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The afterglow photosynthetic luminescence

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Abstract

The afterglow (AG) photosynthetic luminescence is a long-lived chlorophyll fluorescence emitted from PSII after the illumination of photosynthetic materials by FR or white light and placed in darkness. The AG emission corresponds to the fraction of PSII centers in the $S_{2/3}Q_B$ non-radiative state immediately after pre-illumination, in which the arrival of an electron transferred from stroma along cyclic/chlororespiratory pathway(s) produces the $S_{2/3}Q_B^-$ radiative state that emits luminescence. This emission can be optimally recorded by a linear temperature gradient as sharp thermoluminescence (TL) band peaking at about 45°C. The AG emission recorded by TL technique has been proposed as a simple non-invasive tool to investigate the chloroplast energetic state and some of its metabolism processes as cyclic transport of electrons around PSI, chlororespiration or photorespiration. On the other hand, this emission has demonstrated to be a useful probe to study the effect of various stress conditions in photosynthetic materials.

1 | INTRODUCTION

Oxygenic photosynthetic organisms emit a long-lived red light after being illuminated and placed in darkness (Amesz & van Gorkom, 1978; Strehler & Arnold, 1951). This light emission is termed delayed light emission (DLE), delayed fluorescence, or delayed luminescence. The difference between the more widely known prompt chlorophyll fluorescence and DLE is in the origin of the excited single state of the emitting pigment molecule (Jursinic, 1986). DLE originates from the repopulation of excited states of chlorophyll from the stored energy after charge separation, whereas prompt fluorescence reflects the radiative de-excitation of excited chlorophyll molecules before charge separation.

Strehler and Arnold (1951) advanced the hypothesis that DLE is a chemiluminescence process caused by the reversal of photosynthetic electron transfer reactions. Later, it was proposed that DLE is chlorophyll fluorescence originated from photosystem II (PSII), in which the recombination of previously light-separated charge pairs leads, in part, to a radiative process (Amesz & van Gorkom, 1978). Stabilization of the charge pairs on PSII is achieved by activation energy barriers that prevent its recombination. Although charge recombination is a low rate process at physiological temperatures, proceeds following different pathways, one of these leading to the recreation at a low yield of an exciton in the chlorophyll antenna, with a probability to deactivate as fluorescence (Rappaport et al., 2005).

Light-induced charge pairs are stabilized on PSII electron carriers. At the stroma interface of PSII, the electron is located on the secondary quinonic acceptor Q_B or on the primary acceptor Q_A when a diuron-like herbicide is bound at the Q_B site. At the lumen-oriented oxygen-evolving complex (OEC), positive charges are stored as S_1 to S_4 states, corresponding to oxidation steps of a manganese cluster, on which four positive charges are needed to evolve an oxygen molecule (for a review, see Rutherford, Renger, et al., 1984). S_0 and S_1 are stable in the dark and unable to recombine with Q_A^- or Q_B^-, S_4 is unstable since it produces an O_2 molecule. Only the S_2 and S_3 states can recombine with an electron stored on the quinonic acceptors, yielding luminescence.

At a constant temperature, DLE exhibits several decay phases, the rates of which are temperature-dependent (Amesz & van

Abbreviations: AG band, afterglow TL band; B band, TL band due to $S_2/S_3Q_B^-$; CEF, cyclic electron flow around PSI; CR, chlororespiration; DLE, delayed light emission; FQR, ferredoxin plastoquinone reductase; FR, far red light; I_{AG}, the intensity of the AG band; NDH, NAD(P)H-plastoquinone-oxidoreductase; OEC, oxygen-evolving complex; PQ, plastoquinone; PR, photorespiration; PSI, photosystem I; PSII, photosystem II; PTOX, terminal oxidase; Q_A/Q_B, redox-active quinones bound to PSII; $S_{0...4}$, redox states of water oxidation complex; TL, thermoluminescence; t_{max}, temperature of the maximum of a TL band.

This work is a tribute to the memory of Jean-Marc Ducruet.

Gorkom, 1978; Strehler & Arnold, 1951). Arnold and Sherwood (1957) were the first to observe that light-generated precursors of DLE may be stabilized at low temperature. Subsequent heating in the dark resulted in DLE, which in this case is generally referred as thermoluminescence (TL) or thermally stimulated delayed luminescence (Arnold & Sherwood, 1957; Tollin & Calvin, 1957). Decay phases of DLE can be better resolved by TL emission technique (Desai et al., 1983; Ducruet & Miranda, 1992; Miranda & Ducruet, 1995a). This technique consists of recording luminescence emission during the warming of a sample after an irradiation given at a temperature sufficiently low to make negligibly small the recombination rate of the charge pairs under investigation (for a review, see Vass & Inoue, 1992, Inoue, 1996, Vass & Govindjee, 1996, Ducruet, 2003, Ducruet & Vass, 2009, Ducruet et al., 2012, Sane et al., 2012).

By using the TL technique, it is possible to identify the different types of charge pairs as successive emission bands by a progressive warming. After a sequence of short flashes, a so-called B band of TL, peaking around 25°C, is observed in both isolated photosynthetic membranes and intact systems. This emission is due to the recombination of $S_2/S_3Q_B^-$ pairs (Demeter et al., 1982; Demeter & Vass, 1984; Inoue & Shibata, 1982; Rutherford et al., 1982; Rutherford, Zimmermann, & Mathis, 1984). Treatment by a PSII-inhibiting herbicide (diuron, atrazine), which blocks the Q_A to Q_B electron transfer, induces the appearance of a Q band peaking at about 5°C, due to the $S_2Q_A^-$ recombination (Demeter et al., 1982; Demeter & Vass, 1984). A C band at about 55°C can also be detected in particular conditions. This TL band is due to $D^+Q_A^-$ recombination (Demeter et al., 1993; Desai et al., 1975; Johnson et al., 1994), D^+ being the oxidized form of tyrosine D on the inactive branch of PSII.

In 1965, Bertsch and Azzi first reported the occurrence of a delayed rise of luminescence, induced by FR illumination and superimposed over the exponential decay phases recorded at a constant temperature (Bertsch & Azzi, 1965). This slow component of DLE was named afterglow luminescence (AG) because it passed through a relative maximum between 1–4 minutes after the end of illumination (Bertsch & Azzi, 1965; Björn, 1971; Hideg et al., 1991). AG emission has been reported in algal cells (Bertsch & Azzi, 1965; Petrou et al., 2014; Schmidt & Senger, 1987), protoplasts (Nakamoto et al., 1988), whole leaves (Björn, 1971; Desai et al., 1983; Sundblad et al., 1988), and purified spinach chloroplasts with some degree of intactness (Hideg et al., 1991), but not in isolated thylakoids or PSII particles.

The AG emission is stimulated by temperature elevation (Björn, 1971). When recorded at a constant temperature, it usually appears as a broad luminescence burst, which cannot quantitatively be separated from the exponential decay phases, which it overlaps. However, AG emission can be much better resolved when recorded during a progressive warming rather than at a constant temperature (Desai et al., 1983; Miranda & Ducruet, 1995b). Thus, it can be optimally recorded by a linear temperature gradient as a sharp TL band peaking at about 45°C at a 0.5°C s^{-1} warming rate under appropriate experimental conditions (Miranda & Ducruet, 1995b).

2 | THE ORIGIN OF THE AFTERGLOW LIGHT EMISSION

The AG emission, even though generally induced by FR light which preferentially excites PSI, is originating from PSII, as evidenced by its period 4 oscillation, by fluorescence emission spectroscopy and by its suppression by PSII inhibitors such as diuron (Björn, 1971; Nakamoto et al., 1988; Schmidt & Senger, 1987). AG emission results from a heat-induced back-flow of electrons from reductants present in the stroma to PSII centers initially in the non-recombining state $S_{2/3}Q_B$ (Havaux, 1996; Miranda & Ducruet, 1995b; Sundblad et al., 1988). This charge pair enables to emit AG luminescence as soon as a back-electron transfer from stroma reduces Q_B. Therefore, it is proposed that AG emission does not originate from preformed charge pairs but reflects an electron transfer that occurs in the dark (Ducruet, 2003; Ducruet, Roman, Havaux, et al., 2005; Hideg et al., 1991; Miranda & Ducruet, 1995b; Sundblad et al., 1988). While $S_{2/3}Q_B^-$ centers produce a TL B band emission, the $S_{2/3}Q_B$ centers cannot lead to a luminescence emission, unless an electron is transferred from the stroma to Q_B, resulting in an AG emission (Ducruet, 2003, Ducruet, Roman, Havaux, et al., 2005, Hideg et al., 1991, Miranda & Ducruet, 1995b, Sundblad et al., 1988).

This reverse electron flow to PSII via the PQ pool is supported by a transmembrane proton gradient resulting from ATP hydrolysis by thylakoidal ATPases (Rienits et al., 1974; Schreiber, 1984) and can be induced by warming above 30°C (Ducruet, 2003; Ducruet, Roman, Ortega, et al., 2005; Hideg et al., 1991; Miranda & Ducruet, 1995b; Sundblad et al., 1986; Sundblad et al., 1988).

The FR excitation promotes a well-defined state of the electron transfer chain favoring the AG emission (Ducruet, Roman, Ortega, et al., 2005). PSI is preferentially excited by FR light, which consequently causes the oxidation of the PQ pool, the reduction of the PSI acceptor pool and the increase of ΔpH, thus favoring in the dark a back transfer of electrons from stromal reductants to the oxidized Q_B and, finally, to the S_2 and S_3 states of the manganese cluster. PSII excitation by FR is sufficient to create a random distribution of S states (Ducruet, Roman, Havaux, et al., 2005).

The cyclic electron flow around PSI (CEF) seems to relate with the electron pathway leading to the AG emission (Björn, 1971; Nakamoto et al., 1988). It has been shown by photoacoustics and P700 absorption methods that short heat treatments in the same range of temperature as that of AG emission (45°C) trigger a PSI-driven electron flow from stromal reductants to the intersystem electron transport chain (Havaux, 1996). The AG emission arises faster in the presence of phenazine-methosulfate and is inhibited by antimycin, which are respectively an activator and an inhibitor of CEF (Björn, 1971). The AG band has been linked to the induction of the FQR and/or NDH pathways. On the one hand, it has been related to FQR activity since it is suppressed by 5 μM antimycin A (Björn, 1971), a low concentration that also selectively inhibits the ferredoxin-plastoquinone-reductase or FQR pathway but not the NAD(P)H-plastoquinone-oxidoreductase or NDH (Bendall & Manasse, 1995; Ravenel et al., 1994; Scheller, 1996). The suppression of this band by

FQR inhibitor antimycin A has been described in tobacco (Havaux et al., 2005) and *Chlamydomonas* (Ducruet et al., 2011), suggesting that more ferredoxin reduction can occur in the dark from NADPH by a reverse activity of FNR (Okegawa et al., 2008) in these latter species (Peeva et al., 2012). On the other hand, AG emission has been linked to the induction of the NDH pathway but not of the FQR pathway since it is impaired in *Arabidopsis* mutants deficient in NDH activity (Havaux et al., 2005) but unaffected in PGR5 mutants deficient in FQR activity (Okegawa et al., 2008). Therefore, it has been proposed that the participation of the FQR and/or NDH activities in the generation of this band depends on the species studied (Havaux et al., 2005).

The electron back-transfer from the stroma to Q_B, leading to AG emission, seems to also require an activated chlororespiratory pathway (CR) (Bennoun, 1982; Rumeau et al., 2007; Sundblad et al., 1988). CR is a respiratory electron transport chain in interaction with photosynthetic electron transport involving both non-photochemical reduction and oxidation of PQ in thylakoid membranes (Bennoun, 1982; Garab et al., 1989). CR involves mostly the plastid NDH complex, the thylakoid PQ pool, and a terminal oxidase named PTOX (Peltier & Cournac, 2002). A reduction of the PQ pool by CR has been found in diatoms and algae leading to the build-up of a proton gradient without the participation of PSII electron transport (Wilhelm & Duval, 1990).

AG emission is usually induced by FR light and is generally weaker or absent after white light illumination (Palmqvist et al., 1986; Roncel et al., 2007; Roncel et al., 2016; Roncel & Ortega, 2005). However, if the assimilatory potential (NADPH+ATP) in chloroplasts is high enough to allow an electron flow to the PQ pool (Heber et al., 1986), the AG emission can be induced by white light (Palmqvist et al., 1986) or xenon flashes (Ducruet et al., 2011; García-Calderón et al., 2019; Krieger et al., 1998; Miranda & Ducruet, 1995b; Repetto et al., 2015; Roman & Ducruet, 2000; Roncel et al., 2016). Thus, the AG band can usually be induced under different metabolic conditions in which the use of assimilatory potential (NADPH+ATP) is slowed down (Ducruet et al., 2011; García-Calderón et al., 2019; Mellvig & Tillberg, 1986; Palmqvist et al., 1986). Hence, AG band induced by white light appears to reflect the energetic state in the chloroplast (Roman & Ducruet, 2000).

On the other hand, the AG emission can be observed only in intact systems, including intact chloroplasts, but not in isolated thylakoids (Belatik et al., 2012; Cerović et al., 1991). The reason for that can be found in the requirement of a proton gradient and in the role of soluble molecules in stroma (NADPH, ATP, and ferredoxin) and also the phosphoglycerate/dihydroxyacetone phosphate system that determines the NADPH+ATP assimilatory potential (Gerst et al., 1994; Krieger et al., 1998).

In conclusion, the AG band corresponds to the fraction of PSII centers in the $S_{2/3}Q_B$ non radiative state immediately after pre-illumination, in which the arrival of an electron transferred from stroma along cyclic/chlororespiratory pathway(s) produces the $S_{2/3}Q_B^-$ radiative state that emits luminescence (Sundblad et al., 1988). The AG emission, although originating from PSII, is governed by the electron back-transfer to Q_B from the stroma, which requires a sufficient potential gap between the acceptors side of PSI ($NADPH/NADP^+$) and PSII (PQH_2/PQ) (Ducruet, Roman, Havaux, et al., 2005; Heber et al., 1986; Hideg et al., 1991; Miranda & Ducruet, 1995b; Sundblad et al., 1988).

3 | INFORMATION PROVIDED BY AG EMISSION

The AG band obtained by TL technique has been proposed as a simple non-invasive tool to investigate the chloroplast energetic state (Ducruet et al., 2011; Roman & Ducruet, 2000), and some of its metabolism processes as CEF, CR or photorespiration (PR) (García-Calderón et al., 2019; Havaux et al., 2005; Heber et al., 1986).

Specifically, the intensity (I_{AG}) and the temperature of the maximum (t_{max}) of this band give information about: (1) assimilatory potential in the chloroplast (I_{AG} after white light flash excitation), (2) capacity of cyclic/chlororespiratory pathways revealed by warming (I_{AG} after FR light continuous illumination), and (3) activation of cyclic pathways before any treatments (t_{max} downshift after FR light continuous illumination) (Ducruet, 2013; Krieger et al., 1998).

The I_{AG} is an indicator of the assimilatory potential (NADPH +ATP) when it is inducible by a white light illumination (Mellvig & Tillberg, 1986; Palmqvist et al., 1986; Sundblad et al., 1986) or xenon flash excitation (Krieger et al., 1998). After flash excitation, I_{AG} depends not only of the CEF capacity, as the FR light-induced AG band, but also on the dark-stable assimilatory potential of stroma donor pool (NADPH) in equilibrium with the pool of triosephosphate (Krieger et al., 1998; Peeva et al., 2012; Sajnani et al., 2007).

The induction of the AG emission by a single turnover flash has been described in facultative CAM plants when this metabolism is activated by salt treatment (Krieger et al., 1998). Under these conditions, the I_{AG} correlates with changes in the ratio of dihydroxyacetone phosphate/phosphoglycerate (DHAP/PGA), which is an indicator of the energy status of the chloroplast. It has been described that the flash-induced AG band occurs during the phases of the diurnal cycle corresponding to both a high level of phosphorylation and a strong reduction potential. Under these conditions, photosynthetic electron transfer produces NADPH and ATP, building up an energetic potential necessary for CO_2 fixation, which occurs when enzymes of the Calvin cycle are light-activated (Krieger et al., 1998).

The flash-induced AG band proves to be also useful for studying changes in the PR metabolism (García-Calderón et al., 2019). The absence of a functional PR pathway in *L. japonicus* plants under high CO_2 conditions led to a significant increase in the I_{AG} probably due to a greater availability of NADPH and ATP (Urban, 2003; Wingler et al., 2000). PR is an energetically costly process where both energy (ATP) and reducing equivalent (NADPH) are required (Hagemann et al., 2016; Wingler et al., 2000). Therefore, under conditions in which the PR is suppressed (high concentration of CO_2), NADPH and ATP can accumulate, raising the assimilatory potential. Therefore, I_{AG} might be an indicator of this extra ATP and/or NADPH when PR is inactive.

The CEF and CR pathways can be also investigated by measuring the AG band emission (Havaux et al., 2005). The general capacity of the electron transfer of both pathways can be assessed by the I_{AG} induced by FR illumination (Bürling et al., 2014; Havaux et al., 2005; Lintala et al., 2009).

A strong AG band near 45°C indicates that the cyclic pathways are inactive at ambient temperature and are therefore induced by warming (Ducruet, 2013). Electrons stay in the stroma pool of reductants until the inactive cyclic pathway(s) are activated by warming, allowing them to flow towards PSII, as reflected by the AG band. In contrast, when cyclic pathways are active (open) at ambient temperature, the electrons flow freely from the stroma reductants to the intersystem chain and PSII quinonic side and the AG band tends to fuse with the B bands. Thus, a downshift of the t_{max} of AG band, leading ultimately to a fusion with the B band, indicates a progressive induction of a dark-electron transfer to PSII acceptor side, without warming (Apostol et al., 2006; Ducruet, Roman, Havaux, et al., 2005; Havaux et al., 2005).

The downshift of the FR light-induced AG band reflects the activation of cyclic pathways (CEF and CR) in darkness at ambient temperature. Cyclic pathways are normally closed at moderate physiological temperatures. They progressively open during temperature elevation above 35°C (Bukhov et al., 1999; Havaux, 1996), presumably to compensate for the enhanced proton leakage through the thylakoid membrane at warm temperatures by allowing a stronger proton pumping into the lumen (Sharkey, 2005). Thus, the appearance of the AG peak at lower temperatures indicates that the CEF and CR pathways are partly activated before warming despite dark adaptation. Under these conditions, the observed faster re-reduction in darkness of $P700^+$ previously oxidized by FR light correlated well with this activation (Ducruet, Roman, Havaux, et al., 2005).

State transition can also be studied by using the AG band (Havaux et al., 2005). A downshift of AG band below 40°C is caused by type II light (e.g., blue) inducing state 2 that favors CEF, whereas type I light (FR) inducing state 1 restores t_{max} at 45°C in *Arabidopsis thaliana* (Havaux et al., 2005). In tobacco (Havaux et al., 2005) and *Chlamydomonas* (Ducruet et al., 2011), the AG band is almost not downshifted by type II light, suggesting that FQR is not activated by light but mainly depends on the reduction state of PSI electron acceptors (at least in these two species), in contrast to NDH.

4 | AG EMISSION AS A SENSITIVE INDICATOR OF STRESS IN CHLOROPLASTS

Several authors have reported various effects of stress conditions on the FR light-induced AG emission observed as luminescence decay at constant temperature (Mellvig & Tillberg, 1986; Schmidt & Senger, 1987). However, AG emission band detected by TL technique, induced by FR continuous illumination or white light flashes, has been proven to be a useful probe to study the effect of various stress conditions in photosynthetic materials (Janda et al., 1999). The intensity and peak position of the AG band provide valuable information about functioning of the PSII reaction center and about the metabolic state in the chloroplast (Ducruet et al., 2011; Roman & Ducruet, 2000). As previously mentioned, the intensity of the AG band emission induced by flashes is an indicator of the assimilatory potential (NADPH+ATP) in the chloroplasts. Besides, the intensity and the t_{max} of FR light-induced AG band give information about the functioning of the cyclic electron transfer pathways. Thus, the AG band could be used as a very sensitive indicator of the effects of abiotic or biotic stresses in chloroplasts (Janda et al., 1999; Janda et al., 2000).

4.1 | Temperature

The AG emission has been used as a tool to characterize the effect of thermal stress on intact photosynthetic systems and to understand the mechanisms of constitutive or induced tolerance to this stress (Ducruet et al., 1997; Ducruet et al., 2007). The TL AG band reflects the integrity of the chloroplast (Belatik et al., 2012) and is also a good indicator of the assimilatory potential (NADPH+ATP), thus being very sensitive to temperature stress. Besides, AG band seems to be more sensitive to temperature stress than B band (Janda et al., 2000; Miranda & Ducruet, 1995b).

Plants upon severe cold stress or freezing conditions show a significant decrease in the FR and flash induced AG band intensities (Janda et al., 1999; Roman & Ducruet, 2000). Short-term freezing suppressed FR light-induced AG band in several plant species (Janda et al., 1999; Janda et al., 2004; Miranda & Ducruet, 1995a). In cold and chilling-tolerant genotypes, a less pronounced decrease in the intensity of the FR light-induced AG band has been observed compared to sensitive ones after cold or chilling treatments (Janda et al., 2000; Miranda & Ducruet, 1995b; Roman & Ducruet, 2000). This can be linked to the freezing of inner chloroplast water, leading to an irreversible disruption of the proton gradient, that is, to an uncoupling, of the thylakoid membrane by ice crystals. It has been proposed that a part of the induction mechanism of the AG emission, that dependent on ΔpH, is destroyed by freezing (Miranda & Ducruet, 1995a).

The significant decrease of the flash-induced AG emission observed in cold-sensitive pea varieties under cold conditions may reflect a decrease of the assimilatory potential induced by this stress condition (Roman & Ducruet, 2000). Decreasing temperature induces a photosynthesis limitation due to orthophosphate deficiency even in cold-tolerant species, resulting in a low triose-P/PGA ratio and hence of assimilatory potential in the chloroplast (Falk et al., 1996; Labate & Leegood, 1989).

In the same way as cold stress, increasing temperature causes a progressive decrease of the FR light-induced AG band, being more pronounced in cold tolerant than in cold sensitive plants (Janda et al., 1999). The progressive decrease in the AG band between 30 and 40°C demonstrates that increasing temperatures may produce a milder effect on the photosynthetic apparatus, as also evidenced by other methods (Havaux, 1993; Moffatt et al., 1990; Weis, 1984).

4.2 | Drought

Moderate drought stress induces significant changes in the t_{max} of FR and flash induced AG band but not in its intensity (Peeva et al., 2012). In fast dehydrated excised barley and wheat leaves, the I_{AG} remains unchanged but its position (t_{max}) changes toward lower temperatures indicating an activation of CEF and CR pathways in darkness, without any increase of the overall electron transfer capacity (Peeva et al., 2012). The acceleration of $P700^+$ reduction phases observed in barley leaves under these conditions also evidence the induction of CEF (Peeva et al., 2012). The absence of an increase of the I_{AG} shows that no additional synthesis of the cyclic electron transfer components occurred during short period of dehydration in darkness (Peeva et al., 2012).

By contrast, severe drought stress, as slow dehydration, induces changes in the intensity of FR and flash induced AG band but not in its t_{max} (Peeva et al., 2012). After a slow dehydration of wheat and barley plants, the AG position remains almost unchangeable, whereas its intensity strongly increases compared to watered control, indicating respectively that the capacity of cyclic pathways remained inactivated in darkness but that they are enhanced after several days of slow dehydration under a day/night cycle (Bürling et al., 2014). As the cyclic pathways are not activated and CO_2 assimilation is prevented by stomatal closure, the assimilatory potential (NADPH +ATP) might build up enough during light periods, in equilibrium with the pool of triose-phosphate (Gerst et al., 1994). Slow dehydration may also induce an upregulation of protein components of the FQR (Lehtimäki et al., 2010) or NDH pathways (Ibáñez et al., 2010). Thus, it is not possible to conclude if the increase in I_{AG} observed under severe drought stress is due only to a stronger assimilatory potential or also to an upregulation of synthesis of protein components of cyclic pathways.

4.3 | Salt

TL technique has been used to understand the site of action of NaCl on the photosynthetic electron transport chain (Zurita et al., 2005). A significant decrease in the I_{AG} induced both by flashes and FR illumination has been observed in rice leaf fragments incubated 4 h in the presence of 0.5 M NaCl (Zurita et al., 2005). These authors have proposed that NaCl stress could partially inhibit the oxidation of Q_B needed to generation of AG emission band. A suppression of the reduction of $P700^+$, probably by blocking plastocyanin association to PSI, has been described in *Synechococcus* cells under salt stress (Allakhverdiev et al., 2002). Oxygen evolving machinery seems to be inactivated in the presence of NaCl due to destruction of Mn cluster and dissociation of the extrinsic proteins of the OEC (Allakhverdiev et al., 2002). The significant decrease in the total intensity of TL signals corresponding to AG band, and also to B band, induced by salt stress (Zurita et al., 2005) is consistent with the main site of action of high concentration of NaCl on the OEC by blocking the formation of S_2 and S_3 states.

4.4 | Nutrient deficiency

The TL technique has been used to investigate the photosynthetic response of the pennate marine diatom *Phaeodactylum tricornutum* to Fe deficiency (Roncel et al., 2016). The analysis of the emission curves induced by two flashes showed a significant decrease in the I_{AG} in cells grown under Fe-deficient conditions. This effect has been explained by the existence of a lower assimilatory potential (NADPH +ATP) in the stroma that could be a consequence of the severe decline of the photosynthetic electron transport activity induced by Fe deficiency (Roncel et al., 2016). In Fe deficient cells, the contribution of the AG band to the total TL emission after FR illumination did not increase, as in control cells, probably because it is already fused with the lower temperature B band. Fe deficiency could thus induce the activation of the CR pathway (Roncel et al., 2016), which seems to be involved in protective or adaptive mechanisms of photosynthetic organisms to environmental stress conditions (Bennoun, 1982; Morehouse & Mason, 1988; Peltier & Schmidt, 1991; Rumeau et al., 2007).

4.5 | Anoxia

Anoxia causes rapid induction of cyclic pathways (Bukhov et al., 1999; Joët et al., 2002). A brief anoxia in barley and pea leaves caused a downshift of the FR and flash induced AG band with a decrease in t_{max} from about 45 to 30°C (Peeva et al., 2012). This downshift reflects an induction by anoxia of cyclic pathways in darkness, that is, that electrons flow freely from stroma to Q_B without a need for thermal activation (Peeva et al., 2012). The absence of oxygen, by inhibiting respiration, suppresses mitochondrial ATP synthesis that has been shown to induce CEF (Cardol et al., 2009).

4.6 | Chemicals

Infiltration of glucose and fructose in barley leaf segments causes a downshift of the FR light-induced AG band and acceleration of $P700^+$ reduction kinetics (Peeva et al., 2012). Glucose and fructose can enter into the chloroplast (Quick & Schaffer, 1996) where they can be metabolized and provide reducing power directly in the stroma. Feeding glucose and fructose to a leaf is thus expected to stimulate the cyclic electron transport by supplying electrons to PQ pool through NDH activity, as occurs with acetate in *Chlamydomonas* (Alric, 2010). When excess of reducing power produced in the chloroplasts is not totally exported to the cytoplasm and the mitochondrion by the malate valve, NDH activity can feed electrons to PQ pool and interact with cyclic electron transport (Peltier & Cournac, 2002).

The TL technique has been also applied for the toxicological evaluation of some chemicals by using photosynthetic organisms (Repetto et al., 2015). It has been observed that the exposure of *Chlorella vulgaris* cells to a low concentration of the surface-active agent diethanolamine induced the appearance of a very significant

flash induced AG band (Repetto et al., 2015). In *Chlorella* cells grown in the presence of diethanolamine, phospholipids can provide additional NADPH in the stroma through the respiratory pathway (Alric, 2010), thus stimulating the cyclic versus linear electron transfer pathway to maintain the ATP/NADPH ratio required by the Benson-Calvin cycle. The proposed increase of the assimilatory potential by diethanolamine could explain the appearance of the AG band in TL emissions induced by white light flashes (Repetto et al., 2015).

4.7 | Biotic stress

The assimilatory potential monitored by the flash induced AG band intensity provides an interesting tool to study the influence of pathogen infection on metabolic transport in the host plant (Sajnani et al., 2007). A significant increase in the relative intensity of the flash induced AG band has been observed in leaves of *Nicotiana benthamiana* plants infected by two tobamovirus strains (Sajnani et al., 2007). The lower photosynthetic activity measured in those leaves can be attributed to a downstream inhibition of the Calvin cycle already evidenced by other methods (Pérez-Bueno, 2003). Consequently, the assimilatory potential (NADPH+ATP) builds up, as is evident from the increase in the AG emission.

5 | CONCLUSIONS

The AG emission recorded by TL technique has been proposed as a simple non-invasive tool to investigate the chloroplast energetic state and the effect of various stress conditions in photosynthetic materials. The contribution of Jean-Marc Ducruet to the knowledge of the AG emission, as well as its application to studies on plant metabolism and the effects of stress, has been fundamental. This review includes 19 scientific articles signed by Jean-Marc Ducruet.

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AUTHOR CONTRIBUTIONS

José M. Ortega and Mercedes Roncel conceived and designed the project. Both authors wrote and revised the manuscript.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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