REVIEW

Chlorophyll fluorescence as a tool in cereal crop research

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Abstract

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 exceed-ing 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, Andréassson and Vänngård 1988, Bolhàr-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 OIDP) 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 (Bolhàr-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 b_6/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.

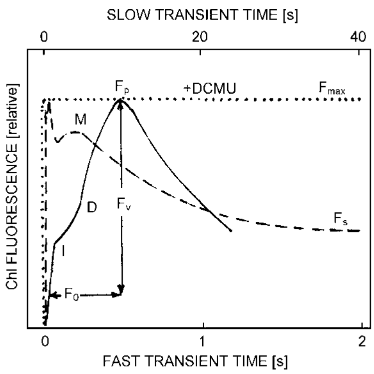

Fig. 1. Chlorophyll fluorescence induction curve. Fast transient (——), slow transient (– – –), fluorescence kinetics in presence of DCMU (· · ·). Minimal fluorescence intensity (F_0), inflection (I), dip (D), peak fluorescence intensity (F_p), variable fluorescence intensity (F_v), maximal fluorescence 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, Bolhàr-Nordenkampf 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, Haitz and Lichtenthaler 1988, Lichtenhaler 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, Bolhàr-Nordenkampf and Öquist 1993, Schreiber and Bilger 1993, 1998, Govindjee 1995, Joshi and Mohanty 1995, Schreiber 1998, Stirbet *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 Miehe 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, Shpiler 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 CO_2 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 photoinhibition 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 CO_2 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 Tollenaarb 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 posessing 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 CO_2 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 CO_2 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 (Masojídek *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 asses-sing 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).

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