

REVIEW

Discovering trends in photosynthesis using modern analytical tools: More than 100 reasons to use chlorophyll fluorescence

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Abstract

In this review, using the network analysis, based on the bibliometric data, collected from *Web of Science Core Collection* database, we followed the development of chlorophyll fluorescence research (CFR) during 1947–2018. We confirmed dramatic increase in diversity of CFR from late 90-ties and vigorous development of this discipline in the last ten years. They are parallel to an increase in number of research areas and institutions involved and were triggered by the accumulation of knowledge and methodological, technological, and communication advances, especially modern fluorimeters and fluorescence techniques. The network analysis of keywords and research areas confirmed CFR changed into modern, multidisciplinary, highly collaborative discipline, in which in spite of many ‘core’ disciplines as plant science, environmental sciences, agronomy/food science and technology, the promising, modern areas developed: biochemistry and molecular biology, remote sensing, and big data artificial intelligence method.

Additional key words: collaboration; globalization; plant physiological status; trends in chlorophyll fluorescence research.

Introduction

Plants live with permanent interactions with other organisms and their environment (Goltsev *et al.* 2016). Photosynthesis is the key process of plant metabolism, which is very sensitive and strongly influenced by environmental conditions (Blankenship 2014, Kalaji *et al.* 2014). The chlorophyll fluorescence (ChlF) is a naturally occurring phenomenon, characteristic to all photosynthetic organisms (Kalaji *et al.* 2017a). It is an electromagnetic radiation emitted by chlorophyll molecule, which is not used in photosynthesis nor dissipated as heat radiation

(Żurek *et al.* 2014). The analysis based on high time-resolution measurements of the ChlF transient represents a method for evaluating the physiological conditions of photosynthesizing organisms and gaining, directly or indirectly, information on all light phases of photosynthesis: water photolysis, electron transport, creation of pH difference across thylakoid membranes, ATP synthesis (Kalaji *et al.* 2017a), and the different regulatory processes (Brestič *et al.* 2012).

There are many examples of successful application of ChlF for studying the reaction of photosynthetic apparatus

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Abbreviations: CFR – chlorophyll fluorescence research; ChlF – chlorophyll *a* fluorescence; cyt *b₆f* – cytochrome *b₆f*; DF – delayed fluorescence; Fd – ferredoxin; FLIM – fluorescence lifetime imaging microscopy; PAM – pulse amplitude modulated fluorescence; PC – plastocyanine, PQ – plastoquinone; Q_A – primary quinone electron acceptors of PSII; TEG – two-electron gate model.

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to different environmental stresses, such as light intensity (Cai and Xu 2002, Živčák *et al.* 2014), high and low temperature (Alam *et al.* 2005, Oukarroum *et al.* 2013, Kalaji *et al.* 2016), drought (Goltsev *et al.* 2012, Abid *et al.* 2017), salinity (Dąbrowski *et al.* 2016, Allel *et al.* 2018), heavy metals (Azevedo *et al.* 2005, Kalaji *et al.* 2016, Baycu *et al.* 2017), herbicides (Ferrell *et al.* 2003) or nutrient deficiency (Cetner *et al.* 2017, Kalaji *et al.* 2017b,c). Moreover, ChlF is used in agriculture (Baker and Rosenqvist 2004, Massacci *et al.* 2008), forestry (Lapa *et al.* 2017, Kučerová *et al.* 2018), ecology (Bussotti 2004, Bąba *et al.* 2012, 2016), climate change studies (Drusch *et al.* 2017, Bałazy *et al.* 2018, Pflug *et al.* 2018), and vegetation research (Li *et al.* 2018).

Lately, Integrated Biomarker Response method was developed in order to combine ChlF data with other proxies characterizing CO₂ assimilation, growth or grain yield (Stirbet *et al.* 2018).

This multidimensionality and multidisciplinary of CFR creates a unique platform for knowledge exchange and cooperation between scientists, both theoreticians and practitioners, from various fields of science, while allows us to follow the growth and development of this fascinating discipline. The close relationship between international cooperation and tremendous growing in a number of articles in well-established journals, plant science journals as well as the number of new titles that appeared in the last 10 years is clearly visible. In this review, we aimed to analyse past and current topics and spatio-temporal trends in CFR, comparing networks of countries and institutions, keywords and research areas with the modern network analysis. Moreover, we tried to identify the current topics and centres of CFR and find its position and relation to photosynthesis research.

Materials and methods

In order to gain the representative sample of research articles related to ChlF we searched *Clarivate Analytics* (former *Thompson Reuters*) *Web of Science*® *Core Collection* database (1945–present; <https://webofknowledge.com>). We used simple query ‘chlorophyll’ AND ‘fluorescence’ within the ‘topic’ in the database, for three periods: before 1994, 1995–2005, and 2006–2018. The search was performed on 24 February 2018. The full record of each article was downloaded and collated into three documents, related to these study periods in the *BibExcell* (Persson *et al.* 2009). Moreover, we searched the ‘photosynthesis’ for identification ChlF position and relationship to other photosynthesis-related research.

Analyses of co-occurrence of keywords field research (disciplines), and co-authorship of countries and institutional networks were performed and visualised with *Bibexcell* and *VOSviewer* software (van Eck and Waltman 2007, Persson *et al.* 2009). We used the default *VOSviewer* settings, in terms of normalization of the strength of the links between items (van Eck and Waltman 2009) and clustering technique is described in van Eck and Waltman (2014).

Results

Taking into account the very extensive bibliographic data of ChlF with more than 50 comprehensive reviews (*i.e.*, Lazár 1999, Papageorgiou and Govindjee 2004, Kalaji *et al.* 2014, 2017b; Stirbet *et al.* 2014, 2018, Stirbet and Govindjee 2011, 2012), we present only few examples of ChlF articles, which contribute to the theoretical and experimental basis of the discipline. Kautsky and Hirsch (1931) introduced chlorophyll *a* fluorescence induction phenomenon. Jabłoński (1933) provided explanation of electronic and vibrational levels of molecules and transitions between them. Munday and Govindjee (1969) provided the theory of thermo-luminescence in plants, and made the first picosecond measurement on the primary photochemistry of PSII. While Strasser and Govindjee (1992), Strasser and Strasser (1995), and Strasser *et al.* (2004, 2010) developed the backgrounds for studies of analysis of OJIP transient with JIP-test, Schreiber *et al.* (1986) and Schreiber (2004) provided efficient system for measurement PAM fluorescence and quenching analysis. The detailed analysis of delayed fluorescence (DF) was provided by Goltsev *et al.* (2009). Holub *et al.* (2000) used fluorescence lifetime imaging microscopy (FLIM) of ChlF for understanding photoprotection against excess light.

The experimental and mathematical modelling approach to study of *in vivo* ChlF was presented by Lazár and Schansker (2009), Lazár (1999, 2006, 2009, 2017), Lazár and Schansker (2009) and Lazár *et al.* (2001, www.e-photosynthesis.org). Lazár *et al.* (1997) constructed two-electron gate model (TEG) in which fluorescence was considered to be proportional to amount of reduced Q_A and considering the energetic connectivity between PSII_s. A model, which gave a quantitative relation between the efficiencies of primary photochemistry, energy trapping, and radical pair recombination in PSII, was presented by Vredenberg (2000, 2018). Lebedeva *et al.* (2002) simulated the chlorophyll induction over the range of light fluxes and incorporated the effect of membrane potential on rate constant of various reactions. Lazár (2003) prepared a very detailed model of PSII reactions that included TEG, reversible-radical pair model (RRP), and Kok's model to simulate the fluorescence induction. In model constructed by Zhu *et al.* (2005), fluorescence emission was calculated directly from the amount of excited singlet-state chlorophyll in the core and peripheral antennae of PSII. A comprehensive model consisting of reactions occurring in thylakoid membrane (PSII, PQ pool, cytb₆/PC, PSI, and Fd), stroma of chloroplast (Calvin-Benson cycle and starch synthesis), and in cytosol of cell (sucrose synthesis) was proposed by Laisk *et al.* (2006).

In order to find the position, mutual relationships, and trends in CFR in relation to photosynthesis research, we used the (1) ‘photosynthesis’ and (2) ‘chlorophyll AND fluorescence’ queries for the 1950–2018 period to *Web of Science Core Collection* database. In the first case, this resulted with 75,014 records, including 65,428 research articles published in 2,098 journals.

The ‘chlorophyll AND fluorescence’ searching resulted in 20,553 records, including 19,249 research

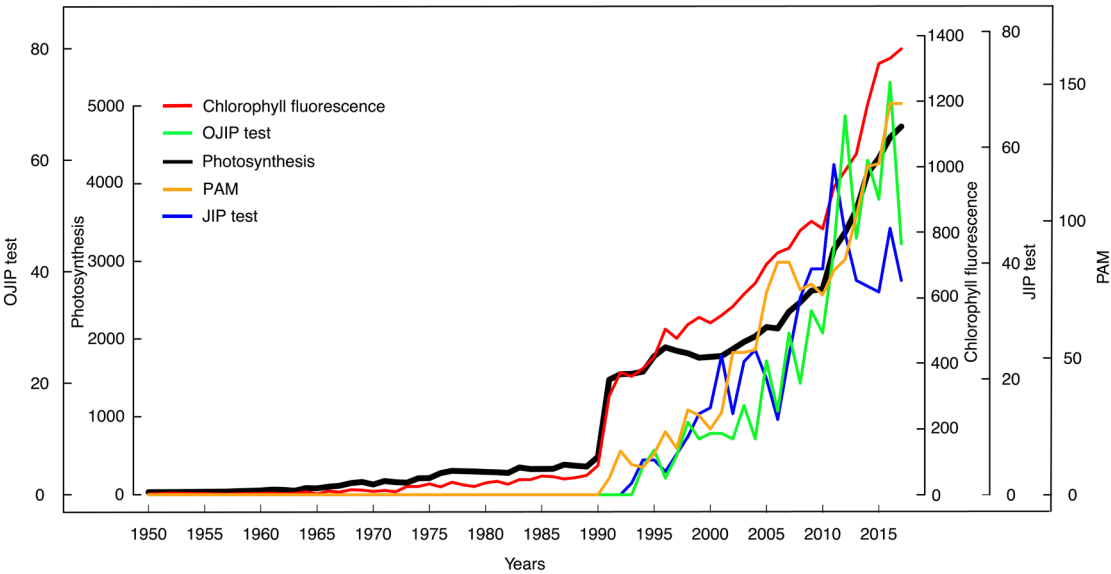


Fig. 1. The changes in number of publications from *Web of Science Core Collection* related to keywords: 'chlorophyll fluorescence', 'photosynthesis', 'JIP test', 'OJIP test', and 'PAM' (Pulse Amplitude Modulated Fluorescence).

Table 1. The number of chlorophyll fluorescence articles collected from *Web of Science Core Collection* database from the three studied periods: before 1994, 1995–2005, and 2006–2018.

Occurrence	Before 1994	1995–2005	2006–2018	Total
Keywords	524	6,307	12,497	19,328
Affiliations	269	2,260	5,886	8,415

articles from 973 journals. The trends in both research areas were very similar. The yearly growth rate in number of photosynthesis-related articles had increased slowly from below 100 in the period before 1990, then increased sharply (more than twenty times) between 1991–1995, and reached 4,000 in the 2015–2017 (Fig. 1).

The first article about ChlF in *Web of Science Core Collection* database was noted in 1947 and 474 articles were published until 1984. Then, the number of papers was increasing quickly: from 1,915 in the period before 1994 to 6,067 and 12,168 in the 1995–2005 and 2006–2018 periods, respectively. Inspection of Fig. 1 clearly indicates that this tremendous development of chlorophyll fluorescence science is related to appearance and rapid advances in modern fluorescence techniques, among them PAM chlorophyll fluorescence and variable chlorophyll fluorescence, especially elaboration of JIP test, which take the dominant position.

Ten top journals that contributed to 21.4% of all articles on this topic were: *Photosynthetica*, *Photosynthesis Research*, *Physiologia Plantarum*, *Plant Physiology*, *Journal of Plant Physiology*, *Biochimica et Biophysica Acta Bioenergetics*, *Plant Cell and Environment*, *Journal of Experimental Botany*, *Environmental and Experimental Botany*, and *Acta Physiologiae Plantarum* (Table 1S, supplement).

The similar trend is visible in keywords use (Table 1,

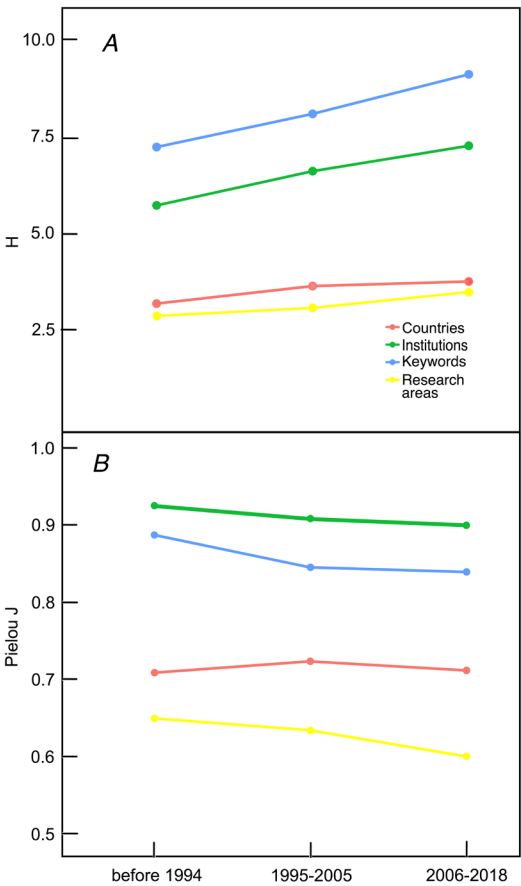


Fig. 2. Diversity (*Shannon's H'*) (A) and evenness (*Pielou's J'*) (B) of bibliometric data on countries, institutions, keywords and research areas on the basis of the 20,553 records from *Web of Science Core Collection* in three study periods: before 1994, 1995–2005, and 2006–2018.

Fig. 2). Number of keywords increased from 542 in the first analysed period (*i.e.*, before 1994) up to 12,497 in the 2006–2018. However, while the diversity, measured

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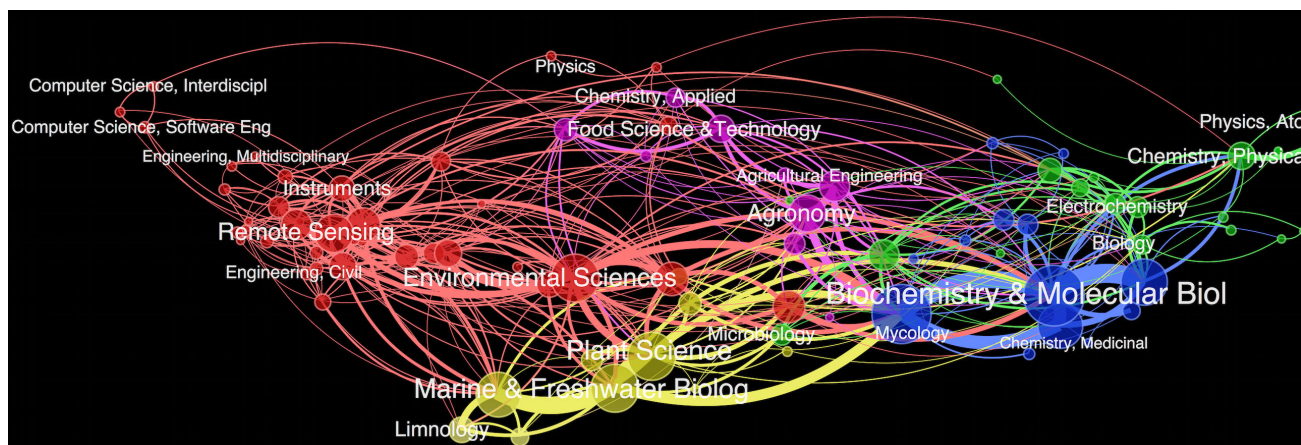


Fig. 5. The network map of co-occurrence of journals research areas for chlorophyll fluorescence articles published between 1995–2005. The networks include 50 most frequently occurred research areas in the studied period. The sizes of circles reflect the percentage of total papers published in journal classified to the particular research area, while the line thickness of the lines reflects the percentage of areas co-occurrence.

‘Chlorophyll fluorescence’, the most common term, which contribution ranged from 6 to 12%, was excluded from the analysis. Over three studied periods, the second most frequent keywords co-occurring with it was general term ‘photosynthesis’. Its frequency sharply increased in all studied periods from 392 before 1994 to 1,857 in 1995–2005 and 3,342 in 2006–2018. Among the next ten most commonly used terms, which all together represented 20–24% of all keywords during the compared periods were: ‘photosystem II’, ‘drought stress’, ‘plants’, ‘leaves’, ‘growth’, ‘light’, ‘photoinhibition’, ‘electron transport’, ‘xanthophyll cycle’, and ‘gas exchange’ (Table 2S, *supplement*). They were more frequently used in 1995–2005, as compared to the first study period. Additionally, ‘drought stress’ and ‘growth’ keywords use continues growing in the 2006–2018 period. The observed discrepancy between the absolute and relative frequency of keywords used is probably consequences of lack of data in period before 1994 and vigorous growth and specializations within discipline (Table 2S).

The analysis of co-occurrence of the 200 most frequent keywords in 1995–2005 and 2006–2018 periods confirmed a distinct structure of the CFR. In 1995–2005, the CFR researches focused on application of ChlF in detection of changes in structure of photosynthetic apparatus (red group in Fig. 3). The second research area was related to acclimatization of photosynthetic apparatus to excess light (violet group) and reaction to different environmental stresses in general (drought, UVB-radiation, low and high temperature; green group in Fig. 3). The distinct CFR branch belonging to agriculture research, focused on applicability of ChlF to increase photosynthetic productivity and crop production (blue group). The last group comprised articles focused both on crop plants and phytoplankton.

The quick progress and specialization within the branches of CFR is visible in the period of 2006–2018. The big group of basic research comprises articles focusing on different aspects of photosystem functioning

(nonphotochemical quenching, photosystem I, cyclic electron flow; green group in Fig. 4).

Although research on response of photosynthetic apparatus to drought stress is still dominant, the tremendous increase in a number of publications dealing with other types of stresses, *i.e.*, excess of light, high and low temperature or oxidative stress, is clearly visible.

Moreover, within environmental stress studies, a strong increase in studies on the reaction of photosynthetic apparatus and adaptation to other stresses, such as: salinity, heavy metals, and nutrient deficiency, was recorded (Fig. 4). In the contemporary CFR, the researchers investigate and compare the reaction(s) of photosynthetic apparatus across plants to different environmental factors on broad level of organization (ultrastructural to ecosystems), while taking into account plant taxonomic position (wheat, barley, maize, tomato), type of photosynthesis (C_3 , C_4 , CAM), genotypes, varieties, and mutants. More often, detailed insights into the structure, function, and dynamics of photosynthetic apparatus using ChlF is possible by comparison the photosynthetic performance of model plants – wild types and its mutants, *e.g.*, *Arabidopsis thaliana*.

The diverse applications of CFR, revealed on the keyword-based data trends, were confirmed, when we analysed the relationships among the research areas. The number of research areas grew from 57 in the period before 1994, to 82 in 1995–2005, and 102 in the 2006–2018 (Table 3S, *supplement*). In the second study period, apart from plant sciences, which took a dominant position, contributing to more than 49% of all publications in the area, the four main research areas of ChlF application can be distinguished: environmental sciences/remote sensing, marine and freshwater biology, biochemistry and molecular biology/biology, agronomy/food science and technology, and physical chemistry (Fig. 5, Table 3S).

In the 2006–2018 period, these groups are divided into several subdisciplines. In the contemporary CFR, geography/geochemistry and geophysics/remote sensing

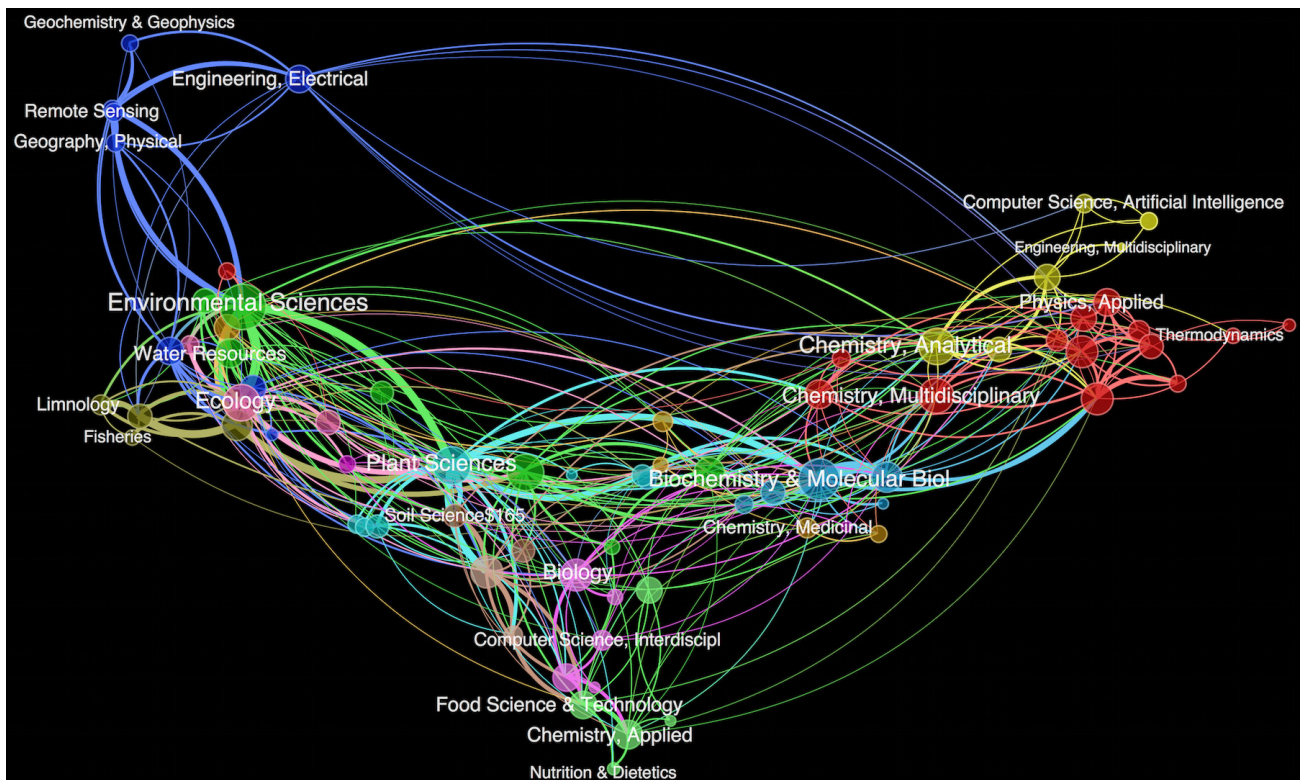


Fig. 6. The network map of co-occurrence of journals research areas for chlorophyll fluorescence articles published between 2006–2018. The networks include 50 most frequently occurred research areas in the studied period. The sizes of circles reflect the percentage of total papers published in journal classified to the particular research area, while the line thickness of the lines reflects the percentage of areas co-occurrence.

form the distinct research area with its own methodology and research techniques. Moreover, the stronger division and increase in number of publications were observed in the other subdisciplines. Environmental sciences formed

strong connections with ecology, limnology, water resource research, and fisheries. The plant sciences preserved its dominant position with strong connections with forestry, food science and technology, and biochemistry and

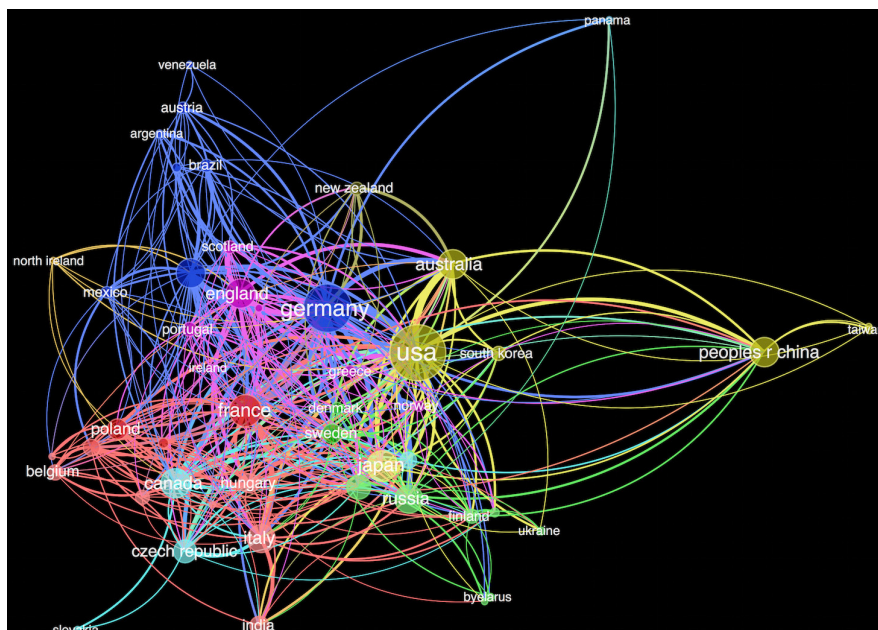


Fig. 7. The network map of country co-authorship network for chlorophyll fluorescence articles published between 1995–2005. The networks include 50 most frequently occurred countries in the studied period. The sizes of circles reflect the percentage of total papers published by authors from particular country, while the line thickness of the lines reflects the percentage of papers co-authorship.

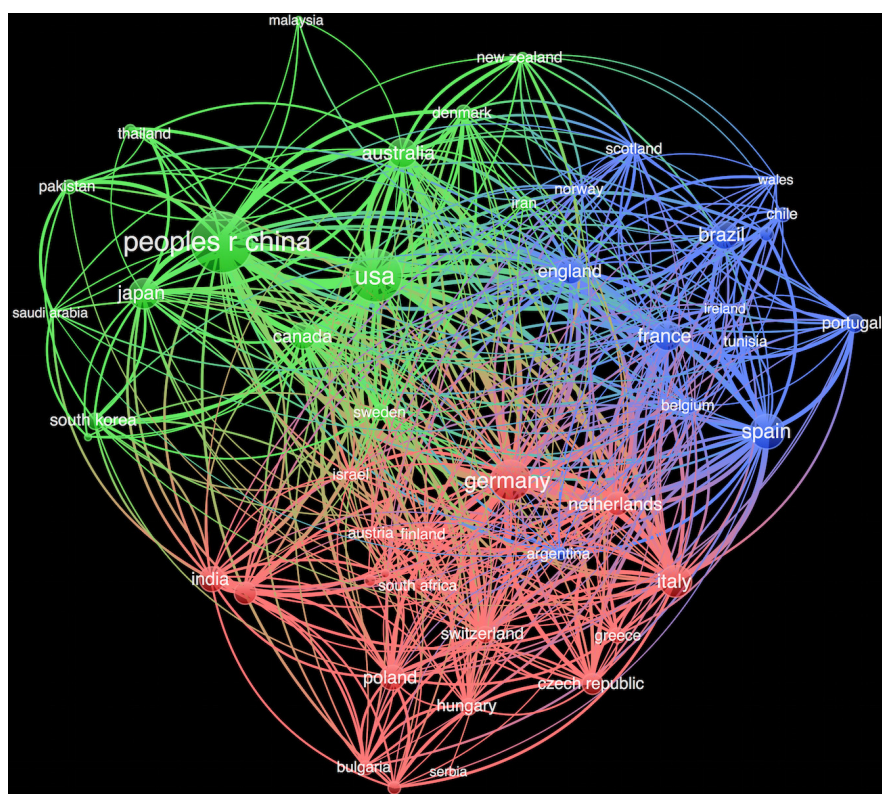


Fig. 8. The network map of country co-authorship network for chlorophyll fluorescence articles published between 2006–2018. The networks include 50 most frequently occurred countries in the studied period. The sizes of circles reflect the percentage of total papers published by authors from particular country, while the line thickness of the lines reflects the percentage of papers co-authorship.

molecular biology (Fig. 6, Table 3S). The last two groups formed research belonging to analytical chemistry and applied physics. The most interesting and promising trend in CFR is the formation of multidisciplinary disciplines, *i.e.*, ‘geochemistry multidisciplinary’, ‘chemistry multidisciplinary’, ‘engineering multidisciplinary’. Moreover, further progress in both base and applied CFR requires

elaboration of novel fluorescence techniques, fluorescence imaging, automation, and methods of big exploratory data analysis and artificial intelligence. This in turn imposes the stronger cooperation between biological and technological sciences which is clearly visible trend.

Analysis of number of publications and co-authorship by countries and research institutions enabled detailed

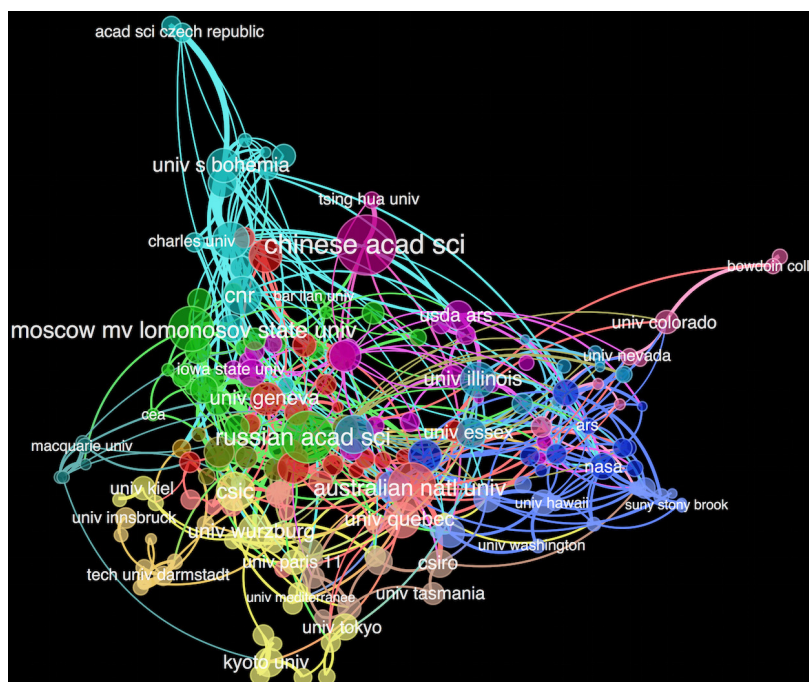


Fig. 9. The network map of institutional co-authorship network for chlorophyll fluorescence articles published between 1995–2005. The networks include 50 most frequently occurred institutions in the studied period. The sizes of circles reflect the percentage of total papers published by particular institution, while the line thickness of the lines reflects the percentage of papers co-authorship.

insights into scientific collaborations and relationships between countries and institutions. Before 1994, the strong domination of US, which contributed to more than 28% of all documents and citations published in this period, and UK, Germany, Canada, France, and Japan in CFR was visible (Table 4S, *supplement*). The inspection of the Fig 7. confirms the strong cooperation in the next study period among the authors from North America and East and West-European countries. The separate groups are formed by China, India, and Latin America countries.

The most astonishing changes are the increase in the number of publications from Chinese authors: from 5 with 87 citations before 1994 to over 2.5 thousand with more than 25,000 citations in the 2006–2018. The next positions belong to US and Germany with 1933 publications and 36,000 citations (Table 4S, Fig. 8).

In this period, the highest changes in author cooperations were noted: the stronger cooperation of Asian countries, Australia, New Zealand with China as a group leader. USA is a country with a stronger cooperation with China and West-European countries. Within Europe, two groups of researchers are formed: the first, which comprises France, UK, and Spain with close cooperation with Brazil, and the second comprising Germany, Netherlands, Italy, Switzerland, Bulgaria, Czech Republic, and Poland. Moreover, the distinct group is formed by India and Russian Federation (Fig. 8).

In the 1995–2005 period, the analysis of the co-authorship among research institutions revealed an interesting difference in contributions between large, national-range and highly structured research institutions, *i.e.*, the PRC and Russian Academy of Science, National Research Council (CNR, Italy), French National Center

for Scientific Research (CNRS) or Spanish National Research Council (CSIC) and universities. The first is characterized by a high number of published articles and closer within-institutional cooperations. The second model is represented by, *e.g.*, US universities with much higher total number of publications but lower scientific contribution per institution (Fig. 9).

In the 2006–2018, in terms of number of publications, the domination of PRC Academy of Science and stronger cooperation with other Chinese universities was observed. Moreover, a close cooperation of authors from Central European universities and scientific institutions is visible: Wageningen University, University of Amsterdam, Sheffield, Geneva, Czech Academy of Science. The separate groups are formed by (1) US, Spanish, and French institutions: University of Illinois, USDA, NASA, University of Paris 06, CNRS, CSIC; (2) Italian CNR and University of Florence; (3) Russian and Bulgarian Academies of Science with Lomonosov University in Moscow; (4) Japan universities: Tokyo University, Hokkaido, and Kyoto University; (5) Polish institutions: Polish Academy of Sciences, Warsaw University of Life Sciences (SGGW), and Jagiellonian University (Fig. 10, Table 5S, *supplement*). The highest number of papers (above 20) per one million citizens in 2006–2018 period was published in Denmark, Finland, Czech Republic, Australia, Switzerland, New Zealand, Netherlands, and Portugal (Table 6S, *supplement*).

Discussion

The primary goal of this review was to characterize the main themes in the contemporary CFR and to show

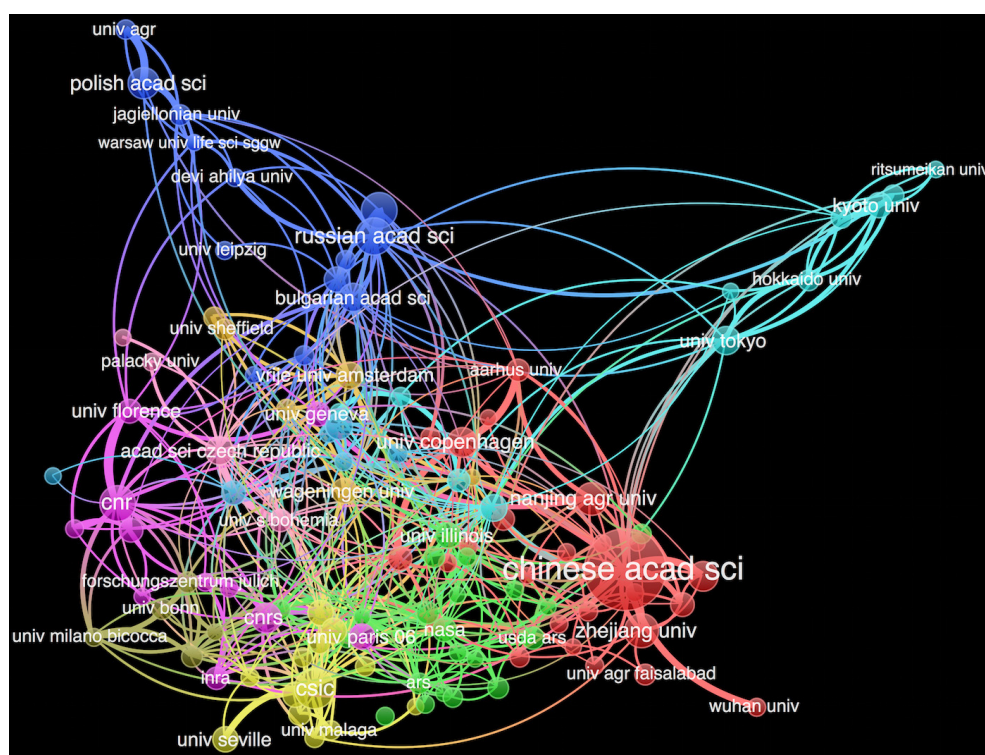


Fig. 10. The network map of institutional co-authorship network for chlorophyll fluorescence articles published between 2006–2018. The networks include 50 most frequently occurred institutions in the studied period. The sizes of circles reflect the percentage of total papers published by particular institution, while the line thickness of the lines reflects the percentage of papers co-authorship.

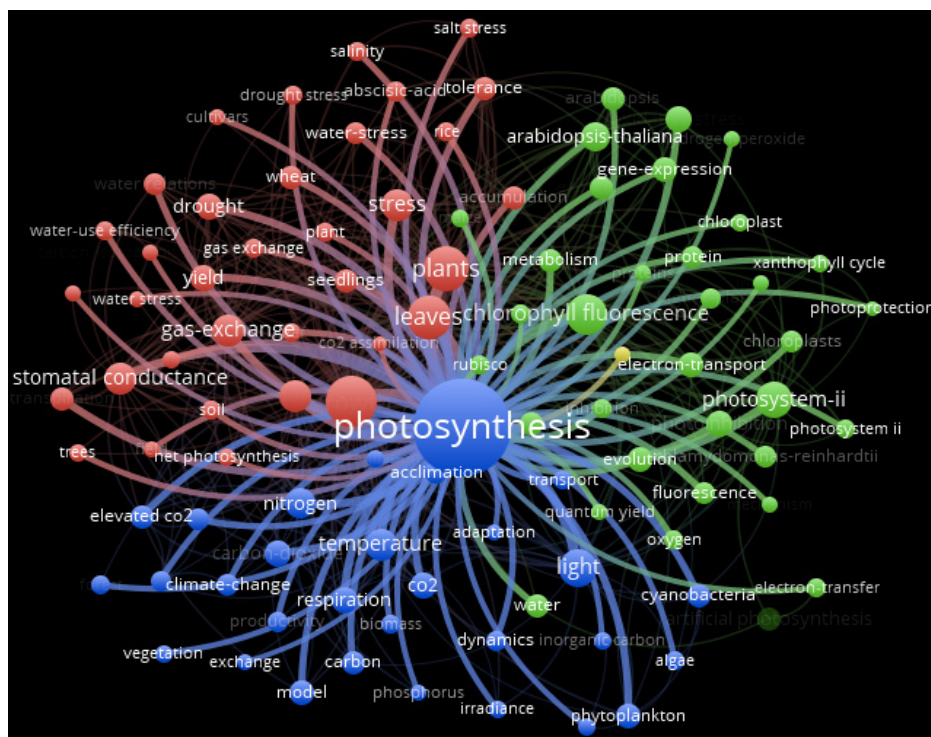


Fig. 11. The network map of keywords co-occurrence for photosynthesis articles published between 2006–2018. The networks include 200 most frequently used keywords in the studied period. The sizes of circles reflect the percentage of total papers published featuring particular keyword. The highlighted nodes are directly connected to the ‘photosynthesis’ keyword.

their changes during the 1995–2018. We confirmed that ChlF is not only an important and common tool (method) for nondestructive probing the various aspects of photosynthesis (Govindjee 1995, Govindjee *et al.* 2005, Papageorgiou and Govindjee 2004, Kalaji *et al.* 2017b) with plethora of applications across different disciplines. The contemporary CFR can be assumed as a novel branch of science, divided into range of subdisciplines: plant sciences, environmental sciences, ecology, agriculture, food science and technology, biochemistry and molecular biology, limnology, water resources research, and fisheries. Moreover, the distinct groups are formed by applied chemistry and applied physics. In the last years, geography, geochemistry, geophysics, and remote sensing are forming the distinct research area with its own methodology and research techniques. The accumulation of ChlF data caused the necessity of application and development of new exploratory methods for analysis of big data, *i.e.*, artificial intelligence (neural networks, support vector machines, *etc.*) (Goltsev *et al.* 2012, Kalaji *et al.* 2017a).

The number and diversity of keywords, disciplines, and research areas increased through the three study periods (Fig. 2). Interestingly, at the same time, the evenness index went down. This confirms, that although the more aspects and research areas appeared within CFR through time, there is still an increase in the proportion of main areas of chlorophyll science research, *i.e.*, plant sciences and environmental sciences.

The same trend is observed in scientific institutions. On one hand, the strong increase in number of institutions was noted (the European Union and US ‘diffuse net model’), on the other hand, the domination of the Chinese Academy of Science and other large national-range institutions:

Russian Academy of Science, Italian National Research Council (CNR), French National Centre for Scientific Research (CNRS), Indian Central Scientific Instruments Organisation (CSIO). The exception is Moscow Lomonosov State University with high contribution to the CFR.

However, when we compare the papers, which mostly influence the CFR discipline on the basis of 144 *Web of Science* ‘highly cited papers’, the resulted pattern was different. Among the ‘top ten’ world’s institutions were: US National Aeronautics Space Administration (NASA) (19), US California Institute of Technology (Caltech) (10), Spanish Consejo Superior de Investigaciones Científicas (CSIC) (10), French Centre National De La Recherche Scientifique (CNRS) (9), US Carnegie Institution For Science (8), French Alternative Energies and Atomic Energy Commission (CEA) (8), German Helmholtz Association (8), Institute National De La Recherche Agronomique (INRA) (8), and Polish Warsaw University of Life Sciences (SGGW) (8).

The slightly different pattern in a number of documents from different countries was observed. After slight increase in 1995–2005, a decrease was recorded to a near initial level. The contemporary domination of US, China, and Germany is observed, where US and German authors contributions to publications influence most the discipline (US: Hirsch index $h = 79$, highly cited papers 51, average citation per item 19.07; Germany: $h = 71$, highly cited papers 29; PRC: $h = 60$, highly cited papers 19, average citation per item 10.34).

In line with changes in contemporary science (Ladle *et al.* 2012), we confirmed the CFR as vigorously growing discipline as it was shown by number of published articles in leading journals and closer international collaboration

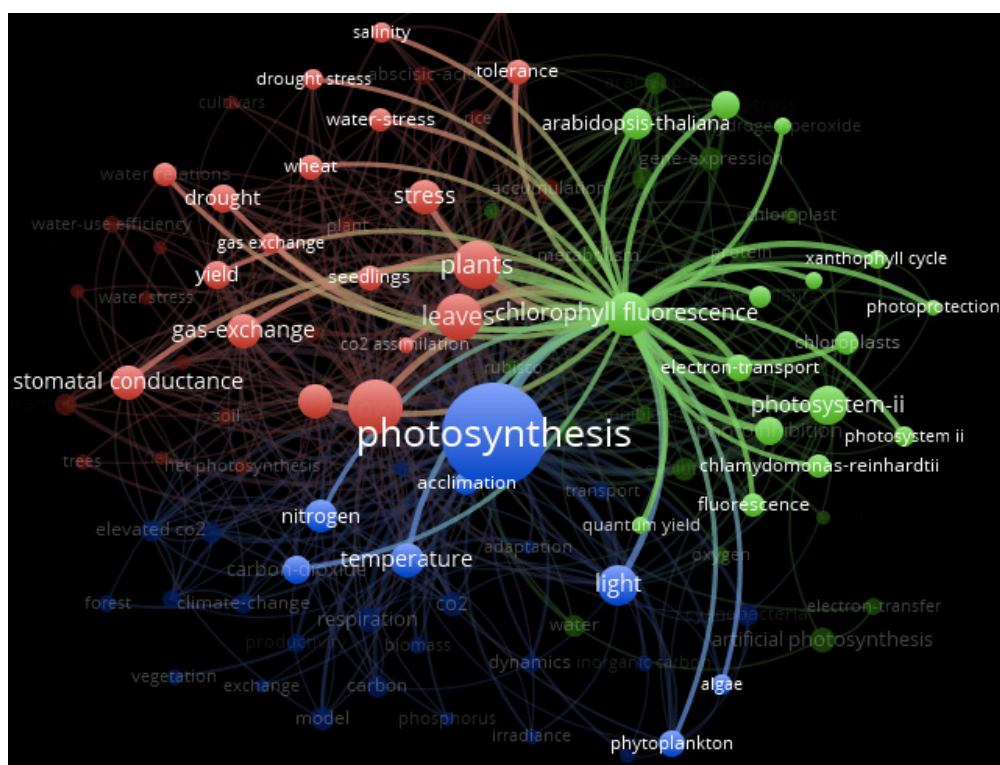


Fig. 12. The network map of keywords co-occurrence for 'photosynthesis' related articles published between 2006–2018. The networks include 200 most frequently used keywords in the studied period. The sizes of circles reflect the percentage of total papers published featuring particular keyword. We highlighted nodes that are directly connected to the 'chlorophyll fluorescence' key-word, in order to find the areas of photosynthesis researches not covered by chlorophyll fluorescence.

and specialization. The comparison of the keywords results of the query for 'chlorophyll fluorescence' and photosynthesis' (Figs. 3, 4, 11, 12), confirmed the tight relationship between photosynthesis and CFR. However, when we highlighted only the branches with the connections with 'chlorophyll fluorescence' keyword in Fig. 12, and analysed the ones confined only to 'photosynthesis', we obtained examples of areas of modern applications or potential future development of CFR: 'nutrient deficiency', 'climate change', 'elevated CO₂', 'vegetation', 'adaptation', 'dynamic' (adaptation and dynamic reaction of plants to environmental factors and stresses). This is often possible due to development and applications of novel technologies.

The FLuorescence EXplorer (FLEX) mission planned by the European Space Agency is intended to launch in 2020 in order to improve our understanding of the way carbon moves between plants and the atmosphere and how photosynthesis affects the carbon and water cycles. Moreover, it will enable to detect and widen the knowledge about effects of different types of stresses (drought, low temperature) on fluorescence and photosynthesis. For example, Walther *et al.* (2016) used space-borne sun-induced fluorescence for monitoring photosynthetic activity of boreal forest. Vialet-Chabrand *et al.* (2017) studied the effect of light fluctuations on plant phenotype and acclimatory response. Joiner *et al.* (2014) tested the application of satellite fluorescence to capture the seasonality in gross primary productivity of terrestrial vegetation, and Samborska *et al.* (2018) presented the combination of confocal microscopy and chlorophyll fluorescence analyses in early detection of magnesium

deficiency. Moreover, Kalaji *et al.* (2017a) used ChlF and statistical procedure combining Principal Component Analysis, hierarchical k-means classification and machine learning methods (super-organizing maps) for automatic identification of nutrient status of plants in field conditions.

At the end of this review, it should be emphasized the significant contribution of articles published in *Photosynthetica*, the oldest existing journal specialized to CFR, to growth and development of the discipline (Govindjee *et al.* 2002).

References

- Abid G., M'hamdi M., Mingeot D. *et al.*: Effect of drought stress on chlorophyll fluorescence, antioxidant enzyme activities and gene expression patterns in faba bean (*Vicia faba* L.). – *Arch. Agron. Soil Sci.* **63**: 536-552, 2017.
- Alam B., Nair D., Jacob J.: Low temperature stress modifies the photochemical efficiency of a tropical tree species *Hevea brasiliensis*: effects of varying concentration of CO₂ and photon flux density. – *Photosynthetica* **43**: 247-252, 2005.
- Allel D., Ben-Amar A., Abdelly C.: Leaf photosynthesis, chlorophyll fluorescence and ion content of barley (*Hordeum vulgare*) in response to salinity. – *J. Plant Nutr.* **41**: 497-508, 2018.
- Azevedo H., Pinto C.G.G., Fernandes J. *et al.*: Cadmium effects on sunflower growth and photosynthesis. – *J. Plant Nutr.* **28**: 2211-2220, 2005.
- Bąba W., Kalaji H.M., Kompała-Bąba A., Goltsev V.: Acclimatization of photosynthetic apparatus of tor grass (*Brachypodium pinnatum*) during expansion. – *PLoS ONE* **11**: e0156201, 2016.
- Bąba W., Kurowska M., Kompała-Bąba A. *et al.*: Genetic diversity of populations of *Brachypodium pinnatum* (L.) P.

- Beauv.: expansive grass in a fragmented landscape. – *Pol. J. Ecol.* **60**: 31-40, 2012.
- Baker N., Rosenqvist E.: Applications of chlorophyll fluorescence can improve crop production strategies: an examination of future possibilities. – *J. Exp. Bot.* **55**: 1607-1621, 2004.
- Bałaży K., Trudnowska E., Wichorowski M., Błachowiak-Samołyk K.: Large versus small zooplankton in relation to temperature in the Arctic shelf region. – *Polar Res.* **37**: 1427409, 2018.
- Baycu G., Gevrek-Kürtüm N., Moustaka J. *et al.*: Cadmium-zinc accumulation and photosystem II responses of *Noccaea caerulea* to Cd and Zn exposure. – *Environ. Sci. Pollut. R.* **24**: 2840-2850, 2017.
- Blankenship R.E.: *Molecular Mechanisms of Photosynthesis*. Pp. 312. Wiley-Blackwell, Chichester 2014.
- Brestič M., Živčák M., Kalaji H.M. *et al.*: Photosystem II thermostability *in situ*: Environmentally induced acclimation and genotype-specific reactions in *Triticum aestivum* L. – *Plant Physiol. Bioch.* **57**: 93-105, 2012.
- Bussotti F.: Assessment of stress conditions in *Quercus ilex* L. leaves by O-J-I-P chlorophyll alpha fluorescence analysis. – *Plant Biosyst.* **138**: 101-109, 2004.
- Cai S., Xu D.: Light intensity-dependent reversible down-regulation and irreversible damage of PSII in soybean leaves. – *Plant Sci.* **163**: 847-853, 2002.
- Cetner M.D., Kalaji H.M., Goltsev V. *et al.*: Effects of nitrogen-deficiency on efficiency of light-harvesting apparatus in radish. – *Plant Physiol. Bioch.* **119**: 81-92, 2017.
- Dąbrowski P., Baczewska A.H., Pawluskiewicz B. *et al.*: Prompt chlorophyll *a* fluorescence as a rapid tool for diagnostic changes in PSII structure inhibited by salt stress in perennial ryegrass. – *J. Photoch. Photobio. B* **157**: 22-31, 2016.
- Drusch M., Moreno J., Del Bello U. *et al.*: The FLuorescence EXplorer mission concept – ESA's Earth Explorer 8. – *IEEE T. Geosci. Remote* **55**: 1273-1284, 2017.
- Ferrell J., Earl H., Vencill W.: The effect of selected herbicides on CO₂ assimilation, chlorophyll fluorescence, and stomatal conductance in johnsongrass (*Sorghum halepense* L.). – *Weed Sci.* **51**: 28-31, 2003.
- Goltsev V., Zaharieva I., Chernev P. *et al.*: Drought-induced modifications of photosynthetic electron transport in intact leaves: Analysis and use of neural networks as a tool for a rapid non-invasive estimation. – *BBA-Bioenergetics* **1817**: 1490-1498, 2012.
- Goltsev V., Zaharieva I., Chernev P., Strasser R.J.: Delayed fluorescence in photosynthesis. – *Photosynth. Res.* **101**: 217-232, 2009.
- Goltsev V.N., Kalaji H.M., Paunov M. *et al.*: Variable chlorophyll fluorescence and its use for assessing physiological condition of plant photosynthetic apparatus. – *Russ. J. Plant Physiol+* **63**: 869-893, 2016.
- Govindjee: Sixty-three years since Kautsky: Chlorophyll *a* fluorescence. – *Aust. J. Plant Physiol.* **22**: 131-160, 1995.
- Govindjee, Beatty T., Gest H., Allen J.F.: *Discoveries in Photosynthesis. Advances in Photosynthesis and Respiration*. Pp. 1304. Springer, Dordrecht 2005.
- Govindjee, Šesták, Z., Peters, W.R.: The early history of "Photosynthetica", "Photosynthesis Research" and their publishers. – *Photosynthetica* **40**: 1-11, 2002.
- Holub O., Seufferheld M., Gohlke C. *et al.*: Fluorescence lifetime imaging (FLI) in real-time – a new technique in photosynthesis research. – *Photosynthetica* **38**: 581-599, 2000.
- Jabłoński A.: Efficiency of anti-stokes fluorescence in dyes. – *Nature* **131**: 839-40, 1933.
- Joiner J., Yoshida Y., Vasilkov A.P. *et al.*: The seasonal cycle of satellite chlorophyll fluorescence observations and its relationship to vegetation phenology and ecosystem atmosphere carbon exchange. – *Remote Sens. Environ.* **152**: 375-391, 2014.
- Kalaji H.M., Bąba W., Gediga K. *et al.*: Chlorophyll fluorescence as a tool for nutrient status identification in rapeseed plants. – *Photosynth. Res.* **136**: 329-343, 2017a.
- Kalaji H.M., Goltsev V.N., Žuk-Golaszewska K. *et al.*: *Chlorophyll Fluorescence. Understanding Crop Performance: Basics and Applications*. Pp. 222. CRC Press, Boca Raton 2017c.
- Kalaji H.M., Jajoo A., Oukarroum A. *et al.*: Chlorophyll *a* fluorescence as a tool to monitor physiological status of plants under abiotic stress conditions. – *Acta Physiol. Plant.* **38**: 102-114, 2016.
- Kalaji H.M., Schansker G., Brestič M. *et al.*: Frequently asked questions about chlorophyll fluorescence, the sequel. – *Photosynth. Res.* **132**: 13-66, 2017b.
- Kalaji H.M., Schansker G., Ladle R.J. *et al.*: Frequently asked questions about *in vivo* chlorophyll fluorescence: practical issues. – *Photosynth. Res.* **122**: 121-158, 2014.
- Kautsky H., Hirsch A.: Neue Versuche zur Kohlensäureassimilation. – *Naturwissenschaften* **19**: 964, 1931.
- Kučerová J., Konôpková A., Pšidová E. *et al.*: Adaptive variation in physiological traits of beech provenances in Central Europe. – *iForest* **11**: 24-31, 2018.
- Ladle R.J., Todd P.A., Malhado A.C.M.: Assessing insularity in global science. – *Scientometrics* **93**: 745-750, 2012.
- Laisk A., Eichelmann H., Oja V. *et al.*: Photosystem II cycle and alternative electron flow in leaves. – *Plant Cell Physiol.* **47**: 972-983, 2006.
- Lapa G., Morandini F., Ferrat L.: Sap flow and photosynthetic response to climate and drought of *Pinus nigra* in a Mediterranean natural forest. – *Trees-Struct. Funct.* **31**: 1711-1721, 2017.
- Lazár D.: Chlorophyll *a* fluorescence induction. – *BBA-Bioenergetics* **1412**: 1-28, 1999.
- Lazár D.: Chlorophyll *a* fluorescence rise induced by high light illumination of dark-adapted plant tissue studied by means of a model of photosystem II and considering photosystem II heterogeneity. – *J. Theor. Biol.* **220**: 469-503, 2003.
- Lazár D.: The polyphasic chlorophyll *a* fluorescence rise measured under high intensity of exciting light. – *Funct. Plant Biol.* **33**: 9-30, 2006.
- Lazár D.: Modelling of light-induced chlorophyll *a* fluorescence rise (O-J-I-P transient) and changes in 820 nm-transmittance signal of photosynthesis. – *Photosynthetica* **47**: 483-498, 2009.
- Lazár D., Nauš J., Matoušková M., Flašarová M.: Mathematical modeling of changes in chlorophyll fluorescence induction caused by herbicides. – *Pestic. Biochem. Phys.* **57**: 200-210, 1997.
- Lazár D., Schansker G.: Models of chlorophyll *a* fluorescence transients. – In: Laisk A., Nedbal L., Govindjee (ed.): *Photosynthesis in silico: Understanding Complexity from Molecules to Ecosystems. Advances in Photosynthesis and Respiration*. Pp. 85-123. Springer, Dordrecht 2009.
- Lazár D., Tomek P., Ilik P., Nauš J.: Determination of the antenna heterogeneity of Photosystem II by direct simultaneous fitting of several fluorescence rise curves measured with DCMU at different light intensities. – *Photosynth. Res.* **68**: 247-57, 2001.
- Lebedeva G.V., Belyaeva N.E., Demin O.V. *et al.*: Kinetic model of primary photosynthetic processes in chloroplasts. Description of the fast phase of chlorophyll fluorescence induction under different light intensities. – *Biophysics* **47**: 968-980, 2002.

- Li S.-H., Ge Z.-M., Xie L.-N. *et al.*: Ecophysiological response of native and exotic salt marsh vegetation to waterlogging and salinity: Implications for the effects of sea-level rise. – *Sci. Rep.-UK* **8**: 2441-2453, 2018.
- Massacci A., Nabiev S.M., Pietrosanti L. *et al.*: Response of the photosynthetic apparatus of cotton (*Gossypium hirsutum*) to the onset of drought stress under field conditions studied by gas-exchange analysis and chlorophyll fluorescence imaging. – *Plant Physiol. Bioch.* **46**: 189-195, 2008.
- Munday J.G., Govindjee: Light-induced changes in the fluorescence yield of chlorophyll *a* *in vivo*. III. The dip and the peak of the fluorescence transient in *Chlorella pyrenoidosa*. – *Biophys. J.* **9**: 1-29, 1969.
- Oukarroum A., Goltsev V., Strasser R.J.: Temperature effects on pea plants probed by simultaneous measurements of the kinetics of prompt fluorescence, delayed fluorescence and modulated 820 nm reflection. – *PLoS ONE* **8**: e59433, 2013.
- Papageorgiou G.C., Govindjee: Chlorophyll *a* Fluorescence: A Signature of Photosynthesis. *Advances in Photosynthesis and Respiration*. Pp. 818. Springer, Dordrecht 2004.
- Persson O., Danell R., Schneider J.: How to use Bibexcel for various types of bibliometric analysis. – In: Åström F., Danell R., Larsen B., Schneider J. (ed.): *Celebrating Scholarly Communication Studies: A Festschrift for Olle Persson at His 60th Birthday*. Pp. 9-24. International Society for Scientometrics and Informetrics, Leuven 2009.
- Pflug E.E., Buchmann N., Siegwolf R.T.W. *et al.*: Resilient leaf physiological response of European beech (*Fagus sylvatica* L.) to summer drought and drought release. – *Front. Plant Sci.* **9**: 187, 2018.
- Samborska I.A., Kalaji H.M., Sieczko L. *et al.*: Structural and functional disorder in the photosynthetic apparatus of radish plants under magnesium deficiency. – *Funct. Plant Biol.* **45**: 668-679, 2018.
- Schreiber U.: Pulse-amplitude-modulation (PAM) fluorometry and saturation pulse method: an overview. – In: Papageorgiou G.C., Govindjee (ed.): *Chlorophyll *a* Fluorescence: A Signature of Photosynthesis. Advances in Photosynthesis and Respiration*. Pp. 279-319. Springer, Dordrecht 2004.
- Schreiber U., Schliwa U., Bilger W.: Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. – *Photosynth. Res.* **10**: 51-62, 1986.
- Stirbet A., Govindjee: On the relation between the Kautsky effect (chlorophyll *a* fluorescence induction) and photosystem II: Basis and applications of the OJIP fluorescence transient. – *J. Photoch. Photobio. B* **104**: 236-257, 2011.
- Stirbet A., Govindjee: Chlorophyll *a* fluorescence induction: a personal perspective of the thermal phase, the J-I-P rise. – *Photosynth. Res.* **113**: 15-61, 2012.
- Stirbet A., Lazár D., Kromdijk J., Govindjee: Chlorophyll *a* fluorescence induction: Can just a one-second measurement be used to quantify abiotic stress responses? – *Photosynthetica* **56**: 86-104, 2018.
- Stirbet A., Riznichenko G.Y., Rubin A.B., Govindjee: Modeling chlorophyll *a* fluorescence transient: relation to photosynthesis. – *Biochemistry-Moscow* **79**: 291-323, 2014.
- Strasser B.J., Strasser R.J.: Measuring fast fluorescence transients to address environmental questions: The JIP test. – In: Mathis P. (ed.): *Photosynthesis: From Light to Biosphere*. Vol. 5. Pp. 977-980. Kluwer Academic Publishers, Dordrecht 1995.
- Strasser R.J., Govindjee: The F_o and the O-J-I-P fluorescence rise in higher plants and algae. – In: Argyroudi-Akoyunoglou J.H. (ed.): *Regulation of Chloroplast Biogenesis*. Pp. 423-26. Springer, Boston 1992.
- Strasser R.J., Tsimilli-Michael M., Qiang S., Goltsev V.: Simultaneous *in vivo* recording of prompt and delayed fluorescence and 820-nm reflection changes during drying and after rehydration of the resurrection plant *Haberlea rhodopensis*. – *BBA-Bioenergetics* **1797**: 1313-1326, 2010.
- Strasser R.J., Tsimilli-Michael M., Srivastava A.: Analysis of the chlorophyll *a* fluorescence transient. – In: Papageorgiou G.C., Govindjee (ed.): *Chlorophyll *a* Fluorescence: A Signature of Photosynthesis. Advances in Photosynthesis and Respiration*. Pp. 321-362. Springer, Dordrecht 2004.
- van Eck N.J., Waltman L.: VOS: A new method for visualizing similarities between objects. – In: Decker R., Lenz H.-J. (ed.): *Advanced Data Analysis*. Pp. 299-306. Springer, Berlin-Heidelberg 2007.
- van Eck N.J., Waltman L.: How to normalize cooccurrence data? An analysis of some well-known similarity measures. – *J. Assoc. Inf. Sci. Tech.* **60**: 1635-1651, 2009.
- van Eck N.J., Waltman L.: Visualizing bibliometric networks. – In: Ding Y., Rousseau R., Wolfram D. (ed.): *Measuring Scholarly Impact*. Pp. 285-320. Springer, Cham 2014.
- Violet-Chabrand S., Matthews J.S.A., Simkin A.J. *et al.*: Importance of fluctuations in light on plant photosynthetic acclimation. – *Plant Physiol.* **173**: 2163-2179, 2017.
- Vredenberg W.J.: A three-state model for energy trapping and chlorophyll fluorescence in photosystem II incorporating radical pair recombination. – *Biophys. J.* **79**: 26-38, 2000.
- Vredenberg W.J.: On the quantitative relation between dark kinetics of NPQ-induced changes in variable fluorescence and the activation state of the CF₀CF₁-ATPase in leaves. – *Photosynthetica* **56**: 139-149, 2018.
- Walther S., Voigt M., Thum T. *et al.*: Satellite chlorophyll fluorescence measurements reveal large-scale decoupling of photosynthesis and greenness dynamics in boreal evergreen forests. – *Glob. Change Biol.* **22**: 2979-2996, 2016.
- Zhu X.G., Govindjee, Baker N.R. *et al.*: Chlorophyll *a* fluorescence induction kinetics in leaves predicted from a model describing each discrete step of excitation energy and electron transfer associated with Photosystem II. – *Planta* **223**: 114-133, 2005.
- Živčák M., Brestič M., Kalaji H.M., Govindjee: Photosynthetic responses of sun- and shade-grown barley leaves to high light: is the lower PSII connectivity in shade leaves associated with protection against excess of light? – *Photosynth. Res.* **119**: 339-354, 2014.
- Žurek G., Rybka K., Pogrzeba M. *et al.*: Chlorophyll *a* fluorescence in evaluation of the effect of heavy metal soil contamination on perennial grasses. – *PLoS ONE* **9**: e91475, 2014.