Short title: Light response curves in photosynthesis modeling

Rapid chlorophyll *a* fluorescence light response curves mechanistically inform photosynthesis modeling

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One-sentence Summary: Chlorophyll *a* fluorescence rapid light response curves improve
mechanistic models of drought limitations to photosynthetic electron transport.
Abstract

Crop improvement is crucial to ensuring global food security under climate change, and hence there is a pressing need for phenotypic observations that are both high throughput and improve mechanistic understanding of plant responses to environmental cues and limitations. In this study, chlorophyll $a$ fluorescence light response curves and gas-exchange observations are combined to test the photosynthetic response to moderate drought in four genotypes of *Brassica rapa*. The quantum yield of photosystem II ($\phi_{\text{PSII}}$) is here analyzed as an exponential decline under changing light intensity and soil moisture. Both the maximum $\phi_{\text{PSII}}$ ($\alpha_{\text{PSII}}$) and the rate of $\phi_{\text{PSII}}$ decline across a large range of light intensities (0–1000 $\mu$mol photons m$^{-2}$ s$^{-1}$) ($\beta_{\text{PSII}}$) are negatively affected by drought. We introduce an alternative photosynthesis model ($\beta_{\text{PSII}}$ model) incorporating parameters from rapid fluorescence response curves. Specifically, the model uses $\beta_{\text{PSII}}$ as an input for estimating the photosynthetic electron transport rate (ETR), which agrees well with two existing photosynthesis models (Farquhar-von Caemmerer-Berry and Yin). The $\beta_{\text{PSII}}$ model represents a major improvement in photosynthesis modeling through the integration of high-throughput fluorescence phenotyping data, resulting in gained parameters of high mechanistic value.

Keywords: Photosynthesis modeling, Chlorophyll $a$ Fluorescence, High-throughput Phenotyping, Drought, *Brassica rapa*

Introduction

Increasing global populations and environmental change require greater mechanistic understanding of plant responses to fluctuating environmental factors along with meaningful phenotyping for tolerance to stress such as drought (Sheffield and Wood, 2008; Jin et al., 2018). Improved phenotyping technologies can also advance our ability to link physiological mechanisms to rapidly improving genetic information. Amongst the challenges towards this goal is the genetic complexity behind drought tolerance traits of interest to breeders (Holland, 2007; Shi et al., 2009). Hence, model-assisted phenotyping has been advocated to separate complex traits such as quantum yield of photosynthesis, stomatal conductance, and water use efficiency.
into manageable mechanistic components (Tardieu, 2003; Martre et al., 2015). Mechanistic modeling formalizes plant physiology using interconnected mathematical equations, which describe primary biochemical and first principle biophysical processes. Improving predictive understanding of crop responses to changing environments will require that mechanistic models directly use phenotypic and environmental data to simulate outcomes sensitive enough to capture possible variation in the expressed traits among unknown genotypes. When these requirements are met, mechanistic models can assist in unraveling the genetic architecture underlying the complex quantitative traits of drought physiology (Reymond et al., 2003; Hammer et al., 2006; Chenu et al., 2009).

Although mechanistic models have evolved to capture the expression of complex plant traits in a changing environment, no current model can dependably capture the impact of drought on photosynthesis (Drake et al., 2017). Photosynthesis models focus on those environmental factors considered critical to net assimilation rates ($A_n$) (de Witt, 1966; Farquhar et al., 1980; Patrick et al., 2009; Yin et al., 2009). Observations of $A_n$ and available CO$_2$ ($A/C_i$) are combined in mechanistic models, such as the Farquhar, von Caemmerer, and Berry model (1980; FvCB model), to reveal biochemical mechanisms underpinning photosynthesis. FvCB estimates $A_n$ as limited by two primary factors. First, RuBisCO-limited $A_n$ ($A_c$) is dominated by the response of the maximum rate of carboxylation ($V_{\text{cmax}}$). Second, light-limited $A_n$ ($A_J$) is constrained by the electron transport rate (ETR) across photosystem II and I (PSII and PSI), which ultimately produces ATP and NADPH needed for the Calvin carboxylation cycle (Farquhar, et al., 1980; von Caemmerer, 2000). Although the FvCB model captures the phenomenological link between ETR and $A_n$, it omits mechanistic details of the photosynthetic electron transport chain (Horton et al., 1994; Allen and Pfannschmidt, 2000; Laisk et al., 2002; Yin et al., 2004). Whereas the conceptual power of a reduced complexity model (FvCB) yields crucial insights under non-stressed conditions, it lacks additional mechanistic detail for plants exposed to environmental stress (Urban et al., 2017).

Drought stress impacts both $A_c$ and $A_J$ via interactive mechanisms (Flexas and Medrano, 2002; Bota et al., 2004; Fini et al., 2012). The initial response to water stress is often a decline in stomatal conductance ($g_s$), which impacts CO$_2$ availability for photosynthesis (Medrano et al., 2002; Grassi and Magnani, 2005). Additional CO$_2$ constraints on $A_c$ are possible via mesophyll conductance ($g_m$), limiting CO$_2$ at the site of carboxylation (Flexas et al., 2002; Niinemets et al., 2004).
Prolonged CO\textsubscript{2} limitation can result in over-reduction of the photosynthetic electron transport chain (Miller \textit{et al.}, 2010), triggering the production of reactive oxygen species (ROS) at different sites of the photosynthetic pathway with the potential for photo-oxidative damage (Krieger-Liszkay \textit{et al.}, 2008; Miller \textit{et al.}, 2010; Sharma \textit{et al.}, 2012). PSII is highly susceptible to oxidative stress, and a variety of mechanisms, collectively called photoprotection, preserve it from irreversible photodamage that causes sustained declines in the overall efficiency of PSII (Murata \textit{et al.}, 2007; Takahashi and Badger, 2011). Heat energy dissipation, state-transitions, augmented PSI energy utilization, and changes in leaf absorbance using alternate pigments or chloroplast avoidance are all known mechanisms of photoprotection (Müller \textit{et al.}, 2001; Kasahara \textit{et al.}, 2002; Takahashi and Badger, 2011).

Photosynthesis models must now progress to reflect these stress-induced mechanisms while using high-throughput phenotyping data, including non-invasive measures of leaf spectral reflectance, absorbance, and chlorophyll \textit{a} fluorescence (Cruz \textit{et al.}, 2016; Kuhlglert \textit{et al.}, 2016; Silva-Perez \textit{et al.}, 2018). Fast and informative techniques provide fine temporal resolution of mechanistic responses to external stressors from mild to lethal stress (Guadagno \textit{et al.}, 2017), which are necessary to improve predictive understanding of photosynthesis responses to drought.

In particular, pulse amplitude modulated (PAM) chlorophyll \textit{a} fluorescence analysis quantifies PSII activity in response to observed photosynthetically active radiation (\(Q\)) and it is informative of the status of the photosynthetic electron transport (Maxwell and Johnson, 2000; Kramer \textit{et al.}, 2004; Baker, 2008). PAM measurements, using the signal of the excitation energy re-emitted by chlorophyll \textit{a} molecule as fluorescence, are used to define the fate of the absorbed light in the leaf and they are currently one of the fastest and most reliable phenotyping tools in photosynthetic measurements (Filek \textit{et al.}, 2015; Gullì \textit{et al.}, 2015; Flood \textit{et al.}, 2016; Gómez \textit{et al.}, 2017; Guadagno \textit{et al.}, 2017). The operating efficiency of PSII (\(\phi_{\text{PSII}}\)) is a fluorescence parameter calculated from the relative difference in light conditions between the steady-state (\(F_s\)) and the maximum fluorescence emitted after a saturating flash that closes (reduces) all PSII reaction centers (\(F_m^{'}\)); i.e. \(\phi_{\text{PSII}} = (F_m^{'} - F_s)/F_m^{'}\) (Genty \textit{et al.}, 1989). A large fraction of the excitation energy not used in PSII photochemistry or re-emitted as fluorescence is dissipated as heat via regulated (\textit{e.g.}, non-photochemical quenching, NPQ) and non-regulated energy dissipation (\textit{e.g.}, NO) mechanisms (Müller \textit{et al.}, 2001; Kramer \textit{et al.}, 2004). Recently, the original derivation of NPQ has also been extended allowing for high-throughput estimates of...
quantum yield NPQ ($\Phi_{NPQ}$) (Tietz et al., 2017). $\Phi_{NPQ}$ can be measured in a few seconds, allowing for high-throughput and field applications, and its calculation does not require full relaxation of quenching processes as for the classic NPQ parameter. The combination of fluorescence observations with leaf gas-exchange data has been shown as a powerful way to inform and test models of photosynthesis (Laisk et al., 2002; Yin et al., 2009; Bellasio et al., 2016).

Alternative models of photosynthetic electron transport have been developed using an increasing number of mechanistic details of the Z-scheme for the electron transport (Fig. 1). Within chloroplasts, photosynthetic electron transport occurs across the thylakoid membranes (Fig. 1a) where a hydrogen ion gradient builds up upon the transfer of excited e\' to ultimately produce ATP and NADPH, which are used as substrates in the Calvin Cycle. Fig. 1 (b) summarizes the ETR derivation of the FvCB model. This model assumes that the electron flow is entirely linear (LEF) from PSII to NAPD\(^+\) reduction with the CO\(_2\) fixation rate from the $A/C_i$ response used to parametrize the maximum ETR ($J_{\text{max}}$). Data from the linear portion of a light response curve can be used to parameterize quantum yield on an $\Delta CO_2/\Delta Q$ basis ($\Phi_{CO_2}$) (Fig. 1b (inset graph)). Although the significance of the correlation between the quantum yield of assimilation and the PSII quantum yield has been previously studied (Oberhuber and Edwards, 1993; Pietrini and Massacci, 1998; Singaas et al., 2000), to the best of our knowledge the effect of drought on its linearity is still unclear. The FvCB model has been recently implemented to include proportional changes between ETR and $A_n$ using observations of $A_n$ and $\Phi_{PSII}$ under low-light conditions ($Q < 200 \, \mu$mol photons m\(^{-2}\) s\(^{-1}\) to estimate ETR and $A_J$ (Yin et al., 2004; Yin et al., 2009; Bellasio et al., 2016) (Fig. 1c). Quantum yield is estimated on an $\Delta e/\Delta Q$ basis using the linear portion of the $\Phi_{PSII}$ light response (Fig. 1c (top inset graph)), but the use of only low-light conditions to characterize PSII quantum yield is limiting. In the Yin model, a lumped parameter, $s$, is estimated to account for the energy partitioning between photosystems ($\rho_2$), leaf absorbance in the antenna complex ($\alpha_{\text{leaf}}$), and the potential use of electron pathways other than LEF ($f_{\text{alt}}$). However, neither FvCB nor the Yin model explicitly address the influence of environmental stress on ETR and $A_n$ and they are not well equipped to capture the $A_J$ responses of the PSII antenna complex to stressors (Govindjee, 2002; Asada, 2006; Murata et al., 2007; Urban et al., 2017).
Here, we introduce an alternative approach ($\beta_{PSII}$ model) that considers PSII activity across a wide range of light conditions and that can better accommodate the role of stress-related mechanisms (Fig. 1d). We observe that data from the $\phi_{PSII}/Q$ response can be modeled as an exponential decline (Fig. 1d (inset graph)). This new parameter as the rate of decline ($\beta_{PSII}$) can be used to calculate ETR, $A_i$, and $A_n$ under stress conditions such as drought. Using a more complete characterization of quantum yield via the $\phi_{PSII}$ light response, the $\beta_{PSII}$ model approach accommodates mechanisms of photoprotection including non-photochemical quenching (NPQ), chloroplast avoidance, and pigment alterations as well as PSII damage relative to repair (Fig. 1d). Our integration of the $\phi_{PSII}$ decline provides a link between gas conductance-based limitations on $A_c$ and photoprotective limitations impacting $A_j$ representing a further step in the mechanistic understanding of the electron transport under stress (incremental yellow shadow in Fig. 1). All model parameters (observed and predicted) for the FvCB, Yin, and $\beta_{PSII}$ models are compared in Table 1, whereas Table 2 describes the equations used in the three photosynthesis models.

We tested the $\beta_{PSII}$ approach in an effort to analyze physiological responses of $A_n$ under different soil moisture conditions from full watering to moderate drought in the species Brassica rapa (Supplemental Fig. 1-2). High intraspecific physiological diversity with respect to complex quantitative traits such as $A_n$ and WUE has previously been shown for Brassica (Edwards et al., 2011; Franks, 2011; Edwards et al., 2012; Baker et al., 2015), making it a perfect model to investigate photosynthesis phenotyping tools. Specifically, we tested a turnip crop type (VT), a cultivated oilseed (R500), and two experimental genotypes (RILs) developed from a cross between a rapid-cycling genotype (Imb211) and an oilseed crop (R500), thus ensuring a broad range of both photosynthetic and biomass allocation diversity (Edwards et al., 2011; Yarkhunova et al., 2016; Pleban et al., 2018).

We developed a $\phi_{PSII}$ light response curve using a three-parameter exponential function,

$$\phi_{PSII} = (\alpha_{PSII} - \kappa_{PSII})e^{Q\beta_{PSII}} + \kappa_{PSII} \quad \text{(Eqn.1)}$$

where the exponential rate of decline for $\phi_{PSII}$ ($\beta_{PSII}$) under increasing light ($Q$) and the intercept of $\phi_{PSII}$ as $Q$ approaches zero ($\alpha_{PSII}$) are used to model the responses. Importantly, $\alpha_{PSII}$ derives from measurements taken in light conditions and it is different that the classic $Fv/Fm$ parameter derived from dark-adapted measurements (Table 1). The $\kappa_{PSII}$ term represents a non-
zero minimum of $\phi_{PSII}$ as $Q$ approaches $\infty$. To evaluate potential differences in photoprotection strategies due to ETR, we validated the $\phi_{PSII}$ light response parameters ($\beta_{PSII}$, $\alpha_{PSII}$) at different soil moisture conditions. Then, we incorporate these parameters in an alternative photosynthesis model that directly incorporates $\phi_{PSII}$ light-response traits into the estimation of ETR and we assessed how the derived parameters relate to known traits, including $V_{cmax}$ and $g_m$.

Using rapid measurements with high mechanistic significance, our approach innovatively connects high-throughput phenotyping and biophysical modeling to better predict plant photoprotective strategies. Gained knowledge will help to clarify the complexity of photosynthetic traits, such as drought tolerance, thus improving breeding and management strategies towards more drought-resistant crops with increased final yield.

**Results**

**Establishing Drought Treatments**

After sowing, plants were immediately randomized and put into different treatment groups (Supplemental Fig. 1). On experimental Day 0 (28 days after sowing) drought was applied via complete water withholding for the droughted cohort. Control pots (Well-Watered) were watered daily throughout the experiment and WW plants measured on experimental days 1, 4, 5, 6, and 9. Droughted plants were assigned to three different groups and replicate plants observed on experimental days 4–7 (treatment group D1), 9–12 (treatment group D2), and 15 (treatment group D3). On experimental day 9, water was re-applied to a subset of droughted plants (R1) and they were observed on experimental day 9–12. On experimental day 15, a second subset of droughted plants (R2) was re-watered and observed 6 h after re-watering. Finally, on day 16 the last subset of droughted plants was re-watered and assessed at 30 h after re-watering (R3). For each experimental day, volumetric soil water content (VWC) was measured across all cohorts of plants for the duration of the experiment (Supplemental Fig. 2).

**Impact of Drought on Leaf Traits and genotypic difference**

The progressive drought and recovery (Supplemental Fig. 1) application inevitably impacted the photosynthetic performance of all genotypes. Table 3 summarizes 14 photosynthetic leaf traits assessed on three different experimental days for each *B. rapa* genotype. As expected, D1 plants were the least impacted by water scarcity for the measured
physiological traits. However, early signs of drought stress were already detected. $g_s$ was reduced in D1 plants of all genotypes by a mean of 0.16 mmol m$^{-2}$ s$^{-1}$ (±0.10), with the biggest decline for $R500$ (0.29 mmol m$^{-2}$ s$^{-1}$). In VT, the electrochromic shift ($ECS_t$) ($\Delta$ absorbance 530 nm), which reflects the trans-thylakoidal $\Delta H^+$ gradient, at 300 and 1000 umol photon m$^{-2}$ s$^{-1}$, increased in D1 plants relative to WW. More sustained drought (D2 and D3 plants) results in pronounced changes across all genotypes (Table 3). $g_s$ showed further reduction in all genotypes but $r46$ in D3 plants. LEF was decreased across genotypes, with $R500$ showing the greatest loss at both 300 and 1000 umol photon m$^{-2}$ s$^{-1}$. $\Phi_{NPQ}$ and $ECS_t$ at both 300 and 1000 umol m$^{-2}$ s$^{-1}$ increased overall in D3 plants. Pigments content as SPAD at 530 nm units and relative chlorophyll content increased in all four genotypes of the D3 cohorts. The changes in $ECS_t$, LEF, and SPAD are reflected in a decreased lumped $s$ parameter in D3 plants, which accounts for potential changes in $f_{alt}$, $\rho_2$, and $\alpha_{leaf}$ (Supplemental Fig.3). These results validate the robustness of high-throughput measurements of fluorescence to pick up early signs of drought stress. The drought treatments applied here can be considered as mild to moderate for B. rapa with an overall recorded VWC never lower than 3% and plants still capable of recovery upon re-watering for all genotypes (Supplemental Fig.1). Changes in physiological traits reflect the expected behavior of the four genotypes under drought (Edwards et al., 2011; Edwards et al., 2012; Baker et al., 2015; Greenham et al., 2017). Genotypes with high biomass accumulation ($R500$, $r301$ and VT) were more impacted at an earlier stage by changes in soil moisture, whereas the small, highly water use-efficient $r46$ was able to tolerate drought and maintain stable level of gas exchange despite the decreased LEF. These genotypic differences in drought behavior were confirmed when looking at the onset of $NPQ_t$ at increased LEF (Supplemental Fig.4), where $R500$ and VT showed earlier changes in $NPQ_t$ values already at lower LEF in comparison to the inbred lines $r46$ and $r301$.

**Analysis of Rapid Light Response Curves of Fluorescence**

Rapid Chlorophyll a fluorescence light response curves were taken on 119 replicate leaves during six different experimental days, with each genotype $\times$ treatment replicated 1–7 times (mean replication rate of 3.3) (Supplemental Fig. 1). The variation in sample size was due to time constraints and destructive measurements occurring during the experiment. Firstly, the rapid light response curves for all genotypes and treatments were pooled together with the mean of
observed $\phi_{PSII}$ at each $Q$ estimated using the median value of the posterior distributions of the parameter from Eqn. 1. The decline was then fitted with an exponential model for each genotype and treatment (Fig.2). All genotypes show a decline in $\phi_{PSII}$ under drought, more pronounced after 15 days (D3), but all plants recovered to pre-stressed values after re-watering (R1, R2, R3). The partial increase of $\phi_{PSII}$ can be found in the rapid leaf development of the utilized genotypes, typical of the Brassicaceae. Since the youngest fully developed leaf was utilized at each measuring point, leaf growth and display changed over the course of 15 days, causing different leaf angles, changes in the photosynthetic complex stoichiometry, and resulting in different responses to incoming radiation and absorbance. Then, to utilize a more rigorous and probabilistic approach to signify differences (Kruschke, 2014), we used the 95% posterior high-density intervals (HDIs) as a Bayesian probabilistic estimator of difference. Figure 3 summarizes the changes in $\beta_{PSII}$ and $\alpha_{PSII}$, estimated following Eqn. 1, at varying VWC. Genotypes VT and r301 showed credible interval differences at 95% HDI in $\beta_{PSII}$ for D2 and D3 relative to the WW treatment, whereas r46 and R500 showed a credible interval difference (95% HDI) only for D3 relative to the WW treatment (Fig. 3a-d).

All genotypes demonstrated similar recovery patterns in $\beta_{PSII}$ with credible differences at 95% HDI for the R2 and R3 treatments relative to D3. For R plants, a less negative $\beta_{PSII}$ was observed at 30 h after re-watering (R3) with respect to the 6-h period (R2) demonstrating ongoing recovery during that time period. Figure 3 (e-h) displays the change of slope in $\phi_{PSII}$ as $Q$ approaches zero, $\alpha_{PSII}$, with 95% posterior HDI. r301, R500 and VT each show credible interval difference at 95% HDI in $\alpha_{PSII}$ for D3 relative to WW treatment whereas r46 remains stable in $\alpha_{PSII}$. The $\alpha_{PSII}$ parameter shows a recovery response similar to $\beta_{PSII}$, with r301, R500, and VT each showing a credible interval difference at 95% HDI for the R3 treatment with respect to pre-stressed values.

Comparison of Photosynthesis Models

All three photosynthesis models (FvCB, Yin, and $\beta_{PSII}$) performed well across genotypes and treatments when comparing observations of leaf gas exchange to simulated results, using the medians of the posterior (i.e. a more rigorous Bayesian estimator that incorporates uncertainty in both measurements and models; McElreath, 2016, Kruschke 2014) parameter distributions. For
the $\beta_{PSII}$ model, a comparison of simulated $A_n$ vs. observed $A_n$ from light response and $A/Ci$
curves results in $0.66 < R < 0.98$ across genotypes and treatments (Supplemental Fig. 5).

The $\beta_{PSII}$ parameter, describing the slope of decline of $\phi_{PSII}$ vs. $Q$, was integrated into the
ETR derivation for estimating light-limited photosynthesis, $A_J$, and the updated ETR description
was compared to both the FvCB and Yin photosynthesis models. To quantitatively evaluate the
alternate modeling approaches estimating ETR, posterior parameters distributions were
compared between the FvCB, Yin, and $\beta_{PSII}$ decline models (Fig. 4, 5). The correlation ($R$) of the
medians of these posterior distributions was chosen to evaluate the strength and direction of a
linear relationship amongst alternative parameterizations. For the parameter $V_{cmax}$, maximum rate
of carboxylation, all models showed close agreement in estimates with $R$ values of 0.97–0.98
(Fig. 4a-c). For mesophyll conductance ($g_m$), the $R$ value between the FvCB model and the $\beta_{PSII}$
model was 0.90, between the Yin model and the $\beta_{PSII}$ model was 0.90, and between the FvCB
model and the Yin model was 0.99 (Fig. 4d-f). Additional posterior parameters not common to
all three models were compared to factors with similar biophysical meaning, such as quantum
yield terms ($\phi_{CO2}$, $\phi_{2ll}$ and $\alpha_{PSII}$) (Fig. 5a-c). Agreement between the quantum yield terms is
particularly strong between $\phi_{2ll}$ (Yin model) and $\alpha_{PSII}$ ($\beta_{PSII}$ model) (Fig. 5b). The $\kappa_{PSII}$ estimates
show little correlation with $J_{max}$ in the FvCB or Yin models (Fig. 5d, e), whereas $J_{max}$ estimates in
FvCB and Yin are highly correlated (Fig. 5f). The Yin model and the $\beta_{PSII}$ model were highly
correlated in the lumped $s$ parameter ($R = 0.83$) (Fig. 5g). The convexity factor, $\theta$, used in FvCB
and Yin models shows a correlation of 0.57 with the Yin estimates closer to the maximum of 1.0
(Fig. 5h). Finally, a comparison was made between $\beta_{PSII}$ as described in Eqn. 1 with the $V_{cmax}$ and
$J_{max}$ estimates from the FvCB model and Yin models. $\beta_{PSII}$ showed an $R$ value of 0.81 with $V_{cmax}$
as described by the FvCB model and 0.83 with $V_{cmax}$ as described by Yin. $\beta_{PSII}$ showed a $R=0.69$
relationship with $J_{max}$ estimates of the FvCB model and $R=0.68$ with Yin (Supplemental Fig.6).

Comparison of High and Low Throughput Fluorescence measurements

Full gas-exchange light response curves coupled with fluorescence were taken on 34 leaves
on four experimental days with each genotype x treatment replicated 1–4 times (mean replication
rate of $2.3 \pm 0.9$) (Supplemental Fig. 1). The variation in sample size was once again due to time
constraints and destructive measurements occurring during the experiment. Specifically, the
assessment of gas-exchange light response curves was done at experimental day 1 and 6 for WW plants, at experimental day 5 and 7 for D1 plants, and at day 9 and 13 for D2 plants. Re-watered plants in the cohorts R2 were observed at experimental day 10 (Supplemental Fig. 1). The assessment of rapid $\phi_{PSII}$ vs. $Q$ curves was done at experimental day 1, 5, and 9 for WW plants, at experimental day 5 for D1 plants, at day 9 and 12 for D2 plants, and day 13 for D3 plants. Re-watered plants had rapid $\phi_{PSII}$ vs. $Q$ observations for cohort R1 on experimental day 9, for cohort R2 on experimental day 13 (6 h after watering was restored), and for cohort R3 on experimental day 14 (30 h after watering was restored). The comparable posterior parameter estimates were matched with posterior parameter estimates from classic gas-exchange light response curves following Eqn. 1 and shown in Supplemental Fig. 7. The median posterior estimates of $\beta_{PSII}$ show a $R$ value of 0.72, whereas median posterior estimates of $\alpha_{PSII}$ parameter show $R = 0.67$ (Supplemental Fig. 7 a, c). Next, the correlation between the posterior estimates for both $\beta_{PSII}$ and $\alpha_{PSII}$ derived using the full $\beta_{PSII}$ photosynthesis model and the rapid fluorescence curves was tested (Supplemental Fig.7b, d). The full $\beta_{PSII}$ photosynthesis model utilizes coupled gas-exchange and fluorescence observations from a low-throughput infrared gas analyzer (LiCor 6400XT), whereas the rapid fluorescence curves of $\phi_{PSII}$ vs. $Q$ curves are obtained using the high-throughput spectrophotometer MultispeQ. Despite the different times of collection, the two methods agree with correlations of 0.66 for $\beta_{PSII}$ and 0.69 for $\alpha_{PSII}$ (Supplemental Fig.7b, d).

**Discussion**

Here we tested how applying alternative descriptions of quantum yield ($\phi_{CO2}$, $\phi_{PSII}$, $\beta_{PSII}$) in photosynthesis models (Fig. 1) can improve the mechanistic realism of electron transport processes and their potential changes under drought. Our $\beta_{PSII}$ photosynthesis model utilized the full $\phi_{PSII}$ vs. $Q$ response accounting for possible photoprotective mechanisms (i.e., NPQ, changes in absorbance, etc.). All these mechanisms decrease photosynthetic ETR and play a crucial role in the $A_n$ magnitude under stress and we have to consider and quantify them to mechanistically improve simulated responses to drought and other environmental changes.

**$\beta_{PSII}$ dynamics**

Our main goal was to explore the use of chlorophyll $a$ fluorescence parameters derived from rapid light curves, collected with a dynamic high-throughput tool, to develop a
photosynthesis model for estimating photosynthetic electron transport rate (ETR). The major
design improvement of the MultispeQ is the quick capture of fluorescence parameters precisely
during steady-state illumination (Kuhlger et al., 2016) and we tested the relationship between
rapid fluorescence data from the MultispeQ and the LiCOR6400-40 fluorimeter (Fig. 6). Single
measurement comparisons grouped by genotype show linear relationships across different light
levels and water treatment with $R^2 > 0.9$ despite the variations in time of the day, duration of the
actinic light, etc. between the low and high-throughput measurements due to the fact that the
LiCOR instrument is primarily utilized to take simultaneous measurements of gas exchange. Our
results build on previous work by Meacham et al. (2017) who posed the question about the use
of rapid fluorescence analysis for photosynthesis modeling. However, we experimented beyond
their results using the high-throughput MultispeQ instead of a monitoring PAM from Walz, thus
avoiding the use of aluminum foil to cover the leaves during the measurements and the possible
increases in temperature with consequent changes in water vapor exchange (Bücher et al., 2018;
Giorio, 2011). Rapid light curves are complex to interpret due to the presence of several
components in the photosynthetic apparatus characterized by different time constants (i.e., the
time to reach ~63% of the full response) involved (Pearcy, 1990; Way and Pearcy, 2012). We
acknowledge that light harvesting and energy transfer respond nearly instantaneously to changes
in the light environment, whereas adjustments in the carbon cycle metabolites can take up to
several seconds (Bowels, 1984; Geiger and Servaites, 1994). However, the use of a fast analysis
is necessary to capture the true light conditions of plants in the field, where they rarely
photosynthesize at full capacity (Zhu et al., 2010; Ort et al., 2011). Fast changes in incoming
radiation, such as that used during the collection of rapid light curves, can be thought to have
similar consequences as for leaves exposed to sunflecks. After an initial uncoupling of the
electron transport from CO$_2$ fixation, the metabolites pool has been shown to re-fill within a few
seconds in healthy leaves (Servaites, 1990; Parry, 2008; McClain and Sharkey, 2019). The
fluorescence calculated parameters have already been shown to have a very dynamic behavior
(Porcar-Castell et al. 2006), which leaves room to accommodate for stress-related mechanisms.

The exponential decline of $\phi_{PSII}$ vs. $Q$ (Eqn. 1) takes into account changes occurring at
PSII antenna-reaction center complexes and is extremely relevant under stress conditions. These
changes are not included in current photosynthesis models (Fig. 1). Identifying the parameter
$\beta_{PSII}$, meaning the slope of decline of $\phi_{PSII}$ at $Q$ increase, and its dynamics at the onset of water
stress is highly valuable to mechanistically elucidate processes of photoprotection and increased
photorespiration, which are relevant for the overall reduction of assimilation under stress (Ort
and Baker, 2002; Souza et al., 2004). The $\phi_{PSII}$ and $Q$ relationship has been previously used to
assess photosynthetic responses using the ETR maximum, showing declines under water stress
(Rascher et al., 2004; Li et al., 2008; Batra et al., 2014).

Our results depict a more complete picture of the changes in $\phi_{PSII}$ vs. $Q$ under drought and the
parameter $\beta_{PSII}$ seems to be better suited to explain a range of stress responses (Fig. 2,3). The
observed declines in $\beta_{PSII}$, here observed under drought, may in fact be the result of more or less
regulated processes, such as NPQ (Table 3), chloroplast light avoidance, and non-regulated
energy dissipation (Müller et al., 2001; Kasahara et al., 2002; Takahashi and Badger, 2011).

Further, the modest recovery after a 6-h period in both $\beta_{PSII}$ and $\alpha_{PSII}$ suggests that these
parameters account for more than just fast-regulated photoprotective mechanisms (Dall’Osto et
al., 2005; Lambrev et al., 2012). Near full recovery by 30 h after the start of re-watering may be
due to slow-relaxing and/or un-regulated processes, along with protein turn-over and repair
processes that require a longer time to return to pre-stress conditions (Nishiyama et al., 2006;
Brooks et al., 2013; Malnoë, 2018). Indeed, both slow and rapid light curves are able to trigger
slow-relaxing NPQ mechanisms with qI having lifetime changes similar to those observed during
the qE (rapid-relaxing) (Ruban, 2016; Lazár, 2015; Müller et al., 2001).

Both $\beta_{PSII}$ and $\alpha_{PSII}$ depicted genotypic variation relative to drought severity, with r301
showing greatest declines, i.e. transgressive segregation with respect to the RIL parents, followed
by R500 and VT which accumulate the highest amount of above-ground biomass (Fig. 3b, f).
Future work should consider how the slope of variation in $\phi_{PSII}$ vs. $Q$ response relates to previous
findings of root:shoot allocation differences occurring under drought (Edwards et al., 2016) as
well as exploring how variance in $\beta_{PSII}$ may influence reactive oxygen species production and,
when more pronounced declines occur, cellular damage (Reddy et al., 2004).

Implementing Photosynthesis Modeling

Using direct observations of $\phi_{PSII}$ vs. $Q$ data as parameters in a leaf photosynthesis model
provided a means of quantifying the impacts of PSII photoprotective mechanisms on ETR.
Although these protective processes are critical to final net photosynthesis, they are abstracted
out of all FvCB-based modeling efforts (Horton et al., 1994; Allen and Pfannschmidt, 2000;
Laisk et al., 2002); therefore, current parameterization approaches may be biased by tuning parameters without mechanistic insight. Our $\beta_{PSII}$ approach extends the development of FvCB-based models using both $A/C_i$ and light response curves in analysis (Holland, 2007; Patrick et al., 2009) to integrate both gas-exchange and fast chlorophyll $a$ fluorescence observations into models (Laisk and Loreto, 1996; Laisk et al., 2002; Yin et al., 2006; Yin et al., 2009). The $\beta_{PSII}$ photosynthesis model maintains the use of commonly employed parameters $V_{cmax}$, $R_d$, and $g_m$, while shifting away from others, such as $J_{max}$ and $\theta$ that do not fully incorporate stress impacts on ETR, for describing ETR and associated processes. Estimates of the common parameters including $V_{cmax}$ show strong similarity across the three considered photosynthetic models (Fig. 4). The correlations between the $\beta_{PSII}$ with $V_{cmax}$ and $J_{max}$ estimates of the FvCB and Yin model is promising for model parameterization. The throughput of $\phi_{PSII}$ vs. $Q$ measurements will also increase the number of genotypes used in models and thus better incorporate mechanistically rigorous, genotype-level informed parameters for crop simulation (Boote et al., 2001; Bertin et al., 2010; Archontoulis et al., 2012; Pleban et al., 2018).

The lumped $s$ parameter has a valuable role in accommodating a number of mechanisms affecting the final ETR and showed declines after 13 days of drought (Supplemental Fig. 3). Our photosynthesis model is able to assess the extent of the mechanisms slowing down ETR as a whole. However, the same MultispeQ collects fluorescence values at each recorded pulses. All components of NPQ ($q_E$, $q_T$, $q_I$) could then be calculated from values of $Fm'$ and $Fm$ over time, allowing for a detailed energy partitioning analysis. These results could benefit the model and separate physiological (feedback mechanisms) and damage consequences of the stress. Future work including the use of knockout mutants, such as those for genes involved in NPQ mechanisms, will be needed to disentangle the three factors lumped in $s$ ($f_{alt}$, $\alpha_{leaf}$, $\rho_2$). Changes in relative chlorophyll and SPAD at 540 nm affect the overall leaf absorbance ($\alpha_{leaf}$) and are partially responsible for changes in $s$ (Table 3). Future work evaluating the light harvesting properties of photosynthetic pigment molecules (Ye et al., 2013) will help clarify the importance of this component on the lumped $s$. Isolating changes in $\alpha_{leaf}$ might also use statistical methods to identify dominate shifts in absorption from spectrophotometric data (Baker et al., 2018). It appears likely that the other two factors, $f_{alt}$ and $\rho_2$, changed during drought progression based on the decline in LEF relative to increases in $ECS_t$ (Table 3). We speculate that the altered relationship between LEF and $ECS_t$ may relate to energetic spillover and changes in cross-
membrane $\Delta H^+$ triggering unbalanced activity in the PSII-PSI duo, ultimately leading to an increased cyclic electron flow around PSI (Livingston et al., 2010; Strand et al., 2015). Future data-model integration could consider saturation pulse estimation of PSI yield parameters to quantify the specific contribution of $f_{alt}$ and $\rho_2$ (Klughammer and Schreiber, 1994). Integration with ECS$_t$ data could also assist in understanding the potential for change how trans-thylakoidal $\Delta H^+$ might be coordinated by the use of cyclic and other non-linear electron transport pathways (Kramer et al., 2004).

Our framework offers opportunities to better evaluate stress limitations on quantum yield and ETR. The coupling of $s$ and $\beta_{PSII}$ as described here are critical for future efforts to model individual photoprotective, photoinhibitory, and photo-damaging mechanisms, which are encompassed in these two parameters albeit in a lumped way. Further implementation of current instrumentation and further modeling approaches may allow for itemizing specific physiological or genetic mechanisms underlining $s$ and $\beta_{PSII}$ responses to drought (Noctor et al., 2002; Miller et al., 2010; Guadagno et al., 2017).

$\beta_{PSII}$ photosynthesis model limitations

Our approach needs additional tests under natural and/or higher intensity light conditions to investigate details of photoprotective mechanisms and their behavior under extreme environmental conditions. For instance, the ratio of carotenoids in the PSII antenna complex responsible for NPQ can vary with growing conditions (Kato et al., 2003). Further, photodamage has been shown to be more severe in the UV range and at 500–600 nm, and the ratio of photodamage to repair is higher as light intensity increases (Nogués and Baker, 2000; Murata et al., 2007; Zavafer et al., 2015). Also, dynamic fluctuations in light, such as those in natural settings, can have relevant effects on photosynthetic rate (Viale-Chabrand et al., 2016; Viale-Chabrand et al., 2017), which we expect are more severe under drought, with subsequent recovery processes possibly delayed (Fig. 3). The repair of PSII damage can also be compromised by temperature stress (Murata et al., 2007). Consequently, how $\beta_{PSII}$, $\alpha_{PSII}$, and $s$ respond to field conditions, drought, and other stresses should be further investigated.

The difficult estimation of $g_m$ may also affect further implementation of our framework and alternative methods of $g_m$ assessment should be considered. The $g_m$ estimation in all three photosynthesis models used the combined fluorometry/gas exchange approach (Harley et al.,
1992, Pons et al., 2009, Archontoulis et al., 2012). Two of the three models (Yin and $\beta_{PSII}$) included the $s$ parameter to consider alternative electron pathways influencing the $g_m$ estimation (Fig. 4d, e, f). State-of-the-art photosynthesis models include a dynamic $g_m$ responding to variations in both internal leaf status and external environments (Tazoe et al., 2009; Moualeu-Ngangue et al., 2017). Coupling online isotope discrimination data to the linear and total electron flow, gathered from gas exchange and fluorometry observations, may help resolve concerns related to $g_m$ estimation and allow for the integration of a dynamic $g_m$ model into the $\beta_{PSII}$ method (Pons et al., 2009; Tazoe et al., 2009; Lianhong and Ying, 2014; Moualeu-Ngangue et al., 2017; Flexas et al., 2018).

Predictive understanding of both photoprotective and $g_m$ mechanisms are still in their infancy; the alternative approach we have successfully tested provides a crucial transfer of high-throughput empirical measurements and analyses to mechanistic simulations that are likely to improve predictive understanding of drought and other stress responses across a range of plant species and genotypes. Our $\beta_{PSII}$ model will further the improvements of current whole-plant crop modeling by the incorporation of first principles mechanisms (Hammer et al., 2006; Chenu et al., 2009; Wang et al., 2019; Müller and Martre, 2019), through the incorporation of more genetic and omic information into the parameters of biophysical-based models.

Material and Methods

Plant material

Four genotypes of *Brassica rapa* were utilized for our analysis: two crop accessions *R500* (oilseed crop, *B. rapa subsp. trilocularis* (Yellow Sarson)) and vegetable turnip (*VT*), VT-089, D’Auvergne Hative); and two recombinant inbred lines (RILs) (*r46* and *r301*). The RILs are part of a population developed from a cross between the *R500 × Imb211* genotypes. The *R500* genotype is an oilseed cultivar planted in India for approximately 3,000 years (Prakash and Hinata, 1980) with large allocation to seed production (Baker et al., 2015). The *Imb211* genotype is a rapid cycling line derived from the Wisconsin Fast Plant™ (Williams and Hill, 1986). The extremely divergent selection history suggests that genetic variation segregating in the RILs may resemble that segregating in crop × wild hybrids found commonly in nature (Adler et al., 1993). The RIL population has been previously described, and the two RILs of interest were chosen based on their transgressively segregating drought stress phenotypes identified in earlier research.
(Iniguez-Luy et al., 2009; Edwards et al., 2011; Edwards et al., 2012; Pleban et al., 2018). Seeds of R500, r46 and r301 were obtained from a single-seed collection bulked at the University of Wyoming in 2011. VT was obtained from the Wageningen UR Center for Genetic Resources (CGN#10995).

**Growth Conditions**

Seeds were germinated and grown in pots (500 ml) filled with a soil mixture (Miracle-Gro Moisture Control Potting Mix (20% v/v), 453 Marysville, OH, USA and Profile Porous Ceramic (PPC) Greens Grade (80% v/v), Buffalo Grove, IL, USA) with the addition of 2 ml of Osmocote 18-6-12 fertilizer (Scotts, Marysville, OH, USA). Experiments occurred during July and August of 2017 at the University at Wyoming in three growth chambers (PGC-9/2 Percival Scientific, Perry, Iowa, USA). Growth chamber conditions were set at a 14-h photoperiod of approximately 250–300 μmol of photons m⁻² s⁻¹, with a 25–30°C /18–22°C day/night cycle and relative humidity maintained at 45–65%. Soil moisture content was monitored daily for all treatment groups (ECH₂O/EC5 probe, Decagon, Pullman, WA, USA). Plants were randomized in three growth chamber compartments with blocks of each treatment with a randomized mix of four genotypes present in each compartment.

For four weeks, all plants were regularly watered to maintain volumetric soil water content at 0.30 ± 5. At 28 days after sowing (DAS), watering was withheld from treatment plants in the droughted and re-watered cohorts (Supplemental Fig. 1). On experimental Day 0, drought was applied via complete water withholding for the droughted cohort. Droughted plants were assigned to three different groups and replicate plants observed on experimental days 4–7 (treatment group D1), 9–12 (treatment group D2), and 15 (treatment group D3). On experimental day 9, water was re-applied to a subset of droughted plants (R1) and they were observed on experimental day 9–12. On experimental day 15, a second subset of droughted plants (R2) was re-watered and observed six h after re-watering. Finally, on day 16 the last subset of droughted plants was re-watered and assessed at 30 h after re-watering (R3). Soil moisture observations in this study were comparable to those from Guadagno et. al. (2017), where the mean VWC was 0.06 (±0.01) after 14 days of drought; here the mean VWC after 13 days of drought was 0.05 (±0.03).

**Plant physiological observations**
Physiological data collection followed the temporal frequency in Supplemental Fig. 1. For evaluation of photosynthesis traits throughout the treatment period, curves of $A_n$ vs. $CO_2$ availability ($A/C_i$ curves) and photosynthetic light response curves were taken (LiCOR 6400XT, LI- COR Biosciences Inc., Lincoln, NE, USA) following established methods (Long and Bernacchi, 2003). Both response curves were measured between 10:00 h and 16:00 h on fully expanded leaves (between 5th and 8th leaf) with cuvette settings at flow rate of 300 μmol s$^{-1}$, relative humidity maintained at 50% (± 8) and temperature maintained at 20°C. $A/C_i$ curves set sample chamber $CO_2$ concentrations to 50, 100, 200, 300, 400, 500, 600, 800, 1000, 1250, 1500, and 2000 μmol CO$_2$ mol$^{-1}$ air. $A/C_i$ curves were taken on WW, D1, and R1 plants. Light response curves were measured across ten light conditions ($Q= 2000, 1500, 1000, 500, 250, 125, 60, 30, 15, 0$ μmol photons m$^{-2}$ s$^{-1}$). Light response curves were taken on WW, D1, and R1 as well as D2 and D3 plants. For both response curves, PAM fluorescence was measured immediately after gas exchange using leaf chamber fluorimeter (Li-COR 6400-40, LiCOR Biosciences Inc., Lincoln, NE, USA). With actinic light maintained at setting of curve protocol ($\lambda = 470$ nm, 10% blue to obtain values of steady-state fluorescence ($F_s$)), a short saturating pulse (0.8 sec; ~8,000 μmol photons m$^{-2}$ s$^{-1}$) was applied to measure maximum fluorescence in light saturating conditions ($F_m'$) with a short Far-Red pulse to record the $F_o'$ value at the end of induction (Baker, 2008). These were used to determine the operating efficiency of photosystem II photochemistry ($F_m' - F_s$)/$F_m' = \phi_{PSII}$, for light acclimated conditions (Genty et al., 1989). Fluorescence measurements were taken in conjunction with all changes in $C_i$ or $Q$ for each $A/C_i$ and light response curve.

Further chlorophyll fluorescence observations used a rapid PAM light response protocol developed for the MultispeQ spectrophotometer (PhotosynQ LLC, East Lancing, MI). The protocol is available on the PhotosynQ platform under project title: B. rapa drought and recovery Chl Fl evaluation (https://photosynq.org/projects/b-rapa-drought-and-recovery-chl-fl-evaluation). In a single 5-minute clamping with a fully expanded leaf (between 5th and 8th leaf), actinic light (655 nm (Lumileds, LXZ1-PA01)) was incremented at ten light intensities (1000, 800, 600, 500, 400, 300, 200, 100, 50, 0 μmol photons m$^{-2}$ s$^{-1}$) for 30 s before a PAM fluorometry sequence was initiated following established methods (Rascher et al., 2000; Datko et al., 2008). After each light acclimation period the PAM sequences used the multiphase flash technique as described in Lorauex, S.D. et al. (2013) with 4 rectangular saturation flashes of 4500, 4050, 3600, and 3150.
A linear regression of each maximum fluorescence ramp vs. $1/Q$ was made to determine expected $F_m$ used for calculating fluorescence parameters. Recently, the original derivation of NPQ has been extended to NPQ_t allowing for high-throughput, under a minute each, yet mechanistically relevant measurements (Tietz *et al.*, 2017). Therefore, this protocol assessed $\phi_{PSII}$, the fraction of $Q$ dissipated safely as heat ($\phi_{NPQ_t}$), and the fraction of $Q$ quenched via unregulated excitation dissipation ($\phi_{NO}$) at each light intensity. $\phi_{NPQ_t}$ assumes a constant theoretical maximum dark-adapted fluorescence yield and $\phi_{NO}$ represents the fraction of light use remaining after accounting for $\phi_{NPQ_t}$ and $\phi_{PSII}$ ($\phi_{NO} = 1 - (\phi_{NPQ_t} + \phi_{PSII})$) (Tietz *et al.*, 2017). From these response curves, linear electron flow (LEF) was calculated for each $Q$ following $LEF = \phi_{PSII} Q \alpha_{leaf} \rho_2$, where $\alpha_{leaf}$ is assumed 0.85 and $\rho_2$ is assumed 0.5. Rapid PAM light response curves were taken on plants from each watering cohort (Supplemental Fig. 1).

Total electrochromic shift (ECSt) measurements were obtained at two $Q$ intensities (300, 1000 $\mu$mol photons m$^{-2}$ s$^{-1}$ at 650 nm) using the MutlispeQ (Kuhlger t *et al.*, 2016). ECSt monitors the proton flow into the thylakoid lumen by evaluating shifts in the absorbance of cross-membrane carotenoid pigments (Fig. 1 (blue H$^+$ arrows)). Carotenoid absorbance spectrum is dependent on the changing electrical gradient produced by proton flow across the thylakoid membrane (Sacksteder *et al.*, 2000). The protocol for these ECSt observations is available on the PhotosynQ platform (https://photosynq.org/projects/b-rapa-drought-and-recovery-ecs-evaluation). ECSt observations were taken on plants of all watering cohorts (Supplemental Fig. 1). Observations of relative chlorophyll content were also measured with a hand-held MultispeQ spectrophotometer on plants of all watering cohorts (Supplemental Fig. 1).

**Exponential decline of $\phi_{PSII}$ vs. $Q$**

Light response data, $\phi_{PSII}$, from both the Li-COR fluorimeter and the MultispeQ rapid fluorescence protocol were used to model the decline in $\phi_{PSII}$ under increasing $Q$. A hierarchical Bayesian framework generated genotype x treatment posterior trait distributions of exponential decline parameters. A three parameters exponential decline function was used following:

$$\phi_{PSII} = (\alpha_{PSII} - \kappa_{PSII})e^{Q\beta_{PSII}} + \kappa_{PSII} \text{(Eqn.1)}$$

where $\alpha_{PSII}$ (y-intercept) represents the maximum light-adapted $\phi_{PSII}$, $\beta_{PSII}$ represents the exponential decline rate in $\phi_{PSII}$ under increasing $Q$, and $\kappa_{PSII}$ represents a non-zero minimum of $\phi_{PSII}$ as $Q$ approaches $\infty$. Eqn. 1 was modeled using rjags (Plummer, 2014) with samples from the
posterior parameter distributions generated from a Gibbs sampling method (Plummer, 2003). Model parameters ($\alpha_{PSII}$, $\beta_{PSII}$, $\kappa_{PSII}$) were estimated using a three-level hierarchical structure with global, genotype by treatment, and individual plant levels. Priors for the means of the exponential decline parameters followed wide informed normal distributions broadly informed with wide variances. Priors for the precision terms used weakly informed normal distributions (Gelman, 2006). The credible interval divergence at 95% high density interval (HDI) was used to evaluate posterior parameter differences for each treatment time. This comparison metric used in Bayesian analysis allows the identification of definitive portions of the posterior distributions characterized by higher probability density than the regions outside those intervals (Kruschke, 2014, Kruschke, 2018, Kruschke and Liddell, 2018), with more rigorous results and higher predictive power.

Photosynthesis Modeling

Utilizing Bayesian statistics, all photosynthesis models describe how quantum yield and underpinning mechanisms are related to CO$_2$ assimilation under changing light conditions and water availability. The three model formulations are similar to those found in photosynthesis process models while hierarchically incorporating uncertainty and providing probabilistic quantification of parameters. Tables 1 and 2 outline the three modeling approaches used to test the utility of $\phi_{PSII}$ light response data for characterizing ETR and light-limited $A_n$. All three approaches estimate $A_n$ following Eqn 2.1 with the estimation of the critical $C_t(C_{crit})$, where $A_c$ shifts to $A_J$, following methods detailed below. All three approaches estimate $A_c$ using Eqn 2.2 and 2.3 (Table 2). The approaches vary in the derivation of photosynthetic ETR. The first approach followed the FvCB model estimating ETR using information from leaf gas exchange (Farquhar et al., 1980; Farquhar and Wong, 1984) (Eqn 2.5) (Fig. 1(a)). This FvCB derivation of ETR for $A_J (J_m)$ requires estimation of three parameters, $J_{max}$, the maximum rate of electron transport; $\phi_{CO2}$, the quantum yield on a CO$_2$ to photon basis; and $\theta_J$, the convexity factor for the response of ETR to $Q$. Two other parameters are fixed a priori in FvCB, an equal fractionation of light between PSI and PSII ($\rho_2 = 0.5$) and leaf absorbance ($\alpha_{leaf}$) is set at 0.85. The second approach, described by Yin et. al. (2009), used a combined gas-exchange and fluorescence approach for modeling ETR ($J_J$) (Fig. 1(b)). The Yin model used $\phi_{PSII}$ data to parameterize PSII efficiency under limiting light ($\phi_{PSII ll}$) as well as the lumped parameter, $s$, which lumps $\alpha_{leaf}$
differences, differences in $\rho_2$ as well as utilization of alternate electron paths, $f_{alt}$, along the Z-scheme (Eqn 2.6). Low-light ($0 < Q < 200$ umol photon m$^{-2}$ s$^{-1}$) response data ($A_n, Q, \phi_{PSII}$) was subset to estimate $R_d, s$, and $\phi_{PSII, ll}$ in the Yin model. $R_d$ is estimated as the y-intercept of linear regression of $A_n$ against $\frac{Q\phi_{PSII}}{4}$. The slope of this regression is used to estimate $s$. The quantum yield parameter for the Yin model, $\phi_{PSII, ll}$, was estimated as the y-intercept of a linear regression of $A_n$ against $\psi_{PSII}$ under low $Q$. Finally, for the third approach, the $\beta_{PSII}$ photosynthesis model derivation ETR ($J_l$), the full light response $\phi_{PSII}$ dataset was passed in the $\beta_{PSII}$ model for estimation of $\alpha_{PSII}, \beta_{PSII}$ or $\kappa_{PSII}$ needed to describe ETR ($J_l$) (Fig. 1(c)). Following Eqn. 1 the $\alpha_{PSII}, \beta_{PSII}$ or $\kappa_{PSII}$ estimates were used to predict $\phi_{PSII}$ at each $Q$, next was $J_l$ solved following Eqn 2.7. $\beta_{PSII}$ implementation used the same $R_d$ and $s$ estimation as Yin.

All models used a temperature response following an Arrhenius function for $K_c, K_o, V_{cmax}, J_{max}, g_m, R_d$, and $J^*$. Each parameter was normalized with respect to 25°C following:

$$X = \frac{E_X(T_{leaf} - 25)}{298 R (T_{leaf} + 273)}$$

(Eqn. 3)

where $T_{leaf}$ is leaf temperature (°C), $X_{25}$ is the parameter normalized with respect to 25°C. $E_X$ is the activation energy of each parameter and R is the universal gas constant (8.314 JK$^{-1}$ mol$^{-1}$).

Other temperature response functions were considered but given the limited variability in $T_{leaf}$ (mean=20.0 ± 0.2) a simple one-parameter equation was selected for analysis.

$C_{crit}$, the $C_i$ at which $A_n$ transitions from $A_c$ to $A_J$, was fixed at 285 ppm in all models based on an analysis of $Fv'Fm'$ under increasing $C_i$. $Fv'Fm'$ increases when $C_i < C_{crit}$ and remains constant when $C_i > C_{crit}$ (Sharkey et al., 2007; Gu et al., 2010; Moualeu-Ngangue et al., 2017). A Bayesian model was employed using a single change point method (Dose and Menzel, 2004) to estimate individual and population-level $C_{crit}$. Results of change point model found the posterior population level estimate had a mean 287.3 of with a 95% HDI of 265.1–318.7 ppm (Supplemental Fig. 8).

All $C_i, A_n, Q$, and $T_{leaf}$ data from $A/C_i$ and light response curves were used to estimate $A_n$ traits, an approached used previously (Patrick et al., 2009; Archontoulis et al., 2012), with $\phi_{PSII}$ data supplied to the Yin and $\beta_{PSII}$ models as described above. Parameter priors for FvCB and shared parameters among the three models were selected based on a recent implementation
(Pleban et al., 2018). The code for all three photosynthesis models as well as the simple $\beta_{PSII}$ decline model are available at https://github.com/jrpleban/.

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Supplemental Data

Supplemental Figure S1. Experimental design and observation schedule.

Supplemental Figure S2. Volumetric soil water content dynamics.

Supplemental Figure S3. Changes in lumped $s$ parameter estimates.

Supplemental Figure S4. Onset of NPQt parameter.

Supplemental Figure S5. Simulated $A_n$ vs observed $A_n$ for three photosynthesis models.

Supplemental Figure S6. Correlations $\beta_{PSII}$ with classic photosynthetic model parameters.

Supplemental Figure S7. Decline rates of Photosystem II efficiency under changing light conditions.

Supplemental Figure S8. Identification of transition point between $A_c$ and $A_J$ ($C_{crit}$).

Conflict of Interest

The authors declare no conflicts of interest. The views expressed here are those of the authors and do not necessarily represent the views of the NSF.

Tables

Table 1.

List of abbreviations used for models (observations, predictions and parameters).

| Abbreviation | Definition                           | Units          |
|--------------|-------------------------------------|----------------|
| $A_n$        | CO$_2$ assimilation rate observed   | $\mu$mol m$^{-2}$ s$^{-1}$ |
| $C_i$        | Intercellular CO$_2$ partial pressure observed | Pa             |
Leaf temperature observed $T_{leaf}$  °C

Conductance to CO$_2$ from atmosphere to intercellular space observed $g_s$  μmol m$^{-2}$ s$^{-1}$

Ambient O$_2$ (assumed 21% atmosphere) $O$  Pa

Photosynthetically active radiation observed $Q$  μmol m$^{-2}$ s$^{-1}$

Operating efficiency of photosystem II $(Fm'-Fs'/Fm')$ observed $\phi_{PSII}$  e$^{-}$/photon

Predicted Rubisco limited rate of CO$_2$ assimilation $A_c$  μmol m$^{-2}$ s$^{-1}$

Predicted electron transport limited rate of CO$_2$ assimilation $A_j$  μmol m$^{-2}$ s$^{-1}$

Predicted rate of electron transport following Farquhar $J_m$  μmol m$^{-2}$ s$^{-1}$

Predicted rate of electron transport following Yin $J_f$  μmol m$^{-2}$ s$^{-1}$

Predicted rate of electron transport following β decay model $J_l$  μmol m$^{-2}$ s$^{-1}$

Predicted rate of electron transport following Yin using Eqn 2.6 $\phi_{PSII}_{ll}$  mol e$^{-}$/mol photon$^{-1}$

Universal gas constant (8.314 J K$^{-1}$ mol$^{-1}$) $R$  J K$^{-1}$ mol$^{-1}$

Absorptance of leaf photosynthetic pigments $\alpha_{leaf}$  %

Partitioning of energy between PSII and PSI $\rho_2$  %

Fraction of electron not using LEF $(1-f_{pseudoe}(1-f_{cyc})$ in Yin et al. 2009 $f_{alt}$  %

Lumped parameter $(\rho_2 a_{leaf}f_{alt})$ (Yin et al. 2009) $s$  %

CO$_2$ photocompensation point (standardized to 25 °C) $\Gamma^{*25}$  Pa

Michaelis-Menten constant for Rubisco for CO$_2$ (standardized to 25 °C) $K_{c25}$  Pa

Michaelis-Menten constant for Rubisco for O$_2$ (standardized to 25 °C) $K_{o25}$  kPa

Activation energy used in Arrhenius function $Ei's$ (Kc, Ko, Rd, Vcmax, $\Gamma^*$, $J_{max}$, gm, $V_{cmax}$)  KJ mol$^{-1}$

Respiration rate in the dark (standardized to 25 °C) $R_{d25}$  μmol m$^{-2}$ s$^{-1}$

Mesophyll conductance (standardized to 25 °C) $g_m$  μmol m$^{-2}$ Pa$^{-1}$ s$^{-1}$

Maximum rate of carboxylation (standardized to 25 °C) $V_{cmax25}$  μmol m$^{-2}$ s$^{-1}$

Maximum rate of electron transport (standardized to 25 °C) $J_{max25}$  μmol m$^{-2}$ s$^{-1}$

Quantum yield of CO$_2$ using Eqn 2.6 $\phi_{CO2}$  mol CO$_2$ mol photon$^{-1}$

Curvature factor on electron transport rates predictions $J_m$ and $J_f$ $\theta_f$  unitless

Maximum quantum efficiency following Yin using Eqn 2.6 $\phi_{PSII}$  mol e$^{-}$/mol photon$^{-1}$

Decay rate in $\phi_{PSII}$ under increasing $Q$ using Eqn 1 $\beta_{PSII}$  Q$^{-1}$

Modeled $\phi_{PSII}$ as $Q$ approaches zero using Eqn 1 $\alpha_{PSII}$  unitless

Modeled $\phi_{PSII}$ as $Q$ approaches $\infty$ using Eqn 1 $\kappa_{PSII}$  unitless
Table 2.
List of equations used in three photosynthesis models (FvCB, Yin, $\beta_{PSII}$ decay).

| Eqn No | Equation | Description |
|--------|----------|-------------|
| 2.1    | $A_n = \begin{cases} A_c & \text{if } C_i < C_{crit} \\ A_j & \text{if } C_i > C_{crit} \end{cases}$ | $A_n$ depending on 2 limiting factors and the critical $C_i$ ($C_{crit}$) |
| 2.2    | $A_i = \frac{-b+\sqrt{b^2-4ac}}{2a}$ | General quadratic form for solving $A_c$, $A_j$, $J_m$, $J_f$ |
| 2.3    | $a = \frac{-1}{g_m}$, $b = \frac{V_{i,max} - R_d}{g_m} + C_i + K_c(\frac{1+O}{K_o})$, $c = R_d(C_i + K_c(\frac{1+O}{K_o})$ | Quadratic roots using intercellular CO$_2$ ($C_i$) and a mesophyll conductance ($g_m$) term for describing $A_c$ |
| 2.4    | $a = \frac{-1}{g_m}$, $b = \frac{1}{g_m} - R_d$, $c = R_d(C_i + 2\Gamma^*) - \frac{1}{4}(C_i - \Gamma^*)$ | Quadratic roots for $A_j$ using $J_m$, $J_f$ or $J_l$ |
| 2.5    | $Q_{abs} = Q_{\alpha_{leaf}}$, $a = \theta_J$, $b = -(Q_{abs} \phi_{CO2}) - J_{max}$, $c = Q_{abs} \phi_{CO2} J_{max}$ | Quadratic roots for whole chain ETR ($J_m$) as described in von Caemmerer (2000) assumes $\alpha_{leaf} = 0.85$ |
| 2.6    | $a = \theta_J$, $b = -(Q s \phi_{HL}) - J_{max}$, $c = Q s \phi_{HL} J_{max}$ | Quadratic roots for combined gas-exchange and chlorophyll fluorescence ETR ($J_f$) as described in Yin (2009) $s = \alpha_{leaf} f falt$ |
| 2.7    | $J_l = \phi_{preact} Q$, $\beta_{PSII}$ model for full $\phi_{PSII}$ vs $Q$ derivation of ETR ($J_l$) using Eqn 1 to predict $\phi_{II}$ from decay with $Q$ |
### Table 3.

Genotype by treatment trait estimates for 14 photosynthesis traits. Modeled traits show median of posterior distribution (95% credible interval range) while observed traits show mean values (standard deviation). Bold indicates significance relative to Well-Watered at \( p < 0.05 \) or for 95% CI's HDI interval difference not intersecting with zero was used to describe a credible trait variance (\( A_{\text{max}} \) and \( s \)).

| Trait           | Treatment       | \( r_{301} \) | \( r_{46} \) | \( R_{500} \) | \( VT \) |
|-----------------|-----------------|--------------|--------------|--------------|---------|
| \( A_{\text{max}} \) (μmol m\(^{-2}\) s\(^{-1}\)) | Well Watered    | 27.70 (25.47, 30.26) | 17.12 (14.99, 19.57) | 25.42 (22.86, 28.13) | 18.25 (15.94, 20.64) |
|                  | Early Drought   | 28.70 (26.02, 31.22) | 14.54 (12.73, 16.43) | 25.62 (23.33, 27.74) | 14.71 (12.91, 16.45) |
| \( s \) unitless | Well Watered    | 0.33 (0.3, 0.37)  | 0.29 (0.25, 0.32)  | 0.32 (0.29, 0.34)  | 0.31 (0.27, 0.35)  |
|                  | Early Drought   | 0.36 (0.33, 0.38) | 0.28 (0.25, 0.31)  | 0.32 (0.3, 0.34)   | 0.29 (0.25, 0.32)  |
| \( ESC_{300} \times 1000 \) | Well Watered    | 1.7 (0.35)       | 1.7 (0.34)       | 1.4 (0.32)       | 1.2 (0.42)       |
| \( \Delta \text{ absorbance} 530 \) | Early Drought   | 1.4 (0.10)       | 1.7 (0.49)       | 1.8 (0.48)       | 1.9 (0.32)       |
| | Late Drought    | 3.0 (0.44)       | 2.4 (0.13)       | 2.7 (0.24)       | 2.7 (0.21)       |
| \( LEF_{300} \) | Well Watered    | 61.07 (2.90)     | 57.37 (0.26)     | 70.25 (4.43)     | 64.06 (3.39)     |
| \( \Delta \text{ absorbance} 530 \) | Early Drought   | 68.72 (0.18)     | 57.46 (7.59)     | 63.27 (4.34)     | 61.23 (3.05)     |
| | Late Drought    | 34.48 (11.38)    | 43.06 (7.59)     | 36.21 (5.70)     | 42.39 (1.53)     |
| \( \phi_{NPQ_{300}} \) (%) | Well Watered    | 0.31 (0.03)      | 0.33 (0.04)      | 0.21 (0.03)      | 0.24 (0.04)      |
| | Early Drought   | 0.24 (0.02)      | 0.32 (0.01)      | 0.27 (0.06)      | 0.28 (0.03)      |
| | Late Drought    | 0.55 (0.05)      | 0.49 (0.07)      | 0.52 (0.08)      | 0.49 (0.03)      |
| \( \phi_{NPQ_{1000}} \) (%) | Well Watered    | 0.64 (0.02)      | 0.66 (0.02)      | 0.57 (0.03)      | 0.59 (0.04)      |
| | Early Drought   | 0.6 (0.01)       | 0.67 (0.01)      | 0.60 (0.06)      | 0.62 (0.03)      |
| | Late Drought    | 0.73 (0.01)      | 0.73 (0.02)      | 0.69 (0.05)      | 0.69 (0.01)      |
| \( \phi_{NO_{300}} \) (%) | Well Watered    | 0.21 (0.019)     | 0.22 (0.009)     | 0.24 (0.011)     | 0.25 (0.028)     |
| | Early Drought   | 0.22 (0.018)     | 0.23 (0.01)      | 0.23 (0.032)     | 0.24 (0.011)     |
| | Late Drought    | 0.18 (0.045)     | 0.17 (0.015)     | 0.20 (0.036)     | 0.18 (0.019)     |
| \( \phi_{NO_{1000}} \) (%) | Well Watered    | 0.15 (0.022)     | 0.15 (0.006)     | 0.18 (0.018)     | 0.20 (0.029)     |
| | Early Drought   | 0.15 (0.005)     | 0.15 (0.011)     | 0.17 (0.021)     | 0.17 (0.008)     |
| | Late Drought    | 0.15 (0.026)     | 0.14 (0.007)     | 0.19 (0.035)     | 0.16 (0.005)     |
| \( SPAD_{530} \) | Well Watered    | 58.66 (3.93)     | 52.42 (6.57)     | 58.53 (5.8)      | 41.54 (8.2)      |
| | Early Drought   | 53.06 (7.57)     | 45.61 (7.39)     | 56.86 (17.02)    | 43.19 (9.4)      |
| | Late Drought    | 98.91 (10.11)    | 72.59 (11.91)    | 102.86 (8.66)    | 84.86 (27.68)    |
| \( gs \) (mmol m\(^{-2}\) s\(^{-1}\)) | Well Watered    | 0.48 (0.07)      | 0.21 (0.06)      | 0.44 (0.12)      | 0.23 (0.11)      |
| | Early Drought   | 0.30 (0.15)      | 0.17 (0.07)      | 0.15 (0.15)      | 0.09 (0.11)      |
| | Late Drought    | 0.19 (0.14)      | 0.17 (0.12)      | 0.04 (0.06)      | 0.06 (0.06)      |
Leaf Temp & Well Watered & -1.2 (1.57) & -0.68 (1.02) & -0.58 (1.19) & -1.03 (0.94) \\
Differential (°C) & Early Drought & -0.17 (0.81) & 0.51 (1.32) & 0.45 (1.48) & **1.76 (0.7)** \\
(Std. Dev) & Late Drought & -0.1 (1.41) & 0.53 (0.57) & 0.33 (0.24) & -0.24 (0.35) \\
Relative Chlorophyll & Well Watered & 45.75 (3.58) & 42.46 (5.91) & 45.72 (3.03) & 29.57 (10.98) \\
(Std. Dev) & Late Drought & **73.52 (2.04)** & **56.82 (5.37)** & **77.85 (3.67)** & **67.44 (10.18)**

**Figure Legends**

Figure 1. Simplified illustration of the light reactions of photosynthesis representing how three conceptual models account for the photosynthetic electron transport. Upon light energy absorption, energy in the form of excited electrons (e) is transferred from light harvesting antennae to the reaction centers of photosystems I and II (PSI and PSII) in the chloroplastic thylakoid membranes (a). This energy transport has been described as a Z-scheme (Hill and Bendall, 1960) whereby e from PSII produce a transmembrane H⁺ gradient (used for ATP production) while e downstream of PSI produce NADPH; both ATP and NADPH are then used for Calvin cycle CO₂ fixation. For modeling applications (inset graphs of panels b, c, and d), photosynthetic quantum yield describes how light energy relates to CO₂ fixation (Long et al 1993, Gentry et al 1989) and assumptions are made about the processes of electron transfer more or less obscuring (gray boxes in b, c, and d) the actual physiological mechanisms. In the traditional FvCB conceptualization, quantum yield is calculated on a photon to CO₂ basis (ϕCO₂) (inset graph of panel b). Here, ETR processes are ignored, assuming 100% linear electron flow (LEF) from PSII to NADPH production, leaf absorbance (αleaf) is fixed (0.85) and an implicit 50/50 fractionalization of Q between PSII and PSI (ρ₂) (b). The Yin conceptualization improved the use of PSII physiology by calculating quantum yield on a photon to e basis, using the relationship between ϕPSII and Q under light limiting conditions (ϕPSII,b) (top inset graph of panel c). Yin also used a lumped s parameter defined by the slope of a linear regression of Aₙ against (Q ϕPSII)/4 using light < 200 μmol m⁻² s⁻¹, where 4 is the number of protons needed to synthesis one ATP. This regression was used to calibrate for three factors, the unknown fraction of non-linear electron flow around PSI (fₐᵲ), αleaf and ρ₂ (bottom inset graph of panel c). Our alternative βPSII conceptualization captures the behavior of energy transfer from the antennae complex to the PSII reaction complex (d). Here, quantum yield is modeled using an exponential decay function (Eqn. 1) across all relevant Q conditions, on a photon to e basis, providing estimates of both maximum light-acclimated quantum yield (αPSII) and the decay rate in ϕPSII under increasing Q (βPSII) (inset graph of panel d). βPSII model maintains the use of the s parameter to address fₐᵲ, αleaf, and ρ₂. Implementations of modeling photosynthetic electron transport in the Yin and βPSII approaches are represented as incrementing highlighted yellow in panels c and d.

Figure 2. Photosystem II operating efficiency (ϕPSII) across photosynthetically active radiation (Q) of 0–1000 μmol photons m⁻² s⁻¹ for four B. rapa genotypes. Observations of r301 (a), r46 (b), R500 (c), and VT (d) occurred over a range of water regimes from well-watered (W1, W2, W3) to increasing drought (D1, D2, D3) and different levels of re-watering (R1, R2, R3). Points are the mean values of replicates (n curves=119, average n curves per replicate = 3.3), fitted lines use median posterior estimate of a three-parameter exponential decline model (Eqn 1) by genotype x treatment.

Figure 3. Photosystem II dynamics in response to different water regimes. Decline rate in Photosystem II efficiency (ϕPSII) under increasing light intensity (βPSII) (Q⁻¹) (a,b,c,d) and maximum light-acclimated Photosystem II efficiency (αPSII) (e,f,g,h) for the four B. rapa genotypes R500 (a,e), r301 (b,f), r46 (c,g), and VT (d,h) over a range of water regimes, as defined in Figure 2, described by volumetric soil moisture content (VWC). Points represent median posterior estimate of βPSII and αPSII from a three-parameter
exponential decline model (Eqn.1) ($\beta_{\text{PSII}}$ and $\alpha_{\text{PSII}}$ derived from $n$ curves=119, average $n$ curves per replicate = 3.3), vertical bars are 95% high density intervals of posterior estimates and horizontal bars are standard deviations on observations of VWC ($n$=153, average $n$ per replicate = 4.25). On the right side of the panels are Bayesian prior distributions of $\beta_{\text{PSII}}$ and $\alpha_{\text{PSII}}$.

Figure 4. Comparison of posterior median estimates of parameters common to the FvCB, Yin, and $\beta_{\text{PSII}}$ photosynthesis models. Comparison of maximum rate of carboxylation ($V_{cmax}$), estimates between $\beta_{\text{PSII}}$ and FvCB, $\beta_{\text{PSII}}$ and Yin, and FvCB and Yin with R for each relationship (a,b,c). Comparison of mesophyll conductance ($g_m$) estimates between $\beta_{\text{PSII}}$ and FvCB, $\beta_{\text{PSII}}$ and Yin and FvCB and Yin with R for each relationship (d,e,f). Genotypes and water regimes are as defined in Figure 2.

Figure 5. Comparison of posterior median estimates of parameters in the FvCB, Yin, and $\beta_{\text{PSII}}$ models. Comparison of quantum yield terms for each model: $\alpha_{\text{PSII}}$ (mol photon/mol e') of $\beta_{\text{PSII}}$ model with $\phi_{\text{CO2}}$ (mol CO$_2$/mol e') of FvCB model (a) $\alpha_{\text{PSII}}$ with $\phi_{\text{PSII, ll}}$ (mol photon/mol e') of Yin model (b), and $\phi_{\text{ll}}$ with $\phi_{\text{PSII, ll}}$ (c) with correlation coefficient (R) for each. Comparison of s parameter between Yin model and $\beta_{\text{PSII}}$ model (d) and comparison of $\theta_s$ between Yin model and FvCB model (e). Genotypes and water regimes are as defined in Figure 2.

Figure 6. Photosystem II efficiency analysis. Comparison of Photosystem II efficiency ($\phi_{\text{PSII}}$) across two instruments, Li-Cor 6400 and Multispec, and three light intensities (0, 500, 1000 $\mu$mol photons m$^{-2}$ s$^{-1}$) for the four $B$. rapa genotypes r301 (a), r46 (b), R500 (c), and VT (d). Each set of observations occurred over a range of water regimes from well-watered (W1) to increasing drought (D1, D2, D3) and re-watering (R2). Points are mean of replicate error bars are standard deviations (total $n$ Li-Cor 6400 = 162, average $n$ per replicate 2.7; total $n$ Multispec = 213, average $n$ per replicate 3.6)
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