A model for the irradiance responses of photosynthesis

Jeremy Harbinson* and Xinyou Yin

*Horticulture and Product Physiology Group, Department of Plant Sciences, Wageningen University and Research, Wageningen 6708 PB, the Netherlands
bCentre for Crop Systems Analysis, Department of Plant Sciences, Wageningen University and Research, Wageningen 6700 AK, the Netherlands

The analysis of the irradiance responses of photosynthetic processes, such as the quantum efficiencies of electron transport by photosystems I and II (PSI and PSII) or the rate of carbon dioxide fixation, is limited by the lack of mechanistically based analytical model for these processes. Starting with a model of P700 redox state, we develop a series of analytical functions which can be used to fit the irradiance responses of the quantum yields for electron transport by PSI and PSII, the irradiance responses of electron transport by PSI and PSII, and even the irradiance response of the fixation rate of carbon dioxide. These functions depend on two or three parameters so they can be fit to typical irradiance response data. We illustrate by example the use of these functions in various applications and discuss further use and development of the basic model described in detail here.

Introduction

Models play an important role in plant physiology and elsewhere. They serve to unambiguously consolidate knowledge acquired by experiment, they provide a tool for analyzing experimental data, they allow simulations of natural processes and they provide a heuristic tool with which to explore what we do and do not understand about nature. In photosynthetic physiology, the model of Farquhar, von Caemmerer and Berry (Farquhar et al. 1980) beautifully illustrates how a model can serve diverse roles (consolidation, analysis, simulation and a heuristic tool). The derivation elegantly focuses on the important, underlying physiological processes for the phenomenon it seeks to reproduce, and the result is a model with an analytical solution that describes in a simple way the responses of C3 photosynthetic systems to carbon dioxide concentration or mole fraction. The model has a small number of parameters that need to be estimated [as few as two (typically V_{cmax} and J_{max})], depending on the assumptions that are made and data available. This makes the model usable as a tool with which to analyze experimental data, which is often limited in the number of datapoints. Its analytical form also makes it easily portable and easy to integrate into more complex models, and the clear physiological meaning underlying all the parameters in the model make it easy to understand in relation to natural phenomena.

The value of the Farquhar, von Caemmerer and Berry equation also reflects another characteristic of plant physiology – we very often characterize processes in terms of their responses to external and internal factors and then seek to simply describe, hopefully in a physiologically insightful way, the data in terms of parameters that summarize the responses obtained. The responses of photosynthesis to irradiance is a commonly used way of characterizing the photosynthetic properties of a leaf, or some other photosynthetic tissue. The responses can be of fluxes, such as the rate of carbon dioxide fixation, or quantum efficiencies, such as that for the efficiencies of charge separation by PSI and PSII (Φ_{PSI} and Φ_{PSII}, respectively). While photosynthetic light-responses of this kind are frequently measured the tools available for the analysis of this data are limited. There are no well-developed,

Abbreviations – P_{c}, plastocyanin; P_{QH2}, plastoquinol; PSI, photosystem I; PSII, photosystem II; RuBP, ribulose-1,5-bisphosphate.
simple, analytical models with a mechanistic foundation for the analysis of light-response data. Various models have been applied to light-responses of carbon dioxide fixation, and some of these have been mechanistic in nature (e.g. Gutschick 1984, Terashima and Saeki 1985, Badeck 1995), but it is the non-rectangular hyperbola model (Farquhar and Wong 1984, Thornley and Johnson 2000) that is most commonly encountered. This model, while it is not deeply mechanistic, accurately reproduces a typical carbon dioxide fixation/irradiance curve, including the linear light-limited region at low irradiances, the light-saturated region at high irradiances and the curvilinear phase that links these two extremes. Insights into the physiological underpinnings of the light-response curve of carbon dioxide fixation make possible a new route to modeling irradiance responses, not only of assimilation, but also of the quantum efficiencies of electron transport rates of PSI and PSII.

In response to an increasing irradiance, $\Phi_{\text{PSI}}$ and $\Phi_{\text{PSII}}$ both decrease (e.g. Harbinson et al. 1989, Genty et al. 1990a, 1990b, Peterson 1991). These decreases are normally linearly related to each other, supporting a predominant role for linear electron transport in photosynthesis. The decrease in $\Phi_{\text{PSI}}$ and $\Phi_{\text{PSII}}$ is linked to a limitation of linear electron transport at the plastoquinol (PQH$_2$)/cytochrome $b_6$f step (e.g. Harbinson and Hedley 1989, Foyer et al. 1990, Laisk and Oja 1994, Genty and Harbinson 1996). This limitation can be summarized as either a first-order rate constant or a half-time. This rate constant is often observed not to change with increasing irradiance, suggesting that in these cases there is no change in the extent of photosynthetic control with increasing irradiance. On the other hand, changes in this rate constant can be brought about by, for example, decreasing the carbon dioxide concentration in the air around a leaf, resulting in largely parallel changes in both the rate constant and $\Phi_{\text{PSI}}$ (Laisk and Oja 1994, Genty and Harbinson 1996). This point towards the rate constant for linear electron transport being of crucial importance in determining the irradiance dependency of $\Phi_{\text{PSI}}$ and $\Phi_{\text{PSII}}$, and estimates of electron transport derived from these measurements. The absence of changes in the rate for electron transport from the PQH$_2$ pool and P$_{700}^+$ also implies that light-response curves are largely electron-transport limited as a shift to metabolic limitation would be reflected in a decrease in the rate constant. At low irradiances at most photosynthetically active wavelengths $\Phi_{\text{PSI}}$ is limited by PSI (Hogewoning et al. 2012). These observations imply that it should be possible to model the light-response of both $\Phi_{\text{PSI}}$ and $\Phi_{\text{PSII}}$ by focusing on the behavior of PSI. This would require combining the irradiance-dependent oxidation of P$_{700}$ with the electron transport-dependent reduction of P$_{700}^+$ into a model describing the irradiance dependency of the steady-state redox state of P$_{700}$.

The irradiance dependency of the light-use efficiency, or quantum yield, of the gross carbon dioxide fixation rate is often found to be linearly related to that of PSII (and PSI, though this is encountered less often in the literature) under non-photorespiratory and sometimes photorespiratory conditions (Genty et al. 1989, Peterson 1991, Genty and Meyer 1995). The relationship between photosynthetic electron transport under photorespiratory conditions can be non-linear (Harbinson et al. 1990), possibly owing to the variation in the relative velocities of carboxylation and oxygenation of ribulose-1,5-bisphosphate (RuBP) with increasing irradiance, and thus the relative activity of photorespiration as a sink for the products of photosynthetic electron transport. A model for the irradiance dependency of photosynthetic electron transport, either in terms of flux or quantum efficiency, could work as a model for the irradiance response of assimilation, either alone or possibly with extra modeling of the relative rates of carboxylation and oxygenation of RuBP.

In this article, we will demonstrate the derivation of a model for the irradiance dependency of $\Phi_{\text{PSI}}$ and PSI electron transport. This is based upon simulating the balance between the photochemical oxidation of P$_{700}$ and the reduction of P$_{700}^+$ by electrons from the PQH$_2$ pool. The model has only two parameters, has an analytical solution and gives rise to a family of different functions that differ in the number of P$_{700}$ donors included in the analysis. In addition, we will show that with the addition of one extra parameter, the model can be used to fit the irradiance responses of $\Phi_{\text{PSI}}$, and even carbon dioxide fixation/irradiance responses. This model has been previously presented in a partial and preliminary form (van Vliet and Harbinson 1992).

Materials and methods

Growth conditions and measurements

Plants of *Juanulloa aurantiaca* were grown at an irradiance of 400 µmol m$^{-2}$ s$^{-1}$, a 12 h day/12 h night, 25°C day/23°C night, 75% relative humidity. Plants were grown in a peat-based compost and fed with Pokon liquid fertilizer at a recommended dilution once per week, and otherwise watered as required. Light-induced absorbance changes at 820 nm, chlorophyll fluorescence and leaf carbon dioxide fixation of a leaf of one of these plants were measured in equipment identical to that described by Kingston-Smith et al. (1999) and provided the specimen data used for most of the analyses shown here. In addition, minor use will be made of data
obtained from leaves of *Pisum sativum* and *Prunus laurocerasus*.

The irradiance responses of $\Phi_{\text{PSI}}$, $\Phi_{\text{PSII}}$ and carbon dioxide fixation rate were measured in response to an increasing irradiance regime. At each light step the rate of carbon dioxide was allowed to stabilize before measuring the quantum yield of electron transport from trap with P700 and Trissl 1995). Second, for PSI it is assumed that the primary stable electron acceptor of PSII (Lavergne et al. 2004), 0.98–0.99 (Wientjes et al. 2011).

***Basic principles of the P700 oxidation model***

We shall make extensive use of a model of P700 oxidation state. This model is fully described in Supporting information Appendix S1 and will only be briefly summarized here. The approach used to model the degree of P700 oxidation is based upon modeling the interconversion between P700 and P700+ (Fig. 1, showing examples of models for different numbers of donors (0, 1 and 2) to P700). Assuming that there are available electron acceptors to support P700 oxidation, its oxidation in a leaf (and elsewhere in a similar way) depends on the irradiance, the efficiency of leaf light absorption, the partitioning of those absorbed photons between photosystems I and II (PSI and PSII; non-photosynthetic pigments could also be included, but for the sake of simplicity we will not include them), the quantum yield of P700 oxidation, and (inversely) on the density of P700 per unit area. Under most experimental conditions and assuming there are no state-transitions or that their effect is minor, all factors influencing the rate of oxidation are constant with the exception of number of P700 per unit area and the irradiance. Consequently, we can combine the factors affecting oxidation of P700, including irradiance, into an apparent rate constant of oxidation, $k_e$, that acts upon an individual P700 to give its rate of oxidation.

The reduction of P700 occurs via the photosynthetic electron chain, with P700+ being immediately reduced via reduced plastocyanin (Pc; Pc−). P700+ can also be reduced by a back reaction from the PSI acceptor pool, though this is not a major activity except when forward electron transport is blocked (e.g. Klughammer and Schreiber 1991, Harbison and Hedley 1993). The models introduced here will not include any allowance for a restriction on electron transport on the PSI acceptor side, though such a component could easily be added. While the reduction of P700+ is via reduced Pc, the rate-limiting step for linear electron transport is the first step in the oxidation of PQH2 by the cytochrome bc/f complex. This is a pH sensitive process that occurs with a half time of 3 ms or longer. It is the kinetics of this step that normally has, all other things being equal, the largest regulatory effect on the degree of oxidation of P700 (Laish and Oja 1994, Genty and Harbison 1996, Ott et al. 1999) and therefore the quantum yield for PSI electron transport. The rate constant of this limiting step will be termed $k_e$. It is commonly observed (though not always;
Fig. 1. The basic physical structures that are reproduced in the models for 0, 1 and 2 donors. “P” is P\textsubscript{700} while “D” is the lumped donor pool within the high-potential chain part of the photosynthetic electron transport chain. Oxidation of P\textsubscript{700} occurs via steps k\textsubscript{x}, while electron transfer from the PQH\textsubscript{2} pool to the lumped donor pool occurs via steps k\textsubscript{e}, and redox equilibration between P\textsubscript{700} and the donor pool occurs via steps ‘K’. The oxidized forms of P\textsubscript{700} are on the right side, and the reduced forms on the left side, of the diagram.

(Ott et al. 1999) that the rate constant, or half-time, for P\textsubscript{700}\textsuperscript{+} reduction from the PQH\textsubscript{2} pool does not vary with irradiance (Harbinson and Hedley 1989, Laisk and Oja 1994, Kramer et al. 1999, Ott et al. 1999, Sacksteder and Kramer 2000). The value for k\textsubscript{e} will therefore be treated as fixed in this model framework, though it could be made dependent on, e.g. irradiance if required. Electrons from the first oxidation of PQH\textsubscript{2} will initially reduce the Reiske FeS complex, then cytochrome f (Cape et al. 2006) before arriving on Pc; this family of electron transfer components, collectively known as the high potential chain, can be seen as an electron buffer that interfaces the PQH\textsubscript{2} pool with the P\textsubscript{700}\textsuperscript{+} pool. Note that the second oxidation of PQH\textsubscript{2} will normally be via the low potential cytochrome b\textsubscript{6}/f complex, plastocyanin and P\textsubscript{700}\textsuperscript{+}, and, on the other, the rate of excitation of each PSI photosynthetic unit. Electron transfer between the components of high potential chain occurs within the sub millisecond time range allowing equilibration in the 150 \(\mu\)s time range (Haehnel 1984, Sacksteder and Kramer 2000). A typical leaf has about 1 \(\mu\)mol m\textsuperscript{-2} of PSI (RC\textsubscript{1}) and PSII reaction centers (Osmond et al. 1980, Schöttler and Tóth 2014), which, assuming equal partitioning of absorbed photons between PSI and PSII, will result in an average excitation of each RC\textsubscript{1} every millisecond at an irradiance of 2000 \(\mu\)mol m\textsuperscript{-2} s\textsuperscript{-1} (compare this with the 3 ms or greater half time of electron transfer from the PQH\textsubscript{2} pool and P\textsubscript{700}\textsuperscript{+}). This gives enough time for the donor side of P\textsubscript{700} to reach near-equilibrium between the excitations rate normally used experimentally (i.e. up to about 2000 \(\mu\)mol m\textsuperscript{-2} s\textsuperscript{-1}). The assumption that P\textsubscript{700} and the components of the high potential chain, such as plastocyanin, are in equilibrium (or very nearly so) under normal experimental conditions is an important simplification of the model. It allows P\textsubscript{700} and the high potential chain to be treated as a single entity, leading to a much simpler model that allows an analytical solution. This simplification is not expected to raise any problems for that application of the model to data from wild-type leaves under normal experimental conditions. Data obtained from, for example, mutants with diminished equilibration rates between P\textsubscript{700} and the high potential chain, data obtained at very high irradiance (for example saturating light pulses), or any other condition where disequilibrium might occur between P\textsubscript{700} and the high potential chain should not be fitted or simulated with this model.

The values of K\textsubscript{1}, K\textsubscript{2} etc. (the ratios of P\textsubscript{700}\textsuperscript{0}/P\textsubscript{700}\textsuperscript{+} following equilibration of the P700 and donor pools at, e.g. step 1, Fig. 1B and steps 1 and 2, Fig. 1C) depend on the equilibrium constant between P\textsubscript{700} and the components of the high potential chain, and the number of donors per P\textsubscript{700}. In vivo, there are several components
in the high potential chain (plastocyanin, cytochrome f and the Reiske FeS) each with its own standard redox potential. Experimentally, it is not certain if there is a complete redox equilibrium between P700 and plastocyanin in vivo. This is normally determined by comparing the actual equilibrium between P700 and plastocyanin and comparing it with that predicted by the redox equilibrium constant (Kirchhoff et al. 2004). Under conditions of active electron transport (e.g. excitation both photosystems and not predominantly PSI, and in the absence of inhibitors of electron transport) equilibrium has been shown (Oja et al. 2010) as has disequilibrium (Kirchhoff et al. 2004). The redox potential is about 465–485 mV for P700 and 355–370 mV for plastocyanin (Kirchhoff et al. 2004) so under equilibrium conditions the oxidation of plastocyanin should occur before that of P700.

The model of P700 oxidation state will therefore include oxidation of P700+ following excitation, the rate of which is governed by a rate constant k−; electron transfer from the PQH2 pool to the electron donor pool of P700+ via the rate-limiting step of linear electron transport (rate constant k+); and, normally, equilibration of oxidizing equivalents between P700+ and its donor pool. The following are also assumed: there is no restriction of P700 oxidation due to a limitation of electron acceptors, and each P700 reaches equilibrium with only a pool of donors that only equilibrate with that P700 and with each other (an extreme restricted diffusion model, though another equilibration model is also described in the Appendix S1).

The models that describe the extent of oxidation of P700 for 0, 1 and 2 donors are derived in terms of P700+/P700− (Kirchhoff et al. 2004) and a stochastic term which is the ratio of combinations between the P700 oxidation state will therefore include oxidation of P700+ following excitation, the rate of which is governed by a rate constant k−; electron transfer from the PQH2 pool to the electron donor pool of P700+ via the rate-limiting step of linear electron transport (rate constant k+); and, normally, equilibration of oxidizing equivalents between P700+ and its donor pool. The following are also assumed: there is no restriction of P700 oxidation due to a limitation of electron acceptors, and each P700 reaches equilibrium with only a pool of donors that only equilibrate with that P700 and with each other (an extreme restricted diffusion model, though another equilibration model is also described in the Appendix S1).

The models that describe the extent of oxidation of P700 for 0, 1 and 2 donors are derived in terms of P700+/P700− in the Appendix S1. Each model version has a different, integer number of donors, and those for 0, 1, 2, 3 and a general case are shown here:

\[ n = 0 : \frac{P700^+}{P700^-} = \frac{1}{k_+} \]

\[ n = 1 : \frac{P700^+}{P700^-} = \frac{1}{k_+ \left( k_+ + 1 \right)} \times \left( 1 + \frac{k_+}{K_1} \right) \]

\[ n = 2 : \frac{P700^+}{P700^-} = \frac{1}{k_+ \left( k_+ + 1 \right)} \times \left( 1 + \frac{k_+}{K_2} + \left( \frac{k_+}{k_1} \right)^2 \right) \times \left( 1 + \frac{k_+}{K_2} + \left( \frac{k_+}{K_1} \right)^2 \right) \]

\[ n = 3 : \frac{P700^+}{P700^-} = \frac{1}{k_+ \left( k_+ + 1 \right)} \times \left( 1 + \frac{k_+}{K_3} + \left( \frac{k_+}{k_1} \right)^3 \right) \times \left( 1 + \frac{k_+}{K_3} + \left( \frac{k_+}{K_1} \right)^3 \right) \]

General case for n donors:

\[ \frac{P700^+}{P700^-} = \frac{1}{k_+ \left( k_+ + 1 \right)} \times \left( 1 + \frac{k_+}{K_n} + \left( \frac{k_+}{K_1} \right)^n \right) \times \left( 1 + \frac{k_+}{K_n} + \left( \frac{k_+}{K_1} \right)^n \right) \]

For each P700 oxidation model, except n=0, there is equilibration between the P700+/P700− and donor+/donor− couples at each oxidation step. The equilibrium ratios P700+/P700− at each step are given by ‘K’s (Fig. 2). For each model, these K values [K1, K2 etc. – note that a function for a K (e.g. for K2 for an n=2 model) is only valid within the specific model (n=2, n=3 etc.) for which it is derived] can be expressed in terms of an effective redox equilibrium constant between the P700+/P700− and donor+/donor− couples and a stochastic term which is the ratio of combinations (see Appendix S1):

\[ n = 1 : K_1 = K_{eq} \]

\[ n = 2, K_1 : K_1 = 2K_{eq} \]

\[ n = 2, K_2 : K_2 = 0.25K_{eq} \]

\[ n = 3, K_1 : K_1 = 3K_{eq} \]

\[ n = 3, K_2 : K_2 = 1K_{eq} \]

\[ n = 3, K_3 : K_3 = 0.3333K_{eq} \]

where K_{eq} is the effective redox equilibrium constant in the restricted diffusion system, which differs from the K_{eq} that is valid in a freely diffusing system (Lavergne et al. 1989). The appropriate equations for the ‘K’ values must be substituted into Eqns 2, 3 and 4 (e.g. ‘K’ Eqns
Fig. 2. (A) The irradiance dependency of $\Phi_{PSI}$ (the relative quantum yield for PSI electron transport) and $k_e$ – the pseudo-first order rate constant for reduction of P700$^+$ by electrons derived from the oxidation of PQH$_2$. These measurements were made on a leaf of *Juanulloa aurantiaca*. These data are (and other similar data from this leaf) presented to demonstrate the use of the models outlined here. (B) A fit using an $n=0$ form (i.e. zero high-potential chain donors to P700) of the $\Phi_{PSI}$/irradiance model to an experimentally measured $\Phi_{PSI}$/irradiance response obtained from a leaf of *J. aurantiaca*.

**9, 10 and 11 must be used in Eqn 4.** As shown here, the model, in its various forms, treats the leaf as single homogeneously illuminated layer and takes no account of radiation gradients within the leaf.

**Fitting**

To fit $\Phi_{PSI}$/irradiance data, the equation of the kind shown in Eqn 2.35 in the Appendix S1 needs some slight modification. $k_e/k_x$ incorporates irradiance (‘irr.’) as part of $k_x$ so $k_x$ needs to be replaced by $k_{x/irr}$. $k_{x/irr}$ therefore becomes $k_{x/(irr. e)}$ and $k_{x/e}$ forms a lumped parameter including the rate-limiting electron transport step from the PQH$_2$ pool and structural and organizational factors linking irradiance to a rate of P$_{700}$ oxidation. $k_x$, if known, (it can be measured via PSI kinetics, for example) can be included separately. Equations to calculate $K_1$ and $K_2$ (etc.) need to be substituted into the main equations for $P_{700}^+/P_{700}^0$ (e.g. Eqns 2, 3 and 4), and this equation needs to substituted into $\Phi_{PSI} = 1/(1 + (P_{700}^+/P_{700}^0))$. For example, for the $n=2$ version of the model this would give:

$$\Phi_{PSI} = \frac{1}{1 + \left(\frac{k_e}{k_{x/irr}}\right) \times \left(1 + \left(\frac{k_e}{K_1}\right) + \left(\frac{k_e}{K_2}\right)\right)}$$

This modified equation can then be used to fit $\Phi_{PSI}$/irradiance data with irradiance as the independent variable and $\Phi_{PSI}$ as the dependent variable, with $K_{eq}$ and $k_{x/irr}$ being the estimated parameters. On a more practical point, the model assumes that $\Phi_{PSI}$ is 1 when the irradiance is zero (i.e. that there is no oxidized P$_{700}$ in the dark) and in light-response curves $\Phi_{PSI}$ is often shown as 1 when the irradiance is zero. Fitting to data with an irradiance of zero will cause a ‘divide by error’ because irradiance, as part of $k_{x/irr}$, becomes $k_{x/(irr. e)}$. It is therefore necessary to either exclude the zero-irradiance value or to replace zero with a small number.

**Results**

**Preliminary observations**

The $\Phi_{PSI}$/irradiance response measured from a leaf of *J. aurantiaca* that will be used to demonstrate the capabilities of the model has the sigmoidal form typical of this type of relationship (Fig. 2A). The rate constant for P$_{700}^+$ reduction ($k_e$), measured from the decay of the 820-nm absorbance change following a light on–off transition, is relatively independent of irradiance, especially at irradiances above 100 μmol m$^{-2}$ s$^{-1}$. These $\Phi_{PSI}$/irradiance data are therefore both apparently normal and reflect a response obtained from a leaf where $k_e$ is essentially independent of irradiance, at least under conditions where $\Phi_{PSI}$ is becoming substantially determined by limitations on electron transport arising from the PQH$_2$/cytochrome $b_6/f$ step.

**Fitting different models to $\Phi_{PSI}$/irradiance responses from different species**

The $\Phi_{PSI}$/irradiance response curve of $\Phi_{PSI}$ obtained from *J. aurantiaca* fitted by the simple $n=0$ model (Eqn 1; Fig. 2B) reveals that the $n=0$ model produces a poor fit to the $\Phi_{PSI}$/irradiance response. In particular, it fails to reproduce the sigmoidicity of the response at
Fig. 3. A fit using an \( n = 1 \) form (i.e. one high-potential chain donor to \( P_{700} \)) of the \( \Phi_{PSI}/\text{irradiance} \) model to an experimentally measured \( \Phi_{PSI}/\text{irradiance} \) response obtained from a leaf of \( \textit{Juanulloa aurantiaca} \). \( K_{eq} \) is unitless, while \( k_{0}/\varepsilon \) has units of \( \text{mol}^{-1} \text{m}^{2} \).

Fig. 4. A fit using an \( n = 2 \) form (i.e. two high-potential chain donors to \( P_{700} \)) of the \( \Phi_{PSI}/\text{irradiance} \) model to an experimentally measured \( \Phi_{PSI}/\text{irradiance} \) response obtained from a leaf of \( \textit{Juanulloa aurantiaca} \).

Fig. 5. A fit using an \( n = 3 \) form (i.e. three high-potential chain donors to \( P_{700} \)) of the \( \Phi_{PSI}/\text{irradiance} \) model to an experimentally measured \( \Phi_{PSI}/\text{irradiance} \) response obtained from a leaf of \( \textit{Juanulloa aurantiaca} \).

The effect of altering parameters in the model on the form of the curve

The effects of varying the lumped parameter \( k_{0}/\varepsilon \) and \( K_{eq} \) on the curves produced by the model (in this case the \( n = 2 \) version of the model; except for \( n = 0 \), the other functions are qualitatively similar) are shown in Figs 7 and 8. The effects are as expected based on the roles played by the parameters in the model. Increasing the value of \( k_{0}/\varepsilon \), which would be equivalent to, for example, increasing the rate constant for electron transport from \( \text{PQH}_{2} \) to the donor pool or increasing the density of PSI reaction centers per unit leaf area, produces an increase in \( \Phi_{PSI} \) at all irradiances, decreasing the rate at which \( \Phi_{PSI} \) decreases with increasing irradiance. Decreases in \( k_{0}/\varepsilon \) decrease the extent of the sigmoidal phase in the \( \Phi_{PSI}/\text{irradiance} \) response. Compared with the effects of changes in \( k_{0}/\varepsilon \), changes in \( K_{eq} \) (note that this is an effective or apparent equilibrium constant owing the way that part of the model is formulated) have smaller effects on the form of the curves. Increases in \( K_{eq} \) results in increased sigmoidicity of the curve at higher values of \( \Phi_{PSI} \) (and low irradiances), but this effect is both non-linear and saturates at relatively low values of \( K_{eq} \). With decreasing values of \( \Phi_{PSI} \), the effect of \( K_{eq} \) on the curve diminishes and it is the value of
Fig. 6. Fits using an $n = 3$ form of the $\Phi_{\text{PSI}}$/irradiance model to experimentally measured $\Phi_{\text{PSI}}$/irradiance responses obtained from leaves of *Pisum sativum* (A) and *Prunus laurocerasus* (B).

$k_{\text{eq}}/\varepsilon$ that increasingly determines the response of $\Phi_{\text{PSI}}$ to irradiance.

**Fitting PSI electron transport ($J_1$)/irradiance relationships**

Given that the functions for the irradiance response of $\Phi_{\text{PSI}}$ fit experimental data well, it is natural to explore their usefulness in other applications. The rate of electron transport through PSI is a function of the product of the irradiance and $\Phi_{\text{PSI}}$ – this may be corrected further by adding terms to adjust for light absorption by the leaf, partitioning of absorbed light to PSI and the actual quantum yield for PSI charge separation. In the results presented here the rate of PSI electron transport will be represented by a simple index of PSI electron transport – the product of $\Phi_{\text{PSI}}$ and incident irradiance, without any further correction. This is expected to be proportional to the actual rate of PSI electron transport, though not to be numerically equivalent to it. A version of the $n = 2$ model modified to fit $J_1$/irradiance responses (i.e. the equation that gives $\Phi_{\text{PSI}}$ is multiplied by irradiance), was fit to a $J_1$/irradiance dataset derived from the *J. aurantiaca* $\Phi_{\text{PSI}}$/irradiance dataset used in Figs 2–5 and 9.
This fit gave similar estimates of the parameters $k_e/\varepsilon$ and $K_{eq}$ to those obtained using an $n=2$ model fit to the $\Phi_{PSI}/$irradiance dataset (cf. Figs 9 and 4), and the model accurately reproduces the form of the $\Phi_{PSI}/$irradiance relationship.

The effects of varying either $k_e/\varepsilon$ and $K_{eq}$ in the function used to model the $J_1$/irradiance relationship (Figs 10 and 11) parallels those shown for the $\Phi_{PSI}/$irradiance responses (Figs 7 and 8). The greatest impact occurs when $k_e/\varepsilon$ is altered, and Fig. 10 shows for the lower values of $k_e/\varepsilon$ what can also be shown mathematically – the curve for each value of $k_e/\varepsilon$ asymptotically approaches a value of $J_1$ equal to $k_e/\varepsilon$ (i.e. $k_e/\varepsilon$ is the value of $J_1$ at an infinite irradiance). This shows the physiological relevance of $k_e/\varepsilon$ – it is the light saturated rate of electron transport in the absence of any external constraints (such as a metabolic limitation) and assuming that the basic quantum yield for charge separation is 1. As with the $\Phi_{PSI}/$irradiance response, the effect on the $J_1$/irradiance relationship of changing $K_{eq}$ is less pronounced than changing $k_e/\varepsilon$, and the effect saturates at low values of $K_{eq}$. Low values of $K_{eq}$ do result in a conspicuously decreased $J_1$ beyond the light-limited region of the response curve, but this effect diminishes with increasing irradiance. Simulation of the $J_1$/irradiance response at low irradiances (Fig. 12; i.e. within what would be normally viewed as the light-limited region, though the irradiance response of $\Phi_{PSI}$ does show some small decreases of light-use efficiency in this region) show that the model can accurately reproduce the light-limited response.

**Fitting $\Phi_{PSI}/$irradiance responses**

It is commonly observed that in response to a range of irradiances (e.g. Harbinson et al. 1989, Genty et al. 1990a, 1990b, Peterson 1991, Genty and Harbinson 1996), and other environmental factors that affect photosynthetic light-use efficiency [such as carbon dioxide or oxygen concentrations (Peterson 1991)], $\Phi_{PSI}$ and $\Phi_{PSII}$ are largely linearly related. This is consistent
with a predominant role for linear electron transport in C3 mesophyll cell chloroplasts. Additionally, the limitations acting on PSII in many ways mirror those acting on PSI – while PSI light-use efficiency is largely limited on the donor side, PSII is largely limited on its acceptor side, and while the PSI donor side has a pool of donors, the PSII acceptor side has a pool of acceptors. At most photosynthetically active wavelengths PSI also seems to limit the efficiency of PSII at low irradiances; at most wavelengths PSII shows small decreases at low irradiances while PSI does not, as if there was overexcitation of PSI relative to PSI (Hogewoning et al. 2012). The overall regulation of PSII is, of course, more complex than PSI because PSI has a distinct, non-reaction center based non-photochemical dissipation mechanism – qE (e.g. Murchie and Harbinson 2014), while in PSI non-photochemical dissipation is achieved via an oxidation of P$_{700}$, which quenches chlorophyll singlets in PSI as well as P$_{700}$$^0$ (Nuijts et al. 1986). The similarities between PSI and PSII and the fact that PSI tends to limit PSII suggested that a $\Phi_{PSII}$ model might also be able to fit $\Phi_{PSII}$/irradiance responses, despite the differences in the regulation of PSI and PSII. The model used for $\Phi_{PSII}$ (Eqn 12) assumes that $\Phi_{PSII}$ at zero irradiance is 1 [which is not fully accurate: (Wientjes et al. 2011)]. The maximum yield for $\Phi_{PSII}$ is only about 0.83 (Björkman and Demmig 1987) (depending somewhat on the contribution from PSI fluorescence, and thus the measuring wavelength (Genty et al. 1990a, 1990b, Pfundel 1998). Therefore Eqn 12 needs to modified by including an extra term, C, to account for the lower maximum of $\Phi_{PSII}$, giving for the $n = 2$ version of the model:

$$\Phi_{PSII} = C \times \frac{1}{1 + \left(\frac{k_e}{\epsilon} + \left(\frac{1}{k_e}\right)^n\right) \times \left(1 + \left(\frac{\left(\frac{k_e}{\epsilon}\right)}{k_e}\right) + \left(\frac{\left(\frac{k_e}{\epsilon}\right)^2}{k_e}\right)\right)}$$

(13)

Including the dark-adapted value of $\Phi_{PSII}$ (the dark-adapted F$_{v}$/F$_{m}$) in the irradiance response curve, this function fits a $\Phi_{PSII}$/irradiance response quite well (Fig. 13), but can be seen to be poor at high values of $\Phi_{PSII}$ and to slightly overestimate $\Phi_{PSII}$ at low values of $\Phi_{PSII}$ (Figs 13 and 14B). This problem appears to be due to the low yield of $\Phi_{PSII}$ that occurs at low irradiances due to the imbalance of the photochemical activity of PSI and PSII under these conditions (Hogewoning et al. 2012). This response is not included in the model and excluding this low irradiance behavior of $\Phi_{PSII}$ (or at least most of it) results in a much-improved fit at high $\Phi_{PSII}$ (Fig. 14A, B) and a better fit at lower values of $\Phi_{PSII}$. When exciting chlorophyll fluorescence using a 560-nm excitation wavelength the values of $\Phi_{PSII}$ obtained are higher than those obtained when using a 660-nm excitation wavelength (Fig. 15). This is most likely due to the deeper penetration of the 560-nm radiation into the leaf and therefore the lower average irradiance experienced by the chlorophyll producing the fluorescence. Fitting the $\Phi_{PSII}$ estimated from fluorescence excited via 560 nm radiation instead of 660 nm gives a similar $K_{eq}$ but a higher $k_e/\epsilon$ for the 560-nm derived $\Phi_{PSII}$ irradiance response compared with the 660-nm derived response ($k_e/\epsilon = 218$ vs $k_e/\epsilon = 162$). Changing the $k_e/\epsilon$ in the 560-nm data fit to 162 causes the 560-nm fit line to follow the trajectory of 660 nm points (Fig. 15). This shows that model can be used to fit $\Phi_{PSII}$/irradiance responses in the same way that can be used to fit those of $\Phi_{PSI}$, and also that it can be used to correct or adjust $\Phi_{PSII}$ or $\Phi_{PSII}$/irradiance relationships for changes in absorbed or effective irradiance (changing $\epsilon$), or, by implication, changes in $k_e$ and thus the light-saturated rate of electron transport.

**Fitting CO$_2$ fixation/irradiance responses**

Carbon dioxide fixation is often closely related to an estimate of linear photosynthetic electron transport derived from $\Phi_{PSII}$. The maximum yield of carbon dioxide fixation in C3 leaves, under non-photorespiratory conditions range from 0.089 to 0.096 (Long et al. 1993, Hogewoning et al. 2012) decreasing under photorespiratory conditions (Ehleringer and Björkman 1977). To become suitable for fitting a carbon dioxide fixation
The estimate of $K_{eq}$ was 2.55 ($SD = 1.00$). The value of $C$ agrees well with the maximum value of $\Phi_{CO_2}$ measured from the leaf (Fig. 17). The product of $C$ and $k_e/\varepsilon$ gives the light-saturated rate of assimilation under electron-transport limited conditions. The model used to fit the $I_{CO_2}/irradiance$ relationship is mechanism so it ought to be capable of extrapolation beyond the limits of data. Selecting only the first 6 datapoints of the 10 available and fitting Eqn 14 to this subset of the data produced estimates for the parameters similar to those estimated using the entire dataset: using only 6 points (Fig. 16) the estimate of $k_e/\varepsilon$ was 109.1 ($SD = 34.8$) and that of $C$ was 0.048 ($SD = 0.005$), while the estimate of
A fit using an \( n = 2 \) form (i.e. derived from the version with two high-potential chain donors to \( P_{700}^0 \)) of the \( \Phi_{PSI}^{n} \)/irradiance model to an experimentally measured \( \Phi_{PSI}^{n} \)/irradiance response obtained from a leaf of *Juanulloa aurantiaca* and using a 560 nm excitation wavelength for chlorophyll fluorescence (open symbols); the values for the estimated parameters shown in the figure are for the 560 nm excitation derived data. The estimated curve for this data can be mapped accurately onto the curve obtained using 660 nm as an excitation wavelength (solid symbols; Fig. 13) by adjusting the value of \( k_{eq}/ \epsilon \) obtained by fitting the 560-nm dataset.

\[ K_{eq} = 7.54, SD = 3.56 \]
\[ k_{eq}/ \epsilon = 218.54, SD = 10.79 \]
\[ \text{intercept} = 0.77, SD = 0.0080 \]

\( K_{eq} \) was 1.57 (SD = 2.60). While the estimate of \( K_{eq} \) based on the reduced dataset is poor (the SD of the estimate exceeds the estimate) the estimate of \( k_{eq}/ \epsilon \) similar to that obtained with the full dataset (approximately 8% difference), though with much less certainty (SD increased by a factor of 10), and the estimate and certainty of \( C \) was hardly affected by using the limited dataset. The projected relationship between \( J_{CO2} \) and irradiance based on the fit to the reduced dataset is only slightly different to that obtained from the complete dataset, which was itself a good representation of the trend shown by the actual data, especially if the data measured at 450 \( \mu \)mol m\(^{-2} \) s\(^{-1} \) is excluded from the fit.

**Discussion**

The results presented here show that by modeling the following processes: (1) the oxidation of \( P_{700}^0 \), (2) the reduction of \( P_{700}^+ \) and (3) equilibration between \( P_{700} \) and its donor pool (the high potential chain within the photosynthetic electron transport chain), it is possible to produce a family of analytical functions that can be used to closely fit and therefore simulate the irradiance response of \( \Phi_{PSI} \) and \( J_1 \). This approach to modeling the irradiance response of \( \Phi_{PSI} \) is mechanistic and the parameters of the model therefore have a clear physiological meaning, implying that the model can easily be linked to the experimentally determined structure, organization and regulation of photosynthesis. It can also easily be used for in silico testing of projected alterations of the structure, organization and regulation of photosynthesis.
In the form presented here, these functions have only two parameters that need to be estimated – an apparent equilibrium constant ($K_{eq}$), and a lumped parameter ($k_e/\epsilon$) that integrates electron transport from the PQH$_2$ pool and the oxidation of P$_{700}^0$. This lumped parameter could potentially be subdivided to contain more elemental parameters describing different steps in the oxidation/reduction processes. The family of functions differ in the number of donors included per function. In most cases a model based on a donor pool of only two donors works well, though the number of plastocyanins per P$_{700}$ can be up to 5 (Schöttler et al. 2004), and cytochrome b$_6$/f/P$_{700}$ ratios of up to 1.25 have been measured (Anderson 1992), giving a potential donor pool/P$_{700}$ of 7.5. So far it has not been necessary to use such a large donor pool to obtain a good fit using the model. The impact of varying $K_{eq}$ and $k_e/\epsilon$ on the $\Phi_{PSII}$/irradiance relationship is similar at high values of $\Phi_{PSII}$. This results in a practical problem: it is difficult to fit the $\Phi_{PSII}$/irradiance model to $\Phi_{PSII}$/irradiance if $\Phi_{PSII}$ does not decrease to the point where there is some obvious curvature in the $\Phi_{PSII}$/irradiance relationship. If it is necessary to fit such data then the most practical option is to fix $K_{eq}$ and fit only $k_e/\epsilon$; $k_e/\epsilon$ is, overall, has a more significant effect on the $\Phi_{PSII}$/irradiance relationship than does $K_{eq}$.

The apparent redox constant required for the fit is much lower than expected based on the redox potential difference between P$_{700}$ and the donor pool: in the case of plastocyanin, for example, the equilibrium constant with P$_{700}$ has been estimated to be around 16 (Hope 2000). A lower effective redox potential between P$_{700}$ and plastocyanin has, however, been observed under conditions of physiological rates of electron transport (Kirchhoff et al. 2004), implying restricted diffusion and disequilibrium, though under similar conditions equilibrium has also been reported (Oja et al. 2010). A low apparent equilibrium constant is also expected due to the presence of radiation gradients through the leaf resulting in a gradient of redox steady-states between P$_{700}$ and its donor pool throughout the leaf. Estimating an equilibrium constant based on the sum of this gradient of redox steady-states will result in lowered estimated equilibrium constant.

Notably, the estimate of $k_e/\epsilon$ is the estimated light saturated rate of PSI electron transport under conditions where it is not limited by any non-electron transport process, such as metabolism (i.e. $k_e$ remains constant and is not decreased as a result of photosynthetic control). While a fixed $k_e$ was assumed in the derivation of the model, this should not be seen as being obligatory, but more a matter of simplicity and convenience. If required, $k_e$ could be allowed to vary based on some other function, resulting in a more complex model with $k_e$ and $\epsilon$ being treated either as separate parameters, or the lumped parameter ($k_e/\epsilon$) being tuned across the irradiance response. We also only illustrate estimation of $k_e/\epsilon$ and $K_{eq}$ with irradiance as an independent variable and $\Phi_{PSII}$ as the dependent variable (typical of light-response curves). It would also be possible to reconfigure the model to estimate $k_e$ and $K_{eq}$ when using $k_e$ as an independent variable and $\Phi_{PSII}$ as a dependent variable (typical of results obtained by varying carbon dioxide concentration under conditions of constant irradiance). That the $J_1$/irradiance relationship can be simulated well at low irradiances shows that the model does simulate well the light-limited part of the irradiance response curve as well as the transition from light-limitation to light-saturation.

The effectiveness of the model in fitting and simulating $\Phi_{PSII}$/irradiance relationships (and by implication PSII electron transport/irradiance data) naturally emerges from the linear relationship that is usually observed between $\Phi_{PSII}$ and $\Phi_{PSII}$. The exception to this is the inability of the model to reproduce the loss of $\Phi_{PSII}$ at low irradiances due to the imbalance between PSII and PSI activity under these conditions (Hogewoning et al. 2012). The ability to sculpt the form of the $\Phi_{PSII}$/irradiance relationship (and by implication of $\Phi_{PSII}$/irradiance relationships), will have obvious applications in the simulation of photosynthetic light-use efficiency. In addition, this will prove useful in comparing more quantitatively $\Phi_{PSII}$/irradiance relationships derived from fluorescence data obtained using different excitation or measurement wavelengths, or comparing fluorescence derived data with light-induced absorption change derived parameters – a situation where differences in the population of chloroplasts being measured can lead to confusion.

The ability of the model, with only the minimum of adaptation, to fit a carbon dioxide fixation irradiance relationship has been demonstrated here. The model can be used to convincingly extrapolate assimilation/irradiance data, though this presumes that the conditions upon which the model is based are met in the region of extrapolation. That a model of photochemical efficiency can be used to fit an assimilation response is consistent with the linear, or nearly linear, relationships shown between $\Phi_{PSII}$, $\Phi_{PSII}$, $J_1$ or $J_0$, and the corresponding parameter describing carbon dioxide fixation. In principle, however, the rate of carbon dioxide fixation could have a complex relationship with electron transport, depending on the ratio of carbon dioxide and oxygen at the site of carboxylation, and therefore on the diffusive resistance for carbon transport from the free air to the site of carboxylation. This could be accounted for by adding components to the model to account for
diffusion and metabolism. While this would make the model more complex it would also make it a more useful tool with which to simulate and explore photosynthetic light-use efficiency.

Author contributions

J. H. helped formulate the model in its basic form, developed the model further and conducted the physiological measurements and applied the model to these data. X. Y. developed the model further beyond the basic version. Both authors contributed to the writing of this article.

Acknowledgements – Much early work on the model was carried out by Pieter van Vliet and we gratefully acknowledge the insights and the major contribution he made to this model. J. H. would like to acknowledge financial support from the EU Marie Curie ITN ‘Harvest’ (grant 238017) and the Dutch national program ‘Biosolar Cells’.

References

Anderson JM (1992) Cytochrome b$_6$f complex: dynamic molecular organization, function and acclimation. Photosynth Res 34: 341–357
Badeck FW (1995) Intra-leaf gradient of assimilation rate and optimal allocation of canopy nitrogen: a model on the implications of the use of homogeneous assimilation functions. Funct Plant Biol 22: 425–439
Baker NR, Harbinson J, Kramer DM (2007) Determining the limitations and regulation of photosynthetic energy transduction in leaves. Plant Cell Environ 30: 1107–1125
Björkman O, Demmig B (1987) Photon yield of O$_2$ evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. Planta 170: 489–504
Cape JL, Bowman MK, Kramer DM (2006) Understanding the cytochrome bc complexes by what they don’t do. The Q-cycle at 30. Trends Plant Sci 11: 46–55
Ehleringer J, Bjorkman O (1977) Quantum yields for CO$_2$ uptake in C$_3$ and C$_4$ plants. Plant Physiol 59: 86–90
Farquhar GD, Wong SC (1984) An empirical model of stomatal conductance. Funct Plant Biol 11: 191–210
Farquhar GD, Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO$_2$ assimilation in leaves of C$_3$ species. Planta 149: 78–90
Foyer C, Furbank R, Harbinson J, Horton P (1990) The mechanisms contributing to photosynthetic control of electron transport by carbon assimilation in leaves. Photosynth Res 25: 83–100
Franck F, Juneau P, Popovic R (2002) Resolution of the photosystem I and photosystem II contributions to chlorophyll fluorescence of intact leaves at room temperature. Biochim Biophys Acta 1556: 239–246
Genty B, Harbinson J (1996) Regulation of light utilization for photosynthetic electron transport. In: Baker NR (ed) Photosynthesis and the Environment. Kluwer Academic Publishers, Dordrecht, pp 67–99
Genty B, Meyer S (1995) Quantitative mapping of leaf photosynthesis using chlorophyll fluorescence imaging. Funct Plant Biol 22: 277–284
Genty B, Briantais J-M, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim Biophys Acta 990: 87–92
Genty B, Harbinson J, Baker NR (1990a) Relative quantum efficiencies of the two photosystems of leaves in photorespiratory and non-photorespiratory conditions. Plant Physiol Biochem 28: 1–10
Genty B, Wonders J, Baker NR (1990b) Non-photochemical quenching of Fo in leaves is emission wavelength dependent: consequences for quenching analysis and its interpretation. Photosynth Res 26: 133–139
Gutschick VP (1984) Photosynthesis model for C$_3$ leaves incorporating CO$_2$ transport, propagation of radiation, and biochemistry, 1: kinetics and their parametrization. Photosynthetica 18: 549–568
Haehnel W (1984) Photosynthetic electron transport in higher plants. Annu Rev Plant Physiol 35: 659–693
Harbinson J, Hedley CL (1989) The kinetics of P700$^+$ reduction in leaves: a novel in situ probe of thylakoid functioning. Plant Cell Environ 12: 357–369
Harbinson J, Hedley CL (1993) Changes in P-700 oxidation during the early stages of the induction of photosynthesis. Plant Physiol 103: 649–660
Harbinson J, Genty B, Baker NR (1989) Relationship between the quantum efficiencies of photosystems I and II in pea leaves. Plant Physiol 90: 1029–1034
Harbinson J, Genty B, Baker NR (1990) The relationship between CO$_2$ assimilation and electron transport in leaves. Photosynth Res 25: 213–224
Hogewoning SW, Wientjes E, Douwstra P, Trouwborst G, van Ieperen W, Croce R, Harbinson J (2012) Photosynthetic quantum yield dynamics: from photosystems to leaves. Plant Cell 24: 1921–1935
Hope A (2000) Electron transfers amongst cytochrome f, plastocyanin and photosystem I: kinetics and mechanisms. Biochim Biophys Acta 1456: 5–26
Kingston-Smith AH, Harbinson J, Foyer CH (1999) Acclimation of photosynthesis, H$_2$O$_2$ content and antioxidants in maize (Zea mays) grown at sub-optimal temperatures. Plant Cell Environ 22: 1071–1083
Kirchhoff H, Schöttler MA, Maurer J, Weis E (2004) Plastocyanin redox kinetics in spinach chloroplasts: evidence for disequilibrium in the high potential chain. Biochim Biophys Acta 1659: 63–72
Klughammer C, Schreiber U (1991) Analysis of light-induced absorbance changes in the near-infrared...
region. I. Characterization of various components in isolated chloroplasts. Z Naturforsch C 46: 233–244
Kramer DM, Sacksteder CA, Cruz JA (1999) How acidic is the lumen? Photosynth Res 60: 151–163
Laik A, Oja V (1994) Range of photosynthetic control of postillumination P700+ reduction rate in sunflower leaves. Photosynth Res 39: 39–50
Lavergne J, Trissl H (1995) Theory of fluorescence induction in photosystem II: derivation of analytical expressions in a model including exciton-radical-pair equilibrium and restricted energy transfer between photosynthetic units. Biophys J 68: 2474–2492
Lavergne J, Joliot P, Vermeglio A (1989) Partial equilibration of photosynthetic electron carriers under weak illumination: a theoretical and experimental study. Biochim Biophys Acta 975: 346–354
Long SP, Postl WF, Bolbar-Nordenkampf HR (1993) Quantum yields for uptake of carbon dioxide in C3 vascular plants of contrasting habitats and taxonomic groupings. Planta 189: 226–234
Murchie EH, Harbinson J (2014) Non-photochemical fluorescence quenching across scales: from chloroplasts to plants to communities. In: Demmig-Adams B, Garab G, et al. (eds) Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria. Springer, Berlin, pp 553–582
Nuijs AM, Shuvalov VA, van Gorkom HJ, Plijter JJ, Duyzens LNM (1986) Picosecond absorbance difference spectroscopy on the primary reactions and the antenna-excited states in Photosystem I particles. Biochim Biophys Acta 850: 310–318
Oja V, Eichelmann H, Anijalg A, Rämma H, Laik A (2010) Equilibrium or disequilibrium? A dual-wavelength investigation of photosystem I donors. Photosynth Res 103: 153–166
Osmond CB, Björkman O, Anderson DJ (1980) Physiological Processes in Plant Ecology: Toward a Synthesis with Atriplex. Springer, Berlin
Ott T, Clarke J, Birks K, Johnson G (1999) Regulation of the photosynthetic electron transport chain. Planta 209: 250–258
Peterson RB (1991) Effects of O2 and CO2 concentrations on quantum yields of photosystem-I and photosystem-II in tobacco leaf tissue. Plant Physiol 97: 1388–1394
Peterson RB, Oja V, Eichelmann H, Bichele I, DallOsto L, Laik A (2014) Fluorescence F0 of photosystems II and I in developing C3 and C4 leaves, and implications on regulation of excitation balance. Photosynth Res 122: 41–56
Pfundel E (1998) Estimating the contribution of photosystem I to total leaf chlorophyll fluorescence. Photosynth Res 56: 185–195
Sacksteder CA, Kramer DM (2000) Dark-interval relaxation kinetics (DIRK) of absorbance changes as a quantitative probe of steady-state electron transfer. Photosynth Res 66: 145–158
Schöttler MA, Tóth SZ (2014) Photosynthetic complex stoichiometry dynamics in higher plants: environmental acclimation and photosynthetic flux control. Front Plant Sci 5: 188
Schöttler MA, Kirchhoff H, Weis E (2004) The role of plastocyanin in the adjustment of the photosynthetic electron transport to the carbon metabolism in tobacco. Plant Physiol 136: 4265–4274
Terasima I, Saeki T (1985) A new model for leaf photosynthesis incorporating the gradients of light environment and of photosynthetic properties of chloroplasts within a leaf. Ann Bot 56: 489–499
Thornley JHM, Johnson IR (2000) Plant and Crop Modelling: A Mathematical Approach to Plant and Crop Physiology. Blackburn Press, Caldwell, NJ
Vasil’ev S, Bruce D (2004) Optimization and evolution of light harvesting in photosynthesis: the role of antenna chlorophyll conserved between photosystem II and photosystem I. Plant Cell 16: 3059–3068
van Vliet PH, Harbinson J (1992) Modeling steady state P700 photooxidation in leaves: the role of plastocyanin. In: Murata N (ed) Research in Photosynthesis, Vol. 2. Kluwer, Dordrecht, pp 527–530
Wientjes E, van Stokkum IH, van Amerongen H, Croce R (2011) The role of the individual Lhcas in photosystem I excitation energy trapping. Biophys J 101: 745–754

Supporting Information
Additional Supporting Information may be found in the online version of this article:
Appendix S1. Modeling the steady-state oxidation of the P700 pool in vivo.