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REVIEW

The Kautsky effect: 60 years of chlorophyll fluorescence induction kinetics

H.K. LICHTENTHALER

Botanisches Institut, University of Karlsruhe, Kaiserstr. 12, D-7500 Karlsruhe, Germany

Abstract

The detection of the Kautsky effect, *i.e.* the chlorophyll (Chl) fluorescence induction kinetics induced in the dark-adapted leaves because of a sudden irradiation, by Hans Kautsky and his students is reviewed here on the occasion of the 60th anniversary of this Chl fluorescence transient discovery and of the 100th birth anniversary of Hans Kautsky in 1991.

The discovery of the fluorescence induction kinetics

In 1931 Hans Kautsky, at that time *dozent* at the Chemical Institute of the Heidelberg University, published his first paper on the Chl fluorescence induction kinetics of pre-darkened leaves entitled "Neue Versuche zur Kohlensäureassimilation" (New experiments on carbon dioxide assimilation). In this paper he described the essential inverse relationship between Chl fluorescence and the photosynthetic carbon dioxide assimilation (Kautsky and Hirsch 1931). He differentiated between three time periods A-B, B-C and C-D in the Chl fluorescence kinetics (Fig. 1):
(*1*) Period A-B: a fast rise from weak to maximum fluorescence. Kautsky recognized this rise as a pure photochemical reaction which was independent of temperature changes and could not be inhibited by cyanide.
(*2*) Period B-C: a slow decrease from maximum fluorescence to a low fluorescence yield. This decrease he described as strongly temperature dependent which was not found at 0 °C and was sensitive to inhibition by cyanide.
(*3*) Period C-D: a period of constant fluorescence (stationary phase) which is reached several minutes after the beginning of irradiation.

Kautsky and Hirsch (1931) already concluded that fluorescence decreasing (period B-C) corresponded to the induction time of CO_2 assimilation and stated that "the larger the proportion of absorbed radiation converted into chemical energy, the lower the fluorescence intensity of the chlorophyll". At the same time they also

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realised that it requires a considerable dark period, before "the fluorescence intensity and decrease proceeded in the same strength as the first time".

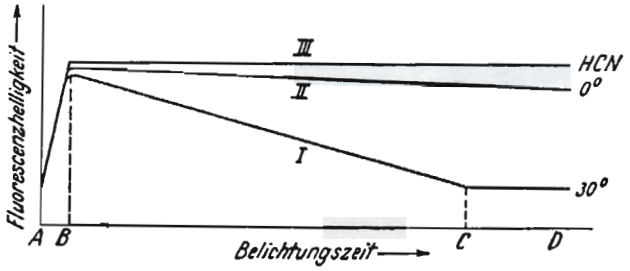

Fig. 1. Original presentation by Kautsky of the changes in the chlorophyll fluorescence intensity of leaves which are observed immediately after onset of irradiation: at 30 °C (I), at 0 °C (II) and after poisoning with cyanide (III). *Abscissa:* irradiation time, *ordinate:* fluorescence intensity. (From Kautsky and Hirsch 1931.)

The Chl fluorescence induction kinetics shown in Fig. 1 were at that time not registered with a recorder but visually observed in a dark room using a red cut-off filter. This is why the fluorescence decrease in Fig. 1 is linear and the exact irradiation time is not indicated on the abscissa. The principles of the visual method applied by Kautsky are described in detail in the booklet of Lichtenthaler and Pfister (1978) and shown in Fig. 2. The actual Chl fluorescence induction kinetics as measured today separately for the 690 and 730 nm regions (*i.e.* the two maxima regions of the *in vivo* Chl fluorescence) are shown in Fig. 3. Though the first paper presented as short communication to Naturwissenschaften (Kautsky and Hirsch 1931) was rather short (one page), it contained the essential elements of the Chl fluorescence induction transient.

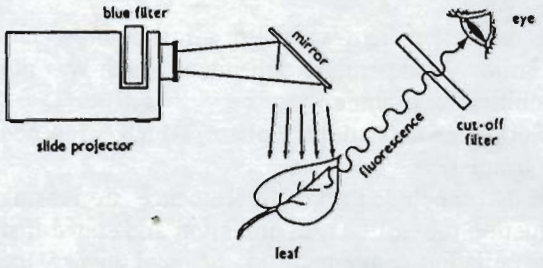

Fig. 2. Experimental set-up for the visual observation of the chlorophyll fluorescence of green leaves. Excitation was performed with either a UV quartz lamp (Kautsky and Hirsch 1931) or a slide projector + blue excitation filter. The red chlorophyll fluorescence is observed through the red cut-off filter which excludes excitation radiation. (From Lichtenthaler and Pfister 1978.)

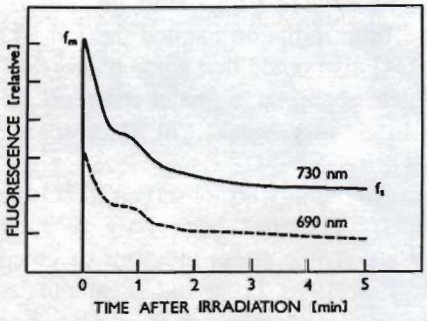

Fig. 3. Chlorophyll fluorescence induction kinetics (Kautsky effect) of green bean leaves separately measured in the two fluorescence maxima near 690 and 730 nm using the two-wavelength fluorometer *LITWAF* as described by Lichtenthaler and Rinderle (1988).

In 1934, two longer original papers were published with the general title "Chlorophyllfluoreszenz und Kohlensäureassimilation" I and II using different subtitles (Kautsky and Hirsch 1934, Kautsky and Spohn 1934). These were the first two of a total 13 communications by H. Kautsky *et al.* using the same overall title. In communication No. I further information on the fluorescence induction kinetics of *Pelargonium* leaves and those of other plants are given together with some details on the measuring principles (see Fig. 4).

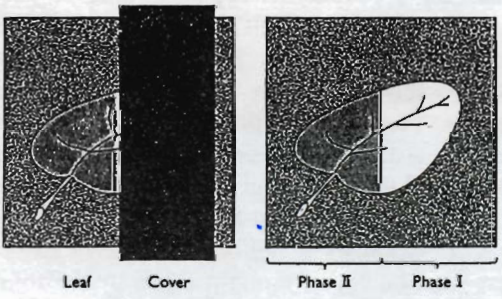

Fig. 4. Schematic presentation of the principles of the original set-up applied by Kautsky and co-workers (Kautsky and Hirsch 1934) to study the chlorophyll fluorescence induction kinetics (known as the Kautsky effect). *Left:* In the left half of the leaf chlorophyll fluorescence is excited, whereas the right half is kept in the dark using a cover. The red fluorescence of the left half goes through a maximum and then declines to a steady state. *Right:* After removal of the cover the red chlorophyll fluorescence of the right half of the leaf is at maximum (phase I) and exhibits a much higher fluorescence intensity than the left half which is in the steady state of fluorescence (phase II). Kautsky and Hirsch (1934) noted that after several minutes both leaf halves are in the steady state and exhibit the same low fluorescence intensity (taken from Lichtenthaler and Pfister 1978).

Kautsky preferred ultraviolet radiation of 350 to 400 nm as excitation radiation, but noted that visible radiation could also induce the same transient in Chl

fluorescence. When using a "white light" source he applied a blue ammonia copper sulfate solution to ensure that mainly violet and blue radiation excited the red Chl fluorescence of the leaf. Kautsky and Hirsch (1934) also noted that some plants (*e.g. Oleander*) contained particular substances which absorbed a major part of the exciting ultraviolet radiation which resulted in a very weak Chl fluorescence transient.

Kautsky and Hirsch were also the first researchers who observed the blue fluorescence of green leaves (communication I). This has been only recently redetected and is being discussed extensively as a possible stress indicator of green vegetation (Chapelle *et al.* 1984, Lichtenthaler *et al.* 1990, Lang and Lichtenthaler 1991). Kautsky and Hirsch (1934) noted that "many plants contain in their interior or on their surface a considerable blue fluorescence which outshines the chlorophyll fluorescence" and that this blue fluorescence did not go through a transient. Furthermore they observed that with respect to Chl fluorescence the "lower leaf sides fluoresce much brighter than the upper leaf sides". These leaf properties have been explained by the fact that in lower leaf halves, which in most plants possess a lower Chl content, the emitted Chl fluorescence is reabsorbed by the leaf Chl to a much lower degree than in the upper leaf halves which exhibit a much higher Chl content (Lichtenthaler and Rinderle 1988).

In communication II (Kautsky and Spohn 1934) an apparatus with many particular devices, *e.g.* a thermostat, was described which allowed measurement of temperature dependent changes of the Chl fluorescence signals, in particular the shortening of the fluorescence rise time with increasing temperature. In this paper it is also noted that the speed of the Chl fluorescence rise is determined by the intensity of the exciting radiation. Already in his first paper Kautsky reported that cyanide blocked the decrease in Chl fluorescence (Kautsky and Hirsch 1931), which was investigated in more detail in communication No. III (Kautsky and Hirsch 1935a). Kautsky thus clearly demonstrated by means of Chl fluorescence induction kinetics that cyanide inhibits photosynthesis, though the target of cyanide, the inhibition of the photosynthetic electron flow at the level of plastocyanin, was detected much later (Trebst 1963, Ouitrakul and Izawa 1973). Not all the communications No. IV to VIII published until 1939 (Kautsky and Hirsch 1935b, Kautsky and Flesch 1936, Kautsky and Marx 1937, Kautsky and Hormuth 1937, Kautsky and Eberlain 1939) can be discussed in detail here. A major progress was, however, brought about by the four papers together with U. Franck (Kautsky and Franck 1943a, b, c, d). These are the communications No. IX to XII which are based on the results of the doctoral thesis of U. Franck of 1941.

In the communication No. IX, Kautsky and Franck (1943a) give details on a measuring apparatus with photocell and photoelectric registration, which allow to register the fluorescence induction curves, and present the complete fluorescence intensity time curves. Contribution X deals with the dependency of the chlorophyll fluorescence of the green alga *Ulva lactuca* upon temperature and irradiance (Kautsky and Franck 1943b). There it is noted that the first fluorescence maximum M1 can be reached within several tenths of a second and then it becomes quenched by acceptor substances which take over the excitation energy of excited Chl. In this paper also the general concept of energy flow from excited Chl (Chl^*) is indicated

"Excitation energy is transferred to other energy forms, mostly into chemical energy and heat":

$$\text{Chl}^* \rightarrow \begin{array}{l}\text{light (fluorescence)}\\ \text{chemical energy (photochemical reaction)}\\ \text{heat (energy dissipation)}\end{array}$$

Kautsky and Franck (1943b) also state that (*a*) the higher the transfer of excitation energy into chemical energy, the higher the concentration of acceptor substances, and (*b*) Chl fluorescence quenching is a function of the concentration of the quenching substances.

Communication XI deals with the dependence and change of the Chl fluorescence induction curves upon the application of narcotics (*e.g.* phenylurethane) as well as under excess or deficiency of oxygen and carbon dioxide. A large number of fluorescence induction kinetics are presented. Phenylurethane and surface active alcohols (*e.g.* octanol) inhibited fluorescence depression in a similar way as we know it today from the photosystem 2 herbicide diuron (DCMU). Kautsky and Franck (1943c) analyzed the first and second fluorescence depression (D1 in the fluorescence rise signal and D2 after reaching the fluorescence maximum M1) and presented evidence that the light reactions of photosynthesis may not only cause an increase but also a decrease of Chl fluorescence. Based on these results they already considered the possibility that during the process of photosynthesis "two light reactions succeed one another almost immediately" ("daβ zwei Lichtreaktionen fast unmittelbar aufeinanderfolgen"), an assumption which was put into evidence only many years later.

In the communication No. XII Kautsky and Franck (1943d) summarized the various results of their Chl fluorescence research and presented theoretical considerations on the relationship of Chl fluorescence, photochemical reactions and photosynthetic CO_2 assimilation. Concerning properties of Chl fluorescence and the shape of fluorescence induction curves twelve general rules ("Gesetzmäβigkeiten") are established, all of which are valid even nowadays, with the sole exception that some of the theoretical interpretations of the underlying photosynthetic reactions have changed. One example may be given here (rule 2): "The fluorescence yield is not constant, but dependent on internal and external factors of the chlorophyll containing cell".

In his last paper on chlorophyll fluorescence (communication No. XIII) Kautsky reinvestigated the effect of anaerobiosis on the fluorescence induction kinetics using *Chlorella* cells, applied intermittent radiation, Hill reagents as well as phenanthroline and phenylurethane and came again to the conclusion that two consecutive light reactions worked in photosynthesis (Kautsky *et al.* 1960). Using the inhibitor phenylurethane he also calculated value of 400 Chl molecules per one photosynthetic unit of the green alga *Chlorella*.

The observation of N.J.C. Müller

Though Kautsky has been the first to describe and analyze in detail the Chl fluorescence induction kinetics which are, indeed, correctly named as "The Kautsky effect", he was not the first scientist who detected the Chl fluorescence. This he

clearly admits in the paper of 1934: "That green plant parts owing to their chlorophyll content fluoresce, is a long known fact (s. Stern 1921); surprising and new is the time-dependent change in fluorescence immediately after the start of illumination" (Kautsky and Hirsch 1934).

In fact, one of the first who investigated the *in vivo* Chl fluorescence of leaves was N.J.C. Müller. He describes that "a diluted chlorophyll solution fluoresces stronger than any living green leaf" (Müller 1874) and concluded on the basis of this and other observations that a reciprocal action would exist between CO_2 assimilation and Chl fluorescence in such a way that one process would exclude the other. He also considered that at lower temperature CO_2 assimilation should be weaker and the fluorescence intensity stronger. By a longer irradiation of leaves, which had been cooled down to 4 °C, he observed that these leaves right upon illumination showed a higher fluorescence than after several minutes when - so is his interpretation - they had been warmed up by the irradiating beams. Whereas Müller attributed this decrease in Chl fluorescence intensity to an increase in the rate of photosynthesis due to an increase in leaf temperature as caused by the excitation radiation, the major part of the fluorescence decrease seen by him was certainly the fluorescence induction kinetics. Though Müller has seen the Chl fluorescence transient, the nature of the Chl fluorescence induction kinetics as a property of dark-adapted leaves remained hidden to him. One can assume that Kautsky was aware of Müller's observation, since he cited the reference of Stern (1921), where access to Müller's work is given. This does not, however, change Kautsky's work and detection at all, since it was he who recognized the true nature of the induction kinetics, analyzed them in detail and introduced them as methods for the study of photosynthesis.

Short curriculum vitae of Hans Kautsky

In 1991 we not only celebrated the 60th anniversary of the detection of the Kautsky effect by Kautsky and Hirsch (1931), but also the 100th birthday of Hans Kautsky, who was born on April 13, 1891 in Vienna. Details on his life are found in the portrait written by G. Fritz (1981). Initially Hans Kautsky saw his future profession as that of a painter and worked with artists in France, the Netherlands, Italy and Switzerland. In 1915 his former interests in chemical experiments took over and he studied chemistry in the laboratory of A. Rosenheim and R.L. Meyer in Berlin. In 1922 he received his doctoral degree at Berlin with an experimental thesis on unsaturated silicium coupounds. He continued to work at the Kaiser-Wilhelm Institut in Berlin investigating problems of energy and substance conversion on boundary layers including phosphorescence, fluorescence and photochemical reactions. After his habilitation Hans Kautsky was appointed in 1928 as head of the Department of inorganic chemistry at the Chemical Institute of the University of Heidelberg. There he extended his research on surface processes and energy conversions on boundary layers by studying the quenching of the fluorescence of dyes by oxygen (Kautsky *et al.* 1932, 1935) and started his research on the energy conversion in carbon dioxide assimilation of green plants using Chl fluorescence.

In 1931, at an age of 40 years, he not only detected the singlet oxygen, but also the chlorophyll fluorescence induction kinetics, today known as the Kautsky effect.

Some details on both processes are to be found in his publication in the Biochemische Zeitschrift (Kautsky and Hirsch 1934). In 1936 H. Kautsky was appointed Professor at the Chemical Laboratory of the University of Leipzig. There he continued his research on Chl fluorescence and carbon dioxide assimilation with his doctorand Ulrich Franck (see Kautsky and Franck 1943a, b, c, d). The war, however, restricted the working possibilities and in 1943 the chemical laboratories in Leipzig were destroyed by bombs. After the Second World War H. Kautsky started with some delay at the University of Marburg, where in 1947 he was appointed director of the newly formed Institut für Siliciumchemie. The lack of laboratories and equipment in these post-war times made the building up of this new institute a difficult task. Kautsky's scientific research was then more concerned with the chemistry of silicium and siloxens. Re-starting of his Chl fluorescence research was therefore much delayed and seems to have begun in the early fifties. This can be judged from his XIII and last communication on Chl fluorescence and carbon dioxide assimilation, which appeared in 1960 (Kautsky *et al.* 1960) and was written after he had been emerited as professor from the University of Marburg in 1959. In this publication Kautsky summarized the results of the Chl fluorescence research undertaken in Marburg since 1955. Hans Kautsky, who liked nature very much as well as hiking in the woods and the Italian Alps, unexpectedly died in 1966 during hiking tour on the Adria.

The effect of Kautsky's discovery on photosynthesis research

Kautsky's research work on Chl fluorescence and CO_2 assimilation has inspired many other scientists who performed research in photosynthesis. Apparently the first photosynthesis researchers, who were stimulated by Kautsky's detection and started research on Chl fluorescence and photosynthesis in the late 30s and beginning 40s, were E.C. Wassink, J. Franck, C.S. French, E.D. McAlister and J.E. Meyers (Franck and Wood 1936, Wassink and Katz 1939, McAlister *et al.* 1940, Franck *et al.* 1941). This early research on *in vivo* Chl fluorescence is summarized in an extensive and excellent review by Wassink (1951) and later by Frank (1960).

After the Second World War Kautsky's former Ph.D. student Ulrich Franck continued the Chl fluorescence research at first at Göttingen and later as professor of physical chemistry at the Technische Hochschule Aachen (Franck *et al.* 1969). One of his students is Ulrich Schreiber who developed the PAM fluorometer (Schreiber *et al.* 1986) which at present is much used in photosynthesis research. Also the author of this article became interested in the application of the Chl fluorescence method as a tool to investigate photosynthetic processes after a visit of the laboratory of Ulrich Franck at Aachen in 1969. Further progress in the understanding of the Chl fluorescence induction kinetics and their relation to photosynthesis came from many different laboratories in the early sixties - *e.g.* Govindjee *et al.* (1960), Butler (1962), Duysens and Sweers (1963) - and helped to establish and confirm the concept of the two photosynthetic photosystems and light-reactions as they are known today.

It is, however, not possible to name all the major contributions in this fast developing field. As a summary one can say that in the last 25 years Chl fluorescence has greatly stimulated photosynthesis research. Chl fluorescence

developed to an essential and intrinsic probe to a further understanding of the complex processes of the photosynthetic light and dark reactions. Some of this research is described in the reviews of Papageorgiou (1975) and other colleagues (Schreiber 1983, Krause and Weis 1984, 1991, Duysens 1986). The application of Chl fluorescence induction kinetics in ecological research and stress detection in plants is reviewed by Lichtenthaler and Rinderle (1988) who also introduced R_{fd}-values and the fluorescence ratio F_{690}/F_{735} in photosynthesis research (Hák *et al.* 1990). Strasser (1974) has introduced a new device for simultaneous measurements of oxygen, fluorescence and absorption changes. With the introduction of further instruments and analytical techniques in the last 10 years (Schreiber *et al.* 1986, Kocsanyi *et al.* 1988, Lichtenthaler and Rinderle 1988, Bolhar-Nordenkampf *et al.* 1989), various different Chl fluorescence parameters are utilized today in the photosynthesis research including fluorescence decay measurements (Holzwarth 1988), in order to determine the potential photosynthetic capacity of leaves and the functional performance of the photosynthetic processes. Many examples of the various practical applications of Chl fluorescence in photosynthesis research, stress physiology, hydrobiology and limnology as well as in the remote sensing of algal bloom and the physiological state of terrestrial vegetation can be found in the contributions to the book "Applications in Chlorophyll Fluorescence" edited by H.K. Lichtenthaler (1988) and in a review by Lichtenthaler (1990). How the detection of the Kautsky effect has changed photosynthesis research may also be seen in the fact, that approximately 50 % of the contributions to the recent international symposium "Photosynthesis and Stress" and the "Workshop on Photoinhibition", held at České Budějovice and Třeboň in August 1991, applied Chl fluorescence in order to define the physiological state of, as well as, damage to the photosynthetic apparatus.

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