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Minireview

Studies of chlorophyll biosynthesis in Russia *

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Abstract

History of the studies of chlorophyll biosynthesis by Russian and Byelorussian scientists starting from those by Kliment Timiriazeff (also spelled as Timiriazev) and Nikolay (also spelled as Nikolai) Monteverde (late 19th century) to the present time are summarized here.

Abbreviations: RC – reaction centers; PS II (or I) – Photosystem II (or I); Chl – chlorophyll; Pchl – protochlorophyll; Chlde – chlorophyllide; Pchlde – protochlorophyllide

Early work: Kliment Timiriazeff, Nikolay Monteverde and Vladimir Lubimenko

In the late 19th century, the main notion for chlorophyll (Chl) biosynthesis in plant leaves was that it is a set of light-induced reactions. It was assumed that Chl precursor is a colorless substance – leucophyll. Russian scientist Kliment Timiriazeff (1843 –1920) (Figure 1), based on the absorption spectra measurements, found in the alcohol extracts from the etiolated seedlings a colored substance 'protophylline.' It was Timiriazeff's opinion that protophylline was transformed into Chl under illumination in plants (Timiriazeff 1889).

In 1894, Nikolay Monteverde (1856–1929) (Figure 2) introduced the generally accepted name of the chlorophyll precursor – *protochlorophyll* (Monteverde 1894). He performed detailed studies of protochlorophyll (Pchl) spectral characteristics and showed that under the action of light Pchl was rapidly transformed into Chl. Monteverde and Lubimenko (1911a, b) using visual spectral methods (microspectrometer with a kerosene lamp as light source) were the first to observe

Figure 1. Kliment A. Timiriazeff (also listed as Timiriazev) (1843–1920). The photograph is reproduced from the book K.A. Timiriazeff, 'Plant Life,' Moscow/Leningrad, 1949.

* Dedicated to my teacher, Professor Felix Litvin.

Figure 2. Nikolay (also known as Nikolai) A. Monteverde (1856–1929). The photograph is reproduced from the book 'Biographies and Literature Works of Botanists and Staff of Imperial Botanical Garden,' Petrograd, 1915.

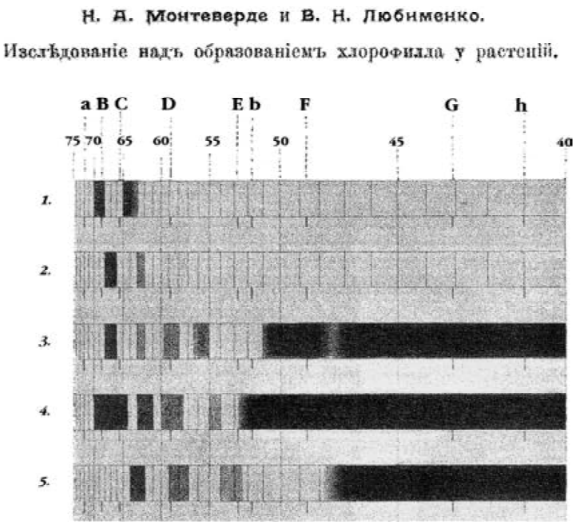

Figure 3. Spectrograms of the greening leaves obtained by Monteverde and Lubimenko (1911b) with microspectromether and oil lamp as light source at room temperature: 1 – absorption spectrum of chlorophyllogen of live etiolated leaves (short-wavelength part of the spectrum was not shown); 2 – first stage of chlorophyllogen transformation into chlorophyll (short-wavelength part of the spectrum was not shown); 3 – second stage of transformation; 4 – absorption spectrum of live green leaves; 5 – absorption spectrum of alcohol solution of Luffa protochlorophyll (Monteverde and Lubimenko 1911b).

Figure 4. Tikhon N. Godnew (also listed as Godnev) (1893–1982). The photograph was obtained from the Photobiology Institute, Minsk.

a number of the intermediate stages of Chl formation, directly in the whole plant leaves. They considered one of the intermediates to be 'chlorophyllogen' (absorption bands at 630–650 nm and 680–700 nm), which was observed at the same time that illumination had begun (Figure 3, spectrum 1), to be a direct chlorophyll precursor. From the current point of view, it seems that chlorophyllogen was a mixture of protochlorophyllide (Pchlde) and primary long-wavelength chlorophyllide (Chlde), which was formed under illumination. The authors observed the short-wavelength shift of the band at 680–700 nm to 660–680 nm, upon illumination (see Figure 3, spectrum 2). This observation of the absorption shift described by Monteverde and Lubimenko preceded the results obtained half a century later by Kazuhiko Shibata – the so-called 'Shibata shift' (Shibata 1956, 1957). They also showed that the red spectral region is more efficient than blue and the blue is more efficient than green in its influence on protochlorophyll transformation to Chl.

New stage of chlorophyll biosynthesis studies: Tikhon Godnev, Alexander Krasnovsky and Alexander Shlyk

At the time Hans Fischer (Nobel Prize in chemistry in 1930) synthesized porphyrin, Russian scientist Tikhon Godnew (also spelled as Godnev) (1893–1982, from 1940 – academician of Byelorussian Academy of Sciences) (Figure 4) advanced a proposal for the primary synthesis of monopyrrols and their subsequent conjugation in the porphine system through the formation of leuco-compounds of porphyrogene type (Godnew 1925; Godnew and Naryshkin 1926).

Figure 5. Alexandr (also known as Alexander) A. Shlyk (1928–1984). The photograph was obtained from the Photobiology Institute, Minsk.

Byelorussian scientist Alexander Shlyk (1928–1984) (Figure 5) was one of the first to apply the method of labeled atoms to the studies of Chl biosynthesis that allowed him to prove the phenomenon of a constant renewal of Chl molecules in plant leaves (Shlyk 1965). The discovery of the metabolic heterogeneity of Chl allowed A. Shlyk and co-workers to advance and develop the hypothesis of the location of the biosynthetic process at certain sites of chloroplasts called 'centers of Chl biosynthesis' (Shlyk 1975; Fradkin and Shlyk 1978; Shlyk et al. 1982; Averina et al. 1993). Fradkin et al. (1988) found that the polyenzymic complexes in the centers of Chl biosynthesis functions in contact with the pigment-protein complexes of the photosynthetic apparatus.

A significant contribution to the studies of Chl formation mechanism was made by academician Alexander Krasnovsky (1913–1993) (Figure 6) and his co-workers. Alexander Krasnovsky and Larisa Kosobutskaya (Vorobyova) (1952) were the first to obtain the active extracts of protochlorophyllide holochrome in aqueous medium. They also showed that in the spectra of homogenates during greening, a bathochromic shift of the absorption band takes place (from 670 to 678 nm). The results of these studies compared with the data on the model systems obtained in the same laboratory confirmed the existence of two different Chl forms, monomer and aggregated, in leaves. It was also shown that protochlorophyll P650 was an aggregated form (Vorobyova and Krasnovsky 1966). P650 was shown to be a phytol-free pigment – protochlorophyllide, while P628 was mostly protochlorophyll (Krasnovsky and Bystrova 1960; Vorobyova et al. 1963). In Krasnovsky's laboratory protochlorophyll photoreduction to chlorophyll was first performed in solution and other model systems (Bystrova et al. 1966, 1983; Krasnovsky et al.1970; Krasnovsky and Bystrova 1974).

Figure 6. Top: A photograph of Alexandr (also known as Alexander) A. Krasnovsky (1913–1993). From www.che.nsk.su/RAN/WIN/14/1447.HTM. *Bottom:* Another photograph of A. Krasnovsky (in his office in Moscow) with the Editor Govindjee.

Studies of the sequence of light and dark reactions from protochlorophyllide to chlorophyll. Felix Litvin and co-workers

At the time Kazuhiko Shibata discovered the so-called Shibata shift (Shibata 1956, 1957) in his absorption spectroscopy studies, the sequence of stages of chloro-

Figure 7. Olga B. Belyaeva (the author), Felix F. Litvin (to whom this article is dedicated) and Nikolay (Nikolai) V. Ignatov (who has contributed much to our understanding of the topic under discussion), Pushchino-na-Oke, Russia, September 2002.

phyll biosynthesis from the precursor in whole plant leaves was studied by Felix Litvin (Figure 7) and Alexander Krasnovsky (1957) with low-temperature fluorescence spectroscopy. In etiolated leaves at 77 K, several fluorescent forms of chlorophyll precursor(s) (maxima at 633, 655, 690, and 705–707 nm) were found and a number of labile intermediates of protochlorophyll photoreduction were registered. Litvin and Krasnovsky proposed that the scheme of Chl formation includes one photochemical reaction and two subsequent dark reactions:

$$\mathrm{P633,\ P655} \xrightarrow{h\nu} \mathrm{Chl690\text{-}695} \rightarrow \mathrm{Chl675\text{-}680} \rightarrow \mathrm{Chl685\text{-}686}$$

where, the numbers show the positions of the fluorescence maxima at a low temperature (77 K); P633 is the inactive form and P655 is the active form of the precursor.

Later, the formation of the native Chl forms *in vivo* was shown to be even a more complicated process. The final stage of Chl formation from protochlorophyllide was shown by Felix Litvin and the author (Olga Belyaeva) (1968, 1971) to be a branching chain of reactions including two sequential photochemical reactions and several dark processes. To describe the process as a whole, the following scheme was proposed (first index shows the fluorescence maximum, second index shows the absorption maximum):

$$\begin{array}{ccccc} \mathrm{Pchlde655/650} & \xrightarrow{h\nu_1} & \mathrm{Chlde684/676} & \xrightarrow{h\nu_2} & \mathrm{Chlde690/680} \\ & & \downarrow & & \downarrow \\ & & \mathrm{Chl675/670} & & \mathrm{Chlde695/685} \\ & & & & \downarrow \\ & & & & \mathrm{Chl683/670} \end{array}$$

The presence of two sequential photoreactions in the Chl biosynthesis chain was confirmed by other investigators (Mathis and Sauer 1973; Henningsen and Thorn 1974).

Using the low-temperature phosphorescence spectroscopy method, triplet states of Chl precursor and intermediate products were found by Alexander Krasnovsky Jr. (son of academician Krasnovsky, cited above) and co-workers in etiolated and greening leaves at 77 K (Krasnovsky Jr. et al. 1975, 1999; Lebedev et al. 1991). However, it is not yet clear if the triplet states of the intermediates are involved in Chl photobiosynthesis.

Litvin and Stadnichuk (1980) found a few minor long-wavelength protochlorophyllide forms *in vivo*. It was later shown that long-wavelength protochlorophyllide forms participate in the photochemical process of Chl biosynthesis (Ignatov et al. 1983; Belyaeva et al. 1984; Ignatov and Litvin 2002a).

Nikolay Ignatov and Felix Litvin have carried out a number of studies on the pathways of pigment formation in the reaction centers of the photosystems. Ignatov and Litvin (1994) found that the side (dark) reaction chain of Chl biosynthesis leads to the formation not only of Chl *a*, but also of pheophytin *a* – primary electron acceptor of Photosystem (PS) II (Klimov et al. 1977; see Klimov 2003). In the juvenile plants (4 days), in addition to the main Pchlde 655/650, another active protochlorophyllide form, Pchlde 653/648, was found which was formed from minor long-wavelength form Pchlde 686/676, under illumination. Pchlde 653/648 initiates the alternative reaction chain, which leads to the formation of non-fluorescent Chl (absorption at 680 nm) of the PS II core:

$$\begin{array}{ccccc} & & & & \mathrm{Chl675/670} \\ & & & & \uparrow \\ \mathrm{Pchlde686/676} & \xrightarrow{h\nu} & \mathrm{Pchlde653/648} & \xrightarrow{h\nu} & \mathrm{Chlde684/676} \\ & & & & \downarrow \\ & & \mathrm{Chl\text{-}/680} & \leftarrow & \mathrm{Chl688/680} \end{array}$$

(Ignatov and Litvin 2002a). The investigation of the biosynthesis of PS I reaction center (RC) pigment (P700) using *Chlorella vulgaris* mutants has shown that this pigment is formed from another long-wavelength Pchlide form Pchlde 682/672 (Ignatov and Litvin 1996).

When the biosynthesis of Chl in green leaves was investigated, it was found that it used the same active Pchlide forms as the etiolated leaves (Litvin et al. 1962; Ignatov and Litvin 2002b).

Figure 8. A 1998 photograph of Andrey Rubin in Budapest, Hungary. Photo by Govindjee.

The structure of the active pigment–protein complex of Chl precursor including the hydrogen donor NADPH (reduced form of *n*icotinamide *a*denine *d*inucleotide *p*hosphate) has been studied extensively, mainly by W.T. Griffiths (1974, 1978). Here, it should be noted that the special role of NADPH in Chl formation was first determined by the Russian scientists Lija Nikolayeva and Elena Porshneva (1970). In their studies it was shown that only NADPH, in contrast to other reductants, stimulated Chl formation in homogenates of etiolated leaves through the activation of the inactive form P630.

Investigation of the primary reactions of protochlorophyll(ide) photoreduction *in vivo* and *in vitro*

Russian scientists have contributed much to the investigation of the mechanism of protochlorophyllide molecule photoreduction, its photophysical and photochemical stages *in vivo* and *in vitro*. In 1962, Andrey (Andre) Rubin (Figure 8) and co-workers found that the protochlorophyll fluorescence life times decreased during illumination of the etiolated leaves at low temperatures (113 K–173 K) without the appearance of any new bands in the fluorescence spectra. Rubin and co-workers advanced a proposal for primary transformation of protochlorophyll molecule into an intermediate state at temperatures lower than 193 K and transformation of this intermediate into Chl in the subsequent dark reaction (the appearance of a Chl fluorescence band was observed only if the temperature of the leaf was increased up to 293 K). A decrease of the Pchlde fluorescence quantum yield after illumination of etiolated leaves at 153 K was observed in The Netherlands by J.H.C. Goedheer and C.A.H. Verhulsdonk (1970) and in Belgium by C. Sironval and P. Kuyper (1972). The hypothesis about the primary formation of the short-lived non-fluorescent intermediate (stabilized at low temperatures) in the process of Pchlide photoreduction was advanced at that time. Byelorussian scientist Viktor Raskin (1976) reported that the absorption band of non-fluorescent intermediate was located at 690 nm. The studies of protochlorophyllide photoreduction *in vivo* at the temperature of liquid nitrogen (77 K) and liquid helium (4 K) performed in our laboratory revealed one more earlier non-fluorescent intermediate, whose formation was characterized by quenching of the active protochlorophyllide fluorescence without alteration of the absorption spectrum (Belyaeva and Litvin 1981; Litvin et al. 1981, 1998; Ignatov et al. 1993). The free-radical nature of the primary non-fluorescent intermediates was proved both for non-fluorescent intermediates formed *in vivo* and in protochlorophyllide photoreduction in model systems (Belyaeva et al. 1988, 20 001; Belyaeva and Litvin 1989; Litvin et al.1998).

The study of Chl biosynthesis continues in Russia despite the difficulties Russian science is experiencing.

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