

# FMS-300

Pulse modulated chlorophyll fluorometer for teaching & research applications

## Parameters Glossary



# FMS-300 Parameters Glossary

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# FMS-300

## An introduction

FMS-300 is a convenient, laboratory-based system for teaching chlorophyll a fluorescence as an ecophysiology technique. It is also a highly capable research instrument offering flexibility, functionality, and data acquisition of exceptional quality. The system provides an extremely user-friendly platform to introduce the fundamentals of chlorophyll a fluorescence measurements. Newcomers to the technique are quickly able to acquire and analyse data associated with both pulse-modulated (PAM) and fast-fluorescence (OJIP) types of fluorometry. Acquired skills and knowledge are transferable into early career plant physiology research and beyond, both in laboratory and field settings.

FMS-300 provides a comprehensive introduction to the world of chlorophyll fluorescence measurements and, in turn, can yield powerful insights into the mechanisms of photosynthesis.

## Parameters

FMS-300 can make measurements of both fast and slow fluorescence kinetics. The FluoroControl software provides 6 pre-set experimental routines, which can be further configured, if wished. This enables rapid learning and efficient, hassle-free data acquisition.

Each routine's protocol consists of saturating pulse events with periods of measurement in the dark or under actinic or ambient light conditions. This allows fluorescence yield measurements under a wide range of environmental conditions. FMS-300 captures extremely high resolution fast fluorescence kinetics during each saturating pulse event. This includes for both light- and dark-adapted sample states, believed to be a first for a commercially available chlorophyll fluorometer.

For each parameter that FMS-300 measures or calculates, this document provides:

- > A definition of the parameter
- > Information on the method of calculation
- > Synonyms or logical equivalents that may be presented in the literature
- > A physiological interpretation of each parameter
- > References to publications describing the use and interpretation of the parameter
- > Graphics to highlight the context of parameters, as appropriate

# Fast Fluorescence & OJIP Analysis

Dark-adapted samples



# FMS-300 Parameters Glossary

## Fast fluorescence kinetics: An Overview



### Analysis of the fast fluorescence rise

Fast fluorescence kinetics from dark-adapted samples have a very definite and widely recognised form. In 1931, Kautsky and Hirsch found that when a dark-adapted leaf is suddenly illuminated with a saturating light source, the fluorescence signal rises quickly from an origin level (O) to the first inflection point known as the J-step at ~2 milliseconds (or  $I_1$  in some publications). The rate of fluorescence intensity increase slows through the I-step at ~30 milliseconds (or  $I_2$ ). The signal then reaches a peak (P) denoting the maximum fluorescence signal somewhere between 300 - 600 milliseconds after the onset of illumination.

The inflection points at the J and I-step represent definite physiological events during the primary photochemical response of Photosystem II (PSII). This can be transposed on to a widely recognised model; the Z-Scheme of Photosynthesis, to assist in interpretation of the physiological events at these steps.

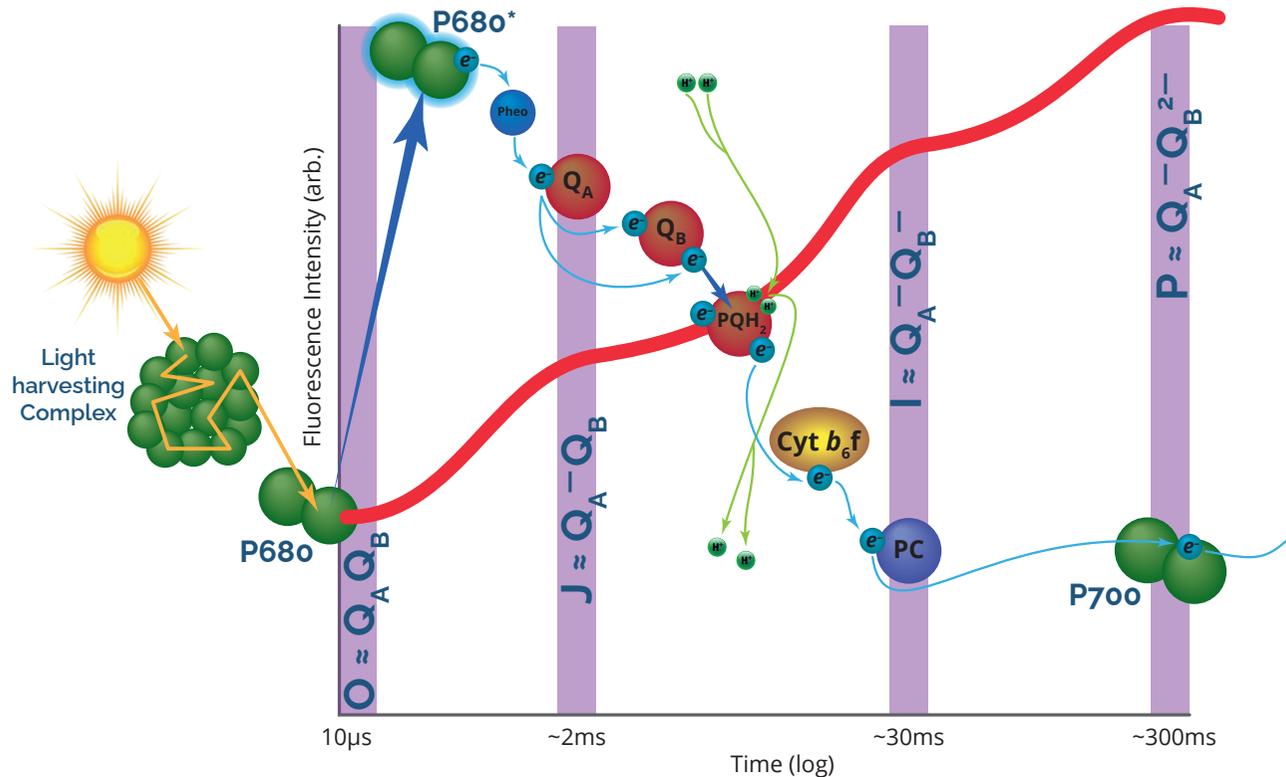
The graphic on the following page shows the first part of the Z-Scheme model overlaid onto a typical fast fluorescence trace. It also highlights redox states of the different elements within PSII and the electron transport chain (ETC) which links PSII to Photosystem I (PSI), shown at relevant time-points during the fast fluorescence measurement.

The fundamental goal of measuring fast fluorescence from dark-adapted samples is to analyse the changes in fluorescence intensity under fully saturating illumination. This begins at the point in time where all reaction centres (RCs) are oxidised (open) in the presence of a non-actinic measuring LED. This point immediately precedes the onset of saturating illumination. During saturating illumination, complete reduction occurs of PSII RCs, it's plastoquinone (PQ) electron acceptors and the ETC carriers that link to the PSI RC and beyond.

The parameters measured and calculated from this fluorescence rise provides valuable data relating to both the photochemical phase between O and J steps and the thermal phase between the J, I and P steps.

# FMS-300 Parameters Glossary

## Fast fluorescence kinetics: An Overview



The fluorescence signal is at the  $F_0$  level at  $T_0$ . Here, the energy states of the light harvesting complex and oxidised P680 are balanced, and the plastoquinone electron acceptors are also oxidised. Therefore,  $O \approx Q_A Q_B$  state.

Upon illumination, P680 becomes excited to P680\* and loses an electron to reduce pheophytin.  $Q_A$  is subsequently reduced to  $Q_A^-$  at the J-step, at approximately 2 ms after the onset of illumination. O - J represents the photochemical phase of the fluorescence rise, since the height of the J-step is dependent on the intensity of the excitation light. The height of the J-step is related to the balance between reduction of  $Q_A$  and its reoxidation by  $Q_B$ . It thus reflects light-driven accumulation of  $Q_A^-$  with  $Q_B$ , the second quinone electron acceptor in PSII, being oxidised. Therefore,  $J \approx Q_A^- Q_B$  state.

$Q_B$  requires 2 electrons from  $Q_A$  to become fully oxidised to  $Q_B^{2-}$ , before detaching from the PSII complex and migrating into the thylakoid membrane. In addition, it collects 2  $H^+$  ions from the chloroplast stroma (to become  $PQH_2$ ). The 2  $H^+$  ions are then released into the thylakoid lumen. Electrons are transferred from  $PQH_2$  to plastocyanin (PC) via Cytochrome  $b_6f$ . Since the J-I phase reflects the light-driven accumulation of  $Q_B^-$  in addition to the accumulation of  $Q_A^-$ ,  $I \approx Q_A^- Q_B^-$  state.

The final stage of the fluorescence rise (I - P), sees electrons transferred to PSI, subsequently reducing PSI electron acceptors. The P-step at between 300 - 600 ms represents complete reduction of PSII RCs and the maximum fluorescence intensity is reached. It represents the light-driven accumulation of  $Q_A^-$  and  $Q_B^{2-}$  and therefore,  $F_m$  (or P)  $\approx Q_A^- Q_B^{2-}$ . The J-I-P steps are collectively known as the thermal phase, since greater light intensities do not result in greater fluorescence intensity. These steps cannot therefore be photochemical in nature.

# FMS-300 Parameters Glossary

## Fast fluorescence kinetics (dark-adapted sample)

Parameter	Synonyms	Calculation	Interpretation	References
F <sub>o</sub>	D <sub>lo</sub> / C <sub>Sm</sub> ABS / C <sub>So</sub>	Calculated from an average of data points preceding a saturating pulse event	<p>The level of fluorescence emission when all the primary quinone acceptors (Q<sub>A</sub>) are in the oxidized or open state.</p> <p>An increase in F<sub>o</sub> has been attributed to the physical separation of the PSII reaction centres from their associated pigment antennae resulting in blocked energy transfer to PSII traps.</p>	<p>Baker (2008)<sup>3</sup> Banks (2017)<sup>9</sup> Srivastava et al. (1997)<sup>29</sup></p>
F <sub>m</sub>	P F <sub>p</sub> ABS / C <sub>Sm</sub>	Maximum average of 4 points during a saturating pulse event (see TF <sub>m</sub> )	<p>Fluorescence intensity recorded from a dark-adapted leaf during a saturating pulse event of sufficient intensity to fully reduce all PSII reaction centres. Represents the light-driven accumulation of Q<sub>A</sub><sup>-</sup> and Q<sub>B</sub><sup>2-</sup> and therefore, F<sub>m</sub> (or P) ≈ Q<sub>A</sub><sup>-</sup>Q<sub>B</sub><sup>2-</sup> state.</p>	<p>Stirbet and Govindjee (2011)<sup>7</sup> Strasser et al. (2004)<sup>8</sup> Samborska et al. (2019)<sup>30</sup></p>
F <sub>v</sub>		F <sub>m</sub> - F <sub>o</sub>	<p>Demonstrates the ability of PSII to perform photochemistry (Q<sub>A</sub> reduction) in a dark-adapted leaf.</p>	<p>Baker (2008)<sup>3</sup> Stirbet and Govindjee (2011)<sup>7</sup> Strasser et al. (2004)<sup>8</sup> Samborska et al. (2019)<sup>30</sup></p>
TF <sub>m</sub>	Tfmax	Finds the average of each group of four consecutive points over the entire range of data, finds the maximum 'average' and then saves the time for the 3rd point in that average	<p>Time to maximal fluorescence (F<sub>m</sub>) and an indicator of Q<sub>A</sub> reduction rate of the PSII acceptor. It is likely that this parameter has a strong sensitivity to the PSII/PSI ratio and the size of the PSI acceptor-side pool.</p>	<p>Strasser et al. (2004)<sup>8</sup> Kalaji et al. (2017)<sup>27</sup> Hassannejad et al. (2020)<sup>28</sup></p>

# FMS-300 Parameters Glossary

## Fast fluorescence kinetics (dark-adapted sample)

Parameter	Synonyms	Calculation	Interpretation	References
Area		The average level between each pair of two points multiplied by the time difference between those two points, summed for all points between the start (TFo or TF1 dependent on user selection) and TFm	The area above the fluorescence induction curve measured on a dark-adapted leaf. It is proportional to the pool size of the electron acceptors $Q_A$ on the reducing side of PSII. A useful parameter to probe electron transport capacity.	Rohacek and Bartak (1999) <sup>31</sup> Strasser et al. (2004) <sup>8</sup> Kalaji et al. (2017) <sup>27</sup>
$F_{20\mu s}$			Fluorescence value at 20 $\mu s$ following onset of a saturating pulse. Used as an estimation of Fo in devices that do not measure Fo using a modulated measuring light.	
$F_L$	L $F_{100\mu s}$		Fluorescence intensity at L step at T100 $\mu s$	
$F_K$	K $F_{300\mu s}$		Fluorescence intensity at K peak at T300 $\mu s$ . A well-documented symptom of heat stress, and is thought to indicate the separation of the OEC complex and electron transport between pheophytin and primary electron acceptor $Q_A$ . The direct cause of the K peak is the outflow of electrons from P680 to PSII acceptors, which over-compensates the inflow of electrons from the donor side of PSII to P680. The K peak is also affected by changes in the energetic relationships between photosystems II. An increase in the $F_K:F_J$ ratio indicates that the heat stress is inhibiting the donation of electrons by the OEC.	Strasser et al. (2000) <sup>32</sup> Lazár (2009) <sup>33</sup> Srivastava et al. (1995) <sup>34</sup> Kalaji et al. (2016) <sup>35</sup>

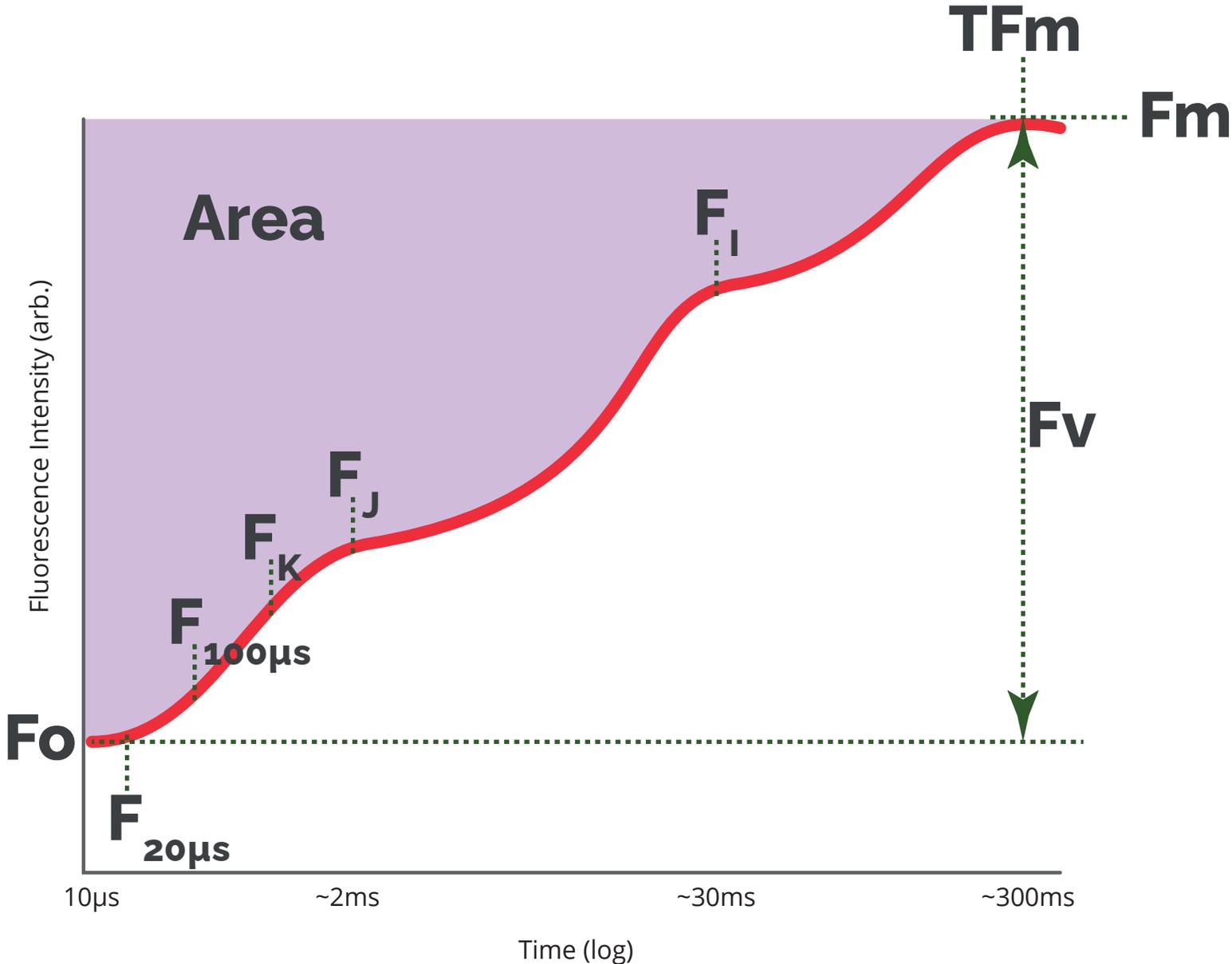
# FMS-300 Parameters Glossary

## Fast fluorescence kinetics (dark-adapted sample)

Parameter	Synonyms	Calculation	Interpretation	References
$F_J$	J $F_{2ms}$		$F_J$ marks the end of the O-J phase of the fluorescence induction. O-J is regarded as the photochemical phase since its height depends on intensity of used excitation light. O-J is related to the balance between reduction of $Q_A$ and its reoxidation by $Q_B$ . The J step therefore reflects light-driven accumulation of $Q_A^-$ with $Q_B$ , the second quinone electron acceptor in PSII, being oxidised. Therefore, $J \approx Q_A^- Q_B$ state.	Bednarikova et al. (2019) <sup>36</sup> Lazár (2006) <sup>33</sup> Strasser and Govindjee (1992) <sup>37</sup>
$F_I$	I $F_{30ms}$		$F_I$ is the mid-point of the J-I-P thermal phase of the fluorescence induction. It is known as the thermal phase since greater light intensities do not result in greater fluorescence intensity and therefore cannot be photochemical in nature. Reflects the light-driven accumulation of $Q_B^-$ in addition to the accumulation of $Q_A^-$ . Therefore, $I \approx Q_A^- Q_B^-$ state.	Lazár (2006) <sup>33</sup> Strasser and Govindjee (1992) <sup>37</sup>

# FMS-300 Parameters Glossary

Fast fluorescence kinetics (dark-adapted sample)



# FMS-300 Parameters Glossary

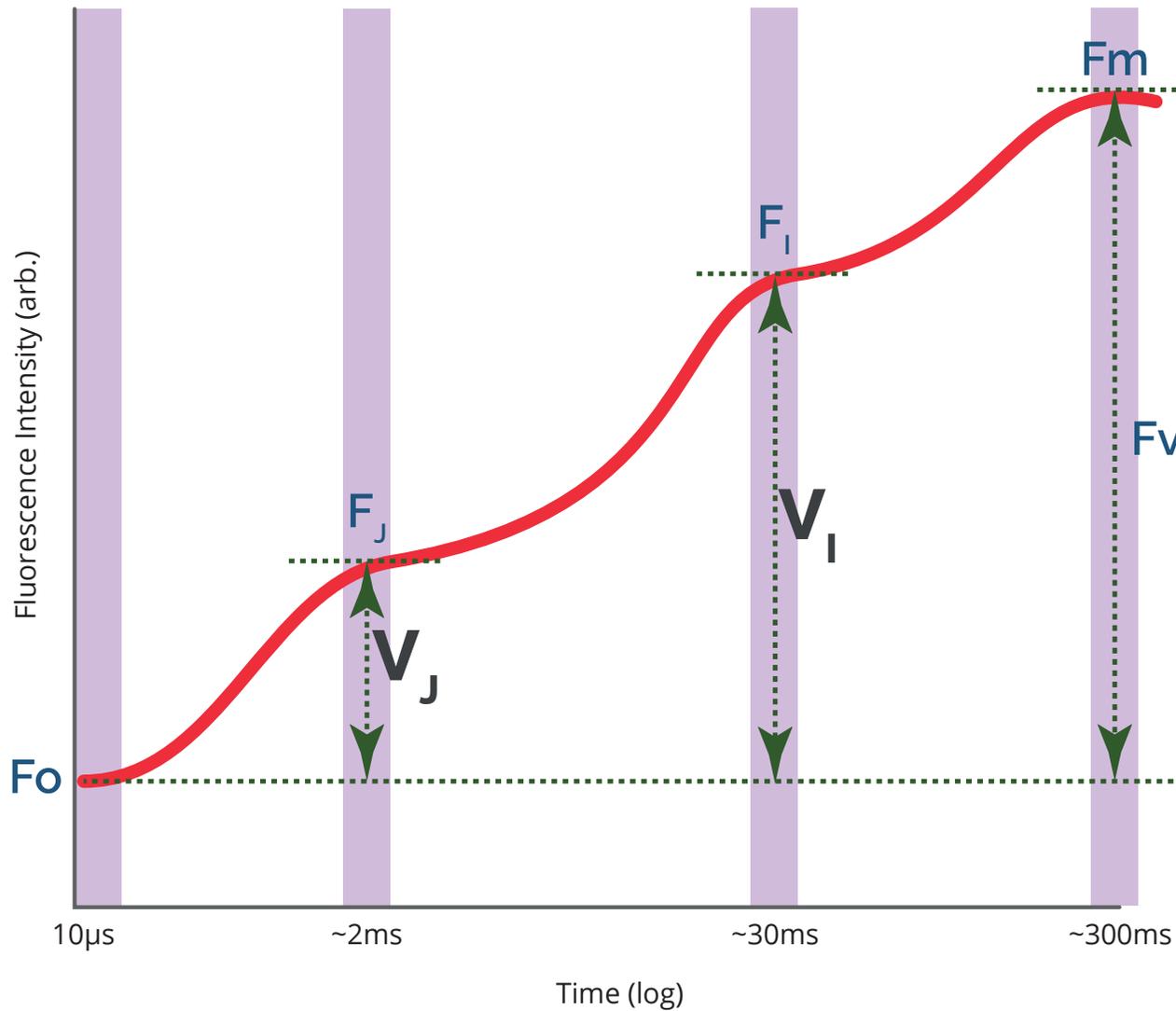
Ratiometric: (dark-adapted sample)



Parameter	Synonyms	Calculation	Interpretation	References
Fv/Fm	$\phi_{Po}$ TRo/ABS	$(F_m - F_o) / F_m$	Maximum quantum efficiency of PSII. Indicates the probability that an absorbed photon will be trapped by the PSII RC with the resultant reduction of $Q_A$ .	Maxwell and Johnson (2000) <sup>1</sup> Rosenqvist and van Kooten (2003) <sup>2</sup> Baker (2008) <sup>3</sup> Force et al. (2003) <sup>4</sup> Murchie and Lawson (2013) <sup>5</sup>
Fv/Fo		$(F_m - F_o) / F_o$	Estimates the maximum primary yield of photochemistry of PSII to provide an estimation of leaf photosynthetic capacity. It is also related to maximal efficiency of the water splitting reaction (also oxygen evolution) on the donor side of PSII.	LI Rong-hua et al. (2006) <sup>6</sup> Stirbet and Govindjee (2011) <sup>7</sup> Strasser et al. (2004) <sup>8</sup>
Fo/Fm		Fo/Fm	Ratio of extrema. An indicator of the physiological state of the photosynthetic apparatus.	Banks (2017) <sup>9</sup> Gliožeris et al. (2007) <sup>10</sup>
V <sub>J</sub>		$(F_J - F_o) / (F_m - F_o)$	Represents the relative emission of variable Chl a fluorescence at 2 ms (the J-step). Estimates the fraction of PSII $Q_A$ acceptors in the reduced state ( $Q_A^-/Q_{A(total)}$ )	Dewez et al. (2018) <sup>11</sup> van Rensburg et al. (1996) <sup>12</sup>
V <sub>I</sub>		$(F_I - F_o) / (F_m - F_o)$	Relative variable fluorescence at 30 ms the (I-step). This expression has no direct reference to changes in PSII	Strasser et al. (2004) <sup>8</sup> Kalaji et al. (2017) <sup>13</sup>

# FMS-300 Parameters Glossary

Ratiometric: (dark-adapted sample)



$$F_v/F_m = (F_m - F_o)/F_m$$

$$F_v/F_o = (F_m - F_o)/F_o$$

$$F_o/F_m = F_o/F_m$$

$$V_j = (F_j - F_o)/(F_m - F_o)$$

$$V_i = (F_i - F_o)/(F_m - F_o)$$

# FMS-300 Parameters Glossary

## Slopes & integrals (dark-adapted sample)

Parameter	Synonyms	Calculation	Interpretation	References
RC/ABS	$\gamma(\text{RC}) / ((1 - \gamma(\text{RC})))$	$(V_j / Mo) \times (Fv / Fm)$	The ratio of the total number of reaction centres to the total number of photons absorbed by the chlorophyll molecules of all reaction centres, and it expresses the average size of the active reaction centre (RC) antennas.	Barboričová et al. (2022) <sup>40</sup>
dVg/dto	$(\Delta Vg/\Delta t)_o$	$(1 \text{ ms} / (TF_L - Tfo)) \times ((F_L - F_{20\mu s}) / (Fm - Fo))$	Express the excitation energy transfer between the reaction centres.	Strasser et al. (2004) <sup>8</sup> Stirbet & Govindjee (2011) <sup>7</sup>
N		$Sm \times Mo \times (1 / V_j)$	Time-dependent turnover number of $Q_A^-$ . Expresses how many times $Q_A^-$ has been reduced in the time interval between Tfo to TFm.	Force et al. (2003) <sup>4</sup> Tsimilli-Michael (2020) <sup>41</sup>
Sm		Area / Fv	Normalization of the Area parameter on the maximum variable fluorescence, necessary to compare samples under different conditions. Provides a measure of the excitation energy needed to be supplied (by open units) in order to close all RCs. It thus expresses a work integral and also provides a measure of the amount (on an arbitrary scale) of all electron carriers reduced from Tfo until TFm. It is assumed proportional to the number of reduction and oxidation of one $Q_A^-$ molecule during the fast OJIP transient, and therefore related to the number of electron carriers per ETC.	Tsimilli-Michael (2020) <sup>41</sup> Stirbet & Govindjee (2011) <sup>7</sup>
Sm/TFm		$Sm / ((TFm) \times 1000)$	Expresses the average redox state of $Q_A^-$ in the time span from 0 to TFm, namely the average fraction of open reaction centres during the time needed to complete their closure. Provides a measure of the average electron transport activity.	Strasser et al. (2004) <sup>8</sup>

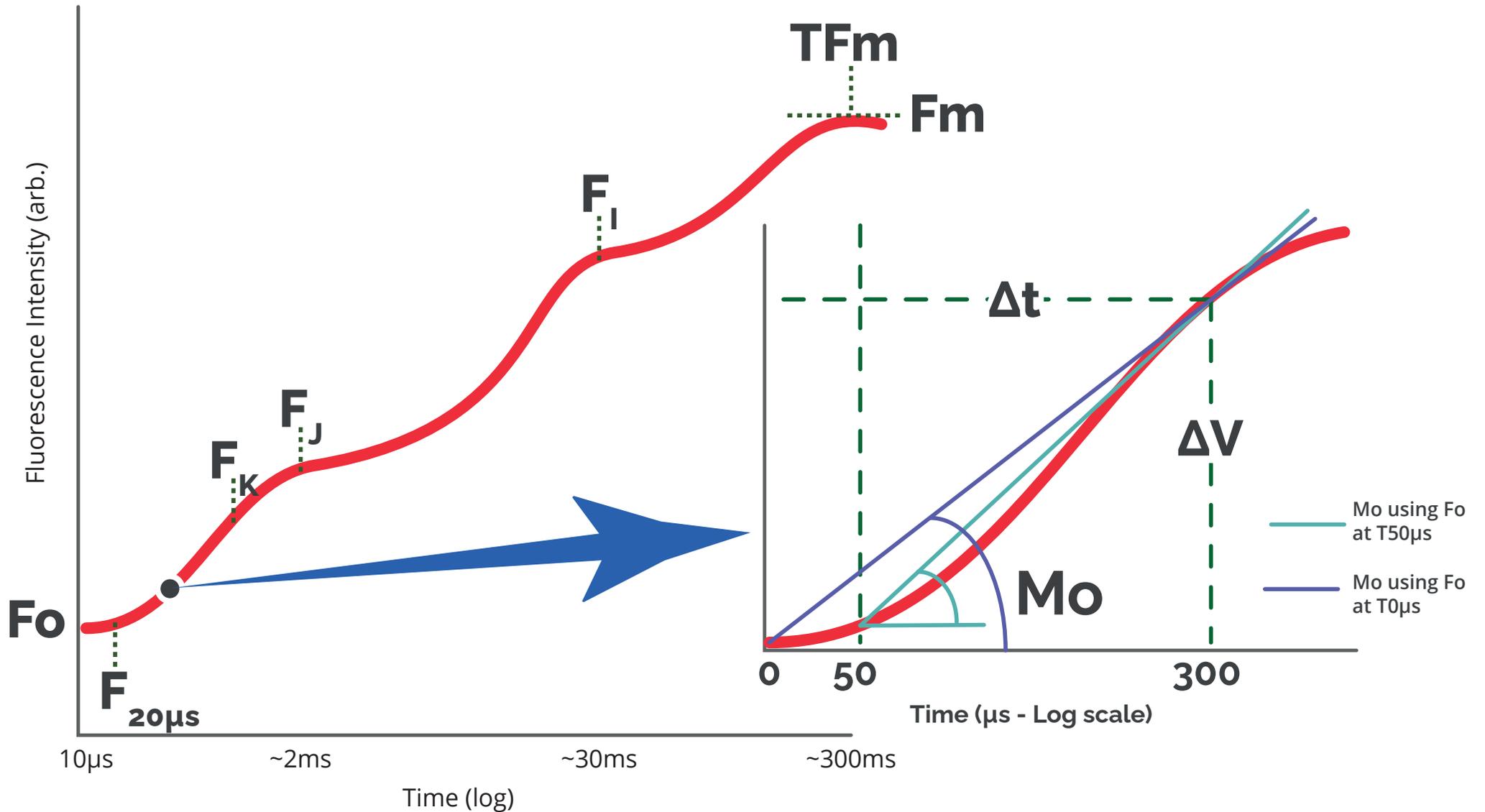
# FMS-300 Parameters Glossary

## Slopes & integrals (dark-adapted sample)

Parameter	Synonyms	Calculation	Interpretation	References
Mo	$(\Delta V/\Delta t)_o$ dV/dto	$\frac{1 \text{ ms}}{(TF_k - T Fo)} \times \frac{(F_k - Fo)}{(F_m - Fo)}$ or $\frac{0.001}{(0.0003 - 0)} \times \frac{(F_k - Fo)}{(F_m - Fo)}$	<p>Net rate of PS II closure in <math>\text{ms}^{-1}</math>. An approximation of the slope at the origin of the fast fluorescence rise <math>(\Delta V/\Delta t)_o</math> which is a measure of the rate of primary photochemistry. It is a net rate because the reduced <math>Q_A</math> can be reoxidised via electron transport beyond <math>Q_A</math>.</p> <p>In many publications, Mo is calculated using the fluorescence value at <math>50\mu\text{s}</math> for Fo. This has historically been regarded as the first "reliable" data point in continuous excitation fluorometers that have typically been used for the measurement of the Mo parameter.</p> <p>Since FMS-300 is a modulated system, it therefore measures a "reliable" dark-adapted Fo under the measuring LED only where all PSII RCs are oxidised (open). FMS-300 will therefore report different Mo values than continuous excitation fluorometers such as Handy PEA, Pocket PEA and M-PEA.</p> <p>If necessary, the Mo value can be recalculated to use <math>F_{50\mu\text{s}}</math> by exporting the FMS-300 data to CSV and using an external software package such as Excel.</p>	<p>Force et al. (2003)<sup>4</sup> Tsimilli-Michael (2020)<sup>41</sup></p>

# FMS-300 Parameters Glossary

Calculation of Mo Parameter: Using a true  $F_0$  rather than  $F_{50\mu s}$



# FMS-300 Parameters Glossary

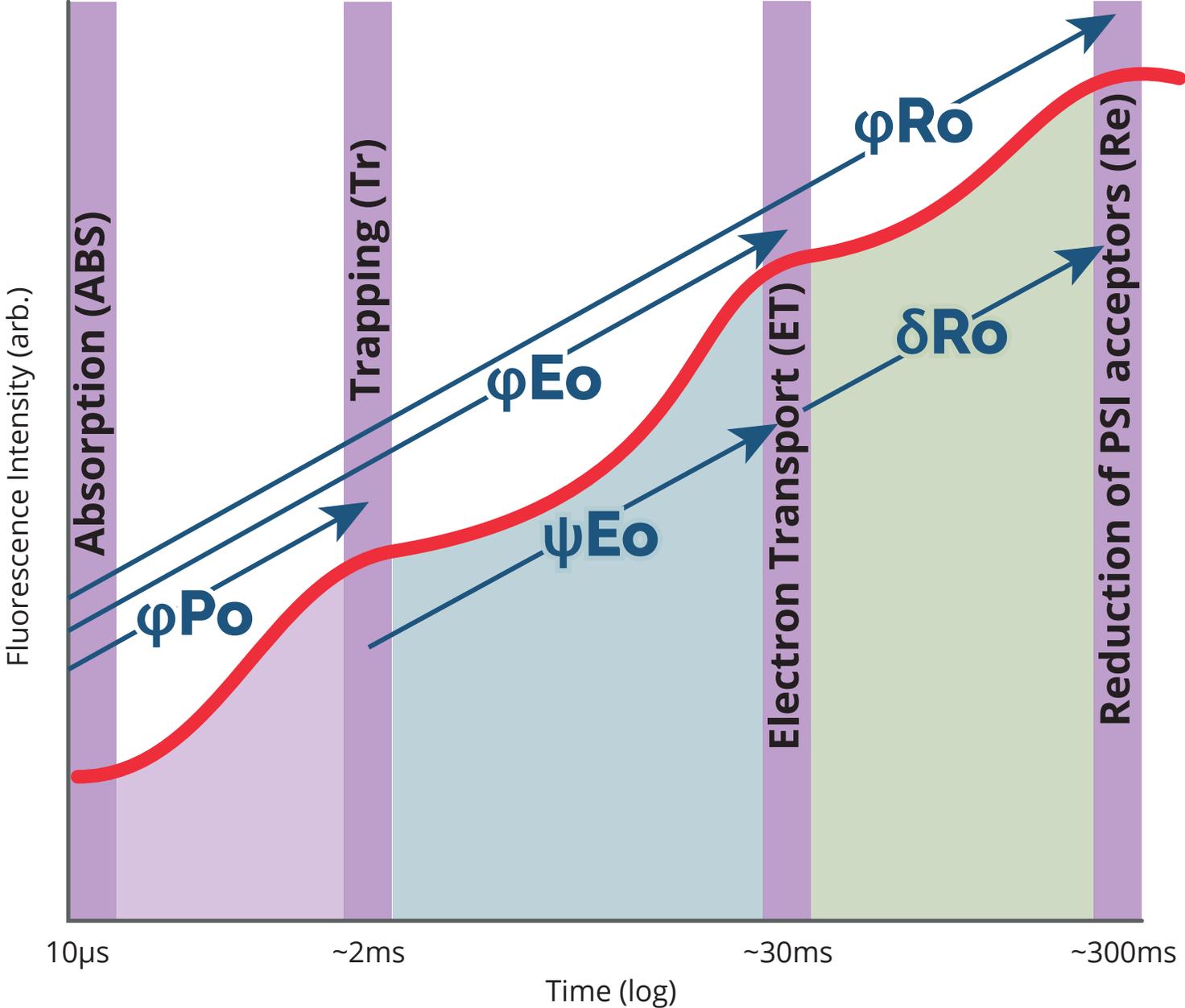
Yield:Flux ratios (dark-adapted sample)



Parameter	Synonyms	Calculation	Interpretation	References
$\phi_{Po}$	TRo / ABS Fv / Fm	$1 - F_o / F_m$	Trapping efficiency/probability (Fv/Fm ratio). The efficiency/probability that an absorbed photon will be trapped by the PSII RC with the resultant reduction of $Q_A$ . Relates to the whole measured sample that may be heterogeneous in terms of $Q_A$ reducing and non-reducing RCs.	Force et al. (2003) <sup>4</sup>
$\phi_{Eo}$	ETo / ABS	$1 - F_j / F_m$	The quantum yield for electron transport. Expresses the probability that an absorbed photon will move an electron into electron transport further than $Q_A^-$ .	Tsimilli-Michael (2020) <sup>41</sup> Gonzalez-Mendoza et al. (2006) <sup>42</sup>
$\phi_{Ro}$	REo / ABS	$(1 - V_i) / (1 - V_j)$	The quantum yield for the reduction of the final PSI electron acceptor per photon absorbed.	Cuchiara et al. (2013) <sup>43</sup>
$\psi_{Eo}$	ETo / Tro	$1 - V_j$	Electron transport efficiency/probability. The efficiency/probability that a trapped exciton, having triggered the reduction of $Q_A$ to $Q_A^-$ , can move an electron further than $Q_A^-$ into the electron transport chain.	Force et al. (2003) <sup>4</sup> Tsimilli-Michael (2020) <sup>41</sup> Gonzalez-Mendoza et al. (2006) <sup>42</sup>
$\delta_{Ro}$	REo / Eto	$1 - F_i / F_m$	The efficiency/probability that an electron of the intersystem electron carriers moves to reduce the final PSI electron acceptors (the likelihood of the reduction of a final PSI acceptor).	Cuchiara et al. (2013) <sup>43</sup>

# FMS-300 Parameters Glossary

Yield: Flux ratios (dark-adapted sample)



# FMS-300 Parameters Glossary

## Performance indices (dark-adapted sample)

Parameter	Synonyms	Calculation	Interpretation	References
$PI_{abs}$		$(\gamma RC / 1 - \gamma RC) \times (\varphi Po / 1 - \varphi Po) \times (\psi Eo / 1 - \psi Eo)$ or $(RC / ABS) \times (Fv / Fo) \times ((1 - V_j) / V_j)$	See Below.	Tsimilli-Michael (2020) <sup>41</sup> Strasser et al. (2000) <sup>32</sup> Strasser et al. (2004) <sup>8</sup> Tsimilli-Michael & Strasser (2008) <sup>44</sup>
$PI_{total}$		$(\gamma RC / 1 - \gamma RC) \times (\varphi Po / 1 - \varphi Po) \times (\psi Eo / 1 - \psi Eo) \times (\delta Ro / 1 - \delta Ro)$ or $(RC / ABS) \times (Fv / Fo) \times ((1 - V_j) / V_j) \times ((1 - V_i) / (V_i - V_j))$		
$DF_{abs}$		$\text{Log}(PI_{abs})$		
$DF_{total}$		$\text{Log}(PI_{total})$		

## Performance Indices and Driving Forces

The performance index  $PI_{abs}$  was introduced as a product of terms expressing energy bifurcations from the absorption events to the reduction of the intersystem electron transport chain. When extended as  $PI_{total}$ , the index also incorporates the energy bifurcation until the reduction of PSI end electron acceptors. As defined, the performance indexes are products of unit-less  $[pi/(1 - pi)]$  terms, where pi (i = 1, 2, ..., n) stands for probability (or fraction); hence, the terms express partial performances.

Such expressions are related to the Nernst equation, where pi is the fraction of the reduced and (1 - pi) the fraction of the oxidised form of a compound; in that case  $\text{log}[pi/(1 - pi)]$  expresses the potential or driving force for the corresponding oxidoreduction reaction. Extrapolating this inference from chemistry, the  $\text{log}(PI_{abs})$  was defined as the total driving forces  $DF_{abs}$ , which is the sum of partial driving forces. Since the calculated values of  $PI_{abs}$  and  $PI_{total}$  are on an arbitrary scale, they cannot be used to characterise a sample. It is their changes upon any environmental change/stress on any (but the same) photosynthetic material, that are meaningful. Hence the  $[PI_{total}]/[PI_{total,control}]$  is mostly used and, accordingly, the  $\Delta[DF_{total}] = [DF_{total}] - [DF_{total,control}]$ .

# FMS-300 Parameters Glossary

## Performance indices (dark-adapted sample)



The performance indexes, being very sensitive parameters (especially  $PI_{total}$ ), have proven to be very useful for routine screening of plants and evaluation of the overall impact of a stress on photosynthetic performance/behaviour. Their individual terms provide information for the impact on the sequential processes.

It is worth clarifying the following:

1. Though both  $PI_{abs}$  and  $PI_{total}$  are determined from the kinetics of PSII fluorescence,  $PI_{total}$  evaluates impacts also on PSI behaviour (via the  $\delta Ro$  term).
2. When introduced,  $PI_{abs}$  was denoted as 'performance index on absorption basis', hence the subscript 'abs'. When the extended  $PI_{total}$  was defined, though, it is also on absorption basis, it had to be distinguished; hence, subscript 'total' was used.
3. Like electrochemical potentials, driving forces  $DF_{abs}$  and  $DF_{total}$ , as well as any partial DF, can be positive, negative or zero, since they are the logarithms of quantities that can be bigger, smaller or equal to unity.

*Tsimilli-Michael M.*

*Revisiting JIP-test: An educative review on concepts, assumptions, approximations, definitions and terminology.*

*Photosynthetica. 2020 Jan 1;58(special issue):275-92.*

# FMS-300 Parameters Glossary

## Specific fluxes (dark-adapted sample)



Parameter	Synonyms	Calculation	Interpretation	References
ABS/RC	Antenna size AZ	$(Mo) \times (1 / V_j) \times (1 / \phi Po)$	Effective antenna size of an active RC. The total number of photons absorbed by chlorophyll molecules of all RCs divided by the total number of active RCs. It is influenced by the ratio of active/ inactive RCs.	Force et al. (2003) <sup>4</sup> Tsimilli-Michael (2020) <sup>41</sup>
TRo/RC		$Mo \times (1 / V_j)$	Maximal trapping rate or trapped energy flux (leading to a $Q_A$ reduction) of an RC. The maximal rate by which an exciton is trapped by the RC resulting in the reduction of $Q_A$ . A situation synonymous with measuring the trapping rate in the presence of DCMU.	Force et al. (2003) <sup>4</sup> Tsimilli-Michael (2020) <sup>41</sup>
ETo/RC		$Mo \times (1 / V_j) \times (1 - V_j)$	Electron transport flux (further than $Q_A$ ) in an active RC. The reoxidation of reduced $Q_A$ via electron transport in an active RC. Only reflects the activity of active RCs.	Force et al. (2003) <sup>4</sup> Tsimilli-Michael (2020) <sup>41</sup>
REo/RC		$Mo \times (1 / V_j) \times (1 - V_l)$	Electron flux reducing end electron acceptors at the PSI acceptor side, per active RC.	Tsimilli-Michael (2020) <sup>41</sup>
Dlo/RC		$(ABS / RC) - (TRo / RC)$	Effective dissipation of an active RC. The ratio of the total dissipation of untrapped excitation energy from all RCs with respect to the number of active RCs. Dissipation occurs as heat, fluorescence and energy transfer to other systems. It is influenced by the ratio of active/inactive RCs.	Force et al. (2003) <sup>4</sup>

# FMS-300 Parameters Glossary

Apparent fluxes (approximated by  $F_o$ , dark-adapted sample)



Parameter	Synonyms	Calculation	Interpretation	References
ABS/CS <sub>o</sub>		$F_o$	Number of photons absorbed by an excited PS II cross-section – the total number of photons absorbed by the antenna molecules of active and inactive PS II RCs over the sample cross-section. It can be represented by the dark adapted $F_o$ value.	Force et al. (2003) <sup>4</sup>
TRo/CS <sub>o</sub>		$F_o \times (1 - F_o / F_m)$	Maximal trapping rate in a PS II cross-section – the maximal trapping rate of an exciton that will lead to $Q_A$ reduction measured over a cross-section of active and inactive RCs. Approximated by $F_o$	Force et al. (2003) <sup>4</sup>
ETo/CS <sub>o</sub>		$F_o \times (1 - F_j / F_m)$	Electron transport in a PS II cross-section – the reoxidation of reduced $Q_A$ via electron transport over a cross-section of active and inactive RCs. Approximated by $F_o$	Force et al. (2003) <sup>4</sup>
REo/CS <sub>o</sub>		$F_o \times (1 - F_i / F_m)$	Electron flux reducing end electron acceptors at the PSI acceptor side, per cross section, approximated by $F_o$	Stirbet and Govindjee (2011) <sup>7</sup> Strasser et al. (2004) <sup>8</sup> Samborska et al. (2019) <sup>30</sup>
Dlo/CS <sub>o</sub>		$F_o \times (F_o / F_m)$	Dissipation in a PS II cross-section - total dissipation measured over the cross-section of the sample that contains active and inactive RCs. Dissipation occurs as heat, fluorescence and energy transfer to other systems. Approximated by $F_o$	Force et al. (2003) <sup>4</sup>

# FMS-300 Parameters Glossary

Apparent fluxes (approximated by  $F_m$ , dark-adapted sample)

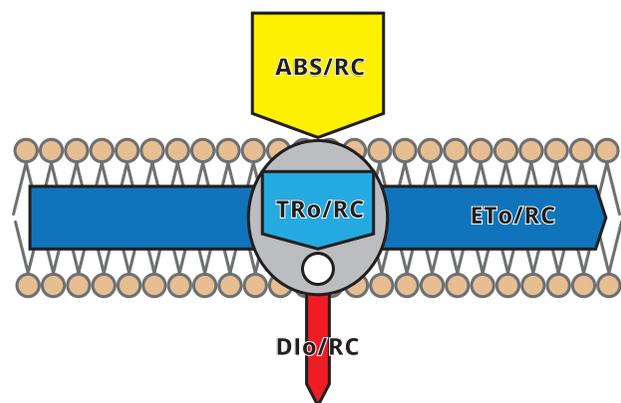


Parameter	Synonyms	Calculation	Interpretation	References
ABS/CSm		$F_m$	Absorption flux per cross section, approximated by $F_m$	Strasser et al. (2004) <sup>8</sup>
TRo/CSm		$F_v$	Trapped energy flux per cross section (at $t = 0$ ), approximated by $F_m$	
ETo/CSm		$F_m \times (1 - F_j / F_m)$	Electron transport flux per cross section (at $t = 0$ ), approximated by $F_m$	
REo/CSm		$F_m \times (1 - F_i / F_m)$	Electron flux reducing end electron acceptors at the PSI acceptor side, per cross section, approximated by $F_m$	
Dlo/CSm		$F_o$	Dissipated energy flux per cross section (at $t = 0$ ), approximated by $F_m$	

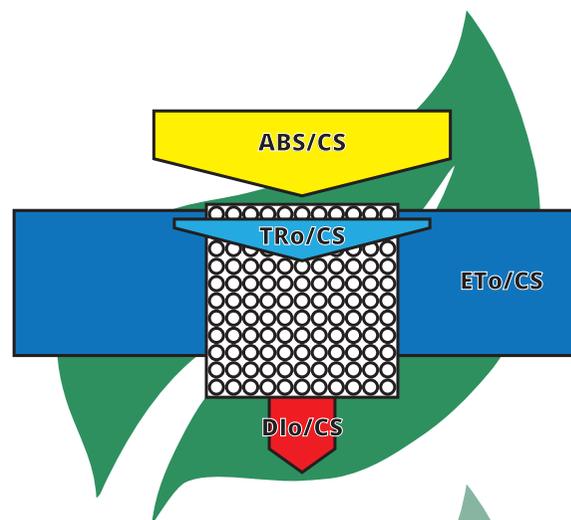
# FMS-300 Parameters Glossary

## Specific and Apparent Energy Flux modelling

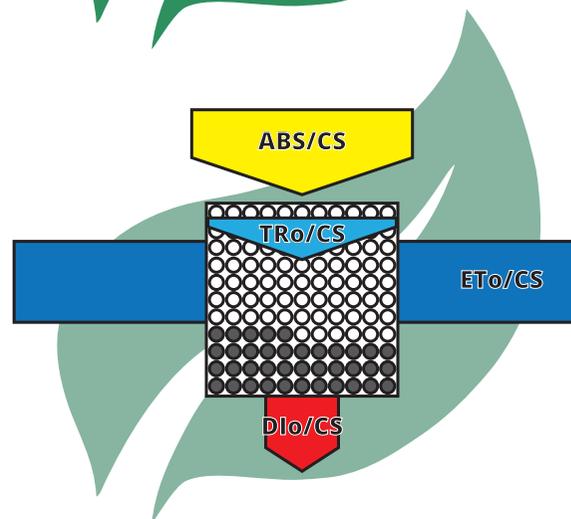
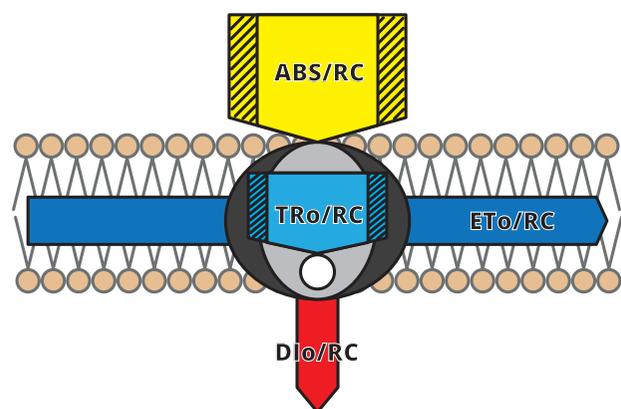
Adapted from Tsimilli-Michael & Strasser (2008) <sup>[1]</sup>.



**A**



**B**



The pipeline model was first proposed by Prof. Reto Strasser in 1987 <sup>[2]</sup> as a method of graphically representing specific and apparent (phenomenological) energy fluxes of the photosynthetic apparatus. The model was subsequently included as a key analysis tool within a piece of software called Biolzyer, which was originally authored and distributed by Prof. Strasser's Bioenergetics Laboratory at the University of Geneva.

The graphics opposite are stylised representations of the pipeline model and demonstrate the concept of comparing control (**A**) and stressed (**B**) samples. They are not based on specific data sets.

The 2 graphics on the left show membrane models for specific energy fluxes per reaction centre (RC). The 2 graphics on the right show leaf models for apparent energy fluxes per excited cross section (CS).

In both model types, parameters for absorption (ABS), trapping (TR), electron transport (ET) and dissipation (DI) are represented by arrows. The overall width of the arrows is dictated by the value of the respective parameter.

In the membrane model, ABS and TR by inactive RCs are indicated by the hatched lateral sections of the arrows. The proportion of antenna belonging to PSII units with inactive centres is indicated by the darker outer ellipse.

In the leaf model, open circles indicate the active RCs and closed circles the inactive centres. The darkness of the foliage indicates, qualitatively, the chlorophyll concentration per leaf cross section.

### References:

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Biolzyer software versions > V3.0.6 is distributed by Fluoromatics ([www.fluoromatics.com](http://www.fluoromatics.com)).

# FMS-300 Parameters Glossary

## De-excitation rate constants of PSII antenna (dark-adapted sample)



Parameter	Synonyms	Calculation	Interpretation	References
kN		$kN = (ABS) \times kF \times (1 / Fm)$	Non-photochemical de-excitation rate constant.	Tsimilli-Michael (2020) <sup>41</sup>
kP		$kP = (ABS) \times kF \times ((1 / Fo) - (1 / Fm))$ or $kN \times (Fv / Fo)$	Photochemical de-excitation rate constant.	

# Fast Fluorescence Analysis

Light-adapted samples



# FMS-300 Parameters Glossary

## Fast fluorescence kinetics (light-adapted sample)

Parameter	Synonyms	Calculation	Interpretation	References
F	F' Fs' Fs Ft' Ft	Steady state yield of fluorescence emission from light-adapted leaf prior to a saturating pulse event.	Provides little information on photosynthetic performance because these parameters are influenced by many factors. F' is sometimes referred to as Fs' when at steady state.	Baker (2008) <sup>3</sup> Maxwell and Johnson (2000) <sup>1</sup>
Fm'		Maximum average of 4 points during a saturating pulse event.	Maximal fluorescence recorded under saturating illumination at when all PSII RCs are closed on a light-adapted sample.	Stirbet and Govindjee (2011) <sup>7</sup> Strasser et al. (2004) <sup>8</sup> Samborska et al. (2019) <sup>30</sup>
Fq'	$\Delta F$	$Fm' - F$	Photochemical quenching of fluorescence by open (oxidised) PSII reaction centres.	Baker (2008) <sup>8</sup>
TFm'		Finds the average of each group of four consecutive points over the entire range of data, finds the maximum 'average' and then saves the time for the 3rd point in that average	Time to maximal fluorescence (Fm') in a light-adapted sample. As far as we are aware, this parameter has not been previously analysed in a light-adapted sample state and therefore, novel research may provide new understanding of the speed of complete PSII reduction in light-adapted leaves.	
Fo'(m)		Measurement of Fo' under far-red illumination.	By transiently shading the sample and illuminating with far-red light, PSI is preferentially excited relative to PSII which allows Q <sub>A</sub> to rapidly become fully oxidised.	Baker (2008) <sup>5</sup> Maxwell and Johnson (2000) <sup>1</sup>

# FMS-300 Parameters Glossary

## Fast fluorescence kinetics (light-adapted sample)

Parameter	Synonyms	Calculation	Interpretation	References
Fo'(c)		$Fo' = Fo / [(Fv/Fm) + (Fo/Fm')]$ <p>Requires previous dark-adapted Fv/Fm and Fm' measurements to calculate.</p>	<p>Measurement of Fo' using far-red illumination can be open to error if the far-red light does not adequately oxidise Q<sub>A</sub>. Additionally, non-photochemical quenching may also relax - both these factors either individually or combined may result in an overestimation of Fo'.</p> <p>Calculating Fo' in situations where plants are stressed and may experience significant photoinhibition has been queried. However, this is not valid, as the only requirements for the calculation of Fo' to be accurate are: (i) that PSII centres are open at the point of measuring Fo; (ii) that there is no reversal of down-regulation between the measurements of Fo and Fm; and (iii) that there is no reversal of photoinhibition between the measurements of Fm' and Fm. It has been argued that the calculation of Fo' is actually more accurate than the measured value, due to the difficulty in measuring Fo'.</p>	<p>Murchie and Lawson (2013)<sup>5</sup> Maxwell and Johnson (2000)<sup>1</sup> Oxborough and Baker (1997)<sup>39</sup></p>
Fv'		Fm' - Fo'	Demonstrates the ability of PSII to perform photochemistry (Q <sub>A</sub> reduction) in a light-adapted leaf.	Baker (2008) <sup>5</sup>

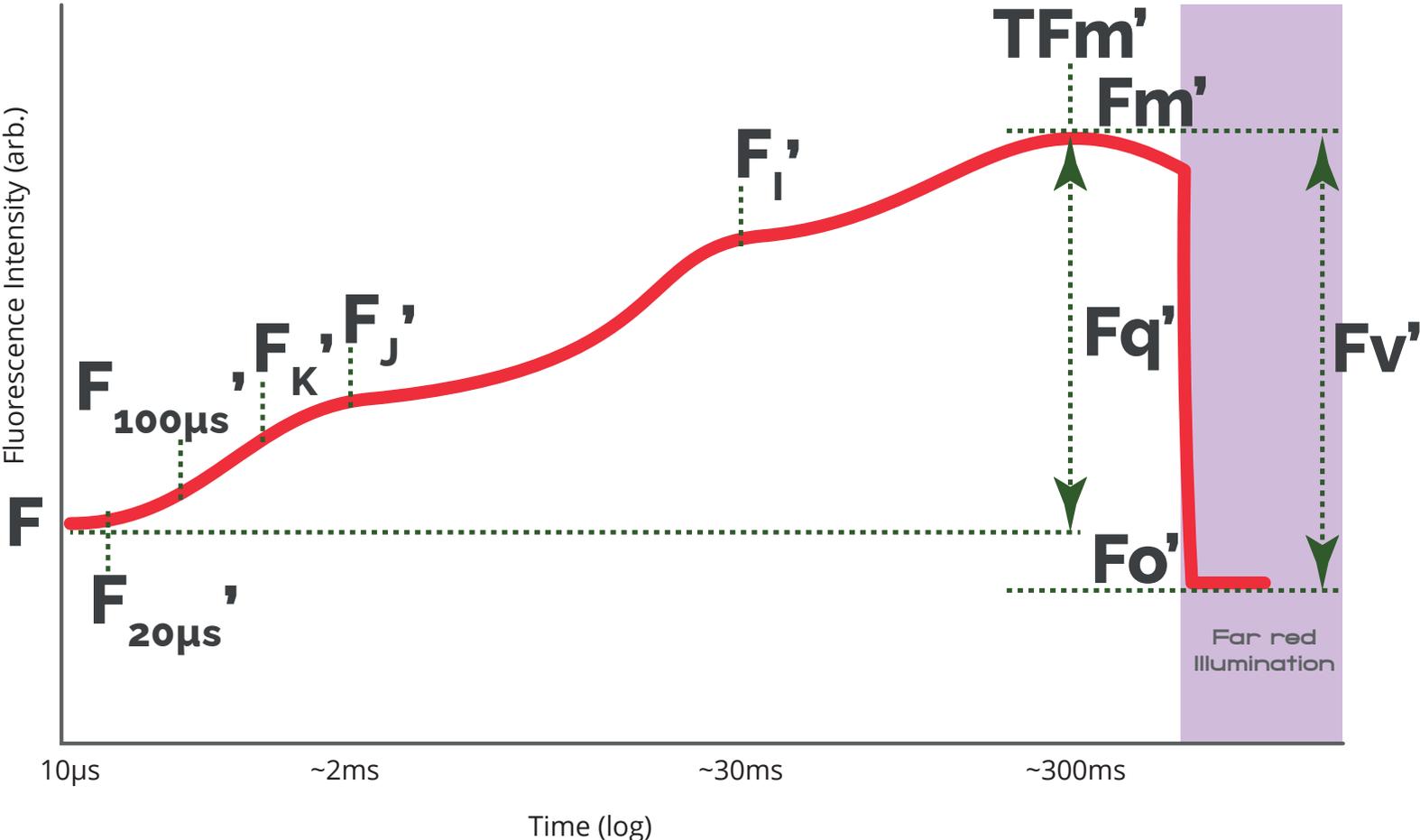
# FMS-300 Parameters Glossary

## Fast fluorescence kinetics (light-adapted sample)

Parameter	Synonyms	Calculation	Interpretation	References
$F'_{20\mu s}$			<p style="text-align: center;"><b>Potentially novel parameters.</b></p> <p>These readings are recorded by FMS-300 at fixed time points during saturating pulses applied to a light-adapted sample. They are thus the logical equivalents of the <math>F_{20\mu s}</math>, <math>F_L</math>, <math>F_K</math>, <math>F_J</math> and <math>F_I</math> parameters listed above for dark-adapted samples.</p> <p>They are presented for comparison with the established parameters for dark-adapted induction kinetics, and as additional data describing the light-adapted response to a saturating pulse.</p>	
$F'_L$	$F'_{100\mu s}$			
$F'_K$	$F'_{300\mu s}$			
$F'_J$	$F'_{2ms}$			
$F'_I$	$F'_{30ms}$			

# FMS-300 Parameters Glossary

Fast fluorescence kinetics (light-adapted sample)



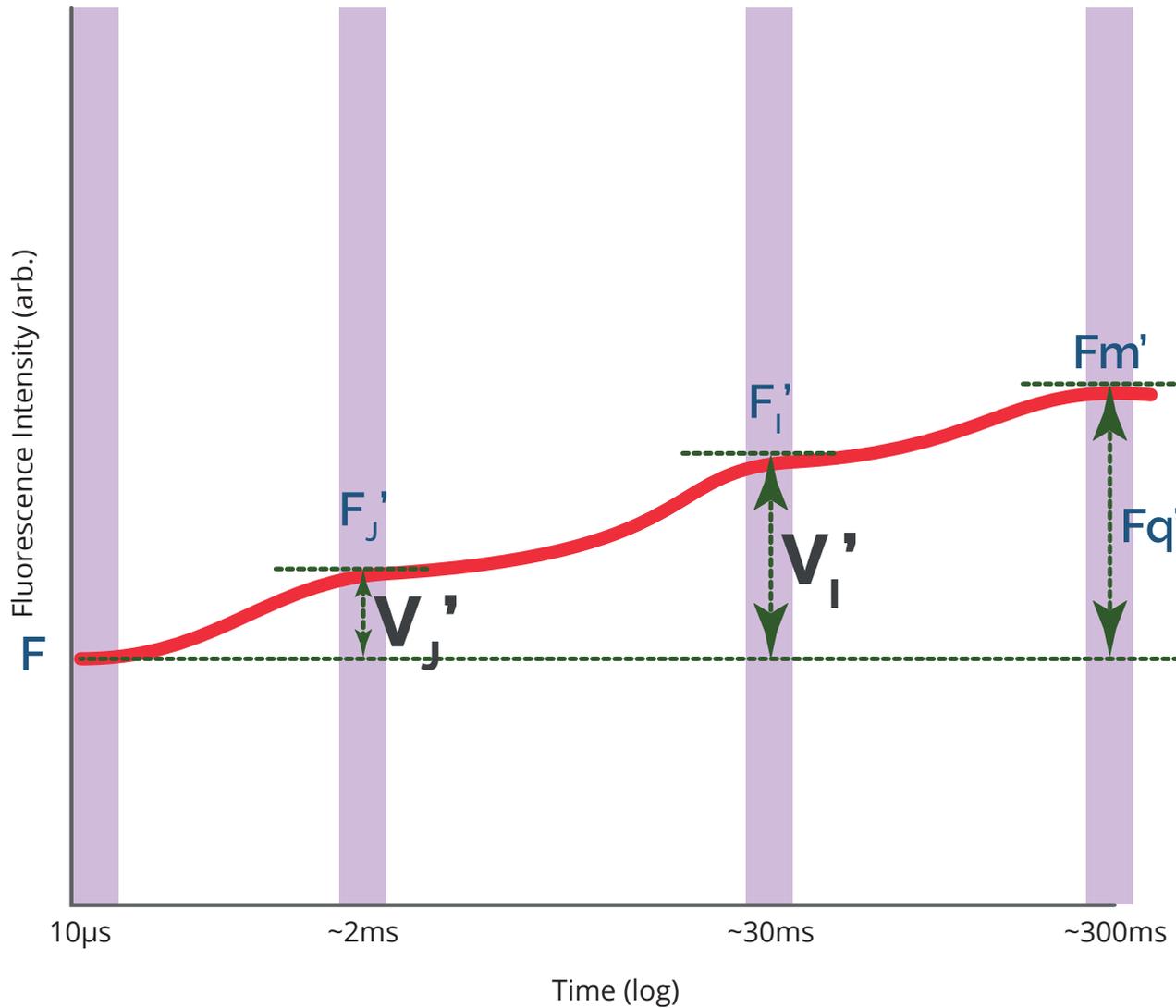
# FMS-300 Parameters Glossary

## Ratiometric (light-adapted sample)

Parameter	Synonyms	Calculation	Interpretation	References
$\Phi_{PSII}$	$Fq'/Fm'$ $\Delta F/Fm'$ Y(II)	$(Fm' - F) / Fm'$	PSII operating efficiency. Estimates the efficiency at which light absorbed by PSII is used for $Q_A$ reduction. At a given photosynthetically active photon flux density (PPFD) this parameter provides an estimate of the quantum yield of linear electron flux through PSII.	Genty et al. (1989) <sup>14</sup> Baker (2008) <sup>3</sup> Maxwell and Johnson (2000) <sup>1</sup>
$Fv'/Fm'$		$(Fm' - Fo') / Fm'$	Provides an estimate of the maximum efficiency of PSII photochemistry at a given PPFD, which is the PSII operating efficiency if all the PSII centres were 'open' ( $Q_A$ oxidized).	Baker (2008) <sup>3</sup>
$V'_j$		$(F'_j - F) / (Fm' - F)$	Proposed new parameter. Represents the relative variable fluorescence at 2 ms which would, in a dark-adapted sample, be the J-step of the OJIP curve. The interpretation of $V'_j$ being an estimation of the fraction of reduced $Q_A$ may still be valid although further research is needed to understand the contribution of reoxidised $Q_A$ given the sample is in a light-adapted state. There may be merit in analysing this parameter against/in conjunction with qL which provides an estimation of open PSII RCs.	
$V'_l$		$(F'_l - F) / (Fm' - F)$	Proposed new parameter. Relative variable fluorescence at 30 ms which, in a dark-adapted sample, would be the I-step of the OJIP curve. As with $V'_j$ above, there may be merit in analysing this parameter with qL.	

# FMS-300 Parameters Glossary

Ratiometric (light-adapted sample)



$$\Phi_{PSII} = (F_m' - F) / F_m'$$

$$F_v' / F_m' = (F_m' - F_o') / F_m' *$$

$$V_j' = (F_j' - F) / (F_m' - F)$$

$$V_i' = (F_i' - F) / (F_m' - F)$$

\*  $F_o'$  can be either calculated from  $F_o' = F_o / ((F_v / F_m) + (F_o / F_m'))$  or by measuring the fluorescence value  $F$  under far red light.

# Slow Fluorescence Analysis

Quenching analysis models



# FMS-300 Parameters Glossary

## Quenching: Puddle Model

Parameter	Synonyms	Calculation	Interpretation	References
NPQ		$\frac{(F_m - F_m')}{F_m'}$ or $F_m / F_m' - 1$	Coefficient of non-photochemical quenching (Stern-Volmer approach). Light-induced photoprotection through thermal dissipation of energy. Can be used to infer activity of the Xanthophyll Cycle as it is more sensitive to energy dissipation within the antennae matrix which contain xanthophylls, where energy dependent quenching occurs. A more robust assessment of non-photochemical quenching, since it is not dependent upon $F_o'$ and is not affected by $F_o$ quenching.	Kramer et al (2004) <sup>15</sup> Murchie and Lawson (2013) <sup>5</sup> Baker (2008) <sup>3</sup> Muller et al (2001) <sup>16</sup> Ruban et al (2012) <sup>17</sup> Schreiber (2004) <sup>18</sup>
qN		$1 - F_v' / F_v$	Used to calculate non-photochemical quenching. This parameter describes the percentage of quenching in a similar manner to $\Phi$ PSII.	Ruban (2016) <sup>19</sup>
qP		$F_q' / F_v'$	Photochemical quenching: relates PSII maximum efficiency to operating efficiency. Non-linearly relates to the proportion of PSII centres in open states based on a puddle model for the photosynthetic unit.	Kramer et al (2004) <sup>15</sup> Murchie and Lawson (2013) <sup>5</sup>

# FMS-300 Parameters Glossary

## Quenching: Lake Model (Kramer)

Parameter	Synonyms	Calculation	Interpretation	References
$\Phi_{PSII}$	$F_q'/F_m'$ $\Delta F/F_m'$ $Y(II)$	$(F_m' - F) / F_m'$	PSII operating efficiency. Estimates the efficiency at which light absorbed by PSII is used for $Q_A$ reduction. At a given photosynthetically active photon flux density (PPFD) this parameter provides an estimate of the quantum yield of linear electron flux through PSII.	Genty et al. (1989) <sup>14</sup> Baker (2008) <sup>3</sup> Maxwell and Johnson (2000) <sup>1</sup>
$Y(NPQ)$	$\Phi_{NPQ}$	$(F / F_m') - (F / F_m)$	Quantum yield of regulated non-photochemical thermal energy dissipation via $\Delta pH$ - and xanthophyll pathways. Competitive pathway with $\Phi_{PSII}$ and $Y(NO)$ i.e. $Y(NPQ) + Y(NO) + \Phi_{PSII} = 1$	Kramer et al (2004) <sup>15</sup> Hendrickson et al (2004) <sup>20</sup> Klughammer & Schreiber (2008) <sup>21</sup> Lazar (2016) <sup>22</sup>
$Y(NO)$	$\Phi(f,D)$ $\Phi(NO)$	$F/F_m$	Quantum yield of primarily constitutive losses, corresponding to the sum of non-regulated heat dissipation and fluorescence emission. Reflects non-light induced (basal or dark) quenching processes. Competitive pathway with $\Phi_{PSII}$ and $Y(NPQ)$ i.e. $Y(NPQ) + Y(NO) + \Phi_{PSII} = 1$	Kramer et al (2004) <sup>15</sup> Hendrickson et al (2004) <sup>20</sup> Klughammer & Schreiber (2008) <sup>21</sup> Lazar (2016) <sup>22</sup>
$q_L$		$(F_q' / F_v') \times (F_o' / F)$	Estimates the fraction of open PSII reaction centres based on a Stern-Volmer approach using a "lake" or "connected units" model which describes photosynthesis consisting of multiple reaction centres connected by shared antenna.	Kramer et al (2004) <sup>15</sup> Baker (2008) <sup>3</sup> Murchie and Lawson (2013) <sup>5</sup>

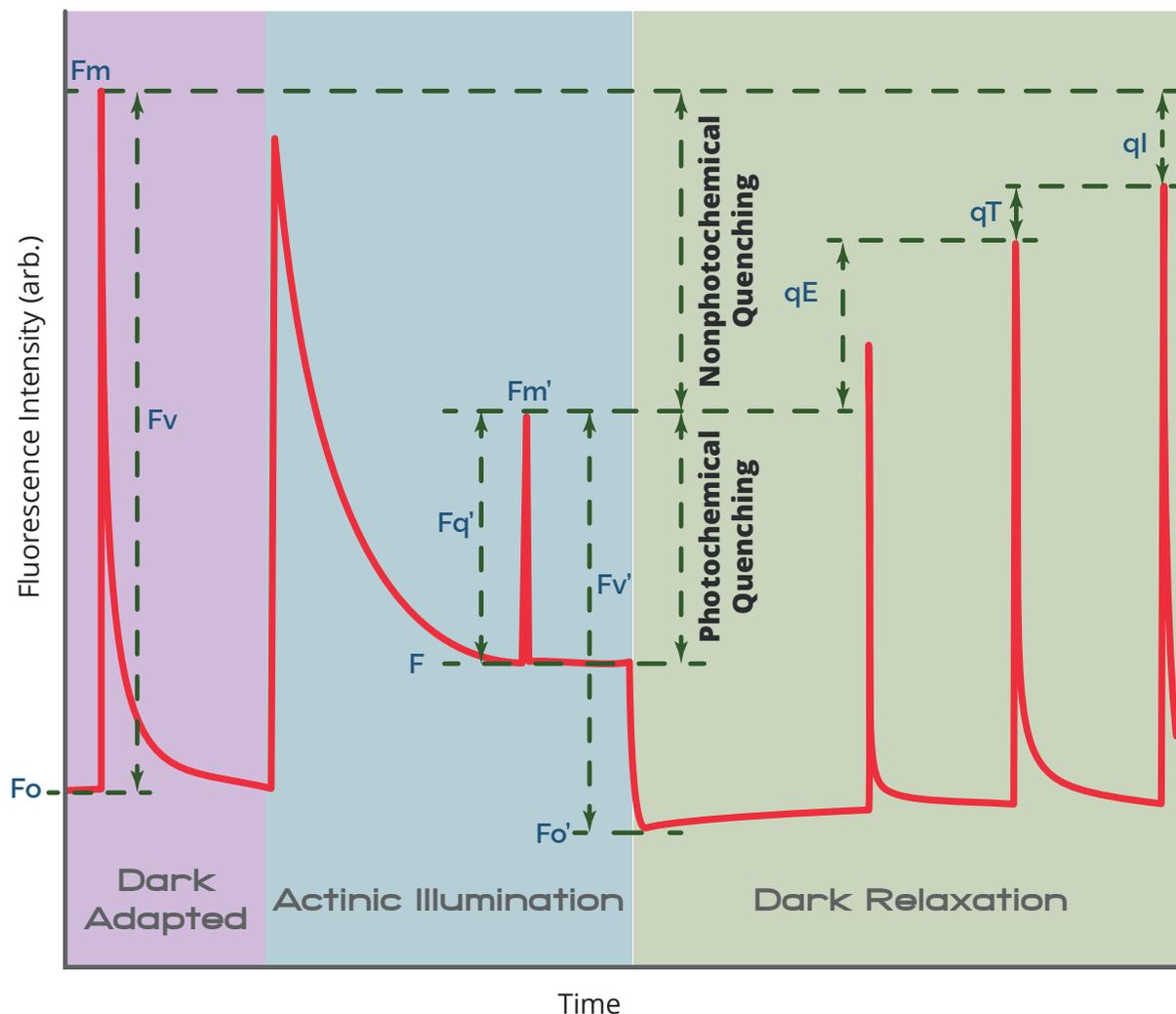
# FMS-300 Parameters Glossary

## Quenching: Lake Model (Hendrickson)

Parameter	Synonyms	Calculation	Interpretation	References
$\Phi_{PSII}$	$F_q'/F_m'$ $\Delta F/F_m'$ $Y(II)$	$(F_m' - F) / F_m'$	PSII operating efficiency. Estimates the efficiency at which light absorbed by PSII is used for $Q_A$ reduction. At a given photosynthetically active photon flux density (PPFD) this parameter provides an estimate of the quantum yield of linear electron flux through PSII.	Genty et al. (1989) <sup>14</sup> Baker (2008) <sup>3</sup> Maxwell and Johnson (2000) <sup>1</sup>
$Y(NPQ)$	$\Phi_{NPQ}$	$(F / F_m') - (F / F_m)$	Quantum yield of regulated non-photochemical thermal energy dissipation via $\Delta pH$ - and xanthophyll pathways. Competitive pathway with $\Phi_{PSII}$ and $Y(NO)$ i.e. $Y(NPQ) + Y(NO) + \Phi_{PSII} = 1$	Kramer et al (2004) <sup>15</sup> Hendrickson et al (2004) <sup>20</sup> Klughhammer & Schreiber (2008) <sup>21</sup> Lazar (2016) <sup>22</sup>
NPQ		$(F_m - F_m') / F_m'$ or $F_m / F_m' - 1$	Coefficient of non-photochemical quenching (Stern-Volmer approach). Light-induced photoprotection through thermal dissipation of energy. Can be used to infer activity of the Xanthophyll Cycle as it is more sensitive to energy dissipation within the antennae matrix which contain xanthophylls, where energy dependent quenching occurs. A more robust assessment of non-photochemical quenching, since it is not dependent upon $F_o'$ and is not affected by $F_o$ quenching.	Kramer et al (2004) <sup>15</sup> Murchie and Lawson (2013) <sup>5</sup> Baker (2008) <sup>3</sup> Muller et al (2001) <sup>16</sup> Ruban et al (2012) <sup>17</sup> Schreiber (2004) <sup>18</sup>
$Y(NO)$	$\Phi(f,D)$ $\Phi(NO)$	$F/F_m$	Quantum yield of primarily constitutive losses, corresponding to the sum of non-regulated heat dissipation and fluorescence emission. Reflects non-light induced (basal or dark) quenching processes. Competitive pathway with $\Phi_{PSII}$ and $Y(NPQ)$ i.e. $Y(NPQ) + Y(NO) + \Phi_{PSII} = 1$	Kramer et al (2004) <sup>15</sup> Hendrickson et al (2004) <sup>20</sup> Klughhammer & Schreiber (2008) <sup>21</sup> Lazar (2016) <sup>22</sup>

# FMS-300 Parameters Glossary

## Quenching Experiments



### Puddle Model

$$\text{NPQ} = (F_m - F_m') / F_m'$$

$$q_N = 1 - F_v' / F_v$$

$$q_P = F_{q'} / F_v$$

### Lake Model (Kramer)

$$\Phi_{\text{PSII}} = (F_m' - F) / F_m'$$

$$Y(\text{NPQ}) = (F / F_m') - (F / F_m)$$

$$Y(\text{NO}) = F / F_m$$

$$q_L = (F_{q'} / F_v') \times (F_o' / F)$$

### Lake Model (Hendrickson)

$$\Phi_{\text{PSII}} = (F_m' - F) / F_m'$$

$$Y(\text{NPQ}) = (F / F_m') - (F / F_m)$$

$$\text{NPQ} = (F_m - F_m') / F_m'$$

$$Y(\text{NO}) = F / F_m$$

# Slow Fluorescence Analysis

Measuring electron transport rates



# FMS-300 Parameters Glossary

## Electron transport rate

Parameter	Synonyms	Calculation	Interpretation	References
ETR	J	$PAR \times PFD_a^* \times \text{fraction}_{PSII}^{**} \times \Phi_{PSII}$	Non-cyclic electron transport rate through PSII	Murchie and Lawson (2013) <sup>5</sup> Baker (2008) <sup>3</sup>
JNPQ		$Y(NPQ) \times PFD_a^* \times \text{fraction}_{PSII}^{**}$	The rate of energy dissipation via $\Delta pH$ and xanthophyll-regulated thermal dissipation	Hendrickson et al (2004) <sup>20</sup>
PAR			Ambient PAR values from the PTL-100 leafclip or user-defined PAR values from routine settings.	
$\alpha$		Levenberg–Marquardt algorithm <sup>***</sup>	Indicates the slope of the rise of ETR vs. PPFD and is proportional to efficiency of light capture (effective quantum yield or $\Phi_{PSII}$ ).	Schreiber (2004) <sup>23</sup> Gavin (2019) <sup>45</sup>
$\beta$		Levenberg–Marquardt algorithm <sup>***</sup>	Where the plant is subjected to supra-saturating light intensities, ETR vs. PPFD curve often tends to decline, which could be associated with photoinhibition. This effect would be more likely to occur with traditional <i>P - E</i> or steady state light curves, where steady-state photosynthetic rates are achieved. However, as steady-state is not achieved in RLC protocols, there isn't normally sufficient time for photodamage to occur. It has been suggested that the decline of ETR at supra-saturating light intensities could be linked to dynamic down-regulation of PSII.	Henley (1993) <sup>25</sup> White and Critchley (1999) <sup>26</sup> Gavin (2019) <sup>45</sup>
ETR <sub>max</sub>		Levenberg–Marquardt algorithm <sup>***</sup>	During the light-saturated phase of a rapid light curve, the capacity of the electron transport chain limits the electron transport rate. When ETR vs. PPFD is plotted. The curve reaches a plateau where maximum ETR occurs.	Schreiber (2004) <sup>23</sup> Gavin (2019) <sup>45</sup>

# FMS-300 Parameters Glossary

## Electron transport rate

Parameter	Synonyms	Calculation	Interpretation	References
$E_k$	$I_k$	Levenberg–Marquardt algorithm. *** The PAR value from the horizontal axis where the intercept between $\alpha$ and $ETR_{max}$ occurs.	The minimum saturating irradiance for electron transport through PSII. Can be related to quenching. Below $E_k$ , photochemical quenching is the dominant pathway whereas non-photochemical quenching is dominant above $E_k$ .	Sakshaug et al (1997) <sup>24</sup> Henley (1993) <sup>25</sup> Gavin (2019) <sup>45</sup>

### \* fraction<sub>PSII</sub>

The assumed proportion of absorbed quanta by PSII reaction centres. 0.5 is readily used for fraction<sub>PSII</sub> although this is likely to be inaccurate for many samples. Variation in concentration of other pigments such as anthocyanins can affect the true fraction<sub>PSII</sub> value.

### \*\* PFD<sub>a</sub>

Frequently assumed to be 0.84, i.e., 84% of incident PPFD is assumed to be absorbed by leaves. This assumption may be reasonable for many mature green leaves, but is not always the case and large deviations from this value can frequently occur (30, 47, 53). Ideally, PFD<sub>a</sub> should be measured using an integrating sphere with a light source similar to that used to drive photosynthesis and a spectroradiometer or quantum sensor.

### \*\*\* Levenberg–Marquardt algorithm

The Levenberg-Marquardt algorithm was developed in the early 1960's to solve non-linear least squares problems. Least squares problems arise in the context of fitting a parametrised mathematical model to a set of data points by minimizing an objective expressed as the sum of the squares of the errors between the model function and a set of data points. If a model is linear in its parameters, the least squares objective is quadratic in the parameters. This objective may be minimized with respect to the parameters in one step via the solution to a linear matrix equation. If the fit function is not linear in its parameters, the least squares problem requires an iterative solution algorithm. Such algorithms reduce the sum of the squares of the errors between the model function and the data points through a sequence of well-chosen updates to values of the model parameters.

Gavin, Henri P. "The Levenberg-Marquardt algorithm for non-linear least squares curve-fitting problems." Department of civil and environmental engineering, Duke University 19 (2019).

# FMS-300 Parameters Glossary

## Electron transport rate

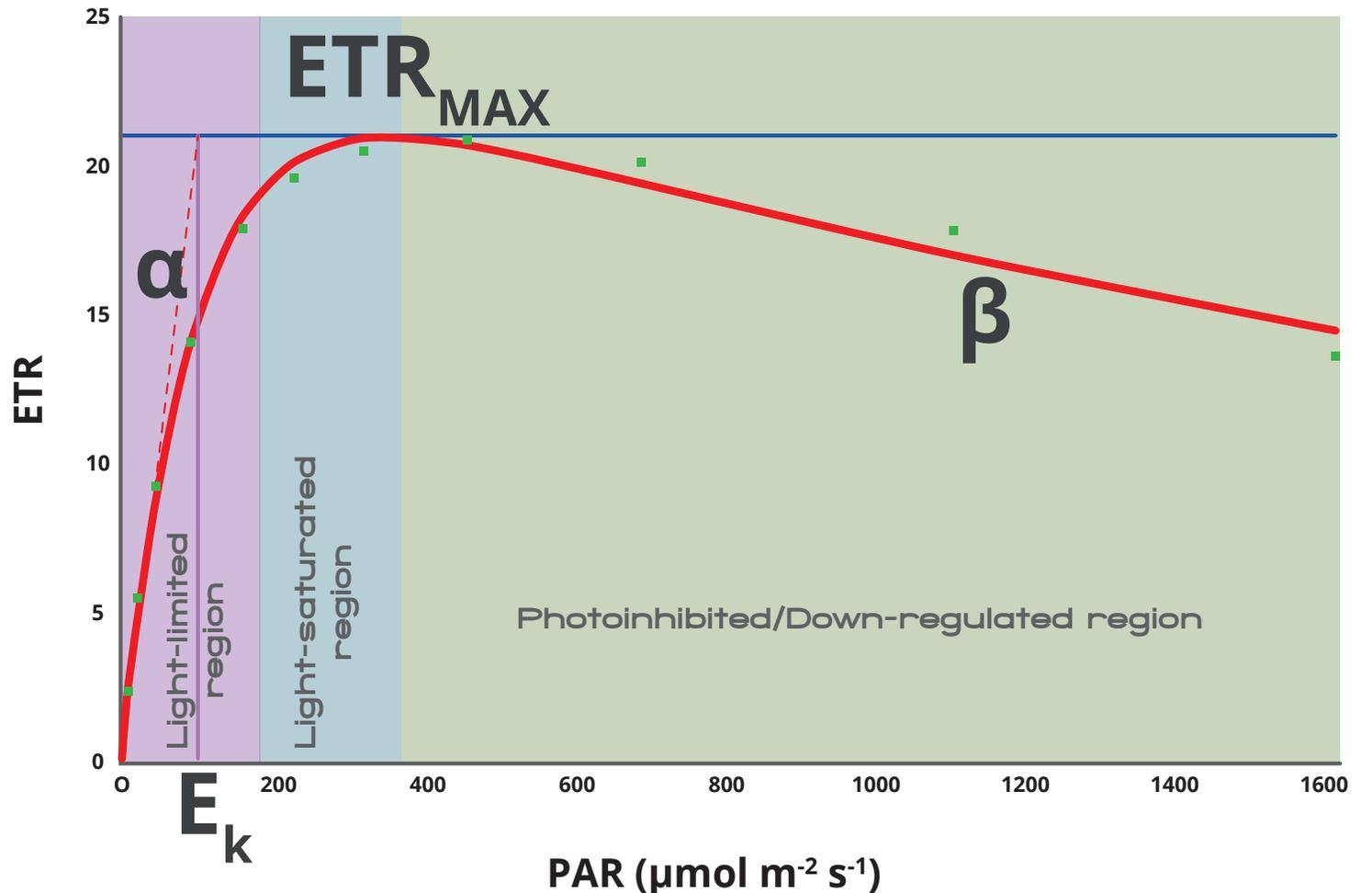
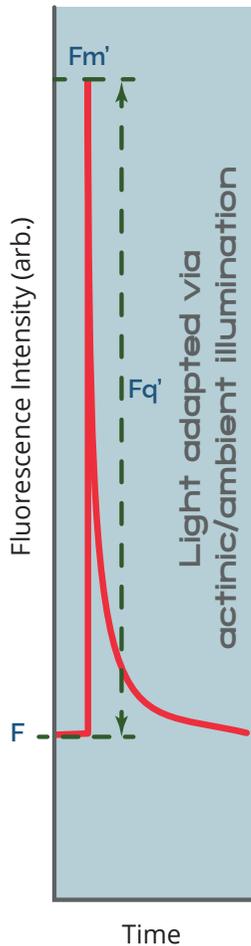
$$\text{ETR} = \Phi_{\text{PSII}} \times \text{PAR} \times \text{fraction}_{\text{PSII}} \times \text{PFD}_a$$

$$\Phi_{\text{PSII}} = (F_m' - F) / F_m'$$

PAR = Ambient or actinic value

$$\text{fraction}_{\text{PSII}} \approx 0.5$$

$$\text{PFD}_a \approx 0.84$$



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