Tribute

Contributions of Henrik Lundegårdh

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Abstract

Henrik Lundegårdh made major contributions in the field of ecology and plant physiology from 1912 to 1969. His early work at Hallands Väderö in the Kattegat pioneered quantitative approaches to plant ecology and laid the understanding of carbon dioxide exchange in natural communities which is still useful today in global carbon accounting. Very early on in this work he invented the flame photometer. In trying to understand salt respiration of plants, he started to formulate hypotheses for the relationship between respiration and ion movement, including protons, hypotheses that were forerunners to the Chemiosmotic Hypothesis of Peter Mitchell. Necessarily, this involved work on plant cytochromes. He invented several early recording spectrophotometers and made many early discoveries in the field of plant cytochromes, including the photo-oxidation of cytochrome $f$ in photosynthesis.

Abbreviations: ABC – ATP-binding cassette; ATP – adenosine triphosphate; Cyt – cytochrome

Life and work

Henrik Lundegårdh was born in 1888 to a rich and well-established Stockholm family. He was a gifted student who played the violin and had a lifetime interest in the visual arts. His early studies were in Stockholm and he obtained his first degree (1907) and Phil Dr (1912) from Stockholm University, Sweden. In these earliest studies he was inspired by Otto Rosenberg and took up the microscopic investigation of plants and cells, resulting in the publication of some 12 papers on cell division. However, as early as 1910, he turned his attention to plant physiology and the permeability of roots to various salts. This led to two periods abroad, in the laboratories of Georg Klebs in Heidelberg (Germany) and Wilhelm Pfeffer in Leipzig (Germany) in 1912–1913. In 1915 he moved to the University of Lund, Sweden, where he stayed until 1926. There he set up (financed to a great extent from personal funds) an experimental station, for ecology and physiology, on the island of Hallands Väderö in the Kattegat (between Sweden and Denmark). This work was characterized by the application of quantitative techniques to measure the exchange between plants and their environment. Here Lundegårdh’s genius for inventing instruments, where no adequate instruments existed, first came to the fore. This work led to several books, the most famous of which was ‘Klima und Boden in Ihrer Wirkung auf dass Pflanzenleben’ ['Climate and Soil and Their Effect on Plant Life'], (first German edition, 1925, fifth edition, 1957; English edition, 1930 (translated by Eric Ashby); Russian edition, 1940; Japanese edition, 1968). In addition, ‘Der Kreislauf der Kohlensäure in der Natur’ ['The Carbonic Acid Cycle in Nature'] was published in 1924 and ‘Die quantitive Spektralanalyse der Elemente’ ['The Spectral Analysis of Elements'] in 1929.

In 1926 Lundegårdh was appointed Professor and Head of the Botany Division of the Central Institution for Agricultural Research at Experimentalffältet, near Stockholm. There he carried out a comprehensive
program on the absorption of salts by plant roots, specializing particularly in wheat roots. This work was carried on when he moved to the Lantbrukshögskolan, just south of Uppsala, as professor of plant physiology in 1935, where he stayed until he retired in 1955. It was during these two periods that he developed the flame photometer, which is described, inter alia, in his book ‘Die Blattan Analysis’ first published in 1944 (English edition, ‘Leaf Analysis,’ 1951), and forerunners of modern autoanalyzers. From 1933 onwards, he worked with Hans Burström, and others, on the relationship of respiration and salt uptake in roots, work which strongly influenced the fields of membrane transport, respiration and energy metabolism and was cited by Peter Mitchell in the development of the chemiosmotic hypothesis (Mitchell 1978).

In 1947, Lundegårdh built a private laboratory at Penningby, 70 km from Stockholm and Uppsala, on the Baltic Sea, near Norrtäije and in the beautiful Stockholm Skärgård (see Figure 1). There he built a number of spectrophotometers and after his retirement, in 1955, he made many discoveries on the role of cytochromes in plant roots and in photosynthesis.

From a very early stage Lundegårdh had had an interest in cytochromes. During the 1930s he entered into a prolonged correspondence with David Keilin in Cambridge (UK), which centred on the operation of cytochromes, which Keilin had discovered. This correspondence is partially contained in the Keilin papers at the University Library, Cambridge, UK (http://www.bath.ac.uk/ncuacs/cambio.htm). In 1943 Lundegårdh was elected to the Royal Swedish Academy of Science. He subsequently led the proposal to get David Keilin awarded the Nobel Prize in Physiology and Medicine. In 1955 both David Keilin and Axel Hugo Theorell were proposed for the award. Since Theorell was Swedish this led to a difficult decision on the part of the Royal Swedish Academy of Science, which eventually made the award to Theorell alone. Thus ended the hopes of many admirers of David Keilin that he would get the ultimate award which it was felt he justly deserved, as the father of cytochromes; David Keilin died in 1963. It was therefore fitting that Peter Mitchell in his Nobel Award Lecture (1978) should entitle it ‘David Keilin’s Respiratory Chain Concept and its Chemiosmotic Consequences.’ Lundegårdh told me, in Penningby in 1960, that he was so upset with the result in 1955 that he had nothing more to do with the Royal Swedish Academy of Science. This and the somewhat autocratic attitude that Lundegårdh took toward his colleagues may account for the lack of suitable appreciations of his life and work, upon his death in 1969. The other reason of course is that he outlived most of his peers.

**Carbon dioxide exchange and global carbon accounting**

In his quantitative ecological investigations of plants at the research station on Hallands Väderö from 1915 to 1926, Lundegårdh obtained quantitative data on the CO₂ exchange of a wide variety of plants and soils, from marsh to forest associations. F.F. Blackman had incorporated the law of limiting factors into plant growth, in which at any instant a single factor was seen to control the integrated response of a plant (see Rabinowitch 1951). In studying photosynthesis, Lundegårdh found that the rate of photosynthesis might be dependent on several factors at the same time, which he saw as a modification of the law (Lundegårdh 1924;