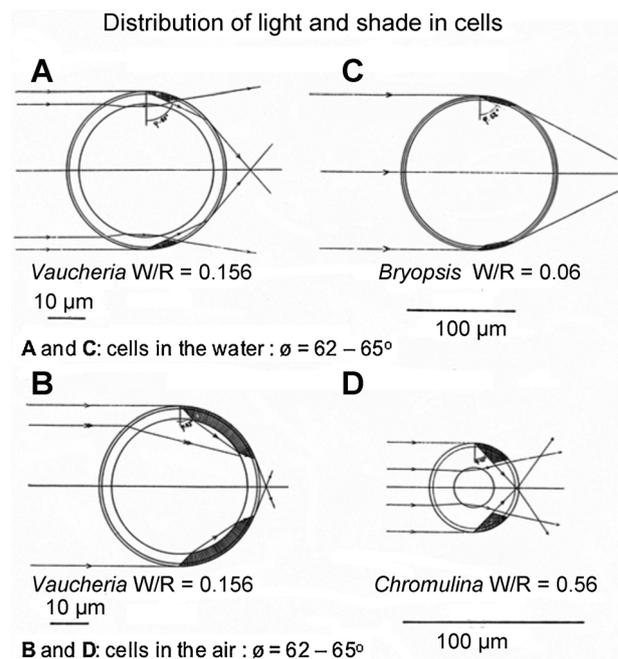
Senn's comprehensive classification of chloroplast photo-migration represents a major accomplishment; however, for present-day photo-physiologists, these detailed classifications may be rather too complicated. In some cases, epistrophe, antistrophe, diastrophe, and escharostrophe can simply be called "the low-intensity position", parastrophe (and rarely systrophe) "the high-intensity position", while apostrophe, peristrophe, and systrophe, as "the dark position" (e.g., Kataoka 1980). Nevertheless, it bears remembering that only a few of these eight specific movement classifications have been studied carefully since Senn and the mechanisms powering them could well turn out to be novel.

To help him understand the patterns of chloroplast orientation and movement, Senn determined the light paths through cells of different shapes and correlated the distribution of light within cells to the destination of chloroplasts or to the orientation of a single chloroplast. Even today, doing so is a formidable problem of optics and Senn's success in this area represents a worthy accomplishment. To determine the light paths, cross-sectional thickness and refractive indices of organelles must be estimated and their light absorption taken into consideration.

Senn did this by fixing materials before and after light treatment, observing and measuring under microscope whole or sectioned samples, and also measuring focal distances of living cells and non-living glass cylinders. He determined refractive indices of the cells of various plants (e.g., *Vaucheria*, *Bryopsis*, *Chromulina*, *Funaria*, *Schistostega*, *Vicia*, *Dipsacus*, *Taraxacum*, and *Viola*) from the angle a light beam was bent when passing through the outer layer of spherical or cylindrical cells. The value of refractive index thus obtained is the average of that of cell wall and cortical cytoplasm, and the thickness of these layers presumably varies widely. Nevertheless, the refractive indices he determined were around 1.5, close to the value usually associated with the cell wall, suggesting that his method was dominated by that structure. This conclusion is strengthened by comparison with contemporary work on *Vaucheria*. Senn described that the refractive indices of four different species of *Vaucheria* were 1.47 to 1.52, considerably higher than as measured by interference microscopy (i.e., 1.36 for *V. geminata*, Kataoka 1975). Using the measured refractive index and relative thickness of cell wall and cytoplasm, he reconstructed the light paths through living cells (Figs. 7 and 8), and confirmed that the intracellular position of chloroplasts was decided by the distribution of light within the cortical protoplasmic layer.

Senn also discussed the mechanism of chloroplast migration in some detail. In his time, chloroplast movement was thought to be passive; the chloroplast had no discernable motile apparatus and was therefore argued to be moved by the cytoplasm. But at the start of the 20<sup>th</sup> century, the concept of "the movement of cytoplasm" was nebulous and there was little consensus about what might be moving chloroplasts in specific or cytoplasm in general (Dietrich 2015).

In those days, perhaps the clearest example of moving cytoplasm was rapid cytoplasmic streaming, frequently observed in Characean intermodal cells and sweeping all



**Figure 7. Distribution of light and shade in a cell. Slightly modified from Senn (1908, Plate IX)**

Light paths through *Vaucheria* (A and B), *Bryopsis* (C) and *Chromulina* (D) cells are reconstructed by calculating refractive indices of the cellular compartments and relative thickness of wall- and cytoplasmic layer (W/R) which vary between 0.06 and 0.56. Maximum refraction angle  $\theta$  were between 62° and 65°.

organelles along in its path. Senn wrote "Nucleus or the migration of nucleus cannot be the cause of the chloroplast migration. Rather to say, migration and settlement of a chloroplast to cortical cytoplasmic layer or to the nucleus is thought to be independent. Instead, as cytoplasmic streaming often acts inversely on chloroplast, chloroplast completes its movement with active mechanisms" (Senn 1908, p. 294). In passages such as this, it seems that Senn envisions that the chloroplasts do have some kind of motile apparatus, endowing them with the ability to move independently. Indeed, the question of whether the chloroplast motility should be considered as intrinsic to the chloroplast or subservient to the cell occurs repeatedly, in Senn's work and up to today.

Senn noted some exceptional cases in which chloroplasts are passively carried by cytoplasm. (i) Movement occurring in a particular region where cytoplasm is regenerated, e.g., at the growing apex of *Bryopsis* filaments or in dividing or auxospore-forming diatom cells. (ii) In cases where intense light or other external stimulus injures chloroplasts (e.g., photodinesis in *Vallisneria* and *Elodea*). (iii) (Related to example ii) Centrifuged Characean intermodal cells contain injured chloroplasts. (iv) Starch-containing heavy chloroplasts or leucoplasts move passively by the influence of gravitational force. "These four examples of passive migration of chloroplasts, which Pfeffer (1904) named argotaxis, are principally different from ordinary active migration," concluded Senn in the summary of section II-2-B of his monograph.

However, the word phototaxis that Senn used for chloroplast photo-migration is defined somewhat differently today. Insofar as chloroplasts are organelles, their movement towards light or shade differs from the movement of unicellular organisms, such as *Chlamydomonas* or *Euglena*, that today defines phototaxis. Senn wrote in the 1908 monograph's conclusion that the migration of chloroplasts could better be expressed as "intensity-difference-sensitive" or "photometric" responses, rather than "phototactic", because the latter word is strongly connected to the idea of "direction-sensitive". Nevertheless, the tactic movement of an organism toward or away from the light share many features with that of chloroplasts within a cell; it seems reasonable to consider each an example of phototaxis.

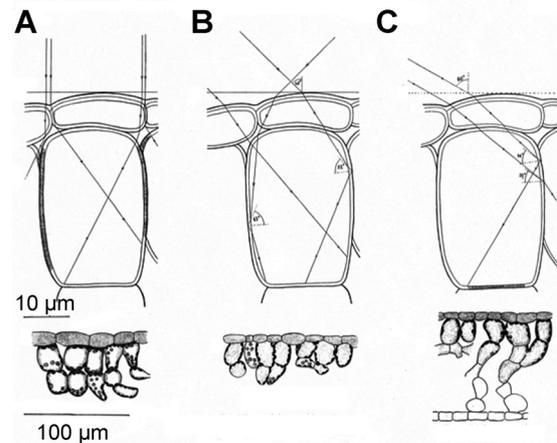
Later, Fischer-Arnold (1963), a student of Haupt, discovered in *Vaucheria* that the chloroplast itself does not need to be irradiated for the induction of migration. This was apparently the first demonstration that chloroplast does not contain the photoreceptor for the movement response and hence that the light stimulus is received elsewhere and transmitted to the chloroplast. Thus, the motility system cannot be completely intrinsic to the chloroplast and has components residing elsewhere in the cell. Today, we know that the responsible photoreceptors are the phototropins, which relay information on the light gradient within the cell to chloroplasts.

It is interesting to note that Senn rejected *Vallisneria* and *Elodea* (*Egeria*) as being unsuitable plants for the study of chloroplast photo-migration, because the chloroplasts are pulled off from cortical cytoplasmic layer and taken away by the cyclosis that is triggered by strong sunlight. He took this response as a kind of injurious effect of harmful sunlight on chloroplast anchorage in the cortical cytoplasm. In the brick-shaped leaf parenchyma of these plants, cyclosis occurs only along anticlinal walls. The cytoplasmic mass beneath the anticlinal walls starts cyclosis immediately after the leaf is exposed to strong blue light, and streaming, viscous cytoplasm washes the chloroplasts away. However, in leaf epidermal cells of *Vallisneria* and *Elodea*, many chloroplasts reside at periclinal walls (epistrophe) in light of moderate intensity, and when the light intensity exceeds a certain value, they quickly migrate towards anticlinal walls (parastrophe). This movement at least cannot be easily explained by the induction of cyclosis by strong light.

Despite Senn's rejection, after three-quarters of a century, chloroplast photo-migration in *Vallisneria* was studied by Konrad Seitz, also a student of Haupt (Seitz 1979, 1982). Seitz hypothesized that the direction moved by a chloroplast is decided by the ATP gradient between periclinal and anticlinal walls, although his group were never able to confirm this. Recently, Shingo Takagi and colleagues discovered that the photoreceptor for the photo-migration response of *Vallisneria* is phototropin (Sakai et al. 2015), contradicting the hypothesis of Seitz but fully validating *Vallisneria* for research on chloroplast motility.

Relating to the question of whether chloroplast migration is active or passive, I would like to add an interesting description of Senn's. He frequently observed chloroplasts to be surrounded by a unique, transparent structure. This was particularly clear when the cortical cytoplasmic layer had become thin following prolonged starvation of the cells. He

### *Taraxacum officinale*, palisade parenchyma

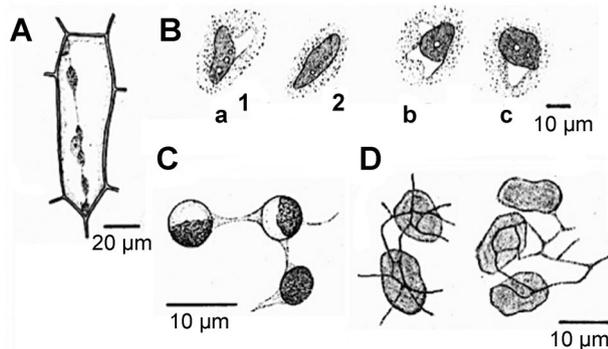


**Figure 8. Light paths through palisade parenchyma cells of *Taraxacum*. Slightly modified from Senn (1908, Plate VII)**

Leaves of *Taraxacum officinale* were irradiated from above with parallel (A) and convergent light beams (B, C). The convergent light beams obliquely shone the leaf at 90° (B) or at 120° (C). Upper row, epidermal- and uppermost layer of palisade parenchyma cells; lower row, sketches of the position of chloroplasts in the palisade parenchyma cells. Note that chloroplasts in palisade parenchyma cells migrate escape from the shaded region (hatched region) towards the lighted regions. If the strongly convergent light beam did not reach the floor of the cell (C), chloroplasts escaped from the floor.

named this structure "the peristromium", from the Greek, π-ε-ρ-ι-σ-τ-ρ-ω-μ-α, and meaning "around the body". Significantly, he observed the peristromium undergoing apparent amoeboid movement at the leading edge of moving chloroplasts (Figure 9). Sometimes, the peristromium formed a kind of network beneath the chloroplasts and appeared to be carrying chloroplasts as they moved some distance. Recent investigations suggest that the peristromium represents a specialized formation of the actin cytoskeleton (Oikawa et al. 2003; Higa et al. 2014). When a small area of a leaf cell is irradiated with intense blue light, a whisker-like actin filament forms at the opposite side from exposure and the chloroplast appears to slide away from the light spot on the newly formed actin railway. Senn's peristromium lacks the specificity of today's chloroplast actin rings or to the actin filaments of *Mougeotia* connecting chloroplast plate and cortical cytoplasmic layer (Mineyuki et al. 1995); nevertheless, that he could see this formation testifies to its substantial nature and careful reading of his observations could yet provide insight into the mechanisms underlying chloroplast motility.

Finally, I would like to add a comment pointing out Senn's insight into the origin of chloroplasts. Although Schimper (1883, cited by Senn 1908) was apparently the first to write that the chloroplast might have originated from a symbiosis between a colorless organism and a cyanobacterium, this idea was then nothing more than speculation that few took seriously. In contrast, Senn acknowledged this idea, recognizing many commonalities between cyanobacteria and



**Figure 9. Peristromia observed in many plant cells. Modified and combined from Senn (1908, Figs. 73, 74, 76 and 77)**

(A) *Selaginella kraussima*. Chloroplasts in the outermost cytoplasmic layer are interconnected. Bar: 20  $\mu\text{m}$ . (B) *Bryopsis* chloroplasts exhibiting characteristic amoeboid movement. Senn (1908) noted that these figures were modified from Noll's sketches, without further explanation about a, b, c, 1 and 2. Bar: ca. 10  $\mu\text{m}$ . (C) Somewhat swollen, partially decomposed *Funaria* chloroplasts are connected with colorless filamentous structure. Bar: 10  $\mu\text{m}$ . (D) *Funaria* chloroplasts with robust peristromial plasmodium that adhere to the ventral surface of the chloroplast. Bar: 10  $\mu\text{m}$ .

chloroplasts, such as the lack of a prominent nucleus, presence of chlorophyll, and as Senn was uniquely placed to appreciate, phototactic behavior. In later years, when Lynn Margulis championed the endosymbiosis origin of chloroplasts (Sagan 1967), one supposes that the arguments over this theory paid little heed to chloroplast motility. But recognizing that any endosymbiont would have had a well developed photo-taxis, Senn would have been disposed to think of chloroplast migration as genuine tactic movement, and we can wonder about the process used to replace a prokaryotic gliding motility with an elaboration of the eukaryotic cytoskeleton. Again, reading about the relationships that Senn drew between the movements of algal cells and chloroplasts offers scope for inspiring us today to understand these processes more deeply.

## ACKNOWLEDGEMENTS

The author is grateful to Dr Tobias Baskin for his critical reading of the manuscript. The author also thanks Ms Nicole Niederhauser of the Library of the Basel University for her help in searching Gustav Senn's Biographical data.

## REFERENCES

- Britz SJ (1979) Chloroplast and nuclear migration. In: Haupt W, Feinleib ME, eds. *Encyclopedia of Plant Physiology NS. Vol. 7*. Springer-Verlag, Berlin-Heidelberg-New York. pp. 170–205
- Bünning E (1975) Wilhelm Pfeffer: Apotheker, Chimiker, Botaniker, Physiologe, 1845–1920, Grosse Naturforscher 37. Wissenschaftliche Verlagsgesellschaft. (Japanese Translation by Tazawa M, Masuda Y, Matsumoto T, Hashimoto A, 1988, Gakkai Shuppan Center)
- Dietrich M (2015) Explaining the “pulse of protoplasm”: The search for molecular mechanisms of protoplasmic streaming. *J Integr Plant Biol* 57: 14–22
- Engler A, Prantl K (1900) Die natürlichen Pflanzenfamilien. Leipzig
- Fischer-Arnold G (1963) Untersuchungen über die Chloroplastenbewegung bei *Vaucheria sessilis*. *Protoplasma* 56: 495–520
- Haupt W (1959) Die Chloroplastendrehung bei *Mougeotia* I. Über den quantitativen und qualitativen Lichtbedarf der Schwachlichtbewegung. *Planta* 53: 484–501
- Haupt W (1977) *Bewegungsphysiologie der Pflanzen*. Georg Thieme-Verlag, Stuttgart
- Haupt W, Schönbohm E (1970) Light-oriented chloroplast movements. In: Halldal P, ed. *Photobiology of Microorganisms*. Wiley-Interscience, London, New York, Sydney, Toronto. pp. 283–307
- Haupt W, Wagner G (1984) Chloroplast movement. In: Colombetti G, Lenci F, eds. *Membranes and Sensory Transduction*. Plenum Publishing Corporation, New York. pp. 331–375
- Higa T, Suetsugu N, Kong SG, Wada M (2014) Actin-dependent plastid movement is required for motive force generation in directional nuclear movement in plants. *Proc Natl Acad Sci USA* 111: 4327–4331
- Higa T, Wada M (2015) Clues to the signals for chloroplast photorelocation from the lifetimes of accumulation and avoidance responses. *J Integr Plant Biol* 57: 120–126
- Kataoka H (2015) *Yohryokutai no Hikari-ten'i-undou* (Japanese translation of Senn 1908). Tohoku University Press, Sendai.
- Kataoka H (1975) Phototropism in *Vaucheria geminata* II. The mechanism of bending and branching. *Plant Cell Physiol* 16: 439–448
- Kataoka H (1980) Photoorientation movement of chloroplasts. In: Furuya M, ed. *Light and Life in Nature* (Hikari-undoh-hannoh, in Japanese) Kyoritsu-Shuppan, Tokyo. pp. 206–241
- Kristiansen J (1995) History of chrysophyte research: Origin and development of concepts and ideas. In: Sandgren CD, Smol JP, Kristiansen J, eds. *Chrysophyte Algae*. Cambridge University Press, Cambridge. pp. 1–22
- Mineyuki Y, Kataoka H, Masuda Y, Nagai R (1995) Dynamic changes in the actin cytoskeleton during the high-fluence rate response of the *Mougeotia* chloroplast. *Protoplasma* 185: 222–229
- Oikawa K, Kasahara M, Kiyosue T, Kagawa T, Suetsugu N, Takahashi F, Kanegae T, Niwa Y, Kadota A, Wada M (2003) Chloroplast unusual positioning1 is essential for proper chloroplast positioning. *Plant Cell* 15: 2805–2815
- Oltmanns F (1892) Ueber die photometrischen Bewegungen der Pflanzen. *Flora* 75: 184–266
- Pfeffer W (1881) *Pflanzenphysiologie-Ein Handbuch des Stoffwechsels und Kraftwechsels in der Pflanze II*. Verlag von Wilhelm Engelmann, Leipzig
- Pfeffer W (1893) Die Reizbarkeit der Pflanzen. In: Verhandlung der Gesellschaft deutschen Naturforscher und Ärzte in Nürnberg, Allgemeine Teilung. pp. 1–31
- Pfeffer W (1904) *Pflanzenphysiologie II. Auflage. Band II. Kraftwechsel*. Wilhelm Engelmann, Leipzig
- Sagan L (1967) On the origin of mitosing cells. *J Theor Biol* 14: 225–274
- Sakai Y, Inoue S, Harada A, Shimazaki K, Takagi S (2015) Blue-light-induced rapid chloroplast de-anchoring in *Vallisneria* epidermal cells. *J Integr Plant Biol* 57: 93–105
- Seitz K (1979) Cytoplasmic streaming and cyclosis of chloroplasts. In: Haupt W, Feinleib ME, eds. *Encyclopedia of Plant Physiology NS. Vol. 7*. Springer-Verlag, Berlin-Heidelberg-New York. pp. 150–169

- Seitz K (1982) Chloroplast motion in response to light in aquatic vascular plants. In: Symoens JJ, Hooper SS, Compère P, eds. *Studies on Aquatic Vascular Plants*. Royal Botanical Society of Belgium, Brussel. pp. 89–101
- Senn G (1906) Sammlung naturwissenschaftlicher Taschenbücher II. Alpen-Flora Carl Winters' Universitätsbuchhandlung, Heidelberg
- Senn G (1908) *Die Gestalts- und Lageveränderung der Pflanzen-Chromatophoren*. Wilhelm Engelmann, Leipzig
- Suetsugu N, Mittmann F, Wagner G, Hughes J, Wada M (2005) A chimeric photoreceptor gene, *Neochrome*, has arisen twice during plant evolution. **Proc Natl Acad Sci USA** 102: 13705–13709
- Takahashi F, Hishinuma T, Kataoka H (2001) Blue light-induced branching in *Vaucheria*. Requirement of nuclear accumulation in the irradiated region. **Plant Cell Physiol** 42: 274–285
- Takahashi F, Yamagata D, Ishikawa M, Fukamatsu Y, Ogura Y, Kasahara M, Kiyosue T, Kikuyama M, Wada M, Kataoka H (2007) AUREOCHROME, a photoreceptor required for photomorphogenesis in stramenopiles. **Proc Natl Acad Sci USA** 104: 19625–19630
- Thompson DW (1945) Dr. Gustav Senn, Obituaries. **Nature** 3958: 289