

REVIEW

Chlorophyll fluorescence as a tool in cereal crop research

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Chlorophyll (Chl) fluorescence is a subtle reflection of primary reactions of photosynthesis. Intricate relationships between fluorescence kinetics and photosynthesis help our understanding of photosynthetic biophysical processes. Chl fluorescence technique is useful as a non-invasive tool in eco-physiological studies, and has extensively been used in assessing plant responses to environmental stress. The review gives a summary of some Chl fluorescence parameters currently used in studies of stress physiology of selected cereal crops, namely water stress, heat stress, salt stress, and chilling stress.

Additional key words: barley; chilling; drought; heat; maize; oat; rice; sorghum; salinity; stress; wheat.

Chlorophyll (Chl) fluorescence

Photon energy absorbed by photosynthetic pigments drives primary photochemical reactions. Energy conversion normally takes place with a high efficiency exceeding 90 % of absorbed quanta (Schreiber *et al.* 2000). Irradiation excites Chl molecules to a first excited singlet state stable for less than 10^{-8} s (Briantais *et al.* 1986, Holzwarth 1991) and charge separation at the reaction centre (RC) takes place within several picoseconds (Cogdell 1983, Glazer and Melis 1987, Andréasson and Vänngård 1988, Bolhär-Nordenkampf and Öquist 1993). If charge separation does not occur, excited pigment molecules return to ground level and absorbed energy is released as heat (radiation-less deactivation) and/or Chl fluorescence (Krause and Weis 1991). At room temperature, Chl fluorescence emanates from Chl *a* of photosystem 2 (PS2) and exhibits changes induced by dark/light transitions (Neubauer and Schreiber 1987, Schreiber and Neubauer 1990, Demmig-Adams and Adams 1992, Strasser *et al.* 1995). However, at liquid nitrogen temperature, the contribution of photosystem 1 (PS1) emission becomes very strong (Stahl *et al.* 1989). Chl fluorescence induction (Fig. 1) involves a fast transient (phase ODP) and a slow transient (phase SMT). Irradiation of a dark-adapted leaf is immediately followed by a fluorescence rise to a minimal level (F_0) emitted by antenna Chl molecules (Krause and Weis 1991). Then fluorescence rises to the peak level (P) *via* level I and dip

(D). The rise to level I denotes fluorescence emission due to decline of photochemistry as the PS2 acceptor Q_A becomes reduced and traps are closed (Schreiber and Bilger 1993, Rascher *et al.* 2000). In addition, two other steps occur in the fast kinetics involving the levels K and J, and the level J is closely related to level I (Guenther and Melis 1990, Klinkovský and Nauš 1994, Tomek *et al.* 2001). As electrons move to the plastoquinone pool *via* Q_B , a transient re-oxidation of Q_A^- occurs denoted by decline of Chl fluorescence to D (Kramer *et al.* 1995, Lazár 1999, Tomek *et al.* 2001). Under strong irradiation all traps become closed and Chl fluorescence rises to a maximal level (F_m). The maximal level can also be attained if no photochemistry is taking place in presence of 3-(3',4'-dichlorophenyl)-1,1-dimethylurea (DCMU) known to block electron transfer after the acceptor Q_A (Krause and Weis 1991). Fast Chl fluorescence transient yield known as variable fluorescence (F_v) equals Chl fluorescence rise from the minimal level F_0 to F_m (Krause and Weis 1991). The ratio F_v/F_m is proportional to potential maximal quantum yield of PS2 (Bolhär-Nordenkampf and Öquist 1993, Hormann *et al.* 1994), and the ratio F_v/F_0 is sensitive to environmental changes that affect efficiency to capture excitation energy by open PS2 RCs (Babani and Lichtenthaler 1996). As electrons are transferred to PS1 *via* cytochrome *b₆/f* complex and plastocyanin, a proton gradient is generated across

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thylakoid membranes (Horton and Bowyer 1990, Schreiber and Neubauer 1990) driving ATP synthesis and causing energy-dependent photochemical quenching (q_p) of Chl fluorescence *via* level S. Additional quenching known as non-photochemical quenching (q_{NP}) also occurs due to increased energy dissipation as heat (Bradbury and Baker 1981, Bilger and Schreiber 1986, Genty *et al.* 1989, Pospíšil 1997, Buschmann 1999, Samson *et al.* 1999). As carbon reduction proceeds and ATP and NADPH are consumed, Chl fluorescence rises to level M.

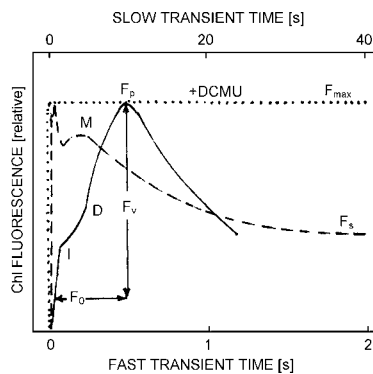


Fig. 1. Chlorophyll fluorescence induction curve. Fast transient (—), slow transient (---), fluorescence kinetics in presence of DCMU (· · ·). Minimal fluorescence intensity (F_0), inflection (I), dip (D), peak fluorescence intensity (F_p), variable fluorescence intensity (F_v), maximal fluorescence intensity (F_m), and steady-state fluorescence intensity (F_s).

Chl fluorescence then attains a steady-state level (T) that was also termed F_s (Lichtenthaler 1988). Chl fluorescence decline ratio (F_{dr}) defined as ($F_{dr} = F_m - F_T/F_m$) is determined by activity of the carbon reduction cycle (Baker *et al.* 1989, Bolhár-Nordenkamp and Öquist 1993,

Jiao *et al.* 2001). Chl fluorescence decrease ratio (Rfd) is also an important parameter defined as Chl fluorescence decrease over steady-state Chl fluorescence ($Rfd = F_d/F_s$) and introduced in the early 1980s (Lichtenthaler *et al.* 1986, Hantz and Lichtenthaler 1988, Lichtenthaler and Rinderle 1988). Rfd correlates to CO_2 fixation capacity, reflects photosynthetic performance under steady-state conditions more than other fluorescence parameters, and was hence termed vitality index (Lichtenthaler *et al.* 1986, Lichtenthaler 1988, Rinderle and Lichtenthaler 1988). Compared to F_v/F_m , the ratio F_d/F_s is a better parameter since the former is less sensitive as changes in its value occur only under strong stress. In addition, while F_v/F_m is measured in non-functional dark-adapted state, Rfd is measured in functional light-adapted state. Several reviews describe relationships between Chl fluorescence and photosynthesis (van der Veen 1951, Kautsky *et al.* 1960, Goedheer 1972, Kitajima and Butler 1975, Butler 1977, Walker 1985, Lichtenthaler 1988, van Kooten and Snel 1990, Krause and Weis 1991, Lichtenthaler 1990, 1992, Bolhár-Nordenkamp and Öquist 1993, Schreiber and Bilger 1993, 1998, Govindjee 1995, Joshi and Mohanty 1995, Schreiber 1998, Stürbet *et al.* 1998, Lazár 1999, Schreiber *et al.* 2000, Maxwell and Johnson 2002). Many reviews describe application of Chl fluorescence techniques in stress physiology (Lichtenthaler *et al.* 1986, 1988, Lichtenthaler and Rinderle 1988, Lichtenthaler 1990, Daley 1995, Guisse *et al.* 1995, Mohammed *et al.* 1995, Šesták and Šiffel 1997, Roháček and Barták 1999, Schreiber *et al.* 2000, Roháček 2002, Zakhidov *et al.* 2002). Furthermore, the future of Chl fluorescence application in stress research lies in the new Chl fluorescence imaging technique (Babani and Lichtenthaler 1996, Lichtenthaler and Miede 1997, Lichtenthaler and Babani 2000, Lichtenthaler *et al.* 2000, Buschmann *et al.* 2000).

Environmental stresses encountered by cereal crops

Water stress is the most common plant stress that is the bottleneck for agricultural development in many regions of the world. Although water stress is associated with regions with botanically ineffective rainfall (Sayed 2001), it may occur under adequate irrigation because plants experience transient water stress during midday hours (Schulze 1986, Sharp and Davies 1989, Mooney *et al.* 1991). Water stress disrupts membrane structure and causes organelle disarray. Deleterious effects of cellular water loss involve mechanical damage due to shrinking of the vacuole and severing of the cytosol from cell wall (Hsiao 1973, Bradford and Hsiao 1982, Schulze 1986, Sharp and Davies 1989, Davies and Zhang 1991, Ingram and Bartels 1996, Frensch 1997). Water exists as both an extra-membrane and intra-membrane component. Membrane water depends on lipid phase, protein hydrophilicity, and temperature (Quinn and Williams 1985, McKersie and Leshem 1994, Leshem 1997). Hence water loss seriously impairs both membrane structure and

function (Cave 1981, Crowe *et al.* 1984, Buchanan *et al.* 2000). When water stress is large enough to cause reduction of turgor, cell expansion is inhibited, vegetative growth is retarded, and carbon gain is reduced (Sharp and Davies 1989). Reduced turgor during reproductive growth leads to abortion of reproductive effort (Nilsen and Orcutt 1999). The impact of water stress on photosynthesis is caused by stomatal closure due to root-sourced and/or leaf-sourced abscisic acid (Davies *et al.* 1987, Sharp and Davies 1989, Davies and Zhang 1991). Water stress-induced stomatal closure depletes intercellular CO_2 leading to accumulation of energy-containing products of electron transport, build-up of free radicals, perturbation of light-harvesting complexes, and photoinhibition (Jones 1985). Under protracted water stress inhibition of photosynthesis involves increased permeability of chloroplast envelope, altered chloroplast ion concentration, and inhibition of CO_2 reduction (Quinn and Williams 1985). Moreover, water stress-induced

inhibition of Chl synthesis causes decrease in content of Chl *a/b* binding proteins leading to preferential reduction of the light-harvesting pigment-protein associated with PS2 (Jones 1985).

Heat stress: Although cereal crops generally tolerate temperatures prevailing in their native habitats, injury occurs when temperature exceeds climatic norms. High temperature affects crop yield by altering radiation interception and use, saccharide partitioning, and yield attributes. Heat stress-induced effects include denaturation of enzymes, alteration of membrane fluidity, unfolding of nucleic acids, and inhibition of electron transport (Quinn and Williams 1985, Sayed *et al.* 1986, 1989a,b, McKersie and Leshem 1994). Heat stress also enhances respiration to a rate exceeding that of photosynthesis causing depletion of saccharide reserve (Teiz and Zeiger 1991) and shortening the period of grain filling (Warrington *et al.* 1977, Shpiller and Blum 1991). In addition, a serious effect of heat stress on photosynthetic performance was envisaged by the discovery of thermal instability of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activase (Eckardt and Portis 1997, Feller *et al.* 1998, Crafts-Brendner and Salvucci 2000, Crafts-Brandner *et al.* 2000).

Salt stress: Saline irrigation water causes progressive salinisation of agricultural land and hampers agricultural productivity in many parts of the world. Saline habitats are those in which soil has a high content of soluble salts (Polyakoff-Mayber and Lerner 1994). Ions commonly found in excess in such soils include anions of chloride, sulphate, and bicarbonate, and cations of sodium, calcium, and magnesium (McKersie and Leshem 1994). Except for barley that possesses an ample degree of salt tolerance, other cereal crops are generally regarded as sensitive to salt stress (McKersie and Leshem 1994). Salt stress-induced effects in cereal crops include reduction of

water uptake by roots due to perturbation of osmotic equilibrium (Waisel *et al.* 1991, Blum and Johnson 1992, Polyakoff-Mayber and Lerner 1994), inhibition of cell expansion due to reduced turgor (Zidan *et al.* 1990, Cramer and Bowman 1991, Newman 1993), photosynthetic area reduction relative to respiratory mass due to salt-induced leaf tip burn and leaf necrosis (Cramer *et al.* 1988), and reduction of cell division due to inhibition of cytokinesis (Waisel 1991).

Chilling stress: Chilling injury occurs in absence of ice formation in the range 0–15 °C adversely affecting growth and development of cereal crops. Primary chilling injury includes metabolic dysfunctions that are reversed with return of temperature to the non-chilling range, whereas the secondary chilling injury includes irreversible metabolic dysfunctions (McKersie and Leshem 1994). During vegetative growth, seedlings are more sensitive to chilling stress than mature plants, and hence chilling injury is manifested by loss of vigour and stunted growth (McKersie and Leshem 1994). However, reproductive organs are most sensitive to chilling, and chilling stress detrimentally inhibits flowering and pollen production (Hume and Jackson 1981). On a cellular level, the major chilling stress-induced effect is membrane lipid phase transition (Murata 1983, Quinn and Williams 1985, Bishop 1986). Chilling-induced inhibition of photosynthesis is more severe when combined with high irradiance. This inhibition involves reduced stomata aperture and reduced CO₂ fixation (McWilliam *et al.* 1982, Guye and Wilson 1987). This inhibition also involves reduced electron transport *via* PS2 due to down-regulation of water splitting and degradation of the D1 protein of PS2 RC (Somersalo and Krause 1990, Krause and Weis 1991). Furthermore, several works reported photo-inhibition of PS1 in barley at chilling temperatures (Lichtenthaler *et al.* 1992, Tjus *et al.* 1998, 1999, Teicher *et al.* 2000).

Chl fluorescence in cereal crop research

Barley: Modulated Chl fluorescence techniques have successfully been used together with measurements of net CO₂ exchange and leaf water potential for rapid screening of barley (*Hordeum vulgare* L.) genotypes for drought tolerance (Nogués *et al.* 1994). Responses of barley to heat stress were assessed using Chl fluorescence temperature curves that proved useful in detecting heat injury of the photosynthetic apparatus at the level of thylakoid membranes (Nauš *et al.* 1992, Lazár and Ilík 1997, Ilík *et al.* 2000). Moreover, increased non-photochemical quenching is a good indicator of enhanced radiation-less dissipation of absorbed photons and hence heat-induced damage of PS2 RCs (Bukhov *et al.* 1997). Chl fluorescence kinetics has also been used to assess responses of barley to salt stress. Chl fluorescence induction kinetics particularly at point I of the induction curve can be used

to screen barley genotypes for salinity tolerance in laboratory experiments (Belkhodja *et al.* 1994, 1999). Chl fluorescence induction kinetics were used to study effects of salinity on photosynthetic pigment composition and stoichiometry in field-grown barley (Abadia *et al.* 1999), and salt stress-induced inhibition of PS2 (Fedina *et al.* 2002). In addition, photochemical quenching and measurements of oxygen evolution were used to assess chilling tolerance and acclimation of cold-hardened and non-hardened barley (Sicher *et al.* 1988, Herzog and Olszewski 1998). Moreover, Chl fluorescence quenching techniques have successfully been used to detect water stress in barley (Matoušková *et al.* 1999).

Maize: Measurements of photochemical and non-photochemical quenching of Chl fluorescence were used to test

water stress-tolerance in different maize (*Zea mays* L.) cultivars (Jovanovic *et al.* 1991). Chl fluorescence parameters were also useful in relating photosynthetic characteristics to morphological traits in maize (Selmani and Wassom 1991). Variable Chl fluorescence was successfully used as a technique for selection for water stress-tolerance in maize cultivars at an early stage of vegetative development (Saccardy *et al.* 1998, Mohammad and Sayed 2002). Fast Chl fluorescence induction kinetics were used in comparing heat-induced effects on radiation use and biomass allocation in maize cultivars from different habitats, and slow Chl fluorescence induction kinetics could be related to effects on carbon exchange rates, dry matter partitioning, and yield attributes (Lafitte and Edmeades 1997). For maize grown under chilling stress, F_v/F_m and Chl fluorescence quenching were useful in monitoring chilling injury (Hetherington and Öquist 1988), in studying maize recovery after exposure to chilling temperatures (Greer and Hardacre 1989), in characterising chilling-induced effects on photosynthetic machinery (Andrews *et al.* 1995, Pasda and Diepenbrock 1996, Aroca *et al.* 2001, Ying *et al.* 2002), in screening maize cultivars for cold tolerance (Schapendonk *et al.* 1989, Dory *et al.* 1990, Aguilera *et al.* 1999, Earla and Tollenaar 1999, Fracheboud *et al.* 1999, Janowiak *et al.* 2000), and in assessing potential acclimation to suboptimal temperatures (Verheul *et al.* 1995, Haldimann *et al.* 1996, Leipner *et al.* 1997, Koscielniak and Biesaga-Koscielniak 1999). Changes in fluorescence kinetics were used also for testing the effects of high temperature in maize (Jin *et al.* 2002).

Oat: Using the ratio F_v/F_m , cold acclimation and freezing tolerance of winter and spring oats (*Avena sativa* L.) could be evaluated and compared in relation to efficiency of excitation capture of PS2 RC and as a rapid method for screening oat cultivars for chilling tolerance (Herzog and Olszewski 1998).

Rice: Salinity-induced senescence in leaves of rice (*Oryza sativa* L.) cultivars differing in salt tolerance was investigated using variable Chl fluorescence that also proved useful in selecting salt-tolerant rice cultivars (Lutts *et al.* 1996). Chl fluorescence quenching was also used to study photosynthetic responses of rice cultivars possessing different potentials of salt tolerance. Chl fluorescence parameters suggested that salt sensitivity in rice is associated with increased shoot sodium levels, decreased photosynthetic efficiency of PS2, and enhanced non-photochemical quenching (Dionisio-Sese and Tobita 2000). Chilling tolerance in rice was also investigated using Chl fluorescence techniques: photochemical efficiency of rice and mechanisms involved in the ability to tolerate photo-oxidative damage under chilling stress could be assessed by the ratio F_v/F_m (Sthapit and Wilson 1992, Kima *et al.* 1997). This ratio was also used to assess

somaclonal variations related to improved chilling tolerance in rice (Bertin *et al.* 1997).

Sorghum: Water stress-induced effects were compared in sorghum (*Sorghum bicolor* L.) cultivars belonging to different parts of the world. These investigations involved simultaneous measurements of CO₂ assimilation and Chl fluorescence in intact leaves, and values were analysed in relation to photosynthetic electron transport and Chl-protein composition in chloroplasts isolated from leaves of these cultivars (Masojidek *et al.* 1991). Results proved that water stress decreased both CO₂ assimilation and electron transport, and that these effects were reflected in reduced Chl fluorescence induction kinetics indicating the value of fluorescence measurements in assessing water stress-induced effects in sorghum (Masojidek *et al.* 1991). Moreover, photochemical quenching and gas exchange were used to investigate photosynthetic performance in response to combined high irradiance and water stress in sorghum. Results indicated that under high irradiance, PS2 efficiency showed a mid-day decline enhanced by water deficit (Corlett *et al.* 1994). In addition, measured variable Chl fluorescence was used to relate salt stress-induced changes at the level of the thylakoid membrane, particularly changes in carotenoid composition, to an observed protection of the photosynthetic apparatus against salinity-induced photoinhibition (Sharma and Hall 1992).

Wheat: Quenching modulated Chl fluorescence was used for screening wheat (*Triticum aestivum* L.) cultivars for water stress tolerance. The easily measurable Chl fluorescence parameter $(FP - FS)/FS$ was used in practice to rapidly estimate the resistance of wheat genotypes to drought (Havaux *et al.* 1988). The same was also true for screening wheat (*Triticum durum* Desf.) for drought tolerance (Pastore *et al.* 1989, Ali *et al.* 1994, Flagella *et al.* 1994, 1996, Tambussi *et al.* 2002). In addition, in wheat, F_v/F_m was used to distinguish stomatal and non-stomatal limitations to photosynthesis under water stress (Kicheva *et al.* 1994), and to separate effects of water stress from photoinhibition (Lu and Zhang 1998). In field-grown wheat cultivars growing under water stress a high correlation existed between various Chl fluorescence indices and mean visual score for leaf vitality in the field during the anthesis-grain filling period (Balota and Lichtenthaler 1999). Moreover, photochemical quenching of modulated Chl fluorescence was used to assess ageing of wheat flag leaf in the field (Hong *et al.* 1999, Yang *et al.* 1999), and to evaluate PS2 photochemistry in wheat exposed to water stress (Lu and Zhang 1999). The ratio F_v/F_m was used to study effects of water stress on PS2 in wheat and components of the xanthophyll cycle (Shangguan *et al.* 2000, Nyachiro *et al.* 2001, Xu *et al.* 2001, Yordanov *et al.* 2001). Furthermore, heat tolerance of different wheat cultivars was investigated by this method. Variable

Chl fluorescence was useful in assessing photosynthetic responses of wheat to heat stress (Sayed *et al.* 1986, 1989b, 1994, Sayed 1992, Dash and Mohanty 2001). Genetic basis of inheritance of heat tolerance could also be characterised by analysing fluorescence profiles. These investigations indicated that recurrent selection based on Chl fluorescence analysis was an appropriate method of accumulating genes that favour heat tolerance in wheat (Moffatt *et al.* 1990). Moreover, Chl fluorescence was used for evaluating heat-induced inhibition and recovery of PS2 in field-grown wheat (Yucel *et al.* 1992), for studying photosynthetic activity and peroxidation of thylakoid lipids during heat-induced photoinhibition in isolated wheat chloroplasts (Mishra and Singhal 1993,

Park *et al.* 1994, Dash and Mohanty 2001), in elucidating effects of heat stress on photosynthesis in relation to heat tolerance of different green organs of wheat during grain-filling (Xu *et al.* 2001, Rekika *et al.* 2002), and in studying genotypic variations in assimilate utilisation during wheat maturation under heat stress and shock (Yang *et al.* 2002). In addition, analysis of Chl fluorescence induction curves indicated that photoinhibition of PS2 RC is the major effect of salt stress in wheat cultivars (Zhu *et al.* 2001), and that salt stress-induced inhibition of PS2 could be related to concomitant loss of variable Chl fluorescence (El-Shintinawy 2000). Chl fluorescence induction and quenching are reliable indicators of salt tolerance of wheat genotypes (Krishnaraj *et al.* 1993).

References

- Abadia, A., Belkhdja, R., Morales, F., Abadia, J.: Effects of salinity on the photosynthetic pigment composition of barley (*Hordeum vulgare* L.) grown under a triple-line-source sprinkler system in the field. – *J. Plant Physiol.* **154**: 392-400, 1999.
- Aguilera, C., Stirling, C.M., Long, S.P.: Genotypic variation within *Zea mays* for susceptibility to and rate of recovery from chill-induced photoinhibition of photosynthesis. – *Physiol. Plant.* **106**: 429-436, 1999.
- Ali, D.T., Monneveux, P., Acevedo, E., Nachit, M.: Evaluation of proline analysis and chlorophyll fluorescence quenching measurements as drought tolerance indicators in durum wheat (*Triticum turgidum* L. var. *durum*). – *Euphytica* **79**: 65-73, 1994.
- Andréasson, L.E., Vänngård, T.: Electron transport in photosystems I and II. – *Annu. Rev. Plant Physiol. Plant mol. Biol.* **39**: 379-411, 1988.
- Andrews, J.R., Fryer, M.J., Baker, N.B.: Characterization of chilling effects on photosynthetic performance of maize crops during early season growth using chlorophyll fluorescence. – *J. exp. Bot.* **46**: 1195-1203, 1995.
- Aroca, R., Irigoyen, J.J., Sánchez-Díaz, M.: Photosynthetic characteristics and protective mechanisms against oxidative stress during chilling and subsequent recovery in two maize varieties differing in chilling sensitivity. – *Plant Sci.* **161**: 719-726, 2001.
- Babani, F., Lichtenthaler, H.K.: Light-induced and age-dependent development of chloroplasts in etiolated barley leaves as visualized by determination of photosynthetic pigments, CO₂ assimilation rates and different kinds of chlorophyll fluorescence ratios. – *J. Plant Physiol.* **148**: 555-566, 1996.
- Baker, N.R., Bradbury, M., Farage, P.K., Ireland, C.R., Long, S.P.: Measurements of quantum yield of carbon assimilation and chlorophyll fluorescence for assessment of photosynthetic performance of crops in the field. – *Phil. Trans. roy. Soc. London B* **323**: 295-308, 1989.
- Balota, M., Lichtenthaler, H.K.: Red chlorophyll fluorescence as an ecophysiological method to assess the behaviour of wheat genotypes under drought and heat. – *Cereal Res. Commun.* **27**: 179-187, 1999.
- Belkhdja, R., Morales, F., Abadia, A., Gómez-Aparisi, J., Abadia, J.: Chlorophyll fluorescence as a possible tool for salinity tolerance screening in barley (*Hordeum vulgare* L.). – *Plant Physiol.* **104**: 667-673, 1994.
- Belkhdja, R., Morales, F., Abadia, A., Medrano, H., Abadia, J.: Effects of salinity on chlorophyll fluorescence and photosynthesis of barley (*Hordeum vulgare* L.) grown under a triple-line-source sprinkler system in the field. – *Photosynthetica* **36**: 375-387, 1999.
- Bertin, P., Bouharmont, J., Kinet, J.M.: Somaclonal variation and improvement of chilling tolerance in rice: Changes in chilling-induced chlorophyll fluorescence. – *Crop Sci.* **37**: 1727-1735, 1997.
- Bilger, W., Schreiber, U.: Energy-dependent quenching of dark-level chlorophyll fluorescence in intact leaves. – *Photosynth. Res.* **10**: 303-308, 1986.
- Bishop, D.G.: Chilling sensitivity in higher plants: The role of phosphatidylglycerol. – *Plant Cell Environ.* **9**: 613-616, 1986.
- Blum, A., Johnson, J.W.: Transfer of water from roots into dry soil and the effect on wheat water relations and growth. – *Plant Soil* **145**: 141-149, 1992.
- Bolhär-Nordenkamp, H.R., Oquist, G.O.: Chlorophyll fluorescence as a tool in photosynthesis research. – In: Hall, D.O., Scurlock, J.M.O., Bolhär-Nordenkamp, H.R., Leegood, R.C., Long, S.P. (ed.): *Photosynthesis and Production in a Changing Environment. A Field and Laboratory Manual*. Pp. 193-206. Chapman & Hall, London – Glasgow – New York – Tokyo – Melbourne – Madras 1993.
- Bradbury, M., Baker, N.R.: Analysis of the slow phases of the *in vivo* chlorophyll fluorescence induction curve. Changes in the redox state of photosystem II electron acceptors and fluorescence emission from photosystems I and II. – *Biochim. biophys. Acta* **63**: 542-551, 1981.
- Bradford, K.J., Hsiao, T.C.: Ecophysiological responses to moderate water stress. – In: *Encyclopedia of Plant Physiology*. Vol. 12B. Pp. 232-253. Springer-Verlag, Berlin 1982.
- Briantais, J.-M., Vernotte, C., Picaud, M., Krause, G.H.: A quantitative study of the slow decline of chlorophyll *a* fluorescence in isolated chloroplasts. – *Biochim. biophys. Acta* **548**: 128-138, 1979.
- Buchanan, B.B., Gruissem, W., Jones, R.L.: *Biochemistry and Molecular Biology of Plants*. – Amer. Soc. Plant Physiol., Rockville 2000.
- Bukhov, N.G., Boucher, N., Carpentier, R.: After effect of short-term heat shock on photosynthetic reactions in barley leaves. – *Fiziol. Rast.* **44**: 605-612, 1997.
- Buschmann, C.: Photochemical and non-photochemical quenching coefficients of the chlorophyll fluorescence:

- comparison of variation and limits. – *Photosynthetica* **37**: 217-224, 1999.
- Buschmann, C., Langsdorf, G., Lichtenthaler, H.K.: Imaging of the blue, green and red fluorescence emission of plants: An overview. – *Photosynthetica* **38**: 483-491, 2000.
- Butler, W.L.: Chlorophyll fluorescence: A probe for electron transfer and energy transfer. – In: Trebst, A., Avron, M. (ed.): *Photosynthesis I*. Pp. 149-166. Springer-Verlag, Berlin – Heidelberg – New York 1977.
- Cave, G.: Water and membranes: The interdependence of their physico-chemical properties in the case of phospholipid head groups. – *Stud. biophys.* **91**: 41-46, 1981.
- Cogdell, R.J.: Photosynthetic reaction centers. – *Annu. Rev. Plant Physiol.* **34**: 21-45, 1983.
- Corlett, J.E., Jones, H.G., Massacci, A., Masojidek, J.: Water deficit, leaf rolling and susceptibility to photoinhibition in field grown sorghum. – *Physiol. Plant.* **92**: 423-430, 1994.
- Crafts-Brandner, S.J., Salvucci, M.E.: Rubisco activase constrains the photosynthetic potential of leaves at high temperature. – *Proc. nat. Acad. Sci. USA* **97**: 13430-13435, 2000.
- Crafts-Brandner, S.J., van den Loo, F.J., Salvucci, M.E.: The two forms of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activase differ in sensitivity to elevated temperatures. – *Plant Physiol.* **114**: 439-444, 2000.
- Cramer, G.R., Bowman, D.C.: Kinetics of maize leaf elongation. I. Increased yield threshold limits short term steady state elongation rates after exposure to salinity. – *J. exp. Bot.* **42**: 1417-1426, 1991.
- Cramer, G.R., Epstein, E., Läuchli, A.: Kinetics of root elongation of maize in response to short-term exposure to NaCl and elevated calcium concentration. – *J. exp. Bot.* **39**: 1573-1582, 1988.
- Crowe, J.H., Crowe, L.M., Chapman, D.: Preservation of membranes in anhydrobiotic organisms. Role of trehalose. – *Science* **223**: 701-703, 1984.
- Daley, P.F.: Chlorophyll fluorescence analysis and imaging in plant stress and disease. – *Can. J. Plant Pathol.* **17**: 167-173, 1995.
- Dash, S., Mohanty, N.: Evaluation of assays for the analysis of thermo-tolerance and recovery potentials of seedlings of wheat (*Triticum aestivum* L.) cultivars. – *J. Plant Physiol.* **158**: 1153-1165, 2001.
- Davies, W.J., Schurr, U., Taylor, G., Zhang, J.: Hormones as chemical signals involved in root to shoot communication of effect of changes in the soil environment. – In: Hoad, G.U., Lenton, J.R., Atkin, R. (ed.): *Hormone Action in Plant Development*. Pp. 201-206. Butterworth, London 1987.
- Davies, W.J., Zhang, J.: Root signals and the regulation of growth and development in plants in drying soils. – *Annu. Rev. Plant Physiol. Plant mol. Biol.* **42**: 55-70, 1991.
- Demmig-Adams, B., Adams, W.W., III: Photoprotection and other responses of plants to high light stress. – *Annu. Rev. Plant Physiol. Plant mol. Biol.* **43**: 599-626, 1992.
- Dionisio-Sese, M.L., Tobita, S.: Effects of salinity on sodium content and photosynthetic responses of rice seedlings differing in salt tolerance. – *J. Plant Physiol.* **157**: 54-58, 2000.
- Dory, I., Boddi, B., Kissimon, J., Paldi, E.: Cold stress responses of inbred maize lines with various degrees of cold tolerance. – *Acta agron. hung.* **39**: 309-318, 1990.
- Earla, H.J., Tollenaar, M.: Using chlorophyll fluorometry to compare photosynthetic performance of commercial maize (*Zea mays* L.) hybrids in the field. – *Field Crops Res.* **61**: 201-210, 1999.
- Eckardt, N.A., Portis, A.R.: Heat denaturation profiles of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and Rubisco activase and the inability of Rubisco activase to restore activity of heat-denatured Rubisco. – *Plant Physiol.* **113**: 243-248, 1997.
- El-Shintinawy, F.: Photosynthesis in two wheat cultivars differing in salt susceptibility. – *Photosynthetica* **38**: 615-620, 2000.
- Fedina, I.S., Georgieva, K., Grigorova, I.: Light-dark changes in proline content of barley leaves under salt stress. – *Biol. Plant.* **45**: 59-63, 2002.
- Feller, U., Crafts-Brandner, S.J., Salvucci, M.E.: Moderately high temperatures inhibit ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activase mediated activation of Rubisco. – *Plant Physiol.* **116**: 539-546, 1998.
- Flagella, Z., Campanile, R.G., Ronga, G., Stoppelli, M.C., Pastore, D., De Caro, A., Di Fonzo, N.: The maintenance of photosynthetic electron transport in relation to osmotic adjustment in durum wheat cultivars differing in drought resistance. – *Plant Sci.* **118**: 127-133, 1996.
- Flagella, Z., Pastore, D., Campanile, R.G., Di Fonzo, N.: Photochemical quenching of chlorophyll fluorescence and drought tolerance in different durum wheat (*Triticum durum*) cultivars. – *J. agr. Sci.* **122**: 183-192, 1994.
- Fracheboud, Y., Haldimann, P., Leipner, J., Stamp, P.: Chlorophyll fluorescence as a selection tool for cold tolerance of photosynthesis in maize (*Zea mays* L.). – *J. exp. Bot.* **50**: 1533-1540, 1999.
- Frensch, J.: Primary responses of root and leaf elongation to water deficits in the atmosphere and soil solution. – *J. exp. Bot.* **48**: 985-999, 1997.
- Genty, B., Briantais, J.-M., Baker, N.R.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – *Biochim. biophys. Acta* **990**: 87-92, 1989.
- Glazer, A.N., Melis, A.: Photochemical reaction centers: structure, organization, and function. – *Annu. Rev. Plant Physiol.* **38**: 11-45, 1987.
- Goedheer, J.C.: Fluorescence in relation to photosynthesis. – *Annu. Rev. Plant Physiol.* **23**: 87-112, 1972.
- Govindjee: Sixty-three years since Kautsky: Chlorophyll *a* fluorescence. – *Aust. J. Plant Physiol.* **22**: 131-160, 1995.
- Greer, D.H., Hardacre, A.K.: Photoinhibition of photosynthesis and its recovery in two maize hybrids varying in low temperature tolerance. – *Aust. J. Plant Physiol.* **16**: 189-198, 1989.
- Guenther, J.E., Melis, A.: Dynamics of photosystem II heterogeneity in *Dunaliella salina* (green algae). – *Photosynth. Res.* **23**: 195-203, 1990.
- Guisse, B., Srivastava, A., Strasser, R.J.: The polyphasic rise of the chlorophyll *a* fluorescence (O-K-J-I-P) in heat-stressed leaves. – *Arch. Sci.* **48**: 147-160, 1995.
- Guye, M.G., Wilson, J.M.: The effects of chilling and chill-hardening temperatures on stomatal behaviour in a range of chilling-sensitive species and cultivars. – *Plant Physiol. Biochem.* **25**: 717-721, 1987.
- Haiz, M., Lichtenthaler, H.K.: The measurement of Rfd-values as plant vitality indices with the portable field fluorometer and the PAM-fluorometer. – In: Lichtenthaler, H.K. (ed.): *Applications of Chlorophyll Fluorescence*. Pp. 249-254. Kluwer Academic Publishers, Dordrecht – Boston – London 1988.
- Haldimann, P., Fracheboud, Y., Stamp, P.: Photosynthetic performance and resistance to photoinhibition of *Zea mays* L. leaves grown at sub-optimal temperature. – *Plant Cell Environ.* **19**: 85-92, 1996.

- Havaux, M., Erne, M., Lannoye, R.: Sélection de variétés de blé dur (*Triticum durum* Desf.) and de blé tendre (*Triticum aestivum* L.) adaptées à la sécheresse par la mesure de l'extinction de la fluorescence de la chlorophylle *in vivo*. – *Agronomie* **8**: 193-199, 1988.
- Herzog, H., Olszewski, A.: A rapid method for measuring freezing resistance in crop plants. – *J. Agron. Crop Sci.* **181**: 71-79, 1998.
- Hetherington, S.E., Öquist, G.: Monitoring chilling injury: comparison of chlorophyll fluorescence measurements, post-chilling growth and visible symptoms of injury in *Zea mays*. – *Physiol. Plant.* **72**: 241-247, 1988.
- Holzwarth, A.R.: Excited-state kinetics in chlorophyll systems and its relationship to the functional organization of the photosystems. – In: Scheer, H. (ed.): *Chlorophylls*. Pp. 1125-1151. CRC Press, Boca Raton – Ann Arbor – Boston – London 1991.
- Hong, S.-S., Hong, T., Jiang, H., Xu, D.-Q.: Changes in the non-photochemical quenching of chlorophyll fluorescence during aging of wheat flag leaves. – *Photosynthetica* **36**: 621-625, 1999.
- Hormann, H., Neubauer, C., Schreiber, U.: On the relationship between chlorophyll fluorescence quenching and the quantum yield of electron transport in isolated thylakoids. – *Photosynth. Res.* **40**: 93-106, 1994.
- Horton, P., Bowyer, J.: Chlorophyll fluorescence transients. – In: Harwood, J., Bowyer, J.R. (ed.): *Methods in Plant Biochemistry*. Pp. 259-296. Academic Press, London 1990.
- Hsiao, T.C.: Plant responses to water stress. – *Annu. Rev. Plant Physiol.* **24**: 519-570, 1973.
- Hume, D.J., Jackson, A.K.: Pod formation in soybeans at low temperature. – *Genetica* **31**: 1-20, 1981.
- Ilik, P., Kouril, R., Fiala, J., Nauš, J., Vacha, F.: Spectral characterization of chlorophyll fluorescence in barley leaves during linear heating. Analysis of high-temperature fluorescence rise around 60°C. – *J. Photochem. Photobiol.* **59**: 103-114, 2000.
- Ingram, J., Bartels, D.: The molecular basis of dehydration tolerance in plants. – *Annu. Rev. Plant Physiol. Plant mol. Biol.* **47**: 377-403, 1996.
- Janowiak, F., Adamczyk, J., Krolikowski, Z.: Differentiation of chilling tolerance among Polish maize lines as measured by chlorophyll fluorescence method. – In: *Proc. 3rd Int. Congress Ecophysiological Aspects of Plant Responses to Stress Factors*. Kraków 2000.
- Jin, M.-X., Li, D.-Y., Mi, H.: Effects of high temperature on chlorophyll fluorescence induction and the kinetics of far red radiation-induced relaxation of apparent F_0 in maize leaves. – *Photosynthetica* **40**: 581-586, 2002.
- Jiao, D.-M., Li, X., Huang, X.-Q., Chi, W., Kuang, T.-Y., Zhang, Q.-D., Ku, M.S.B.: Characteristics of carbon assimilation and chlorophyll fluorescence in C_4 photosynthetic enzymes transgenic rice. – *Photosynth. Res.* **69**: 238, 2001.
- Jones, C.A.: *C₄ Grasses and Cereals*. – John Wiley & Sons, New York 1985.
- Joshi, M.K., Mohanty, P.: Probing photosynthetic performance by chlorophyll *a* fluorescence: Analysis and interpretation of fluorescence parameters. – *J. sci. ind. Res.* **54**: 155-174, 1995.
- Jovanovic, L., Veljovic, S., Janjic, V.: Water regime and photosynthesis parameters in two maize lines differing in drought susceptibility. – *Biol. Vest.* **39**: 103-108, 1991.
- Kautsky, H., Appel, W., Amann, H.: Chlorophyllfluoreszenz und Kohlensäureassimilation. – *Biochem. Z.* **322**: 277-292, 1960.
- Kicheva, M.I., Tsonev, T.D., Popova, L.P.: Stomatal and non-stomatal limitations to photosynthesis in two wheat cultivars subjected to water stress. – *Photosynthetica* **30**: 107-116, 1994.
- Kima, J.H., Hwanga, H.J., Parka, H.S., Leeb, C.B., Myungc, K.Y., Lee, C.H.: Differences in the rate of dephosphorylation of thylakoid proteins during dark incubation after chilling in the light between two rice (*Oryza sativa* L.) varieties. – *Plant Sci.* **128**: 159-168, 1997.
- Kitajima, M., Butler, W.L.: Quenching of chlorophyll fluorescence and primary photochemistry in chloroplasts by dibromothymoquinone. – *Biochim. biophys. Acta* **376**: 105-115, 1975.
- Klinkovský, T., Nauš, J.: Sensitivity of the relative F_{pi} level of chlorophyll fluorescence induction in leaves to the heat stress. – *Photosynth. Res.* **39**: 201-204, 1994.
- Koscielniak, J., Biesaga-Koscielniak, J.: Effects of exposure to short periods of suboptimal temperature during chill (5C) on gas exchange and chlorophyll fluorescence in maize seedlings (*Zea mays* L.). – *J. Agron. Crop Sci.* **183**: 231-241, 1999.
- Kramer, D.M., DiMarco, G., Loreto, F.: Contribution of plastoquinone quenching to saturation pulse-induced rise of chlorophyll fluorescence in leaves. – In: Mathis, P. (ed.): *Photosynthesis: From Light to Biosphere*. Vol. I. Pp. 147-150. Kluwer Scientific Publishers, Dordrecht – Boston – London 1995.
- Krause, G.H., Weis, E.: Chlorophyll fluorescence and photosynthesis. The basics. – *Annu. Rev. Plant Physiol. Plant mol. Biol.* **42**: 313-349, 1991.
- Krishnaraj, S., Mawson, B.T., Yeung, E.C., Thorpe, T.A.: Utilization of induction and quenching kinetics of chlorophyll *a* fluorescence for *in vivo* salinity screening studies in wheat (*Triticum aestivum* vars. Kharchia-65 and Fielder). – *Can. J. Bot.* **71**: 87-92, 1993.
- Lafitte, H.R., Edmeades, G.O.: Temperature effects on radiation use and biomass partitioning in diverse maize cultivars. – *Field Crops Res.* **49**: 231-247, 1997.
- Lazár, D.: Chlorophyll *a* fluorescence induction. – *Biochim. biophys. Acta* **1412**: 1-28, 1999.
- Lazár, D., Ilik, P.: High-temperature induced chlorophyll fluorescence changes in barley leaves. Comparison of the critical temperatures determined from fluorescence induction and from fluorescence temperature curve. – *Plant Sci.* **124**: 159-164, 1997.
- Leipner, J., Fracheboud, Y., Stamp, P.: Acclimation by suboptimal growth temperature diminishes photooxidative damage in maize leaves. – *Plant Cell Environ.* **20**: 366-372, 1997.
- Leshem, Y.Y.: *Plant Membranes. Biophysical Approach to Membrane Structure and Function*. – Kluwer Academic Publishers, Dordrecht 1997.
- Lichtenthaler, H.K.: *In vivo* chlorophyll fluorescence as a tool for stress detection in plants. – In: Lichtenthaler, H.K. (ed.): *Applications of Chlorophyll Fluorescence*. Pp. 129-142. Kluwer Academic Publishers, Dordrecht – Boston – London 1988.
- Lichtenthaler, H.K.: Applications of chlorophyll fluorescence in stress physiology and remote sensing. – In: Steven, M.D., Clark, J.A. (ed.): *Applications of Remote Sensing in Agriculture*. Pp. 287-305. Butterworth Scientific, London 1990.
- Lichtenthaler, H.K.: The Kautsky effect: 60 years of chlorophyll fluorescence induction kinetics. – *Photosynthetica* **27**: 45-55, 1992.
- Lichtenthaler, H.K., Babani, F.: Detection of photosynthetic activity and water stress by imaging the red chlorophyll

- fluorescence. – *Plant Physiol. Biochem.* **38**: 889-895, 2000.
- Lichtenthaler, H.K., Babani, F., Langesdorf, G., Buschmann, C.: Measurement of differences in red chlorophyll fluorescence and photosynthetic activity between sun and shade leaves by fluorescence imaging. – *Photosynthetica* **38**: 521-529, 2000.
- Lichtenthaler, H.K., Burkart, S., Schindler, C., Stober, F.: Changes in photosynthetic pigments and *in vivo* chlorophyll fluorescence parameters under photoinhibitory growth conditions. – *Photosynthetica* **27**: 343-353, 1992.
- Lichtenthaler, H., Buschmann, C., Rinderle, U., Schmuck, G.: Application of chlorophyll fluorescence in ecophysiology. – *Radiat. environ. Biophys.* **25**: 297-308, 1986.
- Lichtenthaler, H.K., Miehe, J.A.: Fluorescence imaging as a diagnostic tool for plant stress. – *Trends Plant Sci.* **2**: 316-320, 1997.
- Lichtenthaler, H.K., Rinderle, U.: The role of chlorophyll fluorescence in the detection of stress conditions in plants. – *CRC crit. Rev. anal. Chem.* **19**: S29-S85, 1988.
- Lichtenthaler, H.K., Wenzel, O., Buschmann, C., Gitelson, A.: Plant stress detection by reflectance and fluorescence. – *Ann. New York Acad. Sci.* **851**: 271-285, 1998.
- Lu, C., Zhang, J.: Effects of water stress on photosynthesis, chlorophyll fluorescence and photoinhibition in wheat plants. – *Aust. J. Plant Physiol.* **25**: 883-892, 1998.
- Lu, C., Zhang, J.: Effects of water stress on photosystem II photochemistry and its thermostability in wheat plants. – *J. exp. Bot.* **50**: 1199-1206, 1999.
- Lutts, S., Kinet, J.M., Bouharmont, J.: NaCl-induced senescence in leaves of rice (*Oryza sativa* L.) cultivars differing in salinity resistance. – *Ann. Bot.* **78**: 389-398, 1996.
- Masojidek, J., Trivedi, S., Halshaw, L., Alexiou, A., Hall, D.O.: Synergistic effect of drought and light stresses in sorghum and pearl millet. – *Plant Physiol.* **96**: 198-207, 1991.
- Matoušková, M., Bartošková, H., Nauš, J., Novotný, R.: Reaction of photosynthetic apparatus to dark desiccation sensitively detected by the induction of chlorophyll fluorescence quenching. – *J. Plant Physiol.* **155**: 399-406, 1999.
- Maxwell, K., Johnson, G.N.: Chlorophyll fluorescence: A practical guide. – *J. exp. Bot.* **345**: 659-668, 2002.
- McKersie, B.D., Leshem, Y.Y.: Stress and Stress Coping in Cultivated Plants. – Kluwer Scientific Publishers, Dordrecht 1994.
- McWilliam, J.R., Kramer, P.J., Musser, R.L.: Temperature induced water stress in chilling-sensitive plants. – *Aust. J. Plant Physiol.* **9**: 343-352, 1982.
- Mishra, R.K., Singhal, G.S.: Photosynthetic activity and peroxidation of thylakoid lipids during photoinhibition and high temperature treatment of isolated wheat chloroplasts. – *J. Plant Physiol.* **141**: 286-292, 1993.
- Moffatt, J.M., Sears, R.G., Cox, T.S., Paulsen, G.M.: Wheat high temperature tolerance during reproductive growth II. Genetic analysis of chlorophyll fluorescence. – *Crop Sci.* **30**: 886-889, 1990.
- Mohammed, G.H., Binder, W.D., Gillies, S.L.: Chlorophyll fluorescence: A review of its practical forestry applications and instrumentation. – *Scand. J. Forest Res.* **10**: 383-410, 1995.
- Mohammad, H.T., Sayed, O.H.: Rescheduling maize irrigation for water conservation. I. Chlorophyll fluorescence, cultivar screening, and yield assessment. – *Bull. Fac. Sci. (Assiut Univ., Egypt)* **31**: 35-41, 2002.
- Mooney, H.A., Winner, W.E., Pell, E.J., Chu, E.: Responses of Plants to Multiple Stress. – Academic Press, London 1991.
- Murata, N.: Molecular species composition of phosphatidylglycerols from chilling-sensitive and chilling-resistant plants. – *Plant Cell Physiol.* **25**: 1241-1245, 1983.
- Nauš, J., Kuropatwa, R., Klinkovský, T., Ilik, P., Lattová, J., Pavlová, Z.: Heat injury of barley leaves detected by the chlorophyll fluorescence temperature curve. – *Biochim. biophys. Acta* **1101**: 359-362, 1992.
- Neubauer, C., Schreiber, U.: The polyphasic rise of chlorophyll fluorescence upon onset of strong continuous illumination. I. Saturation characteristics and partial control by the photosystem II acceptor side. – *Z. Naturforsch.* **42c**: 1246-1254, 1987.
- Newman, P.M.: Wall extensibility and the growth of salt stressed plants. – In: Jackson, M.B., Black, C.R. (ed.): *Interacting Stresses in Plants in Changing Environments*. Pp. 603-615. Springer-Verlag, Berlin 1993.
- Nilsen, E.T., Orcutt, D.M.: *The Physiology of Plants Under Stress. Abiotic Factors*. – John Wiley & Sons, New York 1999.
- Nogués, S., Alegre, L., Araus, J., Perez-Aranda, L., Lannoye, R.: Modulated chlorophyll fluorescence and photosynthetic gas exchange as rapid screening methods for drought tolerance in barley genotypes. – *Photosynthetica* **30**: 465-474, 1994.
- Nyachiro, J.M., Briggs, K.G., Hoddinott, J., Johnson-Flanagan, A.M.: Chlorophyll content, chlorophyll fluorescence and water deficit in spring wheat. – *Cereal Res. Commun.* **29**: 135-142, 2001.
- Park, Y.I., Park, M.C., Hong, Y.N.: Correlative changes between photosynthetic activities and chlorophyll fluorescence in wheat chloroplasts exposed to high temperature. – *J. Plant Biol.* **37**: 37-42, 1994.
- Pasda, G., Diepenbrock, W.: Effects of chilling and genotype on membrane lipids and membrane-dependent characteristics in leaves of maize (*Zea mays* L.): II. Movements of the plastoquinone-pool measured with the chlorophyll fluorescence technique. – *Kuehn Arch.* **90**: 209-224, 1996.
- Pastore, D., Flagella, Z., Rascio, A., Cedola, M., Wittmer, G.: Field studies on chlorophyll fluorescence as drought test in *Triticum durum* Desf. genotypes. – *J. Genet. Breed.* **43**: 45-52, 1989.
- Polyakoff-Mayber, A., Lerner, H.R.: Plants in saline environments. – In: Pessaraki, M. (ed.): *Handbook of Plant Stress*. Pp. 245-278. Marcell Dekker, New York 1994.
- Pospišil, P.: Mechanisms of non-photochemical chlorophyll fluorescence quenching in higher plants. – *Photosynthetica* **34**: 343-355, 1997.
- Quinn, P.J., Williams, W.P.: Environmentally induced changes in chloroplast membranes and their effects on photosynthetic function. – In: Barber, J., Baker, N.R. (ed.): *Photosynthetic Mechanisms and the Environment*. Pp. 1-47. Elsevier, Amsterdam – New York – Oxford 1985.
- Rascher, U., Liebig, M., Lüttge, U.: Evaluation of instant light-response curves of chlorophyll fluorescence parameters obtained with a portable chlorophyll fluorometer on site in the field. – *Plant Cell Environ.* **23**: 1397-1405, 2000.
- Rekika, D., Kara, Y., Souyris, I., Nachit, M., Asbati, A., Monneveux, P.: The tolerance of PSII to high temperatures in durum wheat (*T. turgidum* conv. *durum*): Genetic variation and relationship with yield under heat stress. – *Cereal Res. Commun.* **28**: 395-402, 2002.
- Rinderle, U., Lichtenthaler, H.K.: The chlorophyll fluorescence ratio F690/F735 as a possible stress indicator. – In: Lichtenthaler, H.K. (ed): *Applications of Chlorophyll Fluores-*

- cence. Pp. 189-196. Kluwer Academic Publishers, Dordrecht – Boston – London 1988.
- Roháček, K.: Chlorophyll fluorescence parameters: the definitions, photosynthetic meaning and mutual relationships. – *Photosynthetica* **40**: 13-29, 2002.
- Roháček, K., Barták, M.: Technique of the modulated chlorophyll fluorescence: basic concepts, useful parameters, and some applications. – *Photosynthetica* **37**: 339-363, 1999.
- Saccardy, K., Pineau, B., Roche, O., Cornic, G.: Photochemical efficiency of Photosystem II and xanthophyll cycle components in *Zea mays* leaves exposed to water stress and high light. – *Photosynth. Res.* **56**: 57-66, 1998.
- Samson, G., Prášil, O., Yaakoub, B.: Photochemical and thermal phases of chlorophyll *a* fluorescence. – *Photosynthetica* **37**: 163-182, 1999.
- Sayed, O.H.: Photosynthetic acclimation to high temperature in wheat. – *Acta bot. neerl.* **41**: 299-304, 1992.
- Sayed, O.H.: Aridity and plant survival in desert environments. – In: Prakash, I. (ed.): *Ecology of Desert Environments*. Pp. 87-103. Scientific Publishers, Jodhpur 2001.
- Sayed, O.H., Earnshaw, M.J., Emes, M.J.: Photosynthetic responses of different varieties of wheat to high temperature. II. Effect of heat stress on photosynthetic electron transport. – *J. exp. Bot.* **40**: 633-638, 1989a.
- Sayed, O.H., Earnshaw, M.J., Emes, M.J.: Characterization of the heat-induced stimulation of Photosystem-I-mediated electron transport. – *Acta bot. neerl.* **43**: 137-143, 1994.
- Sayed, O.H., Emes, M.J., Butler, R.D., Earnshaw, M.J.: High temperature induced changes in chloroplast ultrastructure, leaf fluorescence, and photosynthesis in wheat varieties. – *Biochem. Soc. Trans.* **14**: 59, 1986.
- Sayed, O.H., Emes, M.J., Earnshaw, M.J., Butler, R.D.: Photosynthetic responses of different varieties of wheat to high temperature. I. Effect of growth temperature on development and photosynthetic performance. – *J. exp. Bot.* **40**: 625-631, 1989b.
- Shapendonk, A.H.C.M., Dolstra, O., Van Kooten, O.: The use of chlorophyll fluorescence as a screening method for cold tolerance in maize. – *Photosynth. Res.* **20**: 235-247, 1989.
- Schreiber, U.: Chlorophyll fluorescence: New instruments for special applications. – In: Garab, G. (ed.): *Photosynthesis: Mechanisms and Effects*. Vol. V. Pp. 4253-4258. Kluwer Academic Publishers, Dordrecht – Boston – London 1998.
- Schreiber, U., Bilger, W.: Progress in chlorophyll fluorescence research: major developments during the past years in retrospect. – *Progress Bot.* **54**: 151-173, 1993.
- Schreiber, U., Bilger, W.: Rapid assessment of stress effects on plant leaves by chlorophyll fluorescence measurements. – In: Tenhunen, J.D., Catarino, F.M., Lange, O.L., Oechel, W.C. (ed.): *Plant Responses to Stress*. Pp. 27-53. Springer-Verlag, Berlin 1998.
- Schreiber, U., Bilger, W., Hormann, H., Neubauer, C.: Chlorophyll fluorescence as a diagnostic tool: Basics and some aspects of practical relevance. – In: Raghavendra, A.S. (ed.): *Photosynthesis. Comprehensive Treatise*. Pp. 320-336. Cambridge University Press, Cambridge 2000.
- Schreiber, U., Neubauer, C.: O₂-dependent electron flow, membrane energization and the mechanism of non-photochemical quenching of chlorophyll fluorescence. – *Photosynth. Res.* **25**: 279-293, 1990.
- Schulze, E.-D.: Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. – *Annu. Rev. Plant Physiol.* **37**: 247-274, 1986.
- Selmani, A., Wassom, C.E.: Effect of mild drought on chlorophyll fluorescence and morphological traits in young maize seedlings. – *Trans. Kansas Acad. Sci.* **94**: 85-94, 1991.
- Šesták, Z., Šiffel, P.: Leaf-age related differences in chlorophyll fluorescence. – *Photosynthetica* **33**: 347-369, 1997.
- Shangguan, Z., Shao, M.G., Dyckmans, J.: Effects of nitrogen nutrition and water deficit on net photosynthetic rate and chlorophyll fluorescence in winter wheat. – *J. Plant Physiol.* **156**: 46-51, 2000.
- Sharma, P.K., Hall, D.O.: Changes in carotenoid composition and photosynthesis in sorghum under high light and salt stresses. – *J. Plant Physiol.* **140**: 661-666, 1992.
- Sharp, R.E., Davies, W.J.: Regulation of growth and development of plants growing with a restricted supply of water. – In: Hamlyn, G.J., Flowers, T.J., Jones, M.B. (ed.): *Plants Under Stress*. Pp. 71-93. Cambridge University Press, Cambridge 1989.
- Shpiler, L., Blum, A.: Heat tolerance for yield and its components in different wheat cultivars. – *Euphytica* **51**: 257-263, 1991.
- Sicher, R.C., Sundblad, L.-G., Öquist, G.: Effects of low temperature acclimation upon photosynthetic induction in barley primary leaves. – *Physiol. Plant.* **73**: 206-210, 1988.
- Somersalo, S., Krause, G.H.: Reversible photoinhibition of unhardened and cold acclimated spinach leaves at chilling temperatures. – *Planta* **180**: 181-187, 1990.
- Stahl, U., Tusov, V.B., Paschenko, V.Z., Voigt, J.: Spectroscopic investigations of fluorescence behaviour, role and function of the long-wavelength pigments of Photosystem I. – *Biochim. biophys. Acta* **973**: 198-200, 1989.
- Sthapit, B.R., Wilson, J.: Chilling tolerance in February seeded Chaita rice (*Oryza sativa* L.) of Nepal. – *Ann. appl. Biol.* **121**: 189-197, 1992.
- Strasser, R.J., Srivastava, A., Govindjee: Polyphasic chlorophyll *a* fluorescence transient in plants and cyanobacteria. – *Photochem. Photobiol.* **61**: 32-42, 1995.
- Stirbet, A., Govindjee, Strasser, B.J., Strasser, R.J.: Chlorophyll *a* fluorescence induction in higher plants: Modelling and numerical simulation. – *J. theor. Biol.* **193**: 131-151, 1998.
- Tambussi, E.A., Casadesus, J., Munné-Bosch, S., Araus, J.L.: Photoprotection in water-stressed plants of durum wheat (*Triticum turgidum* var. *durum*): changes in chlorophyll fluorescence, spectral signature and photosynthetic pigments. – *Funct. Plant Biol.* **29**: 35-44, 2002.
- Teicher, H.B., Møller, B.L., Scheller, H.V.: Photoinhibition of Photosystem I in field-grown barley (*Hordeum vulgare* L.): Induction, recovery and acclimation. – *Photosynth. Res.* **64**: 53-61, 2000.
- Teiz, L., Zeiger, E.: *Plant Physiology*. – Benjamin-Cummings Publishers, New York 1991.
- Tjus, S.E., Møller, B.L., Scheller, H.V.: Photosystem I is an early target of photoinhibition in barley illuminated at chilling temperatures. – *Plant Physiol.* **116**: 755-764, 1998.
- Tjus, S.E., Møller, B.L., Scheller, H.V.: Photoinhibition of Photosystem I damages both reaction centre proteins PSI-A and PSI-B and acceptor-side located small Photosystem I polypeptides. – *Photosynth. Res.* **60**: 75-86, 1999.
- Tomek, P., Lazár, D., Ilik, P., Nauš, J.: On the intermediate steps between the O and P steps in chlorophyll *a* fluorescence rise measured at different intensities of exciting light. – *Aust. J. Plant Physiol.* **28**: 1151-1160, 2001.
- van der Veen, R.: Fluorescence and induction phenomena in photosynthesis. – *Physiol. Plant.* **4**: 486-494, 1951.

- van Kooten, O., Snel, J.F.: The use of chlorophyll fluorescence nomenclature in plant stress physiology. – *Photosynth. Res.* **25**: 147-150, 1990.
- Verheul, M.J., Van Hassel, P.R., Stamp, P.: Comparison of maize inbred lines differing in low temperature tolerance: Effect of acclimation at suboptimal temperature on chloroplast functioning. – *Ann. Bot.* **76**: 7-14, 1995.
- Waisel, Y.: Adaptation to salinity. – In: Raghavendra, A.S. (ed.): *Physiology of Stress*. Pp. 359-383. John Wiley & Sons, New York 1991.
- Waisel, Y., Eshel, A., Kafkafi, U.: *Plant Roots. The Hidden Part*. – Marcel Dekker, New York 1991.
- Walker, D.A.: Measurement of oxygen and chlorophyll fluorescence measurement. – In: Coombs, J., Hall, D.O., Long, S.P., Scurlock, J.M. (ed.): *Techniques in Bioproductivity and Photosynthesis*. 2nd Ed. Pp. 95-106. Pergamon Press, Oxford – New York – Sydney – Frankfurt 1985.
- Warrington, I.J., Dunstone, R.I., Green, L.M.: Temperature effects at three developmental stages on the yield of the wheat ear. – *Aust. J. agr. Res.* **28**: 11-27, 1977.
- Xu, X.L., Wang, Z.M., Zhang, J.P.: Effect of heat stress on photosynthetic characteristics of different green organs of winter wheat during grain-filling stage. – *Acta bot. sin.* **43**: 571-577, 2001.
- Yang, Q.F., Jiang, H., Xu, D.Q.: Changes in photosynthetic efficiency of flag leaves of wheat during development. – *Acta phytophysiol. sin.* **25**: 408-412, 1999.
- Yang, J., Sears, R.G., Gill, B.S., Paulsen, G.M.: Genotypic differences in utilization of assimilate sources during maturation of wheat under chronic heat and heat shock stresses – Utilization of assimilate sources by wheat under heat stresses. – *Euphytica* **125**: 179-188, 2002.
- Ying, J., Lee, E.A., Tollenaar, M.: Response of maize leaf photosynthesis to low temperature during the grain-filling period. – *Field Crops Res.* **68**: 87-96, 2002.
- Yordanov, I., Georgieva, K., Velikova, V., Tsonev, T., Merakchiiska-Nikolova, M., Paunova, S., Stefanov, D.: Response of the photosynthetic apparatus of different wheat genotypes to drought: I. Laboratory experiments under controlled light and temperature conditions. – *Dokl. bolg. Akad. Nauk* **54**: 79-84, 2001.
- Yucel, M., Burke, J.J., Nguyen, H.T.: Inhibition and recovery of photosystem II following exposure of wheat to heat shock. – *Environ. exp. Bot.* **32**: 125-135, 1992.
- Zakhidov, E.A., Zakhidova, M.A., Kasymdzhanov, M.A., Kurbanov, S.S., Mirtadzhiev, F.M., Khabibullaev, P.: Chlorophyll fluorescence as a tool for diagnostics of optimal temperatures of photosynthesis in plants. – *Dokl. ross. Akad. Nauk* **382**: 563-566, 2002.
- Zhu, X.G., Wang, Q., Zhang, Q.D., Lu, C.M., Kuang, T.V.: Effects of photoinhibition and its recovery on photosynthetic functions of winter wheat under salt stress. – *Acta bot. sin.* **43**: 1250-1254, 2001.
- Zidan, I., Azaizeh, H., Newmann, P.M.: Does salinity reduce growth in maize root epidermal cells by inhibiting their capacity for cell wall acidification? – *Plant Physiol.* **93**: 7-11, 1990.