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Minireview

Photosynthesis research in India: transition from yield physiology into molecular biology*

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Abstract

Photosynthesis research in India can be traced back several thousand years, with the mention of the Sun energizing the plants, which form food for all living creatures on the earth (from the Mahabharata, the great epic, ca. 2600 B.C.) and the report of Sage Parasara (ca. 100 B.C.) on the ability of plants to make their own food, due to their pigments. With the pioneering studies by Sir Jagdish Chandra Bose, work on photosynthesis proceeded steadily during the first half of the 20th century. Some of the classic reports during this period are: malate metabolism in *Hydrilla*, spectrophotometric estimation of chlorophylls, importance of spectral quality for photosynthesis – an indication of two photosystems, photoinactivation of photosynthesis, and importance of flag leaf photosynthesis to grain yield. After the 1960s, there was a burst of research in the areas of physiology and biochemistry of carbon assimilation and photochemistry. A significant transition occurred, before the beginning of new millennium, into the area of molecular biology of chloroplasts, regulation of photosynthesis and stress tolerance. Future research work in India is geared to focus on the following aspects of photosynthesis: elucidation/analysis of genes, molecular biology/evolution of enzymes, development/use of transgenics and modeling.

Abbreviations: CAM – crassulacean acid metabolism; Chl – chlorophyll; LHC – light harvesting complex; ME – malic enzyme; OEC – oxygen-evolving complex; PEPC – phosphoenolpyruvate carboxylase; PS – photosystem; Rubisco – ribulose-1,5-bisphosphate carboxylase oxygenase; TL – thermoluminescence

> 'If the photosynthetic process takes place in more than one photochemical stage it is probable that for one stage a particular wave-length of light is more efficient than for the other.'
> – R.H. Dastur and R.J. Mehta (Annals of Botany, Vol. XLIX, No. CXCVI. October, 1935)

Introduction

References to plants are abundant in ancient Indian Sanskrit scriptures: Vedas, Epics, Charaka Samhita and Susruta Samhita (D.M. Bose et al. 1971). A reference to the photosynthetic process is found in 'The Mahabharata', an epic more than 4600 years old (Figure 1). The report by Sage Parasara (ca. 100 BC), on plant pigments and their ability to make food, is noteworthy (Majumdar and Banerji 1960). Sage Parasara

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* Dedicated to the memory of Professor Suresh Kumar Sinha (1934–2002).

Shloka From:
The Mahabharata
Vana Parva, Section 3

In Devanagari Script

निषिक्तश्चन्द्रतेजोभिः सूयते जगतो रविः।
ओषध्यः षड्रसा मेध्यास्तदन्नं प्राणिनां भुवि।।
एवं भानुमयं ह्यन्नं भूतानां प्राणधारणम्।
नाथोय्यं सर्वभूतानां तस्मात्तं शरणं व्रज।।

In Roman Script

Niṣiktaścandratējōbhiḥ Sūyatē Jagatō Raviḥ.
Ōṣadhyaḥ Ṣaḍrasā Mēdhyāstadannaṃ Prāṇināṃ Bhuvi.
Ēvaṃ Bhānumayaṃ Hyannaṃ Bhūtānāṃ Prāṇadhāraṇam.
Nāthōyyaṃ Sarvabhūtānāṃ Tasmāttaṃ Śaraṇaṃ Vraja.

Transliteration

Niṣiktaścandratējōbhiḥ = Infused with/by light of the Moon; Sūyatē = Produced;
Jagatō = the World; Raviḥ = the Sun; Ōṣadhyaḥ = The herbs (Plants);
Ṣaḍrasā = Six tastes; Mēdhyāstadannaṃ = Vigorous food;
Prāṇināṃ = Living beings; Bhuvi = the Earth.
Ēvaṃ = Thus; Bhānumayaṃ = Filled with the Sun; Hyannaṃ = The food;
Bhūtānāṃ = Creatures; Prāṇadhāraṇam = Support for life;
Nathōyyaṃ = This Lord (the Sun); Sarvabhūtānāṃ = All Living things;
Tasmāttaṃ = Therefore the Sun; Śaraṇaṃ = Protection; Vraja = Seek.

Translation

With the Moon, infused by its light, the Sun energizes the plants with six tastes, which constitute the food for all living beings on the earth.
Thus, the food that supports the lives of creatures is filled with solar energy and the Sun is the father of all living things. Therefore, seek protection from the Sun God.

Figure 1. A *shloka* (poem) in Sanskrit from 'The Mahabharata,' one of the ancient Indian epics (dating back to ca. 2600 BC), describing the role of plants in harnessing the solar energy into food, and being the source of energy for other living beings on the earth. The physiology of plants ('Vriksh-Ayurveda') is discussed in Rig-Veda, one of the four Indian Vedas, more than 5000 years back.

is called 'the father of Botany,' because he classified flowering plants into various families, nearly 2000 years before Linnaeus. Parasara also described plant cells (the outer/inner walls and sap coloring matter), which were rediscovered by Robert Hooke, with the help of microscope. Photosynthesis research in India has been reviewed by S. Bose and Rao (1988), Bhagwat (1990) and R. Singh (1990).

The earliest studies during the modern period were by Sir J.C. Bose and others, at Calcutta (now called Kolkata), Banaras (Varanasi) in Uttar Pradesh, and New Delhi. These are described below. Studies on photosynthesis intensified with the return of young Indian scientists trained abroad (see the section on 'Photochemical reactions'). Soon, international level research progressed at Bhabha Atomic Research Center in Bombay (now called Mumbai) in Maharashtra, Jawaharlal Nehru University (JNU) and Indian Agricultural Research Institute (IARI) (both at New Delhi), Madurai Kamaraj University (Madurai, Tamilnadu), Sri Venkateswara University (Tirupati, Andhra Pradesh) and Haryana Agricultural University (Hisar, Haryana). Their success led to additional centers at National Botanical Research Institute (Lucknow, Uttar Pradesh), University of Delhi (Delhi), Sambalpur University (Sambalpur, Orissa), University of Hyderabad (Hyderabad, Andhra Pradesh), and a few other places. The locations of the current centers are indicated in Figure 2, where research on a variety of aspects of photosynthesis (from primary photochemistry to ecology and global environment), is being carried out.

Although several Indians have contributed significantly to photosynthesis research while working abroad, this article describes only their work done in

Figure 2. Some of the active centers of photosynthesis research in India (in alphabetical order): Bangalore (University of Agricultural Sciences), Bhubaneshwar (Regional Plant Resource Centre, Utkal University, Institute of Life Sciences), Delhi (Indian Agricultural Research Institute, Jawaharlal Nehru University, University of Delhi, International Centre for Genetic Engineering and Biotechnology), Goa (University of Goa), Hisar (Haryana Agricultural University), Hyderabad (University of Hyderabad), Indore (University of Indore), Jodhpur (Jodhpur University) , Kolkata/Calcutta/Kalyani (Bose Institute, University of Kalyani), Lucknow (National Botanical Research Institute), Madurai (Madurai Kamaraj University), Mumbai/Bombay (Bhabha Atomic Research Centre), Pondicherry (Pondicherry University), Pune (University of Pune), Sambalpur (Sambalpur University), Tirupati (Sri Venkateswara University) and Varanasi (Banaras Hindu University).

Figure 3. Some of the pioneers of photosynthesis research in India during the pre-1960 period. A. Sir J.C. Bose (1858–1937); B. Bhola Nath Singh (1898–1984); C. R.H. Dastur (1896–1961); D. R.D. Asana (1908–1999).

India. Among those of Indian origin, and who work abroad, we list P.N. (Dan) Avadhani, Parag Chitnis, Henry Daniell, Govindjee, Arun Goyal, Autar Mattoo, Himadri Pakrasi, Krishna Rao, Sabeeha Merchant, Krishna Niyogi, Bijay K. Singh, A.R. Subramanian, Krishna K. Tiwari and Vittal Yachandra.

In view of the overwhelming literature, references are made to selected publications that originated in work done in India. However, we mention some collaborative research wherever pertinent.

Classic work during the pre-1960 era

Sir Jagdish Chandra[1] Bose, a pioneer in photosynthesis (as well as plant physiology) research in India (Figure 3A) demonstrated, early in 1924,[2] that the rate of photosynthesis versus light intensity followed a curvilinear pattern. He recorded action spectra, as well as quantum yields (using an ingenious CS_2 prism), and malate metabolism in summer grown *Hydrilla* (J.C. Bose 1923, 1924). These findings are amazing, as simple instruments were fabricated and used to record novel responses.

Ghosh and Sen-Gupta (1931) analyzed the absorbance of chlorophyll (Chl) in acetone and developed formulae to determine the content of Chl *a* as well as Chl *b*, based on their absorption at 650 and 460 nm. It was not until 1941 and 1949 that G. Mackinney and Daniel Arnon developed the formulae for Chl determination (for a minireview, see Porra 2002). Rustom Hormusji Dastur and co-workers (K.M. Samant, R.Y. Mehta, and S. Solomon), of the Botany Department of the Royal Institute of Science, Bombay, studied the effect of monochromatic red and blue-violet, obtained by filtering lights with carmine and copper sulphate solutions; they concluded that photosynthesis was dependent not only on the intensity, but also had cooperative and specific effects of different colors on photosynthesis (see Dastur and Mehta 1935; Figure

3C). This seems to be one of the earliest indications of the two light effect in photosynthesis (see quotation at the beginning of this paper). Although Eugene Rabinowitch (1951, p. 1167) had raised concerns based on the use of optically dense tissues, and it is not clear if the light intensities were in the linear range of the 'light curves', the observations were clear, and, perhaps, much ahead of the time. B.N. Singh and Kumar (1935) observed inactivation of carbon assimilation in leaves at high light, obviously an indication of the phenomenon of photoinhibition (see Adir et al., this issue). (See Figure 3B for a photograph of B.N. Singh.)

Other classic contributions during the pre-1960 period are: a sigmoidal type curve of photosynthetic response to light, suggesting a saturation kinetic rather than the Blackman's break (B.N. Singh and Lal 1935), and the importance of flag leaf photosynthesis to grain yield (Rustom Darasha Asana and Mani 1949, see Figure 3D).

The studies of Shri Ranjan (University of Allahabad), on the importance of mineral nutrition to photosynthesis and modulation of respiration in light, were of great vision (Ranjan 1940; Ranjan et al. 1962). In 1940, he also worked on the temperature coefficient of photosynthesis in *Eugenia jambolana* (cited by Rabinowitch 1956). He was instrumental in encouraging and molding the career of the editor of this special issue, Govindjee (University of Illinois, Urbana, USA), a pioneer of photosynthesis research.

Research during the post-1960 period

Most of the work in early 1960s was related to the physiology of photosynthesis, mineral nutrition and crop yields (Asana et al. 1969) and later diversified into biochemistry, photochemistry and molecular biology. The consolidation of photosynthesis research was facilitated by the interaction of Indian Scientists with others in India as well as from abroad (Figures 4A–G).

Carbon metabolism: physiology and biochemistry

The physiology and biochemistry of carbon fixation have been studied by several groups led by (in alphabetical order): Yash P. Abrol (Indian Agricultural Research Institute, New Delhi), Anil S. Bhagwat (Bhabha Atomic Research Centre, Mumbai), V.S. Rama Das (Sri Venkateswara University, Tirupati and later University of Hyderabad, Hyderabad; both in Andhra Pradesh), Arumugham Gnanam (Madurai Kamaraj University, Madurai, Tamilnadu), late G.V. Joshi (Shivaji University, Kolhapur, Maharashtra), Renu Khanna-Chopra (Indian Agricultural Research Institute, New Delhi), Aditya N. Purohit (Garhwal University, Garhwal, Uttar Pradesh), Agepati S. Raghavendra (Ragha to his friends; see Figures 4E and 4F) (University of Hyderabad, Hyderabad), Prafullachandra Vishnu Sane (Raj to his friends; see Figures 4B and 4C) (Bhabha Atomic Research Centre, Mumbai, Maharashtra), Randhir Singh (Haryana Agricultural University, Hisar, Haryana), late Suresh K. Sinha (Indian Agricultural Research Institute, New Delhi) and M. Udaya Kumar (University of Agricultural Sciences, Bangalore, Karnataka) These studies focused on C_3-, C_4-, and Crassulacean Acid Metabolism (CAM) photosyntheses as well as C_3–C_4 intermediates (see C.C. Black and B. Osmond, this issue, for a history of CAM).

C_3-, C_4- and CAM plants

Despite being a C_3 plant, the leaves of rice incorporate CO_2 into C_4 acids under blue light (V.S.R. Das and Raju 1965) or during leaf development. Photosynthetically active mesophyll cells were isolated from leaves of several C_3 plants (Gnanam and Kulandaivelu 1969; Kulandaivelu and Gnanam 1974). Carbon fixation in autotrophic cultures of C_3 (*Arachis hypogaea*), C_4 (*Gisekia pharnacoides*) and CAM (*Chamaecereus sylvestrii*) species was studied by Seeni and Gnanam (1980, 1982).

Several C_4 plants were discovered among the Indian flora (V.S.R. Das and Raghavendra 1973; Sankhla et al. 1975; Raghavendra and Das 1976). A check-list of C_4 plants, based on these reports (Raghavendra and Das 1978a) is highly cited. The PhD thesis of Agepati Raghavendra (advisor: V.S. Rama Das) presented a comprehensive study of carbon assimilation in a selected range of C_3 and C_4 plants, chosen from Indian flora.

The carbon assimilation during C_4 pathway was elucidated in detail in millet crops, such as *Eleusine coracana*, *Pennisetum typhoides* and *Setaria italica* (Rathnam and Das 1975; Raghavendra and Das 1978b). A shift from C_4 to C_3 type photosynthesis after anthesis was discovered in leaves of sorghum (Khanna and Sinha 1973). The activities of photosynthetic enzymes in both C_3 and C_4 plants were shown

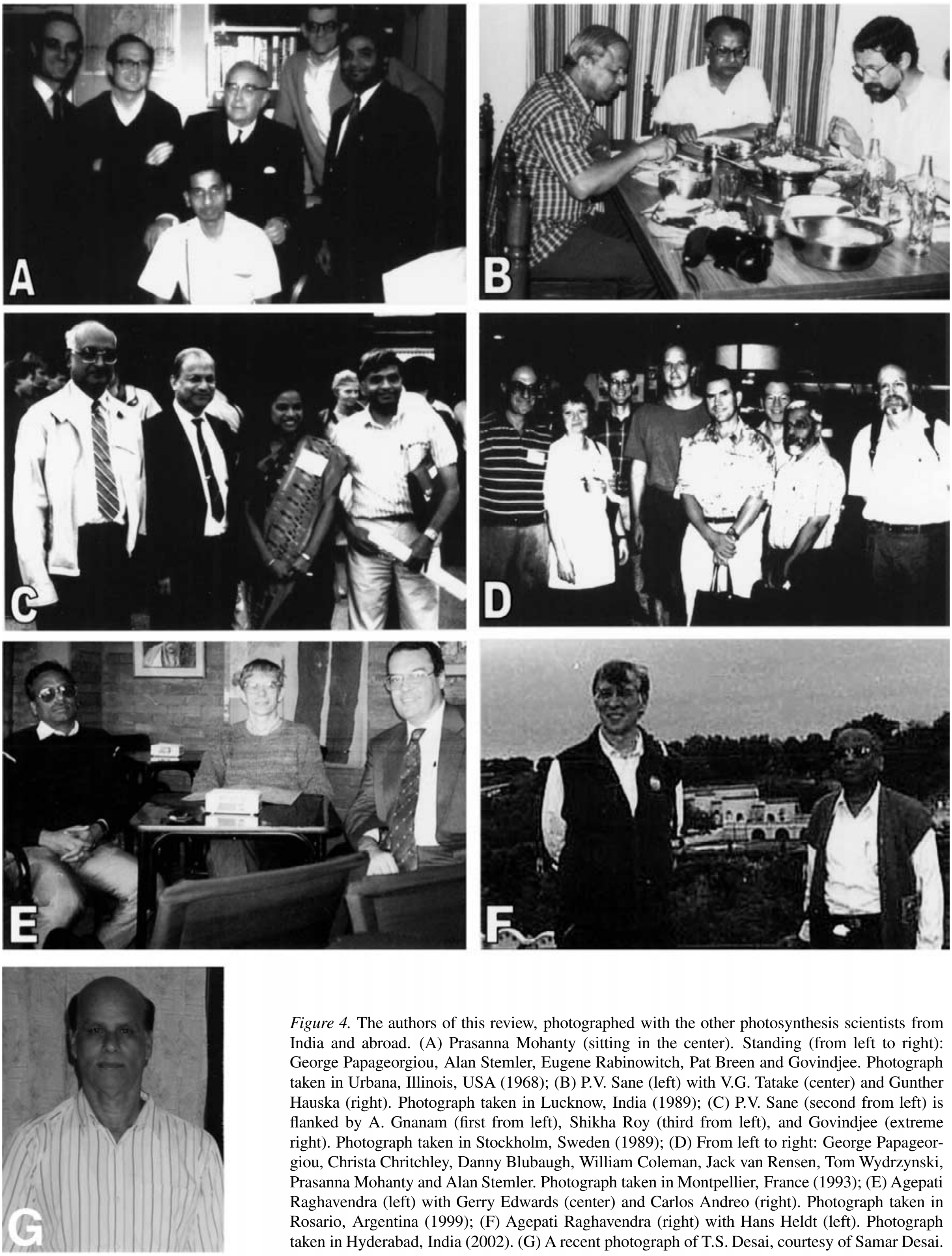

Figure 4. The authors of this review, photographed with the other photosynthesis scientists from India and abroad. (A) Prasanna Mohanty (sitting in the center). Standing (from left to right): George Papageorgiou, Alan Stemler, Eugene Rabinowitch, Pat Breen and Govindjee. Photograph taken in Urbana, Illinois, USA (1968); (B) P.V. Sane (left) with V.G. Tatake (center) and Gunther Hauska (right). Photograph taken in Lucknow, India (1989); (C) P.V. Sane (second from left) is flanked by A. Gnanam (first from left), Shikha Roy (third from left), and Govindjee (extreme right). Photograph taken in Stockholm, Sweden (1989); (D) From left to right: George Papageorgiou, Christa Chritchley, Danny Blubaugh, William Coleman, Jack van Rensen, Tom Wydrzynski, Prasanna Mohanty and Alan Stemler. Photograph taken in Montpellier, France (1993); (E) Agepati Raghavendra (left) with Gerry Edwards (center) and Carlos Andreo (right). Photograph taken in Rosario, Argentina (1999); (F) Agepati Raghavendra (right) with Hans Heldt (left). Photograph taken in Hyderabad, India (2002). (G) A recent photograph of T.S. Desai, courtesy of Samar Desai.

to be influenced by altitude and growth temperatures (Pandey et al. 1980).

C_3–C_4 intermediates, discovered in the genera of *Mollugo* and *Alternanthera* (Raghavendra et al. 1978; Rajendrudu et al. 1986), provided a model system to study the mechanism of reduced photorespiration (Raghavendra 1980). The C_3–C_4 intermediates have imperfect Kranz anatomy, low activities of photorespiratory enzymes and predominant localization of enzymes such as glycine decarboxylase in bundle sheath cells (Devi et al. 1995). Further studies on these C_3–C_4 intermediates are crucial and are promising for the understanding of the mechanism and evolution of not only C_3–C_4 intermediacy but also C_4 photosynthesis.

Studies on CAM date back to 1924, with the reports of acidification and malate accumulation in leaves of *Hydrilla,* particularly at warm temperatures (J.C. Bose 1924). The phenomenon of CAM was detected in several plants, including some nonsucculents (Rao et al. 1979).

The properties of selected C_3- or C_4-enzymes, e.g., ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco), phosphoenolpyruvate carboxylase (PEPC) and NADP malic enzyme (ME), were studied and the enzymes purified (Bhagwat and Sane 1975; Bhagwat 1981; Jawali and Bhagwat 1987; Rajagopalan et al. 1994). Fluorescence probes indicated the importance of tryptophan and histidine residues in the active site of spinach Rubisco (N.C. Verma and Bhagwat 1985). Protein phosphorylation mediates the light activation of C_4-PEPC (Rajagopalan et al. 1994; Parvathi et al. 2000) and regulates small subunit of Rubisco (Kaul et al. 1986). Some of the Calvin–Benson cycle enzymes can exist as multienzyme complexes (Sainis et al. 2003), a phenomenon which warrants further attention. During ageing, marked changes occur in the activities of rubisco and PEPC in even the submerged aquatic angiosperms (Jana and Chaudhuri 1982).

Carbon metabolism in tissues other than leaves

It may be surprising, but the fruiting structures contribute significantly to the crop yield, as they are capable of photosynthetic CO_2 fixation (Sinha and Sane 1976) and can also reassimilate respiratory CO_2. The reproductive parts of wheat, chickpea (*Cicer arientinum*) and rapeseed (*Brassica campestris*) contain high activities of C_4-enzymes, but exhibit intermediate status between C_3-, and C_4/CAM photosynthesis (Singal et al. 1987; R. Singh 1993). Key enzymes of carbon metabolism in these pods, such as PEPC and NADP-ME were purified and characterized by S. Das et al. (1986) and Singal and Singh (1986).

Alternative pathways of CO_2 fixation were reported. The chloroplasts of greening potatoes fixed carbon into formate (through CO_2 reductase) and channeled it into mevalonate (Ramaswamy et al. 1976; Arora et al. 1985). This phenomenon is highly interesting and needs to be studied further.

Interaction of carbon assimilation with other metabolic processes

Mesophyll protoplasts from pea leaves provided a model system to demonstrate the dependence of photosynthetic carbon assimilation on mitochondrial metabolism. Mitochondrial oxidative electron transport helps to dissipate excess reductants from chloroplasts (Raghavendra et al. 1994), optimizes photosynthesis (Padmasree et al. 2002) and protects chloroplasts against photoinhibition (Saradadevi and Raghavendra 1992). This work attracted considerable attention and the phenomenon of mitochondrial influence on photosynthesis is now widely accepted (Gardeström et al. 2002).

Carbon metabolism is essential for fatty acid biosynthesis, particularly in plastids of oilseeds (Gupta and Singh 1996). Glycolate also supports secondary metabolism, by enhanced rubber (polyisoprene) formation in guayule *(Parthenium argentatum)* (A.R. Reddy et al. 1987).

The availability and mode of nitrogen has a profound influence on photosynthesis and photorespiration (Kumar et al. 1993). Besides nitrogen, sulphur also modulates photosynthesis, as in *Brassica* (Ahmad and Abdin 2000). There has been renewed interest in the interaction between photosynthesis and nitrogen metabolism and the relevant literature has been reviewed recently (Kumar et al. 2002).

Crop productivity and stress responses

Photosynthesis by flag leaf is crucial for grain yield (Asana and Mani 1949). The photosynthetic efficiency varies among cultivars. However, high rates of photosynthesis alone would not increase crop yields. Heterotic hybrids of sorghum or wheat produce high biomass, despite their low photosynthesis (Khanna-Chopra 2000). Conventional breeding for water use efficiency could not improve crop performance, because stomatal closure limits photosynthetic carbon assimilation too (Udayakumar et al. 1998).

Accumulation of proline, induced by heat or salt stress, protects thylakoids against membrane peroxidation by scavenging singlet oxygen species (Alia et al. 1997). Proline also seems to promote the dissociation of the small subunits of rubisco and suppress its activity (Sivakumar et al. 2001) suggesting that proline accumulation during stress may have multiple functions.

The effects of water stress, heavy metals and elevated CO_2 on carbon fixation and related enzymes were studied by several groups. These stress factors (e.g., water, heat and light) interact while modulating photosynthesis (Jagtap et al. 1998). Differential degradation of rubisco has been observed, in heat-sensitive and heat-tolerant rice varieties, on exposure to thermal stress (A. Bose et al. 1999). Heavy metals, such as Cd^{2+} and Ni^{2+}, affect the enzymes of Calvin–Benson cycle in chickpea leaves (Sheoran et al. 1990). Exposure to elevated CO_2 reduces photorespiration and increases photosynthesis in *Brassica* (Uprety and Mahalakshmi 2000). Further research on these aspects is essential to understand the adaptive mechanisms and to evolve a strategy of exploiting plants for alleviating the effects of heavy metals and elevated CO_2.

Photochemical reactions

As in the case of carbon assimilation, several research groups in India studied the photochemical reactions of photosynthesis, that involved light emission, excitation energy distribution, state changes, electron transport, photoinhibition and stress responses of photosystems. Sane (1977) suggested the most likely locations of electron transport components along and across the thylakoid membranes resulting in vectorial electron transport, based on his earlier studies and from several other research groups.

One of the strengths of several Indian scientists has been the training received in laboratories abroad. The excellent training received from abroad was then complemented with ingenious adaptation to local environment. Prasanna Mohanty, one of the authors of this review, received his PhD degree from the University of Illinois at Urbana, USA (advisor: Govindjee). His PhD thesis was one of the first studies on the regulation of excitation energy distribution and redistribution in intact algal cells through the use of Chl fluorescence. A major contribution of Mohanty was the first observation of the 'O-I-D-P' Chl fluorescence (Kautsky) curve in cyanobacteria, and the analysis of the non-Q_A-related chlorophyll fluorescence changes through the use of various uncouplers, electron carriers, and inhibitors of electron transfer, also in cyanobacteria (P. Mohanty and Govindjee 1973a, b; see P. Mohanty et al., 1971, for the site of hydroxylamine action in red algae).

P.V. Sane obtained his PhD from the University of Alberta, Edmonton, Canada (advisor: Saul Zalik). Sane's work for PhD was a detailed biochemical analysis of carbon assimilation and reactions of Chl biosynthesis in a mutant of Gateway barley, in comparison with those of wild type (Sane and Zalik 1970). Later, working with Roderick Park, Sane analyzed the ultrastructure and biochemistry of the chloroplast membranes, employing a novel method of isolating PS I and PS II without detergents (Sane et al. 1970). On the basis of these studies, they proposed a model for the distribution of two photosystems in the chloroplast lamellar structure, in an article of *Annual Reviews of Plant Physiology* (Park and Sane 1971), which has become a citation classic.

Thermoluminescence (TL)

Using a novel homemade setup, P.V. Sane, V.G. Tatake and their co-workers, particularly T.S. Desai (Figure 4G), at Bhabha Atomic Research Centre (Mumbai), discovered 7 distinct TL-glow peaks from oxygenic photosynthetic membranes, originating from PS II (Desai et al 1975, 1983; Sane et al. 1977; Tatake et al. 1980). Thermoluminescence was discovered by the late William Arnold, and some fundamental work was already known (for a historical minireview on TL, see Imre Vass, this issue). Using inhibitors, artificial electron donors/acceptors and excitation of PS II/PS I, the origin of TL-peaks in the back reactions of electron transport was identified: the one at −20 °C (due to $Z^+Q_A^-$), 0 °C ($S_2/S_3Q_A^-$), 10 °C ($S_3Q_B^-$), 25 °C ($S_2Q_B^-$) and 50 °C (PS I). The report of light emission from PS I at high temperature (Sane et al. 1980) was interesting and stimulated further work in other laboratories around the world. A major spin off of the activation energy calculations of the TL peaks by Tatake et al. (1980), that led to unusual numbers, was the theory for TL proposed by Don DeVault et al. (1983). Anoxygenic bacterium *Rhodopseudomonas* also exhibits interesting TL peaks (Govindjee et al. 1977). The research on TL was reviewed by Sane and Rutherford (1986). Sane's interest in TL work continues (see, e.g., Sane et al. 2002).

The thermoluminescence technique has provided a very useful tool in understanding the mechanism of delayed light emission. Further work on thermoluminescence was initiated in India by Pandit Vidyasagar and his colleagues at the University of Pune, Pune (Maharashtra), using a setup similar to that developed by Tatake et al. (1971). Vidyasagar et al. (1993) developed mathematical models, based on the general order kinetics of thermoluminescence peaks, to provide acceptable values of activation energy and frequency factor. They suggested that the events of retrapping of electrons during TL peak formation are important while considering the acceptor side but not so dominant on the donor side (Thomas et al. 1996).

Photosystems: structure, function and responses to stress

Several research groups in India are interested in the function and regulation of photosystems, electron transport, and their responses to abiotic or biotic stresses. The group of P.V. Sane discovered heat-induced state changes (Sane et al. 1984). The development of state I was dependent on phosphorylation, whereas the state II development was associated with the redox levels of electron transport components located between the two pigment systems of photosynthesis (Sane et al. 1982). In a recent report, P. Mohanty et al. (2002) provided the final evidence demonstrating that elevated temperature treatment enhances the phosphorylation of light-harvesting complex IIb (LHC IIb) and physically increases the transfer of LHC IIb from PS II region to PS I region. (For a historical account of the discovery of such changes, see Allen 2002.)

The research groups of Prasanna Mohanty and Gauri Singhal at Jawaharlal Nehru University (JNU, New Delhi) studied several aspects of electron transport, energy transfer and transduction processes of PS II/PS I under a variety of stresses. Among the findings of Mohanty's group are: non-circadian out-of-phase oscillations in electron transport activities of PS II and PS I and the association of these oscillations with phosphorylation (Sayeed and Mohanty 1987), *in vivo* multiphasic dark relaxation kinetics of Chl a fluorescence, related to Q^{-}oxidation (Bukhov et al. 1992), elevated temperature induced alterations in PS II acceptor side (Bukhov et al. 1990), subsequent recovery of this phenomenon (N. Mohanty et al. 1987), and use of crown ethers as PS II inhibitors and the site of their action (Sabat et al. 1991).

The group of Gauri S. Singhal studied extensively the synergistic responses of photosynthesis in wheat leaves to stresses, such as high light and low temperature. On exposure to high light, there was not only an increase in lipid peroxidation but also *de novo* synthesis of protective antioxidant enzymes (R.K. Mishra and Singhal 1992; N.P. Mishra et al. 1993; Sharma and Singhal 1992). They observed also that high temperature or water stress alters the membrane organization and the absorbance/fluorescence properties of chloroplasts (Bharadwaj and Singhal 1981; B.R. Singh and Singhal 1984).

Udaya Biswal (Sambalpur University) studied the oxygen evolving complex (OEC) of PS II and proposed one of the earliest models for the Mn-cluster (Raval and Biswal 1985). Salil Bose (Madurai Kamaraj University, MKU) studied changes in photochemical reactions due to cation induced stacking and energy distribution between PS II and PS I (Ramanujam and Bose 1983). Like inorganic cations, anions were shown, at the University of Indore, India, to induce state changes in spinach thylakoids (Jajoo et al. 1998). Lack of usual cation effects on the electron transport activity in thylakoids of *Hydrilla verticillata* has been reported (S.R. Mishra and Sabat 1998). This could be due to altered stacking characteristics of chloroplasts in *Hydrilla.*

Because of the threats of heavy metal pollution to agriculture, several workers in India studied the mode of action and sensitivity to heavy metals of photosynthesis *in vivo* as well as *in vitro*. In higher plant chloroplasts, Zn^{2+}affected reversibly the donor side (OEC) of PS II, while Ni^{2+} affected light-harvesting antennae irreversibly (Tripathy and Mohanty 1980; Tripathy et al. 1981). These authors elucidated three types of heavy metal ion specific changes in chloroplast structure and function. Subsequent work elucidated the effects of Hg^{2+}, Al^{3+} and Na^{+} on the electron transport (Tripathy et al. 1983; Waware and Mohanty 1985; Murthy et al. 1989). Similar inhibition of photosynthetic reactions by heavy metals has been observed in algae and cyanobacteria (D.P. Singh and Singh 1987).

G. Kulandaivelu (MKU) observed that UV-B radiation affected the PS II reaction center of *Phaseolus* leaves (Noorudeeen and Kulandaivelu 1982) and changed the pattern of PS II polypeptides (Nedunchezian and Kulaindaivelu 1991). UV-B changed levels of D1 protein and *psbA* transcripts in wheat leaves (Chaturvedi et al. 1998).

Changes during leaf senescence

Another area of studies initiated by Mohanty's lab in JNU is photosynthesis during senescence, using chloroplasts as well as leaves of barley, wheat and *Cucumis*. The OEC was damaged and the activities of key enzymes, such as rubisco were affected during senescence (U.C. Biswal and Mohanty 1976, 1978). Further, senescence induces not only loss of Chl-protein complexes, with differential sensitivity of various forms of Chl a (A. Grover et al. 1986), but also causes the migration (due to phosphorylation) of LHC II to PS I in stromal region (Prakash et al. 2001). The group of Udaya Biswal continued to study leaf senescence and the chloroplast stability *in vitro* (Panigrahi and Biswal 1979; U.C. Biswal and Biswal 1988; B. Biswal 1997a).

Several groups in India have contributed towards our understanding of changes in chloroplast structure function relationships by a variety of stresses, such as light, UV-B, temperature and drought (e.g., B. Biswal 1997b). These studies have now been extended to several crop species.

Protein synthesis and chlorophyll development

The group of A. Gnanam (MKU) reconstituted an *in vitro* translation system using isolated mesophyll chloroplasts of sorghum (Geetha and Gnanam 1980). The isolated chloroplasts were able to synthesize proteins using ATP generated by photophosphorylation; thus, a very unique protein synthesizing machinery was demonstrated. They studied the synthesis of heat-shock proteins by isolated chloroplasts (Krishnasamy et al. 1988).

Baishnab Tripathy (JNU) studied the Chl biosynthesis and its regulation. The biosynthesis of Chl was regulated by chloroplast envelope (Manohara and Tripathy 2000) and was impaired during temperature stress or senescence (Tewari and Tripathy 1998). The regulation of Chl biosynthesis by intraplastidic distribution is interesting and has recently been further validated by the distribution of biosynthetic intermediates (Mohapatra and Tripathy 2003). A novel protochlorophyllide oxidoreductase C (*porC*) gene, cloned from *Arabidopsis*, mediates chlorophyll biosynthesis (Pattanayak and Tripathy 2002).

5-Aminolevulinic acid acts as a photodynamic herbicide by accumulating tetrapyrroles and hypersensitizing the plant tissue to light due to the over-production of singlet oxygen (Tripathy and Chakraborthy 1991). Prolonged exposure to sub-lethal doses of Sandoz 9785 (a herbicide, decreasing membrane fatty acids) affects the energy distribution process but makes wheat seedlings heat-tolerant (Mannan and Bose 1986).

Molecular biology of chloroplasts

The molecular biology of the chloroplast, including photosynthetic genes, is studied by three groups: Akhilesh K. Tyagi (University of Delhi), P.V. Sane (National Botanical Research Institute, Lucknow) and the team at *I*nternational *C*entre for *G*enetic *E*ngineering and *B*iotechnology (ICGEB, New Delhi, earlier led by Krishna Tewari, and now by Sudhir Sopory). A historical account on the molecular biology of chloroplasts is provided by L. Bogorad, this issue, and of the chloroplast genome by M. Sugiura (also in this issue).

The research group of Tyagi has characterized the chloroplast genome of indica rice, *Vigna* and *Arabidopsis*; they have cloned and sequenced nuclear genes encoding the precursors of 33, 23 and 16 kDa polypeptides of OEC from *Arabidopsis thaliana* (Kochhar et al. 1996; Jain et al. 1998). They have studied the promoters of spinach *psaF* and *petH* (Tyagi et al. 1999), developmental control (Kapoor et al. 1994) and the role of secondary messengers in the plastidic gene expression (M. Grover et al. 1998). In a recent study, Tyagi's group has achieved salt tolerance in indica rice by introducing the gene of choline oxidase, which produces glycine betaine (A. Mohanty et al. 2002).

The group of P.V. Sane has sequenced about 80% of the chloroplast genome, including several PS II/PS I and house keeping genes, from *Populus deltoides.* They have studied several *psb* operons (B to F, L, J) (Naithani et al. 1997; Dixit et al. 1999), as well as seasonal and diurnal changes in the expression of PS II genes (Trivedi et al. 2000).

Among the findings by the group at ICGEB are: the presence of two cis-elements, in the light regulated promoter of *psaF,* chloroplast replication *in vitro*, stimulation of DNA polymerase activity by a glycoprotein, cloning of genes encoding topoisomerases I/II and their promoters (Mukherjee et al. 1994; M.K. Reddy et al. 2001; for further details, see Sopory and Maheswari 2001).

Figure 5. Participants at the International Satellite Conference on Chloroplasts, held in Indian National Science Academy, New Delhi during August 13–15, 2001. This conference was organized in conjunction with the International Photosynthesis Congress held at Brisbane, Australia during August 18–23, 2001. There were 87 participants from India and 26 from abroad, including scientists from Canada, Finland, Germany, Japan, Sweden, Switzerland, UK and USA. Many Indian scientists referred in this article are indicated with numbers: Sitting (from left to right): [1] B. C. Tripathy, [2] V. S. Rama Das, [3] S. K. Sopory, [4] P. V. Sane, [5] A. Gnanam, [6] A. S. Raghavendra, [7] K. C. Bansal, [8] P. Mohanty. Standing (from left to right and bottom to top): [9] S. K. Mukherjee, [10] B. Biswal, [11] J. K. Sainis, [12] G. Kulandaivelu, [13] V. Jagtap, [14] U.C. Biswal, [15] A. S. Bhagwat, [16] R. Khanna-Chopra, [17] A. N. Misra, [18] N. K. Ramaswamy, [19] A. R. Reddy, [20] M. Z. Abdin, [21] H. S. Misra. The readers may also recognize several photosynthesis experts from countries other than India. Photograph taken in New Delhi, India (2001).

Tree photosynthesis

Photosynthesis in trees was studied, e.g., in mango (Shivashankara and Mathai 2000), rubber (Devakumar et al. 1999), tea (Joshi and Palni 1998), and *Populus* (Pathre et al. 1998). Sucrose phosphate synthase in the leaves of *Prosopis juliflora* was activated on illumination, due to protein dephosphorylation (Pathre et al. 2000). (The work on chloroplast genome in *Populus* has already been mentioned in the previous section on 'Molecular biology of chloroplasts.')

Cyanobacterial photosynthesis

Joseph Thomas (while at BARC, Mumbai) provided the first evidence that heterocysts of cyanobacteria lack PS II and maintain the anaerobic milieu essential for their nitrogen fixation (Thomas 1970). He also measured the absorption spectrum of a single cyanobacterial cell. Several groups studied the characteristics of phycobilisomes and photosystems and their responses to a variety of stresses in cyanobacteria. (For a historical account on phycobilisomes, see N. Tandeau de Marsac, this issue.) One of the important findings is the existence of variable long wavelength 77K fluorescence emission originating from PS I, the yield of which was linked to the reduced state of P700, the primary electron donor of PS I (Shubin et al. 1991). Excitation energy transfer from phycobilisomes to photosystems was an important link during the temporal separation of photosynthesis and nitrogen fixation in *Plectonema boryanum* (Misra and Mahajan 2000). (For a historical account on energy transfer in plants and algae, see M. Mimuro 2002.) In a recent and very interesting report, Misra et al. (2003) observed an alternate photosynthetic donor system for PS I supported light dependent nitrogen fixation in *P. boryanum*.

High light causes photooxidative damage due to rise in lipid peroxidation (D.P. Singh et al. 1995). PS II was found to be susceptible to NaCl stress (K. Verma and Mohanty 2000), UV-B (Pandey et al. 1997; Rajagopal et al. 1998) or heavy metals (Murthy et al. 1989; D.P. Singh and Singh 1987). Cobalt ions enhanced the light tolerance and altered the energy distribution in *Synechocystis* (Tiwari and Mohanty 1993). Besides quinones, phycobilisomes serve as the primary targets of UV-B triggered dissociation of PS II in intact cyanobacteria (Rajagopal et al. 1998).

Mutants have been found which are tolerant to high light and other stresses (D.P. Singh and Singh 1997; D.P. Singh and Verma 1995). These mutants would be very useful to further examine the mechanism of tolerance of photosynthesis to different stresses.

Concluding remarks

Besides several original significant and interesting contributions, the Indian researchers have edited and authored several books, conference proceedings and special issues of journals, which serve as excellent additions to the international photosynthesis literature (see Appendix). Despite being from a developing country, Indian Scientists have thrived hard to excel in research. A major part of the research in Indian laboratories is carried out by the PhD students. For example, the doctoral students, from several Indian laboratories, have contributed immensely to the progress of photosynthesis research in India. As an example, we list here the past PhD students[3] of the authors of this paper.

Most of the early research was on the physiology and biochemistry of photosynthesis. During recent years, focus has shifted onto the molecular biology of chloroplasts (Sopory and Maheswari 2001) and this was evident at an International Conference held in New Delhi (Figure 5). Such approach is appropriate to strengthen research in plant biotechnology, including areas such as chloroplast transformation and genomics/proteomics of photosynthesis (Raghuram 2002).

India is an agriculturally important country and photosynthesis research in India has always found support from the people and the government. We envisage that the research on this unique aspect of plant science would make further progress.

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Notes

[1] In the 1924 book, the first and the middle names of J. C. Bose are listed as Jagdis and Chunder instead of Jagdish and Chandra.

[2] At about the same time as J.C. Bose, Dastur (1924) studied the importance of water content in aging leaves. This work was followed by Dastur in 1925, and, then with N.A. Buhariwalla in 1928. Several scientists from the Indian subcontinent, however, studied respiration under the English plant physiologist F. F. Blackman (1866–1947), known since 1905 for the 'law of limiting factors' in photosynthesis. These included T. Ekambaram, R.S. Inamdar, Rafique Ahmad Khan, P. Parija, Shri Ranjan and S.B. Singh (see Blackman 1954, pp. 230–231). This book was actually produced by G.E. Briggs after Blackman's death, and shows the extensive contributions of Parija to Blackman's research.

[3] A partial list of PhD (graduate) students of the authors of this article: Students of *A.S. Raghavendra*: Thurumella Vani, Rita Ghosh, Madhumanchi T. Devi, A.V. Rajagopalan, Kanakagiri Saradadevi, Jagannath Gayathri, Kota Parvathi and Kollipara Padmasree. Students of *P.V. Sane*: Jayashree K. Sainis, Anuj K. Singh, Munna Singh, Jaspreet Arora, Vidhu Bijola, Prabodh K. Trivedi, Pankaj Jaiswal, Purnima Seth, Rekha Sharma, M.S.S. Reddy, Aashish Srivastava, Puneet Dhawan, Sangeeta Saxena, Vipin Hallan, Nidhi Agarwal, Alok K. Sinha and Promod A. Shirke. Students of *P. Mohanty*: Baishnab C. Tripathy, Sabeer A. Sayeed, Ramakrishna A. Wavare, Narendra Mohanty, S.D. Srinivasa Murthy, Bagawatula Vani, Jogadhenu S.S. Prakash, Manoj Joshi, Madhulika Srivastava, Swati Tiwari, Neelima Atal, Sangeeta Dawar and Jerome F. Sah.

Appendix

Books, conference proceedings and special issues of scientific journals on photosynthesis edited by Indian scientists (in chronological order)

Books

Biswal UC and Britton G (eds) **(1989)** Trends in Photosynthesis Research. Agrobotanical Publishers, Bikaner, India

Abrol YP, Mohanty P and Govindjee (eds) **(1993)** Photosynthesis: Photoreactions to Plant Productivity. IBH Publishing Co. Pvt. Ltd, New Delhi, India / Kluwer Academic Publishers, Dordrecht, The Netherlands

Raghavendra AS (ed) **(1998)** Photosynthesis: a Comprehensive Treatise. Cambridge University Press, Cambridge, UK

Singhal GS, Renger G, Sopory SK, Irrgang K-D and Govindjee (eds) **(1999)** Concepts in Photobiology: Photosynthesis and Photomorphogenesis. Narosa Publishing House, New Delhi, India / Kluwer Academic Publishers, Dordrecht, The Netherlands

Yunus M, Pathre U and Mohanty P (eds) **(2000)** Probing Photosynthesis: Mechanisms, Regulation and Adaptation. Taylor & Francis, London

Conference proceedings and special issues of journals

Mohanty P (ed) **(1987)** Indo-USSR Symposium on Photosynthesis under Environmental Stress. Proc Indian National Sci Acad B53: 369–574

Singhal GS, Barber J, Dilley RA, Govindjee, Haselkorn R and Mohanty P (eds) **(1989)** Photosynthesis: Molecular Biology and Bioenergetics. Proceedings of International Workshop on Application of Molecular Biology and Bioenergetics of Photosynthesis. Narosa Publishing House, New Delhi, India

Singhal GS and Bhagwat AS (eds) **(1993)** Proceedings of DAE Symposium on Photosynthesis and Plant Molecular Biology. Department of Atomic Energy, Bombay & Jawarharlal Nehru University, New Delhi

Chitnis PR and Mohanty P (eds) **(2000)** Photosynthesis Research in the Post-Genomic Era. Indian J Biochem Biophys 37: 351–520

Mohanty P and Raghavendra AS (eds) **(2003)** Special Issue on Chloroplast Function. J Plant Physiol 160: 1–96

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Alia, Saradhi PP and Mohanty P (1997) Involvement of proline in protecting thylakoid membranes against free radical-induced photodamage. J Photochem Photobiol 38: 253–257

Allen JF (2002) Plastoquinone redox control of chloroplast thylakoid protein phosphorylation and distribution of excitation energy between photosystems: discovery, background, implications. Photosynth Res 73: 139–148

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Bharadwaj R and Singhal G (1981) Effect of water stress on photochemical activity and membrane organization of chloroplasts during greening of barley seedlings. Plant Cell Physiol 22: 155–162

Biswal B (1997a) Chloroplast metabolism during leaf greening and degreening. In: Pessarakli M (ed) Handbook of Photosynthesis, pp 71–81. Marcel Dekker, New York

Biswal B (1997b) Chloroplasts, pigments and molecular responses of photosynthesis under stess. In: Pessarakli M (ed) Handbook of Photosynthesis, pp 877–885. Marcel Dekker, New York

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