Reprinted from

Journal of
PHOTOCHEMISTRY
AND
PHOTOBIOLOGY
B: BIOLOGY

ELSEVIER
SEQUOIA

New Trends in Photobiology (Invited Review)

History of photoinhibition research

Rafael Ball and Aloysius Wild†
Institut für Allgemeine Botanik der Johannes Gutenberg-Universität Mainz, Saarstraße 21, W-55099 Mainz (Germany)

(Received March 23, 1993; accepted April 30, 1993)

Abstract

At the beginning of our century few scientists paid attention to the phenomenon of inactivation of photosynthesis by high light intensities which was later called photoinhibition. In the period 1925–1950, the idea was established that photoinhibition is a reversible inactivation, determined by light intensity and exposure time, followed by irreversible damage of the photosynthetic apparatus. However, the absence of a uniform terminology demonstrates that photoinhibition was not completely perceived and understood. In 1956, B. Kok gave the first definition of photoinhibition as a photochemical inactivation of pigment complexes.

Key words: Photoinhibition research; History; Development; Investigators; Terminology

1. Introduction

The current discussion on the phenomenon and causes of photoinhibition neglects to deal with the historical development. Reports on photoinhibition-like phenomena can be found as long ago as the middle of the 19th century. This review does not go back so far, but is restricted to a summary from the beginning of our century to the first definition of photoinhibition in 1956. In a further article, the review will be continued to the 1980s.

2. The beginning

Pantanelli (1881–1951), Professor at the University of Bari, Italy, experimented in 1904 with *Elodea canadensis*. He exposed it to variable light intensities (1/36 to 54 times the intensity of full sunlight, achieved by a complicated system of lenses and mirrors) at a constant CO_2 content. By measuring gas bubbles he determined the rate of oxygen evolution [1]. As a result he measured an optimum oxygen evolution at light intensities from 1/4 to four times that of sunlight. A strong decrease in oxygen production was observed at four to nine times the intensity of sunlight. On restoring the experimental plants to optimal conditions the oxygen evolution recovered and Pantanelli was able to maintain this state at any time without decrease. The recovery was faster for shorter exposures to light and for lower light intensities.

These results are very similar to the phenomenon of photoinhibition, as it is currently described. Furthermore, Pantanelli was able to exclude damage of the pigments by keeping the exposure times short so that the plants were able to recover oxygen evolution. Under these conditions we can presume that Pantanelli, for the first time in our century, had described the inhibition of photosynthesis by intense light without bleaching of the pigments.

This phenomenon of inactivation of photosynthesis by intense light was not given much attention until Ursprung [2] (University of Freiburg, Germany) published an article entitled "On starch formation in the light spectrum". He described experiments with attached leaves of various plant species (*Phaseolus*, *Impatiens*, *Tropaeolum*, etc.)

†Author to whom correspondence should be addressed.

1011-1344/93/$6.00

exposed to light of different intensities and wavelengths. Before starting the experiments, the plants were kept in darkness, *i.e.* they were starch free. After an iodine test, the grade of density indicated the formation of starch. From the technical point of view this experiment was completely different from Pantanelli's experimental approach, as Ursprung determined the rate of photosynthesis through measuring its final product. He obtained surprising results.

After long exposure of the leaves to intense light, a decrease in density occurred, *i.e.* there was a decrease in starch formation in intense light. The density began to fall if the irradiation intensity exceeded a certain maximum. Depending on the wavelength and light intensity (unfortunately there is no quantitative information on the light intensity), after an exposure time of 4–6 h, the leaves showed significant signs of "Entstärkung" (loss of starch). A leaf of *Phaseolus* exposed for 5 h vertically to sunlight showed high density, but the border zone of the leaf showed an even higher density. Later tests showed less and less starch formation during the experiments. After 8.5 h there was only a weak reaction colouring due to the formation of the iodine–starch complex, with the exception of the border zones whose maximum had not been exceeded.

This phenomena of "Entstärkung" (loss of starch), *i.e.* the halting of starch production and the continuation of starch decrease at light intensities or long exposure times, was termed by Ursprung, "solarization". This term was introduced by him in botany for the first time. (He derived this term from photography. Here this term denotes the converse of a photograph, *i.e.* a decreasing density in spite of increasing exposure.)

According to Ursprung, the cause of solarization is the inactivation without damage of the chloroplasts. He suggested that this phenomenon was due to a rapid decrease in starch (it is now clear that a decrease in starch is inhibited by light) and a temperature effect, because he could not exclude increasing temperature by intense insolation. As a further (and it seems more modern) explanation, he presumed that a high oxygen partial pressure produced by assimilation let to the inactivation of chloroplasts.

Ursprung attempted to determine the biological sense of solarization: the plants are organized in such a way that assimilation is near optimum within a range of low and normal light intensities. Exceptionally high light intensities will not produce a surplus assimilation but, at the same time, high light intensities are not injurious for the plant.

An interpretation of solarization as photoinhibition seems possible (inactivation of chloroplasts without bleaching, reversibility of inactivation), but the technical arrangement and the use of starch formation as a criterion for photosynthesis effect are in many respects inexact and vague. In addition, the evaluation of density and the missing information on light intensities limit the evidence of these experiments. Further development in the investigation of photoinhibition showed that the final product of photosynthesis was not a suitable measure of the light reaction. The whole system is too complex and there are too many diverse influencing factors from light reaction to starch. Holman [3] repeated the experiments of Ursprung and in principal recorded the same results.

3. The phenomenon of photoinhibition from 1925 to 1950

The discovery of the inhibition of assimilation by intense light was an accidental result at the beginning of the 20th century and not intended in the experiments. In the period from 1925 to 1950, however, many articles dealing with this problem were published. The inhibition of assimilation and the inactivation of chloroplasts were explained and established as a subject of experimental research. Initially this problem was investigated from an ecological point of view and in connection with the light conditions of plants in their natural habitat. The physiological approach to photoinhibition did become apparent until the 1940s. At this point a transfer from ecological to physiological questioning occurred and the cause and mechanisms of photoinhibition were the subjects of interest.

In 1926, Kostytschew [4], Professor of Plant Anatomy and Physiology at St. Petersburg (Russia), talked about the "inactivation of photosynthesis by sunstroke", *i.e.* a stagnation of CO_2 assimilation despite the continuation of light. During the night recovery took place; sunstroke was therefore a reversible inactivation. Thus the phenomenon of the inhibition of assimilation by light was formulated and the term "sunstroke", first utilized by Kostytschew, was introduced into science.

In 1928, Marshall and Orr [5] (Marine Station Millport, England) published experiments on the photosynthesis of diatoms, "The photosynthesis of diatom cultures in sea". They described their observations on the oxygen production of algae in the sea at various depths and weather conditions. If the sky was overcast the O_2 maximum was on

the surface; if the sky was clear the O_2 maximum was situated at a depth of about 5 m and sunlight caused a decrease in oxygen production within a depth of 5 m from the surface. It was concluded that this inhibition was caused only by a light effect, because an influence of temperature on the results could be excluded. It seems that these observations can also be explained by photoinhibition, but Marshall and Orr did not examine the phenomena in detail and did not try to find an explanation for their results.

From experiments examining the light adaptation of algae, Camill Montfort (University of Halle/Saale, Germany) also observed the inhibition of photosynthesis by intense light. In 1928, Montfort and Neydel [6] published an article entitled "On estimation of 'inactivation' and of the 'time factor' of light effects at assimilation of stomata-less shade-type ferns". In discussions on the inhibition of assimilation it had been suggested that the closing of stomata was the only reason for the decrease in photosynthetic rate. Therefore the experiments of Montfort and Neydel [6] were carried out with ferns which do not have stomata. During the treatment with sunlight of various intensities the ferns were kept submerged at a constant temperature. The oxygen evolution was measured by the method of Winkler [28]. The ferns showed an onset of assimilation inhibition in the range of $\frac{1}{4}$ to $\frac{1}{3}$ of the intensity of full sunlight. (In comparison with the result of Pantanelli, who found inhibition of photosynthesis at four times the intensity of sunlight, it should be noted that Pantanelli worked with *Elodea canadensis*, *i.e.* a heliophyte [1], whereas Montfort worked with an extreme shade-type fern.) Furthermore, Montfort and Neydel [6] detected a recovery of inhibition, *i.e.* inactivation was reversible. Because there were no stomatal effects and the temperature was constant, it was concluded that this inhibition was a photic inactivation. Furthermore, they observed a displacement of chloroplasts (so-called side wall position). However, this could not be the cause of the decrease in assimilation as a further increase in light intensity should have led to an increase in assimilation. Therefore, it was concluded that the inhibition was due to a combined effect of a simple chloroplast displacement and a photic (photochemical) inactivation. When light exposure was prolonged a "sunstroke" effect was observed (Montfort and Neydel used the term coined by Kostytschew in 1926); on further prolonged exposure an "extreme sunstroke effect" was found, which causes irreversible structural changes, for example bleaching of chlorophyll, imbibition of the stroma, etc., leading to "sundeath" of the cell. Montfort and Neydel saw a similarity between their observations and the solarization effects of Pantanelli, but they did not presume a direct relation between the two phenomena because of the different methods applied. The work done by Montfort and Neydel [6] distinguished between a reversible photic inactivation and an irreversible bleaching of chlorophyll. Thus photoinhibition itself became an independent subject of research.

In further investigations of Montfort and coworkers the reversible inactivation of photosynthesis by intense sunlight in relation to habitat was repeatedly described. In 1930, Montfort's scholar Neydel (University of Halle/Saale, Germany) continued the experiments on photic inactivation. In his article, "Comparative studies about the effect of light and increasing temperature on CO_2 assimilation by various light intensities", he described experiments on the effect of various light intensities on CO_2 assimilation with the stomata-less shade-type fern *Trichomanes radicans* and the heliophyte alga *Cladophora spec.* [7]. When the light intensity was increased from L78 to L118, the maximal photosynthetic activity of *Cladophora* decreased to 50% (unfortunately Neydel operated only with relative degrees of light intensity; L118 denotes full sunlight). This "photic inactivation" was reversible even with shade-adapted *Cladophora* and did not induce changes in the structure of chloroplasts, whereas permanent exposure of a frond of the shade-type fern to high light intensity produced sunstroke effects associated with morphological and physiological changes. It is important to note that in this work Neydel differentiated between an always reversible photic inactivation (we can compare this with photoinhibition) and sunstroke (accompanied by bleaching and photo-oxidation).

In 1933, Harder [8] (University of Göttingen, Germany) published an article on the decrease in photosynthesis in the light. He obtained interesting results from his experiments with *Fontinalis antipyretica*: "The strong decrease of capacity appears only if the light intensity of assimilation experiments is more intense than the intensity to which the plant has been adapted" [8]. The new concept was that not the absolute intensity of the experimental light, but the difference between the latter and the light intensity during cultivation, is responsible for the decrease in capacity. The observed decrease was compared with the photic inactivation described by Neydel in 1930.

In 1935, Singh and Kumar [9] (Benares Hindu University, India) reported the inactivation of chloroplasts without damage to the leaves and without

bleaching of the chlorophyll during experiments with radish leaves.

In the same year, Blagoweschtschenski [10] (Professor of Physiology at Tashkent, USSR) ascertained, by experiments in the high mountain chains of the Pamir, a strong decrease in CO_2 assimilation in the light. In a region with extreme changes in temperature, permanent clear sky, high solar radiation and a very low CO_2 content (up to contents of 0.18–0.19 mg l^{-1}), Blagoweschtschenski measured a very early maximum assimilation (0730–1000 hours), followed by a strong decrease with the rising sun, and at 1200 hours the assimilation curve no longer reached the compensation point. According to present theory we can presume that this phenomenon represents the (chronic?) photoinhibition of high mountain plants. Nowadays, it is generally accepted that a low CO_2 content promotes photoinhibition. Under these ecological conditions additional water stress and low temperature may produce or reinforce photoinhibition. In addition, the high UV intensity in high mountains may be a reason for photoinhibition.

In 1937, Montfort reported that increasing respiration in the light may also be a cause of inhibition of assimilation [11]. The results of further investigations on enhanced respiration in the light by the coworkers of Montfort are not considered here. Montfort concluded that the effect of light depends on the photic resistance of complex protein compounds, which are very unstable in plants adapted to low light intensities. In later publications, Montfort called these protein compounds pigment–protein complexes. Their photic resistance determines whether or not a plant suffers photoinhibition. It is interesting to compare Montfort's early findings with the currently discussed concept of the involvement of D1 protein turnover in photoinhibition [12–15].

In further research we meet Montfort again. In 1938, he and his scholar Föckler published an article about the significance of light respiration [16]. The results are not important for our discussion, but the method is worth mentioning. So that photosynthesis did not affect photo respiration data, it was eliminated by means of "sunstroke". This is the first time, in photosynthesis research, that photoinhibition was not the subject of research, but was instead used as a means. The method of inhibition of photosynthesis by sunstroke was applied to facilitate the distinction between different overlapping phenomena in the light.

In 1939, Föckler (University of Halle/Saale, Germany) in his article entitled "About the influence of light on respiration of colourless and assimilating tissue and its role by 'functional sunstroke'" clarified the role of photo respiration in the inhibition of assimilation in the light [17]. He was able to show in his experiments with the shade-type fern *Trichomanes* a significant enhancement of respiration in light-exposed fronds. However, the extent of photo respiration was not great enough to explain the inhibition of assimilation. Thus he could not exclude a participation of respiration while measuring photoinhibition, but it was not sufficient to be the exclusive cause.

Föckler postulated a two-step damage mechanism of chlorophyll by oxidation processes increased by light as the cause of inhibition of CO_2 assimilation in the light. Initially there is a reversible damage step and subsequently an irreversible damage step. These two steps correspond to reversible and irreversible sunstroke. At this time this mechanism was generally accepted.

In 1939, Stalfelt [18] (University of Stockholm) published a very comprehensive study entitled, "Light and temperature inhibition of carbon dioxide assimilation", in which he discussed reversibility and epistemological problems in photosynthesis research. He concluded that the recovery time is an important factor. Pathological changes, *e.g.* by light, may seem reversible if there is enough time for recovery. In experiments with lichen, Stalfelt took 12 h in darkness as a recovery time. (Whether or not, within 12 h, the repair processes involved in the recovery from irreversible damage may have begun cannot be decided here. This shows the difficulty of the terminological basis of reversibility without a concrete reference quantity in time and subject.)

In an article entitled, "Light-paralysis and light-bleaching of water plants", Montfort [19] reported experiments which aim directly at the relationship between the bleaching of chloroplasts and the inactivation of photosynthesis. In this study, various shade-type water plants were tested for their photosynthetic rate and content of chlorophyll. Extreme shade-type plants showed a strong decrease in photosynthesis, and an anatropus curve of light intensity and photosynthetic capacity was observed over time. From the measurement of the chlorophyll content it was clear that light paralysis may be associated with bleaching, but there was a significant difference in the time course between these two phenomena. The beginning of chlorophyll loss occurred long after the onset of photosynthetic inactivation. Because of the significant later damage of the pigment, Montfort [19] presumed that

the damage to chlorophyll was a consequence of the previous inactivation of photosynthesis. Further experiments showed a very rapid inactivation of photosynthesis by UV light, which could not be caused by photo-oxidative damage to pigments and protoplasm, because (after a short exposure) the inactivation was completely reversible.

Because both, the enrichment of photosynthesis products and the photo-oxidation of pigments could be excluded, Montfort concluded that the unstable architecture of certain protein complexes inside and outside the grana may be the reason for the light paralysis. According to Montfort this is caused by the "deciding effects of primary photochemical changes of pigment-binding to protein compounds in certain grana layers" [19]. The reversibility of this phenomenon, where very strong inhibition of photosynthesis occurs without pigment damage, shows that the chlorophyll–protein complex, after a pause, is able to recover completely from the harmful photochemical reaction.

The theory of chlorophyll–pigment complexes as the primary site of light paralysis (photoinhibition) suggests an analogy with D1 protein degradation during photoinhibition. Of course, Montfort and the other workers at that time could not have known very much about the molecular organization of the photosynthetic apparatus. Nevertheless, the suggestion of chlorophyll–protein complexes as the primary site was, in principle, verified 40 years later.

Further fundamental work at this time originated from the USA. Myers and Burr [20] (University of Minnesota) published a report entitled, "Studies on photosynthesis: some effects of light of high intensity on *Chlorella*". These workers established a new definition of the term "solarization": a decrease in photosynthetic rate during a longer exposure time. The aim of the experiments was to show solarization (in its new interpretation!) of a suspension of *Chlorella vulgaris* in a special buffer as a function of time and light intensity at constant temperature. The oxygen evolution was measured. The result was a decreasing O_2 curve as a function of time. At higher light intensities the course of the curve was steeper, and the same degree of inhibition of photosynthesis occurred earlier. These results, in principle, were similar to those obtained previously.

The new approach in this publication was the measurement of the recovery curve of the photosynthetic rate after a short pause of 30 min (and not after about 12 h or even 5 days as performed by Stalfelt [18]). The results showed that the longer the exposure and the stronger the damage, the slower and more incomplete the recovery. It is interesting that the recovery also occurred in the dark. If the curve of inhibition and subsequent recovery was plotted as a function of exposure time to high light intensity, a significant dependence of oxygen evolution and recovery on the exposure time was seen. If the exposure was prolonged for a long period, *e.g.* 200 min, there was no recovery detectable in the dark, *i.e.* a prolonged exposure time was followed by progressive damage.

These results show that, above a critical light intensity, which depends on the history of the organism, the oxygen evolution decreases with increasing light intensity up to O_2 uptake. (This verified the suggestion of Harder [8], according to which the relationship between cultivation and experimental light plays the decisive role.)

From the experimental data, the following hypothesis was derived. In the first 20–30 min, complete inactivation of the photosynthetic mechanism occurs, followed by progressive destruction of cellular material. The process of inactivation may be based on the damage of an unknown factor of the photosynthetic mechanism. This inhibition is initially a completely reversible process, which changes to progressive damage of the photosynthetic mechanism.

In 1942, the Danish botanist Steemann-Nielsen [21] (Royal Danish School of Pharmacy) published a comprehensive article on the mechanism of photosynthesis, in which he reported on the inhibition of photosynthesis in the light. This process increases with increasing light intensity and counteracts the rate of photosynthesis. The effects soon neutralize each other and result in a horizontal assimilation curve. If the exposure becomes stronger and stronger, the inhibition will exceed the rate of photosynthesis and the curve begins to fall. This inhibition factor, induced by light, will regulate or reduce the effect of photosynthesis. According to Steemann-Nielsen the cause is an enzymatic factor, which regulates the activation of chlorophyll molecules, inactivated by assimilation.

This concept of the inhibition of photosynthesis was formulated more precisely by Steemann-Nielsen in 1949 [22]. From experiments with *Cladophora insignis* he obtained the following results. The process of reactivation was independent of light and seemed to be chemical, regulated by one or more enzymes. In contrast, the process of inactivation is photochemical. Steemann-Nielsen clearly differentiated between inactivation of photosynthesis and photo-oxidation. He noted that

reversible inactivation (inhibition) of photosynthesis by intense light (up to 40 000 lux, approximately 160 W m^{-2}) is a part of photosynthesis itself. The photo-oxidation processes will only occur at higher light intensities, but will not result in severe damage such as complete bleaching or even cell death.

This review of the most important publications in the period 1925–1950 shows the development of the concept in which a reversible inactivation of photosynthesis is followed by irreversible damage. The former is determined by the exposure time and light intensity.

4. The 1950s

The 1950s were not a period of great innovation in photoinhibition research. The chloroplast isolation technique was applied and Kok [23] produced the first definition of photoinhibition. Steemann-Nielsen [24] questioned whether the mathematical product of exposure time and light intensity could be the criterion of inhibition of photosynthesis, because he obtained very similar results when the product of these two parameters was identical.

Zurzycki [25] (University of Kraków, Poland) described the three effects of intense light observed on plants up to this time: chloroplast displacement, chlorophyll destruction and inhibition of photosynthesis. From his experiments he concluded that neither chloroplast displacement nor chlorophyll destruction causes photoinhibition. Inactivation of photosynthesis proceeds more quickly than both processes. In addition, he distinguished between the measuring light and the inhibitory light, *e.g.* the rate of photosynthesis was measured at 2500 lx, but the light treatment before measurement was carried out at 100 000 lux.

In 1956, Kok [23] (University of Wageningen, Netherlands) published a paper entitled "On the inhibition of photosynthesis by intense light". This article deals with the short-term effects of the inhibition of photosynthesis of a *Chlorella* suspension by high light intensities. The experiments, which were performed at light intensities up to 100 000 foot candles (about 1000 lux or 4000 W m^{-2}) showed a decrease in photosynthetic rate to zero or even below the compensation point for very strong light intensities. For an explanation of these curves, Kok made the following assertion: the rate of photosynthesis is proportional to the concentration of a light-sensitive compound U. If the synthesis of this compound is in equilibrium with its destruction in the light, the concentration of U is still constant and with it the rate of photosynthesis. However, if with increasing light intensity the destruction rate of U exceeds its rate of synthesis, the concentration of U and the rate of photosynthesis fall. According to Kok we can talk about a photochemical inactivation of the pigment system, because the process of photoinhibition in only slightly affected by temperature. In the history of the inactivation of photosynthesis by light, Kok [23] gave the first definition of photoinhibition: "We therefore reach the conclusion that photoinhibition is to be conceived as the photochemical inactivation of complete pigment complexes or photosynthetic units" [23].

The new and important factor here is the understanding of photoinhibition as a process which depends on one or more intermediate steps. So, in addition to light, other factors may also cause, directly or indirectly (through their influence on the light effect), phenomena similar to photoinhibition. From this it is clear that the term "photoinhibition" used by Kok, suffered a generalization which has been preserved until today.

Kok explicitly emphasized that the investigation of photoinhibition could serve as a means to increase our knowledge of pigment organization and to obtain new information in other fields of photosynthesis research.

5. On the terminology used in the publications in the above-mentioned period

In 1956, Kok [23] first used the term photoinhibition. However, before this time many articles on this subject had been published. The terminology used was not uniform, but often varied even within the same publication. Initially, the observed effects (the phenomena) were described. Workers talked about inhibition of assimilation (this reflects the method) and about "fatigue" and "inactivation" of chloroplasts [1]. Cause and consequence were not separated.

In his description of the still unknown phenomenon, Ursprung [2] referred to photography and introduced the term "solarization" by means of an analogy into the discussion. The level of information in this term was raised: the final cause of inhibition was the supraoptimal light intensity. Unfortunately, this term was associated with the method of starch detection as a criterion of photosynthetic rate, which made a general application impossible.

By means of an analogy with a similar phenomenon, the term "sunstroke" was introduced in 1926 [4]. To render this term concrete, Montfort and Neydel [6] talked about "functional sunstroke",

which effected a "photic inactivation". In this context these workers also used terms such as "photic fatigue", but it was not clear what was the cause and what was the effect. Montfort also made use of terms such as "photoinactivation" [26, 27], "pure photochemical inhibition" of chloroplasts [11], "light paralysis" and "photochemical paralysis" [19] to determine the same phenomenon. Neydel, who defined the photic inactivation of Montfort as a reversible phenomenon and sunstroke as an irreversible phenomenon, did not succeed in standardization of the terminology. Nevertheless, Neydel [7] reached a separation of photoinhibition and photo-oxidation.

The utilization of the terms "reversible and irreversible sunstroke" by Föckler [17] a few years later showed clearly the lack of standardization of the terminology. Myers and Burr [20] interpreted the term "solarization" in a new way, *i.e.* the decrease in photosynthesis rate by prolonged exposure time. Therefore, this term, established by Ursprung [2], was liberated from its methodical chains, but nevertheless did not become popular.

The coexistence of the various terms demonstrates that the problem of photoinhibition was not completely understood up to the 1950s. The uncertainty of dealing with this phenomenon is reflected in the wide variability of the terminology.

Acknowledgment

Our thanks are due to Dr. M. Richter for helpful criticism.

References

1 E. Pantanelli, Abhängigkeit der Sauerstoffausscheidung belichteter Pflanzen von äußeren Bedingungen, *Jhb. Wiss, Bot., 39* (1904) 167–228c.
2 A. Ursprung, Über die Stärkebildung im Spektrum, *Ber. Dtsch. Bot. Ges., 35* (1917) 44–69.
3 R. Holman, On solarization of leaves *Univ. Calif., Berkeley, Publ. Bot., 16* (4) (1930) 139–151.
4 S. Kostytschew, *Lehrbuch der Pflanzenphysiologie, Bd. 1; Chemische Physiologie,* Springer, Berlin, 1926.
5 S.M. Marshall and A.P. Orr, The photosynthesis of Diatom cultures in the sea, *J. Mar. Biol. Assoc. UK, 15* (1) (1928) 321–360.
6 C. Montfort and K. Neydel, Zur Beurteilung der 'Inaktivierung' und des 'Zeitfaktors' der Lichtwirkung in der Assimilation stomata-freier Schatten-Farne, *Jhb. Wiss. Bot., 68* (1928) 801–843.
7 K. Neydel, Vergleichende Studien über die Wirkung des Lichtes und ansteigender Temperatur auf die CO_2-Assimilation bei verschiedener Lichteinstellung, *Biochem. Z., 228* (1930) 451–486.
8 R. Harder, Über die Assimilation der Kohlensäure bei konstanten Außenbedingungen II. [Das Verhalten von Sonnen- und Schattenpflanzen], *Planta, 20* (1933) 699–733.
9 B.N. Singh and K. Kumar, The reactions of the assimilatory system to alterations of light intensity, *Proc. Indian Acad. Sci., 1* (11) (1935) 754–762.
10 W.A. Blagoweschtschenski, *Über den Verlauf der Photosynthese im Hochgebirge des Pamir, Planta, 24* (1935) 276–287.
11 C. Montfort, Umwelt, Erbgut und physiologische Gestalt. I. Lichttod und Starklichtresistenz bei Assimilationsgeweben, *Jhb. Wiss. Bot., 84* (1937) 1–57.
12 D.J. Kyle, C.J. Arntzen and I. Ohad, The herbicide binding 32 kDa polypeptide is the primary site of photoinhibition damage, *Plant Physiol., 72* (1) (1983) 52 (Suppl.).
13 C.J. Arntzen, D.J. Kyle, M. Wettern and I. Ohad, Photoinhibition: a consequence of the accelerated breakdown of the apoprotein of the secondary electron acceptor of photosystem II, in Hallick, Stachelin and Thoruber (eds.), *Biosynthesis of the Photosynthetic Apparatus: Molecular Biology, Development and Regulation, 1984,* A.R. Liss, pp. 313–324.
14 M. Richter, W. Rühle and A. Wild, Studies on the mechanism of photosystem II photoinhibition I. A two step degradation of D1-protein, *Photosynth. Res., 24* (1990) 229–235.
15 M. Richter, W. Rühle and A. Wild, Studies on the mechanism of photosystem II photoinhibition II. The involvement of toxic oxygen species, *Photosynth. Res., 24* (1990) 237–243.
16 C. Montfort and H. Föckler, Licht und Atmung bei Licht- und Dunkelgeweben, grünen und farblosen Organen, *Planta, 28* (3) (1938) 515–534.
17 H. Föckler, Über den Einfluß des Lichtes auf die Atmung farbloser und assimilierender Gewebe und seine Rolle beim 'funktionellen Sonnenstich', *Jhb. Wiss. Bot., 87* (1) (1939) 45–92.
18 M.G. Stalfelt, Licht- und Temperaturhemmung in der Kohlensäureassimilation, *Planta, 30* (3) (1939) 384–421.
19 C. Montfort, Lichtlähmung und Lichtbleichung bei Wasserpflanzen. [Grundsätzliches zur physiologischen Gestalt der submersen Blütenpflanzen] *Planta, 32* (1941) 121–149.
20 J. Myers and G. Burr, Studies on photosynthesis: some effects of light of high intensity on *Chlorella, J. Gen. Physiol., 24* (1940) 45–67.
21 E. Steemann-Nielsen, Der Mechanismus der Photosynthese, Dan. Bot. Ark., 11 (2) (1942) 1–95.
22 E. Steemann-Nielsen, A reversible inactivation of chlorophyll *in vivo, Physiol. Plant., 2* (1949) 247–265.
23 B. Kok, On the inhibition of photosynthesis by intense light, *Biochim. Biophys. Acta, 21* (1956) 235–244.
24 E. Steemann-Nielsen, On detrimental effects of high light intensities on the photosynthetic mechanism, *Physiol. Plant., 5* (1952) 334–344.
25 J. Zurzycki, The destructive effect of intense light on the photosynthetic apparatus, *Acta Soc. Bot. Pol., 26* (1957) 157–175.
26 C. Montfort, Fucus und die physiologische Licht-Einstellung der Wasserpflanzen, [Studien zur vergleichenden Ökologie der Assimilation I], *Jhb. Wiss. Bot., 71* (1929) 52–105.
27 C. Montfort, Die funktionelle Einstellung verschieden gefärbter Meeresalgen auf die Lichtintensität, [Studien zur vergleichenden Ökologie der Assimilation II], *Jhb. Wiss. Bot., 71* (1929) 106–148.
28 G. Alsterberg, Die Winklersche Bestimmungsmethode für in Wassergelösten elementaren Sauerstoff sowie ihre Anwendung bei Anwesenheit oxydierbarer Substanzen, *Biochem. Zeitsch., 170* (1926) 30–75.