Chapter 1 Sir Jagadish Chandra Bose (1858–1937): A Pioneer in Photosynthesis Research and Discoverer of Unique Carbon Assimilation in Hydrilla

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Chapter 1

Sir Jagadish Chandra Bose (1858–1937): A Pioneer in Photosynthesis Research and Discoverer of Unique Carbon Assimilation in *Hydrilla*

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Summary

Sir Jagadish Chandra Bose (1858–1937) is acknowledged as the greatest interdisciplinary scientist in India; he was a pioneer of not only Physics, but of Plant Biology. Essentially, he was the father of Biophysics, long before it became a field. He was almost 60 years ahead of his time in his ideas, research and analysis. Bose had several out-of-box concepts and designed his own innovative instruments to facilitate his research. He made several discoveries during his studies on physiology and biophysics of plants, particularly the electrical nature of conduction of various stimuli. His interest shifted during early 1920s from physics towards the physiology of plant movements and then photosynthesis. He fabricated and used a unique photosynthesis recorder to study extensively the carbon assimilation pattern, actually measured through oxygen evolution, in an aquatic plant, *Hydrilla verticillata*. Bose made a phenomenal discovery that a unique type of carbon fixation pathway operated in *Hydrilla*. The plants of *Hydrilla* during summer time were more efficient in utilizing CO_2 and light. The summer-type plants used malate as

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a source of CO_2 and appeared to be different from Crasulacean Acid Metabolism (CAM) plants. These findings of Bose appeared anomalous at his time but are now known to illustrate an instance of non-Kranz single cell type C_4-mechanism. In view of his major research contributions, we consider J.C. Bose as a pioneer of photosynthesis research not only in India but also in the world.

I. Introduction

Two prominent names come up when we consider the scientific research in contemporary India: Sir Jagadish Chandra Bose (also known as Jagdish Chander Basu; November 30, 1858 to November 23, 1937), popularly known as J.C. Bose and Sir Chandrasekhara Venkata Raman (November 7, 1888 to November 21, 1970), who was a 1930 Nobel laureate in Physics, for the discovery of the Raman Effect. In biology, the contributions of Sir J.C. Bose (Fig. 1) are awesome and outstanding. Bose was an outstanding physicist as well as a biologist, a pioneer of Biophysics. With his initial interest in electromagnetism and exploitation of electromagnetic waves, he invented several devices for radio-communication with short waves. Later, his attention turned towards the movements and electrical responses in biological systems, mainly of plants. He was a rare genius who was highly versatile and contributed to diverse fields of not only science (physics/biology/botany/biophysics/ archaeology) but also the Bengali literature; he also wrote science fiction in Bengali. See Geddes (1920), Ray and Bhattacharya (1963) and Salwi (2002) for his biography.

II. Life of Sir J.C. Bose

Sir Jagadish Chandra Bose was born on 30 November 1858, at Mymensingh, now in Bangladesh. He had a graduate degree in science from St. Xaviers College, Calcutta (now Kolkata) and obtained an honors degree, as well as a National Science Tripos in Physics, from Cambridge University, UK, in 1884. Soon after his return from Cambridge in 1885, he was appointed a Professor of Physics in Presidency College, Calcutta. Here, he initiated his experiments in various areas in physics and botany. He received the D.Sc. degree of London University in 1896 for his work on the determination of wavelength of electric radiation by diffraction grating (Ray and Bhattacharya, 1963).

Bose retired from the Presidency College in 1915 and joined in the same year as an Emeritus Professor in the newly founded Department of Physics in the University College of Science, Calcutta. He utilized his scholarly background in

Fig. 1. (**a**) Portrait of J.C. Bose. (**b**) J.C. Bose at the Royal Institution, London, with his radio equipment. The date is 1897, prior to his plant research. (**c**) The Museum located in Bose institute, displaying the work and several innovative instruments developed by J.C. Bose. (**d**) Bust of Sir J.C. Bose, in the Museum; on the right of the bust, a potted plant of *Mimosa pudica* can be seen. (**e**) Plaque of J.C. Bose, in the museum, Bose Institute, Kolkata. (**f**) *Samadhi* (holy grave) of Sir J.C. Bose, in the courtyard of the main campus of the Bose Institute (Courtesy: Bose Institute).

Abbreviations: CAM – Crassulacean acid metabolism; J.C. Bose – Sir Jagadish Chandra Bose

Physics to initiate path-breaking work in Plant Biology, specifically Plant Physiology. He could unequivocally demonstrate scientifically that plants had life, something everyone knew, and responded to stimuli, as in the case of animals (Sen, 1997). Bose was conferred the Knighthood in 1916 and was elected a Fellow of the Royal Society, England, in 1920. He is respected throughout India as 'Acharya', meaning the most revered teacher. He established the Bose Institute (then called Basu Bigyan Mandir) in 1917. The Bose Institute (Fig. 2) was then devoted mainly to the study of plants. The Institute's research interests expanded gradually into several other related subjects. At present, Bose Institute is one of the pioneering research institutions in India (for further details of the Bose Institute, visit their website: http://www.boseinst.ernet.in). J.C. Bose passed away on 23 November 1937 at Giridih in Bihar, India.

The extensive studies of J.C. Bose on the photosynthetic characteristics of *Hydrilla*, and his leading contributions to photosynthesis research in India are highlighted in several articles (see S. Bose, 1982; S. Bose and Rao, 1988; Raghavendra et al., 2003; Mukherjee and Sen, 2007).

His basic approach was to study electromagnetic waves, their properties and their practical applications in both living and nonliving objects. This approach of applying physical principles to biological system developed into the exciting field of biophysics. Despite his inventing the radio, contemporarily with Marconi of Italy, Bose did not get proper recognition, as he did not patent the device. One of the innovative concepts of Bose was that plants and metals have 'life' on the basis of their electrical responses. We, of course, know that life, as we understand it today, is not in 'metals': it was only a way of expressing himself at that time because he was trying to bridge physics and biology! He proved that plants as well as animals use electric signals to carry and convey information.

III. Out of Box Concepts and Innovative Instruments for Biological Experiments

Several of the concepts/explanations proposed by Sir J.C. Bose were all of out-of-box approach at those times. His comprehensive experiments in photosynthesis, physiology, physics, his monumental monographs and his innovative work on plant physiology, made him a pioneer and an icon of biological research in India. His contributions to the communication systems in biology as well as physics are amazing. He devoted strong attention to studies on the biology of movements, feelings and nervous system. The word 'feelings' was used for plants, but clearly this is a matter of semantics; plants react both chemically and physically to touch, but to use the word 'feeling' or 'sensation' as we know it is quite different. The simple experiments

Fig. 2. Bose Institute, Kolkata. On the left (**a**) is the Main Campus, started in 1917 and located on Acharya Prafulla Chandra Road, near Raja Bazaar in Kolkata. On the right (**b**) is New Building, in the "Acharya J.C. Bose Centenary Campus" at Kankurgachi, Kolkata. This campus was built to commemorate the birth centenary of Sir J.C. Bose (Courtesy: Bose Institute, Kolkata, 2008).

of Bose revealed a high degree of similarity in the responses of plant and animal tissues to external stimuli. This principle was amply demonstrated later by biophysicists, using highly sophisticated instruments (Shepherd, 1999, 2005).

The areas of Bose's research included electrophysiology, physiology of ascent of sap, movement in plants, mechanisms of plant response to varieties of stimuli, and physiology of photosynthesis. Three notable features/objectives of his research were: (a) to measure the responses *quantitatively;* (b) to design and to build the physical instruments required for the purpose; and (c) to interpret the results quantitatively in terms of the physicochemical principles known at that time to him. During his research career, Bose designed and utilized several innovative instruments, which looked simple, but were very sensitive and capable of measuring minute changes (Table 1). Only some of these instruments were patented. One of these most fascinating instruments was the Photosynthesis Recorder that can detect the formation of carbohydrate as a millionth of a gram per minute, and record the rate of photosynthetic activity (Fig. 3).

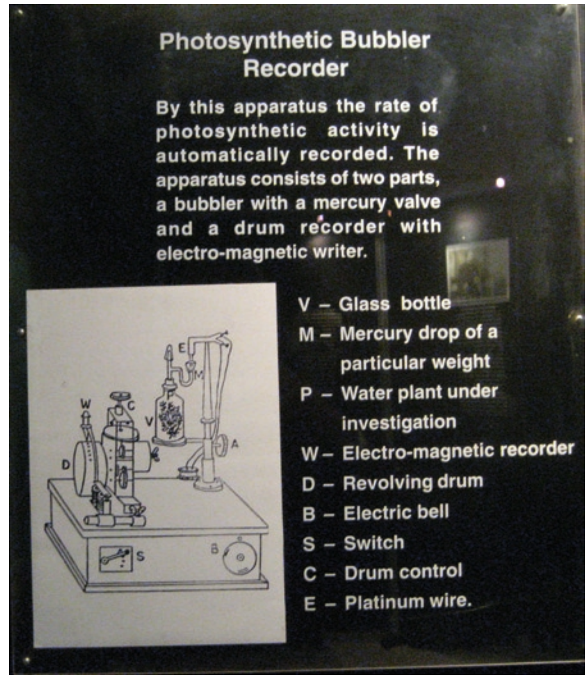

Fig. 3. The *Photosynthesis Recorder* fabricated by J.C .Bose and used extensively for his experiments on photosynthesis in *Hydrilla* (Bose, 1924). This photograph is that of an exhibit in the J.C. Bose Museum in Kolkota, taken by one of us (Govindjee) in January, 2008.

IV. Classic and Comprehensive Monographs on Physiology of Plants

Sir J.C. Bose was never in a hurry to publish small scientific articles. He studied the phenomena in detail and then published his observations comprehensively in the form of books – monographs. This apparently had the disadvantage of his research being not in a format for scrutiny by the peers since often experimental details were not available. One of his books was on "*Responses in the Living and Non-living*", published by Longman in 1902. This monograph made him a celebrity in the world of science. His other important publications again were mostly monographs, including the one on "*Physiology of Photosynthesis*", published in 1924 (Table 2). His observations have been published in several volumes by Longmans, Green and Co. Ltd., England during 1902–1928.

Table 1. A partial list of the novel and innovative instruments fabricated by Sir J.C. Bose.

Instrument	Purpose/parameter of measurement
Oscillating recorder	Ascent of sap
Photosynthetic recorder	Rate of carbon assimilation by plants
Crescograph	Growth of a plant
Magnetic Crescograph	Movements beyond the magnifying capacity of light microscope
Transpirograph	Quantity of water transpired by a single stoma of the leaf
Magnetic radiometer	Measure energy of every ray in the solar spectrum
Resonant recorder	Determination of the latent period of the plant within millisecond
Conductivity balance	Determine the effect of various drugs on electrical impulse

V. Work on Photosynthesis and Focus on *Hydrilla*

During his research life, Bose carried out important and thought-provoking experiments on photosynthesis, particularly on its physiological aspects. In the simplest terms, photosynthesis in plants may be described as the process by which

Table 2. Books written by J.C. Bose on physiology and physics of plant cells, including photosynthesis.

Bose JC (1902) Response in the living and nonliving. Longmans, Green & Co., London
Bose JC (1906) Plant response as a means of physiological investigation. Longmans, Green & Co., London
Bose JC (1907) Comparative electrophysiology. Longmans, Green & Co., London
Bose JC (1913) Researches on the irritability of plants. Longmans, Green & Co. London
Bose JC (1923) The physiology of the ascent of sap. Longmans, Green & Co., London
Bose JC (1924) The physiology of photosynthesis. Longmans, Green & Co., London
Bose JC (1926) The nervous mechanism of plants. Longmans, Green & Co., London
Bose JC (1927) The plant autographs and their revelations. The Macmillan Company, New York
Bose JC (1928a) The motor mechanism of plants. Longmans, Green & Co., London
Bose JC (1928b) Growth and tropic movements of plants. Longmans, Green & Co. London
Bose JC (1985) Life movements in plants. Reprinted and distributed by D.K. Publishers' Distributors, Kolkata

CO_2 and H_2O are taken up, forming carbohydrate and releasing oxygen, using Light. Bose presented the results of his comprehensive studies on photosynthesis, in the form of a book, '*The Physiology of Photosynthesis*' (Bose, 1924). The comparative results and discussion of Bose's investigation with *Hydrilla* in summer and winter seasons are available in the articles of S. Bose (1982) and S. Bose and Rao (1988). During J.C. Bose's time, biochemical interpretations were not available. Subsequent work provided detailed explanations of unique photosynthetic characteristics of *Hydrilla*, which could be ascribed to a variant of carbon assimilation or CO_2 concentrating mechanism called C_4-pathway (Leegood et al., 2000).

J.C. Bose had selected the aquatic plant *Hydrilla* and used it extensively for his studies. He ascribed the following reasons for selecting the plant (Bose, 1924): (a) The plant can be maintained under normal conditions in a vessel of water; (b) The leaves have no stomata and there is no transpiration, making the system very simple; and (c) The oxygen released into intercellular species can easily escape out into the medium. Bose (1924) investigated the relation between CO_2 supply and photosynthesis and defined the coefficient for CO_2 concentration as a measure of the efficiency of CO_2 utilization. The average value of CO_2 coefficient of *Hydrilla* in winter was about 40, which nearly doubled in summer (Table 3). This was a clear demonstration of the marked increase in the photosynthetic efficiency of carbon assimilation in *Hydrilla* during summer time.

VI. Importance of Malate and Operation of C_4-like Pathway

In the early 1920s, Sir J.C. Bose showed that in the aquatic plant, *Hydrilla,* the photosynthetic characteristics in summer were quite different from those in winter. Some of his major observations are summarized in Table 3. Bose (1924) further observed that 'while the juice of the plant was practically neutral in winter and spring, it was very strongly acid in summer'. Furthermore, 'the acidity of the plants was found to be due to the presence of malic and oxalic acids, the latter in small quantities'.

Bose (1924) observed that photosynthesis in *Hydrilla* was unique, because of the following features: (a) Acids, mainly malate, accumulated; (b) Malic acid was a source/substitute for CO_2; and (c) Photosynthesis could occur without external addition of CO_2. *Hydrilla* plants, at high temperatures of summer, became acidic. Photosynthesis, measured by the evolution of oxygen, apparently, occurred also in the complete absence of externally added CO_2. Bose studied the assimilation of organic acids by substituting malic acid for CO_2 and found that the photosynthesis curves of *Hydrilla* under increasing concentration of CO_2 or of malic acid solutions were quite similar (Bose, 1924; see S. Bose and Rao, 1988). Thus, he demonstrated that during photosynthesis, *Hydrilla* assimilated malate instead of CO_2 and that uptake of CO_2 by these plants is less than normal. It is quite astonishing that as early as 1924, Bose had visualized the idea of the operation, in *Hydrilla*, of a quite different photosynthetic pathway, which utilizes malate.

VII. Contemporary View of his Observations on Hydrilla

The primary route of carbon assimilation through Calvin-Benson-Bassham cycle or C_3-pathway was established by the research group of Melvin

Table 3. Photosynthetic characteristics of winter and summer *Hydrilla.*

	Form of hydrilla	
Characteristic	Winter	Summer
Optimum temperature of photosynthesis (°C)	28	33
Light-saturated rate of photosynthesis (arbitrary units, cm m^{-1} h^{-1})[a]	147	362
Light compensation point (in lux)	205	25
Relative quantum yield (initial slope of photosynthesis *versus* light intensity curve)	12	25
Efficiency of CO_2 utilization (initial slope of photosynthesis *versus* CO_2 concentration curve)	40	71
CO_2 compensation point (mg CO_2 water (100 mL)$^{-1}$)	1.2	0

Data adapted from Bose (1924); average values are shown
[a]Displacement of air column by O_2

Calvin and Andy Benson and their coworkers (Bassham and Calvin, 1957; Benson, 2002; Bassham, 2003). The variant of carbon assimilation through C-4 acids was identified and characterized more than a decade later (see e.g., Hatch, 2002). The third type of carbon assimilation is Crassulacean Acid metabolism (CAM) that also uses malate and other acids for concentrating CO_2 inside the cells during darkness (or night); they use these acids up during subsequent day time (Black and Osmond, 2003).

Bose was aware that his observation with summer *Hydrilla* was different from the phenomenon of acid accumulation by many succulent or CAM plants. He said: ‘The organic acids stored during the night (in succulent plants) provide *indirect* material for photosynthesis during the day in the form of CO_2. The *Hydrilla* plant appeared to be most suitable for further investigation on the subject that the organic acid served *directly* for photosynthesis’ (Bose, 1924). Although he proposed that malic acid was used *directly* as a substitute of CO_2 by summer plants, Bose’s observations and the available biochemistry were not detailed enough to suggest any C_4-mechanism in *Hydrilla*. Although the knowledge of biochemistry of photosynthesis was almost nonexistent in the 1920s, his observations and inference, nevertheless, clearly indicated a mechanism different from CAM and which is now known as the C_4-pathway (Bowes et al., 2002).

The physiology, biochemistry and molecular biology of photosynthetic carbon assimilation in aquatic plants, including *Hydrilla verticillata*, were studied in detail after more than 50 years, by the research group of George Bowes. Their results offered a candid explanation of several of the observations made by J.C. Bose (Table 4). The carbon assimilation pathway in *Hydrilla* turned out to be quite unique and is now being termed as an example of non-Kranz single cell C_4-pathway operating in aquatic angiosperms (see Chapter 5, by Bowes, this volume).

VIII. Observations on Inhibitors/Stimulants on Photosynthesis in *Hydrilla*

J.C. Bose examined the effects of several compounds which either stimulated or inhibited the rate of photosynthesis depending on the nature and concentration of the compounds (Bose, 1923). His observations on the stimulatory effects by almost infinitesimal quantities of different chemical agents were triggered by a casual observation that the rate of photosynthesis of certain water plants increased sharply during a thunderstorm. Bose attributed this phenomenon to the oxides of nitrogen produced by electric discharges in the atmosphere; this conclusion induced him to investigate the effects on photosynthesis of various stimulants. He found that the photosynthesis of *Hydrilla verticillata* was tripled by *nitric acid* and doubled by *thyroid gland extract. Iodine* and *formaldehyde* increased the photosynthetic rate 60% and 80%, respectively.

Table 4. The simple observations by J.C. Bose and the independent biochemical characterization of photosynthesis in *Hydrilla*, made by the group of George Bowes.

Observation by J.C. Bose[a]	Biochemical basis	Reference[b]
Low light compensation in summer	Low light compensation point compared to other hydrophytes, such as *Myriophyllum* or *Ceratophyllum*	Van et al., 1976
Summer/winter type	Result of daylength and the temperature. Summer type at 27°C/14-h photoperiod and winter type at 11°C/9-h photoperiod	Holaday and Bowes, 1980
Malate is a major product of photosynthesis	Over 50% of carbon assimilated into malate, as shown by the incorporation of $^{14}CO_2$	Salvucci and Bowes, 1983
CO_2 compensation point	Measured precisely; CO_2 compensation points of >50 mL L^{-1} in summer type and 1–25 mL L^{-1} in winter type	Magnin et al., 1997
Photosynthetic rate in summer type plants is 2.5 times greater than that of winter type	Activity of PEP (phospho-enol pyruvate)carboxylase, the key enzyme for carbon fixation, is enhanced nearly 10 times in summer forms (C_4-type), compared to winter form (C_3-type)	Rao et al., 2006
Malate is a source of CO_2 for photosynthesis	Efficient utilization of malate leading to a reduction in photorespiration; Malate decarboxylated by NADP malic enzyme	Estavillo et al., 2007

[a]From Bose (1924)
[b]Arranged in chronological order

IX. Concluding Remarks: Inspiration for Biology Research in India and a Pioneer of Photosynthesis Research on *Hydrilla*

The observations of Sir Jagadish Chandra Bose on "feelings" and movements in plants can be treated as the earliest studies on the "intelligence" of plants, which is being termed by some as 'plant neurobiology' (Brenner et al., 2006). As mentioned earlier, the use of the words "feelings" and "intelligence" for plants is a matter of semantics, and we need to caution the readers against their misinterpretation. However, the experiments of J.C. Bose to measure minute electrical signals in plants have been recognized and have paved the way for the biophysics of plant cells (Shepherd, 1999, 2005). The anomalies recorded by Bose in the patterns of plant growth are now confirmed to be due to their oscillatory behavior, found by much sophisticated computer based image analysis system (Jaffe et al., 1985). The biological significance of seasonal and diurnal adaptation became the subject matter of modern research in chronobiology (Chandrasekharan, 1998). Bose's, 1924 work on photosynthesis with *Hydrilla* is a landmark in photosynthetic research. Sir J.C. Bose is therefore rightly considered as an early pioneer in research in the field of photosynthesis, particularly carbon assimilation. It seems that Eugene Rabinowitch did not discuss Bose's work, perhaps because it was not published in regular journals, yet Rabinowitch (1951, p. 1079) did mention his 1924 book.

Bose's thoughts and vision have illuminated the path of research since 1920s and they became a source of inspiration to several of his students, who all became great scientists in either physics or biology. Among these stalwarts are: Meghnad Saha, J.C. Ghosh, S. Dutta, Satyendra Nath Bose, D.M. Bose, N.R. Sen, J.N. Mukherjee and N.C. Nag, to name a few. Among his students, Satyendra Nath Bose (January 1, 1891 to February 4, 1974) was the most famous as he is known the world-over for the Bose-Einstein's statistics, and for the particle 'Boson' named after him. The (J.C.) Bose Institute in Kolkata is keeping up his motto and is training several young Indian scientists and offering state-of-the-art facilities in physics and biology. The Bose Institute organized an year-long celebrations of the 150th birth anniversary of its founder during 2008 (Fig. 4). It is no wonder that Sir J.C. Bose is treated as the first Modern Scientist and a pioneer in India (Salwi, 2002; Yadugiri, 2010).

Fig. 4. One of us (Govindjee) honoring Sir J.C. Bose by lighting a lamp on November 24, 2008, in front of his statue, located at the entrance of Acharya Jagadish Chandra Bose's Museum, on the Main campus of Bose Institute, Kolkata. This photograph was taken on the occasion of the Inaugural function of an International Symposium, commemorating the 150th birth year of Sir J.C. Bose. Prof. Arun Lahiri Majumder and three Ph. D. students, of the Bose Institute, are also in the picture (Courtesy: Arun Lahiri Majumder and Sampa Das, 2008).

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