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## REVIEW PAPER

# A model-guided holistic review of exploiting natural variation of photosynthesis traits in crop improvement

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## Abstract

**Breeding for improved leaf photosynthesis is considered as a viable approach to increase crop yield. Whether it should be improved in combination with other traits has not been assessed critically. Based on the quantitative crop model GECROS that interconnects various traits to crop productivity, we review natural variation in relevant traits, from biochemical aspects of leaf photosynthesis to morpho-physiological crop characteristics. While large phenotypic variations (sometimes >2-fold) for leaf photosynthesis and its underlying biochemical parameters were reported, few quantitative trait loci (QTL) were identified, accounting for a small percentage of phenotypic variation. More QTL were reported for sink size (that feeds back on photosynthesis) or morpho-physiological traits (that affect canopy productivity and duration), together explaining a much greater percentage of their phenotypic variation. Traits for both photosynthetic rate and sustaining it during grain filling were strongly related to nitrogen-related traits. Much of the molecular basis of known photosynthesis QTL thus resides in genes controlling photosynthesis indirectly. Simulation using GECROS demonstrated the overwhelming importance of electron transport parameters, compared with the maximum Rubisco activity that largely determines the commonly studied light-saturated photosynthetic rate. Exploiting photosynthetic natural variation might significantly improve crop yield if nitrogen uptake, sink capacity, and other morpho-physiological traits are co-selected synergistically.**

**Keywords:** Canopy traits, crop model, electron transport, QTL, source–sink relationships, trait synergy, yield improvement.

## Introduction

Crop yield needs improving in the face of growing populations, accelerating climate change, and diminishing land resources available for crop production. Photosynthesis scholars argue that this improvement most probably has to come from an enhanced photosynthesis (e.g. Long *et al.*, 2015; Ort *et al.*, 2015; Furbank *et al.*, 2020; Walter and Kromdijk, 2022).

Photosynthesis can be improved via a synthetic biology approach through genetic modification. For example, introducing multigenic C<sub>4</sub> photosynthesis into C<sub>3</sub> crops (von Caemmerer *et al.*, 2012) was predicted to increase yield significantly (Yin and Struik, 2017), but it is a long-shot challenge that will take many years to accomplish

(Long *et al.*, 2015). Genetic modifications for simpler processes, such as accelerating recovery from photoprotection under fluctuating light (Kromdijk *et al.*, 2016) or bypassing photorespiration (South *et al.*, 2019), have resulted in more productive model plants under field conditions. However, inserting such modifications into major crops remains a challenge. Another approach is to exploit natural variation in photosynthesis among and within species (Flood *et al.*, 2011). Within species, natural variation in leaf photosynthesis has been reported for major crops (e.g. Gu *et al.*, 2012a; Driever *et al.*, 2014; Meena *et al.*, 2021). Exploiting such natural variation via conventional breeding is most likely to be the best short-term option.

While past yield improvements rarely came from increased photosynthesis and genotypic yields rarely correlate with leaf photosynthetic rates (e.g. Driever *et al.*, 2014; Gu *et al.*, 2014b), increased photosynthesis generally increases yield, for example in FACE (free-air CO<sub>2</sub> enrichment) trials (e.g. Lv *et al.*, 2020). Increased photosynthetic rates, if achievable beyond those attained in modern cultivars, would thus be a promising objective. However, limited success has been achieved from various efforts in exploiting natural variation of photosynthetic traits to improve crops (e.g. Flexas, 2016), probably because natural variation in photosynthesis above the levels of present standard cultivars may be small. In addition, crop physiologists (e.g. Sinclair *et al.*, 2019; Araus *et al.*, 2021) argue that yield is a very complex trait, depending little on leaf photosynthesis but rather on many other physiological processes. This probably means that breeders should exploit variations in multiple traits and aggregate them synergistically in order to improve crop yield.

In this review, we first describe a whole-plant physiology framework (Box 1), based on a quantitative crop model with parameters that capture multiple traits underlying yield hierarchy from photosynthetic biochemistry to leaf, to canopy, to crop scales (Fig. 1). Based on this framework, we review the extent of natural variation in relevant parameters along the yield hierarchy. We further review quantitative trait loci (QTL) for some of these parameters. We then use the same crop model to assess potential benefits from pyramiding favourable traits, and to identify most important parameters for improving yield beyond that of best-performing cultivars. We focus on C<sub>3</sub> crops, given their economic importance and their greater improvement potential than C<sub>4</sub> crops (Yin and Struik, 2015).

## Natural variation of photosynthetic parameters

### *A*<sub>max</sub> and its underlying biochemical parameters

According to the (extended) model of Farquhar *et al.* (1980), light-saturated photosynthesis capacity (*A*<sub>max</sub>) can be expressed as:

$$A_{\max} = \begin{cases} \frac{(C_c - \Gamma_*)V_{\max}}{C_c + K_{mC}(1 + O/K_{mO})} - R_d & \text{if Rubisco activity limits} \\ \frac{(C_c - \Gamma_*)J_{\max}}{4(C_c + 2\Gamma_*)} - R_d & \text{if electron transport limits} \\ \frac{(C_c - \Gamma_*)(3T_p)}{C_c - (1 + 4\alpha_S)\Gamma_*} - R_d & \text{if TPU limits} \end{cases} \quad (1)$$

where *C*<sub>c</sub> is the level of CO<sub>2</sub> in the chloroplast,  $\Gamma_*$  is the CO<sub>2</sub> compensation point in the absence of day respiration (*R*<sub>d</sub>), *K*<sub>mC</sub> and *K*<sub>mO</sub> are the Michaelis–Menten constants of Rubisco for CO<sub>2</sub> and O<sub>2</sub>, respectively, *V*<sub>max</sub> is the maximum carboxylation capacity of Rubisco, *J*<sub>max</sub> is the maximum capacity of linear electron transport, *T*<sub>p</sub> is the rate of triose phosphate utilization (TPU), and  $\alpha_S$  is the fraction of the glycolate–carbon that does not return to chloroplasts but exits via the photorespiratory pathway (with  $0 \leq \alpha_S \leq 0.75$ ), assuming that serine is the major form of carbon that exits (see Busch *et al.*, 2018; Yin *et al.*, 2021). As *C*<sub>c</sub> for a given ambient [CO<sub>2</sub>] depends on stomatal and mesophyll conductance as discussed later, and  $\Gamma_*$ , *K*<sub>mC</sub>, and *K*<sub>mO</sub> are Rubisco kinetic parameters that are very conserved within C<sub>3</sub> species, *A*<sub>max</sub> depends mainly on biochemical capacity parameters *V*<sub>max</sub>, *J*<sub>max</sub>, or *T*<sub>p</sub>.

A large variation in *A*<sub>max</sub> has been reported for various crops. Ye *et al.* (2019) showed ~2-fold variation of *A*<sub>max</sub> among 121 rice cultivars, ranging from 15.5 μmol m<sup>-2</sup> s<sup>-1</sup> to 32.6 μmol m<sup>-2</sup> s<sup>-1</sup>, while Qu *et al.* (2017) showed *A*<sub>max</sub> varying from 13.7 μmol m<sup>-2</sup> s<sup>-1</sup> to 28.2 μmol m<sup>-2</sup> s<sup>-1</sup> among 214 rice genotypes. A variation of *A*<sub>max</sub> among 64 wheat cultivars was reported by Driever *et al.* (2014), ranging from 20.5 μmol m<sup>-2</sup> s<sup>-1</sup> to 31.5 μmol m<sup>-2</sup> s<sup>-1</sup>. Sadras *et al.* (2012) showed a variation of *A*<sub>max</sub> from 9.3 μmol m<sup>-2</sup> s<sup>-1</sup> to 19.6 μmol m<sup>-2</sup> s<sup>-1</sup> for 13 Australian wheat cultivars released between 1958 and 2007. Shrestha *et al.* (2018) showed an ~1.7-fold range in *A*<sub>max</sub> among 20 chickpea genotypes. Jin *et al.* (2010) showed a 33% increase in *A*<sub>max</sub> for 45 soybean cultivars released in 1950 to 2006 in China, an increase of 0.067 μmol m<sup>-2</sup> s<sup>-1</sup> year<sup>-1</sup>.

Where CO<sub>2</sub> or light response curves are measured that allow the estimation of *V*<sub>max</sub> and *J*<sub>max</sub>, the variation of *A*<sub>max</sub> is often associated with *V*<sub>max</sub> or *J*<sub>max</sub>, or both (Driever *et al.*, 2014; Jahan *et al.*, 2014; Carmo-Silva *et al.*, 2017; Silva-Perez *et al.*, 2020; Acevedo-Siaca *et al.*, 2021). In general, *V*<sub>max</sub> and *J*<sub>max</sub> estimated across genotypes/accessions are highly correlated (Driever *et al.*, 2014; McAusland *et al.*, 2020; Mathan *et al.*, 2021). Carmo-Silva *et al.* (2017) and Acevedo-Siaca *et al.* (2021) showed that both parameters had high heritabilities.

*A*<sub>max</sub>, *V*<sub>max</sub>, and *J*<sub>max</sub> are commonly expressed on a leaf area basis, and their genotypic variation may be related to leaf thickness or to nitrogen content (e.g. Mathan *et al.*, 2021; Fig. 1). An increase in *A*<sub>max</sub> resulting from thicker leaves is not desirable (Austin, 1989) because of trade-offs with leaf expansion, and thus light interception, potentially causing a decrease in whole-plant photosynthesis (Boote and Tollenaar, 1994; Richards, 2000). Likewise, variation in *A*<sub>max</sub> depends on leaf

**Box 1. A general whole-plant physiology framework based on the crop model GECROS**

Crop yield depends on intercepted light or radiation ( $I_{\text{intercept}}$ ), radiation use efficiency (RUE) for conversion of  $I_{\text{intercept}}$  into biomass, and harvest index (HI), the fraction of biomass constituting the harvestable product. Yield improvement from the 1960s Green Revolution for major food crops resulted mainly from increased HI via dwarfing genes (Mifflin, 2000; Hedden, 2003), although increased  $I_{\text{intercept}}$  and/or RUE also contributed in some cases (Sadras *et al.*, 2012; Koester *et al.*, 2014). As HI has reached a plateau, further yield improvement will require improving either  $I_{\text{intercept}}$  or RUE (e.g. Long *et al.*, 2015; Furbank *et al.*, 2020). In order to identify the components that can be exploited to improve yield, we describe biochemical and morpho-physiological components affecting  $I_{\text{intercept}}$ , RUE, and HI (Fig. 1), according to the principles as captured in the crop model GECROS (Yin and Struik, 2017).

During the growing season,  $I_{\text{intercept}}$  is set by the green surface area duration [integrating the green surface area index (GAI) and how long it is sustained] and light extinction coefficient ( $k_L$ ) of the canopy. Early vigour promotes early canopy closure, and stay-green traits extend terminal GAI duration. For a given leaf mass, a high specific leaf area (SLA) enables rapid leaf expansion and increase of  $I_{\text{intercept}}$  (Dingkuhn *et al.*, 2001).

RUE depends on canopy photosynthesis ( $A_{\text{canopy}}$ ), the photosynthates lost by crop respiration ( $R_{\text{crop}}$ ), and the conversion efficiency of net photosynthates into biomass. The latter efficiency (Penning de Vries *et al.*, 1989) and the  $R_{\text{crop}}$  versus  $A_{\text{canopy}}$  ratio (Amthor, 2010) are conservative for a given species under favourable conditions. Photosynthetic competence of individual leaves affects  $A_{\text{canopy}}$ ; however, for given photosynthetic resources (especially nitrogen), their vertical distribution among canopy strata is also crucial. This distribution is described by the nitrogen extinction coefficient ( $k_N$ ). A canopy with similar  $k_N$  and  $k_L$  achieves a high  $A_{\text{canopy}}$  (Goudriaan, 1995; Sands, 1995).

Leaf photosynthetic competence ( $A_{\text{leaf}}$ ) depends on light-saturated photosynthetic capacity ( $A_{\text{max}}$ ) and the initial light-response slope of  $\text{CO}_2$  assimilation (syn. quantum yield,  $\Phi_{\text{CO}_2}$ ). The  $A_{\text{max}}$  mainly depends on either the maximum rate of linear electron transport ( $J_{\text{max}}$ ) or metabolic capacity parameters such as Rubisco activity ( $V_{\text{cmax}}$ ) and the capacity for triose phosphate utilization ( $T_p$ ) (see Equation 1). In theory,  $\Phi_{\text{CO}_2}$  depends primarily on the photochemical efficiency of PSII electron transport and whether there are cyclic and pseudo-cyclic pathways that drain electrons from  $\text{CO}_2$  assimilation (Yin *et al.*, 2006; see Equation 2A). As  $\text{CO}_2$  and  $\text{O}_2$  compete for active catalytic sites of Rubisco, the relative partial pressure of  $\text{CO}_2$  versus  $\text{O}_2$  at Rubisco-carboxylating sites will affect the amount of photorespiration. Therefore, parameters governing  $\text{CO}_2$  diffusion, including stomatal conductance ( $g_s$ ) and mesophyll conductance ( $g_m$ ) (see Equation 3), affect both  $A_{\text{max}}$  and  $\Phi_{\text{CO}_2}$ .

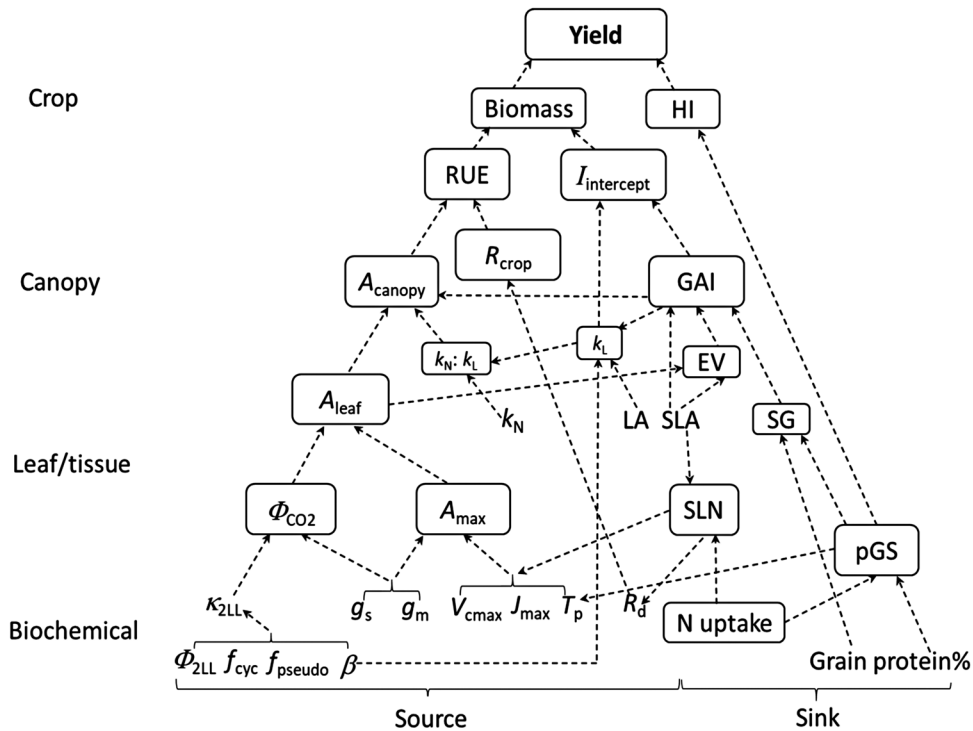
Some of these parameters act at the canopy level while others act at the (sub)-foliar level. Some are morpho-physiological and others are biochemical. However, they are not independent. For example, SLA is a morphological parameter but influences biochemical parameters  $J_{\text{max}}$ ,  $V_{\text{cmax}}$ , and  $T_p$  as they are commonly expressed per leaf area. A smaller SLA (thicker leaves) results in higher aerial nitrogen content, and higher values of  $A_{\text{max}}$  (Boote and Tollenaar, 1994) and underlying biochemical components  $J_{\text{max}}$ ,  $V_{\text{cmax}}$ , and  $T_p$ . In addition, while  $T_p$  is a biochemical parameter reflecting the local sink size for sucrose and starch synthesis in the leaf (Sharkey, 1985), recent evidence suggests that  $T_p$  is regulated by whole-plant source-sink relations (Fabre *et al.*, 2019, 2020).

A greater potential sink demand for photosynthates via larger panicles can increase HI, yet this may impede 'stay-green' traits as grain growth requires nitrogen (Sinclair and de Wit, 1976) and most grain nitrogen comes from remobilization from vegetative organs, particularly leaves. Leaves are source organs, but also sink organs while growing. Increasing photosynthesis has a feedforward effect on leaf production and tillering/branching, and thus early vigour, enabling early canopy closure. However, leaf and tiller production as a sink may also feed back on leaf photosynthesis by removing sink limitation set by  $T_p$ . This has been evidenced by genotypes with superior sink capacity responding more strongly to  $\text{CO}_2$  enrichment (Hasegawa *et al.*, 2013; Dingkuhn *et al.*, 2020; Yiotis *et al.*, 2021).

In short, exploiting natural variation of photosynthesis to increase crop yield potential is not a matter of increasing photosynthesis alone, but should be approached from a whole-plant perspective to exploit synergisms among multiple traits.

nitrogen, which probably results from differences in root uptake (Hikosaka, 2010). Thus, it is useful to correct  $A_{\text{max}}$  for the difference in specific leaf nitrogen (SLN,  $\text{g N m}^{-2}$ ) that captures both leaf thickness and leaf nitrogen concentration;

that is, expressing leaf photosynthetic capacity as so-called photosynthetic nitrogen use efficiency ( $\text{PNUE} = A_{\text{max}}/\text{SLN}$ ). However, PNUE still varied by ~2-fold among rice genotypes, from  $10.0 \mu\text{mol (g N)}^{-1} \text{s}^{-1}$  to  $22.6 \mu\text{mol (g N)}^{-1} \text{s}^{-1}$  (Ye *et al.*,



**Fig. 1.** A simplified qualitative scheme of the quantitative crop model GECROS connecting hierarchical scales from biochemical parameters to crop yield, and covering both photosynthetic (source) and morpho-physiological (sink) traits. Items in rectangles are traits quantified in the model along the hierarchical scales, while those without rectangles are model parameters. Abbreviations and symbols:  $A_{canopy}$ , canopy photosynthesis rate;  $A_{leaf}$ , leaf photosynthesis rate;  $A_{max}$ , maximum rate of light-saturated  $A_{leaf}$ ; EV, early vigour;  $f_{cyc}$ , fraction for cyclic electron transport;  $f_{pseudo}$ , fraction for pseudocyclic electron transport; GAI, green surface area index;  $g_m$ , mesophyll conductance;  $g_s$ , stomatal conductance; HI, harvest index;  $I_{intercept}$ , photosynthetically active radiation intercepted by canopy;  $J_{max}$ , maximum capacity of light-saturated linear electron transport;  $k_L$ , light extinction coefficient in canopy;  $k_N$ , leaf nitrogen extinction coefficient in canopy; LA, leaf angle; pGS, potential grain size;  $R_d$ , leaf day respiration;  $R_{crop}$ , crop respiration; RUE, radiation use efficiency; SG: stay-green; SLA, specific leaf area; SLN, specific leaf nitrogen content;  $T_p$ , rate of triose phosphate utilization;  $V_{cmax}$ , maximum carboxylation capacity of Rubisco;  $\beta$ , absorbance by leaf photosynthetic pigments;  $\Phi_{2LL}$ , quantum efficiency of electron transport of PSII under limiting light;  $\Phi_{CO2}$ , quantum efficiency of  $CO_2$  assimilation under limiting light;  $\kappa_{2LL}$ , efficiency of converting incident light into linear electron transport under limiting light conditions. Further details of the scheme are described in [Box 1](#) and in the main text.

2019). [Silva-Perez et al. \(2020\)](#) also showed significant genotypic variations in  $V_{cmax}$  or  $J_{max}$  to SLN ratios.

$\Phi_{CO2}$  and its components

The initial slope of the photosynthetic light response curve, also called photosynthetic quantum efficiency ( $\Phi_{CO2}$ ), is a composite parameter ([Yin et al., 2006](#)):

$$\Phi_{CO2} = \Phi_{2LL} \frac{1 - f_{cyc} - f_{pseudo}}{\Phi_{2LL}/\Phi_{ILL} + (1 - f_{cyc})} \frac{C_c - \Gamma_*}{4(C_c + 2\Gamma_*)} \tag{2A}$$

where  $\Phi_{2LL}$  is the photochemical efficiency of PSII under limiting light conditions,  $f_{cyc}$  and  $f_{pseudo}$  are the fractions for cyclic and pseudocyclic electron transport, and  $\Phi_{2LL}/\Phi_{ILL}$  is the PSII to PSI photochemical efficiency ratio, which is presumably conserved (~0.85; see [Yin et al., 2021](#), and references therein). If photosynthetic quantum efficiency is expressed on the incident light basis ( $\Phi_{CO2,inc}$ ), it can be set as:

$\Phi_{CO2,inc} = \beta \Phi_{CO2}$ , where  $\beta$  is absorbance by leaf photosynthetic pigments. As  $f_{cyc}$  and  $f_{pseudo}$  are hard to determine and may be conserved within  $C_3$  species under limiting light ([Yin et al., 2006](#)),  $\Phi_{CO2,inc}$  is commonly expressed as:

$$\Phi_{CO2,inc} = \kappa_{2LL} \frac{C_c - \Gamma_*}{4(C_c + 2\Gamma_*)} \tag{2B}$$

where  $\kappa_{2LL}$ , lumping  $\beta$ ,  $\Phi_{2LL}$ , and the second term of Equation 2A, represents the efficiency of converting incident light into linear electron transport.

Values of  $\Phi_{CO2}$  or  $\Phi_{CO2,inc}$  are obtained from linear regression of photosynthetic light–response curves within a limiting light range, or from curvilinear regression of the light–response curves over a broader light range. Consequently, phenotyping  $\Phi_{CO2}$  for a large number of genotypes is time consuming. Furthermore,  $\Phi_{CO2}$  is very conserved ([Austin, 1989](#)), even across various  $C_3$  species ([Björkman and Demmig, 1987](#)), and measurement or curve-fitting errors can obscure differences

among genotypes. For example, Carmo-Silva *et al.* (2017) detected little genotypic differences for wheat in  $\Phi_{\text{CO}_2, \text{inc}}$  estimated from curvilinear regression.

Instead of measuring  $\Phi_{\text{CO}_2}$ , phenotyping  $A$  at a low light level (e.g.  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ )  $A_{\text{low}}$ , or phenotyping the components of  $\Phi_{\text{CO}_2}$  may help find genetic differences in  $\Phi_{\text{CO}_2}$ . Qu *et al.* (2017) phenotyped  $A_{\text{low}}$  for ~200 rice genotypes at two locations and found >2-fold genotypic differences at each location, although location effect and location×genotype interaction were more significant than genotype effect.

Of the components determining  $\Phi_{\text{CO}_2}$ , only  $\Phi_{2\text{LL}}$  (Equation 2A, B) can be relatively easily phenotyped from assessing chlorophyll fluorescence parameter  $F'_v/F'_m$ . A good proxy is the more widely available parameter  $F_v/F_m$ , the quantum efficiency of PSII photochemistry in dark-adapted leaves. Carmo-Silva *et al.* (2017) showed a significant correlation between  $F'_v/F'_m$  and  $F_v/F_m$ , and both were highly heritable in 64 wheat cultivars. Similarly, Czyczyło-Mysza *et al.* (2013) reported small but significant differences in  $F_v/F_m$  among 91 wheat genotypes. Qu *et al.* (2017) showed that  $F_v/F_m$  positively correlated with  $A_{\text{low}}$  among 214 rice genotypes.

Leaf absorbance  $\beta$  is relevant for improving  $\Phi_{\text{CO}_2, \text{inc}}$ . It depends on leaf chlorophyll content [CHL] which is easily assessed with a SPAD leaf greenness meter. [CHL] systematically increased with the year of release of 24 soybean cultivars (Koester *et al.*, 2016). The SPAD values varied significantly among genotypes in wheat (Giunta *et al.*, 2002; Sadras *et al.*, 2012; Czyczyło-Mysza *et al.*, 2013; Carmo-Silva *et al.*, 2017; Silva-Perez *et al.*, 2020), rice (Qu *et al.*, 2017; Zhu *et al.*, 2020), and barley (Giunta *et al.*, 2002). However, while increasing  $\beta$  is beneficial for improving leaf-level  $\Phi_{\text{CO}_2, \text{inc}}$ , in the canopy context an increased  $\beta$  leads to an increased light extinction coefficient ( $k_L$ ), decreasing the contribution of lower leaves to canopy photosynthesis (see a later section).

### CO<sub>2</sub> diffusion parameters $g_s$ and $g_m$

Both  $A_{\text{max}}$  and  $\Phi_{\text{CO}_2}$  depend on the level of chloroplast CO<sub>2</sub> ( $C_c$ ) (see Equations 1, 2A). CO<sub>2</sub> molecules from the atmosphere have to cross resistance barriers to reach chloroplasts which can be expressed as:

$$C_c = C_i - A/g_m = C_a - A \left( \frac{1}{g_m} + \frac{1}{g_s} \right) \quad (3)$$

where  $C_a$  and  $C_i$  are the level of CO<sub>2</sub> at the atmosphere and intercellular air spaces, respectively, and  $g_s$  and  $g_m$  are stomatal and mesophyll conductance, respectively (where  $1/g_s$  also includes the boundary layer resistance).

$g_s$  varies with environment. When assessed under given conditions,  $g_s$  for water vapour has been reported to vary: 0.14–1.16 mol m<sup>-2</sup> s<sup>-1</sup> for ~200 rice genotypes under saturating light and 0.17–0.26 mol m<sup>-2</sup> s<sup>-1</sup> under low-light conditions (Qu *et al.*, 2017), and 0.2–1.0 mol m<sup>-2</sup> s<sup>-1</sup> for various sets

of wheat panels (Silva-Perez *et al.*, 2020). Genotypic differences in  $g_s$  were also significant within samples of a smaller number of genotypes in rice (Jahn *et al.*, 2011), wheat (Jahan *et al.*, 2014), soybean (Koester *et al.*, 2016; Tomeo and Rosenthal, 2017), and chickpea (Shrestha *et al.*, 2018). The heritability of  $g_s$  was high (mostly >0.5) in wheat (Carmo-Silva *et al.*, 2017; Silva-Perez *et al.*, 2020). Anatomical parameters (e.g. stomatal density, stomatal length, and stomatal width) underlying  $g_s$  also varied among genotypes in wheat (Sadras *et al.*, 2012; Ouyang *et al.*, 2017) and in rice (Ouyang *et al.*, 2017). Further information on natural variation of  $g_s$  can be found in recent reviews (Nunes-Nesi *et al.*, 2016; Faralli and Lawson, 2020), and many studies demonstrated a yield increase associated with increased  $g_s$  (Fischer *et al.*, 1998; Richards, 2000).

Compared with the information on  $g_s$  for large genetic panels, datasets for  $g_m$  are smaller, probably because  $g_m$  is difficult to measure. When estimated by the carbon isotope method,  $g_m$  varied from 0.05 mol m<sup>-2</sup> s<sup>-1</sup> bar<sup>-1</sup> to 0.50 mol m<sup>-2</sup> s<sup>-1</sup> bar<sup>-1</sup> in six barley genotypes (Barbour *et al.*, 2010), from 0.5 mol m<sup>-2</sup> s<sup>-1</sup> bar<sup>-1</sup> to 1.0 mol m<sup>-2</sup> s<sup>-1</sup> bar<sup>-1</sup> in 10 wheat genotypes (Jahan *et al.*, 2014), and from 0.29 mol m<sup>-2</sup> s<sup>-1</sup> bar<sup>-1</sup> to 0.88 mol m<sup>-2</sup> s<sup>-1</sup> bar<sup>-1</sup> among 20 chickpea genotypes (Shrestha *et al.*, 2018). Using the constant J method, Koester *et al.* (2016) showed that  $g_m$  in 24 soybean genotypes varied from 0.10 mol m<sup>-2</sup> s<sup>-1</sup> bar<sup>-1</sup> to 0.26 mol m<sup>-2</sup> s<sup>-1</sup> bar<sup>-1</sup>, and the values were not related to the cultivars' year of release. Using a chlorophyll fluorescence-based method, Tomeo and Rosenthal (2017) showed for 12 soybean cultivars that  $g_m$  varied by >2-fold, with 38% of this variation caused by genotype. Using a similar method, Ouyang *et al.* (2017) showed that  $g_m$  of upland rice genotypes was ~50% lower than that of lowland rice genotypes, and  $g_m$  of lowland rice was ~50% lower than that of wheat genotypes, confirming the high values of  $g_m$  reported by Jahan *et al.* (2014) for wheat. Ouyang *et al.* (2017) further showed that  $S_c/S_m$  (ratio of the exposed surface area of chloroplasts to the exposed surface area of mesophyll cell walls) contributed most to variation in  $g_m$  among rice genotypes, whereas  $T_w$  (thickness of the mesophyll cell wall) was the main determinant of  $g_m$  in wheat. Scafaro *et al.* (2011) and Giuliani *et al.* (2013) reported that  $T_w$  in rice and its wild relatives was highly correlated with  $g_m$ .

Increasing  $g_s$  can increase both leaf photosynthesis and transpiration, whereas  $g_m$  increases leaf photosynthesis but not transpiration. A high  $g_m$  or a high  $g_m:g_s$  ratio can thus improve leaf-level transpiration efficiency (Flexas *et al.*, 2013). A good correlation of transpiration efficiency versus  $g_m:g_s$  has been reported across 15 soybean cultivars (Bunce, 2016), nine rice and wheat genotypes (Ouyang *et al.*, 2017), and across 24 accessions of cultivated rice and its wild relatives (Giuliani *et al.*, 2013).

### Stimulating photosynthesis by increasing sink size

The effect of sink activity on photosynthesis has long been known (e.g. Paul *et al.*, 1992), and occurs at both leaf- and whole-plant scales. The sink limitation at leaf level for a short

time scale is reflected by the ability to utilize triose phosphate, the product of carbon reduction in the Calvin–Benson cycle, for sucrose or starch synthesis (Sharkey 1985; see Equation 1). As the half-life time of the intermediates in the Calvin–Benson cycle is shorter than that in sucrose or starch synthesis, the limitation set by TPU can build up and disappear quickly. Therefore, the TPU limitation is not always observable as other components such as electron transport are regulated to counteract TPU limitation (e.g. Sharkey, 2019). At the whole-plant scale over a longer time span, the sink–source (im)balance often refers to whether available photosynthates satisfy or exceed the demand for growth of panicles, stems, roots, and leaves. It has been observed that larger sinks can stimulate photosynthesis of source organs (reviewed by Dingkuhn *et al.*, 2020). For example, Kikuchi *et al.* (2017) demonstrated that genotypic tiling capacity increased rice yield response to elevated [CO<sub>2</sub>]. Hasegawa *et al.* (2013) showed that among eight rice cultivars in Japan, those that responded most to the elevated [CO<sub>2</sub>] under FACE environments had larger reproductive sinks. The importance of sink traits was shown for a larger FACE dataset covering rice genotypes from Japan and China (Lv *et al.*, 2020). Gao *et al.* (2021) confirmed that a high sink/source ratio is necessary for higher photosynthesis and productivity under elevated [CO<sub>2</sub>].

There has been little communication between photosynthesis biologists working on TPU limitation and crop physiologists working on whole-plant sink limitation. Fabre *et al.* (2019) attempted to link sink limitation at both scales and showed that TPU limitation was more prevalent in panicle-pruned rice plants, especially when grown under 800 μmol mol<sup>-1</sup> [CO<sub>2</sub>]. The photosynthetic stimulation by elevated [CO<sub>2</sub>] was smaller in pruned plants than in control plants. The dependency of the [CO<sub>2</sub>] response on sink size was also found when comparing five rice genotypes having contrasting panicle/leaf size ratios or sink/source ratios (Fabre *et al.*, 2020). The rate of TPU ( $T_p$ ), thus  $A_{\max}$  (see Equation 1), declined under sink limitation, increasingly after midday in a diurnal cycle, associated with sucrose accumulation in the flag leaf (Fabre *et al.*, 2019). These findings suggest that TPU limitation to leaf photosynthesis may be regulated by sink feedback at the whole-plant scale. Acevedo-Siaca *et al.* (2021) showed that like  $V_{\text{cmax}}$  and  $J_{\text{max}}$ ,  $T_p$  estimated for 30 rice accessions had high heritability. Data of Acevedo-Siaca *et al.* (2021) further showed that rice  $A_{\max}$  at CO<sub>2</sub> saturation was highly heritable but  $A_{\max}$  at ambient [CO<sub>2</sub>] was not, suggesting that genotypic variation in  $A_{\max}$  might be caused by genotypic sink limitation (Fabre and Dingkuhn, 2022).

### Canopy extinction coefficients

The decrease in light incident on leaves at increasing canopy depth commonly follows the Beer–Lambert law:

$$I_i = I_0 e^{-k_L L_i} \quad (4)$$

where  $I_0$  and  $I_i$  are incoming irradiances at the canopy top and at the layer where the leaf area index (LAI) accrued from the top is  $L_i$ , and  $k_L$  is called the canopy light extinction coefficient. The value of  $k_L$  depends somewhat on solar zenith angle, direct versus diffuse light intensity, and canopy size, causing some variation with time of day, cloudiness, and crop development. For a closed canopy under given light conditions,  $k_L$  primarily depends on leaf angle distribution (e.g. Ouyang *et al.*, 2021) and leaf [CHL] (e.g. Gu *et al.*, 2017). Like [CHL] (see above), leaf angle shows significant genetic variation (Li *et al.*, 2015; Truong *et al.*, 2015; Lu *et al.*, 2018). More erect leaves and lower [CHL] allow more light to reach the lower leaf strata, enabling them to contribute more to canopy photosynthesis. In that sense, more prostrate leaves during early growth and erect leaves after canopy closure are beneficial for the whole-season light interception. Likewise, more prostrate leaves at the canopy bottom and more upright leaves at the top allow greater crop light interception. Erect orientation also reduces the risk of photoinhibition in top leaves under high irradiances at noon on sunny days (Horton, 2000; Jaikumar *et al.*, 2021).

There has been recent interest in reducing top-leaf [CHL] to reduce photoinhibition and increase canopy light interception and productivity (Ort *et al.*, 2011; Gu *et al.*, 2017; Walker *et al.*, 2018). However, canopy photosynthesis ( $A_{\text{canopy}}$ ) depends not only on the light interception achievable with a given amount of photosynthetic resources, but also on how these resources are distributed in the canopy. Mathematical optimization showed that  $A_{\text{canopy}}$  is maximal if these resources are distributed in such a way that the  $A_{\max}$  gradient is comparable with the vertical light profile (Goudriaan, 1995; Sands, 1995). Nitrogen is the most important photosynthetic resource, and leaf nitrogen is observed to decrease with canopy depth (e.g. Evans, 1993), which can be described in analogy to Equation 4:

$$n_i = (n_0 - n_b) e^{-k_N L_i} + n_b \quad (5)$$

where  $n_0$  and  $n_i$  are nitrogen content of uppermost leaves and of those at the layer  $i$ , respectively;  $n_b$  is the base leaf nitrogen content, at or below which photosynthesis is nil; and  $k_N$  is the canopy nitrogen extinction coefficient. Assuming a linear increase of  $A_{\max}$  with leaf nitrogen (e.g. Setter *et al.*, 1994; Dreccer *et al.*, 2000; Hikosaka, 2010), the optimization theory predicts that  $k_N = k_L$ . However, often the observed  $k_N$  is lower than  $k_L$  (Hikosaka *et al.*, 2016), indicating the possibility of improving  $A_{\text{canopy}}$  via optimizing nitrogen versus light profiles.

Indeed, genotypic variations have been reported in various crop species for  $k_N$ ,  $k_L$ , and their ratio (Dingkuhn *et al.*, 1991; Bertheloot *et al.*, 2008; Sadras *et al.*, 2012; Gu *et al.*, 2017; Zhu *et al.*, 2020; Ouyang *et al.*, 2021). Moreau *et al.* (2012) reported for 16 cultivars that variation is larger for  $k_N:k_L$  than for the  $k_L$  itself, suggesting a potential for optimizing this ratio. Ouyang *et al.* (2021) showed that superior carbon gain between stem-elongating and flowering stages in rice genotypes was mainly explained by a higher  $k_N:k_L$  ratio. However, contrary to the theory, Sadras *et al.* (2012) showed a negative correlation

between radiation use efficiency (RUE) and the  $k_N:k_L$  ratio for 13 Australian wheat cultivars released between 1958 and 2007. The negative correlation may result from confounding effects of other traits (e.g. leaf greenness) that also varied with the year of release.

### *Stay-green and feedback of nitrogen balance on photosynthesis*

Maintaining green surface area longer (stay-green) increases crop photosynthetic duration. There are several types of stay-green (Thomas and Howarth, 2000). Here we focus on stay-green achieved by optimizing nitrogen uptake and allocation to grains. Grain nitrogen comes partly from *de novo* uptake by roots, but also largely from remobilization of nitrogen from vegetative green tissues (Gaju *et al.*, 2014; Shao *et al.*, 2021), especially from photosynthetic enzymes (Mu *et al.*, 2018). Remobilization results in leaf senescence (Sinclair and de Wit, 1976). Without provision of additional nitrogen, grain nitrogen (and thus protein content) generally decreases with yield increases. Such negative relations result from not only dilution by photoassimilates but more from remobilization.

While remobilization is a general process occurring in many crops (Monaghan *et al.*, 2001; Bogard *et al.*, 2010; Wei *et al.*, 2018), genetic differences were observed. Some wheat genotypes are able to accumulate more grain protein than others at the same yield level (Monaghan *et al.*, 2001). This can be achieved by higher post-anthesis nitrogen uptake, according to data on 27 wheat genotypes (Bogard *et al.*, 2010) and 15 doubled haploid wheat lines (Hebbar *et al.*, 2014). Likewise, variation in onset and extent of leaf senescence among nine sorghum genotypes was explained by differences in SLN and post-floral nitrogen uptake (Borrell *et al.*, 2001). Using wheat stay-green mutants, Chapman *et al.* (2021) also showed the link between onset of senescence and grain-filling duration, with an ~14% increase in final grain weight in stay-green genotypes.

There were significant genotypic differences in the amount of nitrogen remobilized from vegetative organs during grain filling among 20 genotypes of wheat (Barracough *et al.*, 2014). Post-anthesis nitrogen remobilization and the onset of rapid canopy senescence were correlated among 16 wheat cultivars grown in the UK and France (Gaju *et al.*, 2014). Grain demand for nitrogen can also strongly affect source-sink balance during grain filling. Genotypes with higher grain nitrogen concentration tend to be more source limited in rice (Wei *et al.*, 2018), probably due to faster nitrogen remobilization and accelerated leaf senescence. It is unknown if there is any genetic variation in the dynamics of grain nitrogen demand during filling. One can hypothesize that genotypes having lower nitrogen demand in the earlier than in the later grain-filling phase would remobilize less and maintain canopy photosynthesis longer than those that have constant or earlier nitrogen demand.

### *Early vigour, partly as a feedforward result of increased photosynthesis*

Another way to increase photosynthetic duration is to have an earlier canopy closure, which ensures more interception of light as well as more effective suppression of weeds (Richards, 2000). This can be achieved by increased tillering or branching, or with thinner leaves [higher specific leaf area (SLA)] that would allow faster leaf expansion (Dingkuhn *et al.*, 1999). Selection for high  $A_{\max}$  is not conducive for early vigour if it is achieved at the cost of thicker leaves (Boote and Tollenaar, 1994). Record values of  $C_3 A_{\max}$ ,  $>60 \mu\text{mol m}^{-2} \text{s}^{-1}$  at ambient  $[\text{CO}_2]$  (e.g. Percy and Ehleringer, 1984), were observed for desert plants. Such high values of  $A_{\max}$  associated with thick leaves are not useful for crop plants that require rapid leaf expansion and canopy closure for more light interception during crop establishment.

However, improving leaf photosynthesis without reducing SLA may increase early leaf expansion. In recent studies where leaf photosynthesis was improved by genetic modification (Kromdijk *et al.*, 2016; Driever *et al.*, 2017; Simkin *et al.*, 2017; Shen *et al.*, 2019; South *et al.*, 2019; López-Calcano *et al.*, 2020; Yoon *et al.*, 2020), improved photosynthesis also resulted in greater leaf area or larger plants that in turn intercept more light. It would be worthwhile assessing to what extent the reported increased biomass was directly caused by higher leaf photosynthetic rates versus indirectly by increased leaf expansion. Using 40 genotypes of ryegrass, Yiotis *et al.* (2021) showed that greater yield gain under elevated  $[\text{CO}_2]$  is more likely to occur through exploiting genetic differences in tillering and leaf area rather than in leaf photosynthesis. For different photosynthesis types (among which differences in  $A_{\max}$  are generally large), Atkinson *et al.* (2016) compared 382 grass species. They found that  $C_4$  species had a 19–88% daily growth advantage over  $C_3$  grasses at the seedling stage, but this advantage was driven largely by a high SLA (enabling faster leaf expansion), rather than by fast biomass gain per unit leaf area.

In view of the above considerations, SLA should ideally be larger in early growth phases (to accelerate canopy closure) and smaller in later phases (to increase  $A_{\max}$ ). Domestication and selection seem to have enhanced such SLA dynamics for some crops (rice: Peng *et al.*, 1993), as opposed to others (barley: Yin *et al.*, 1999). Genotypic differences in SLA are significant (Peng *et al.*, 1993; Yin *et al.*, 1999; Zhu *et al.*, 2020). Dingkuhn *et al.* (2001) further showed that the early relative growth rate of rice genotypes was correlated with tillering ability, and SLA was largely responsible for differences in tillering ability and LAI, thereby supporting SLA being a key trait for early vigour.

### *Photosynthetic contribution of non-leaf tissues*

The contribution of non-leaf tissues to whole-plant photosynthesis and source-sink balance has long been reported



(e.g. [Biscoe \*et al.\*, 1975](#)) and was recently reviewed by [Tambussi \*et al.\*, \(2021\)](#). Using the method of covering ears, [Maydup \*et al.\*, \(2012\)](#) estimated that ear photosynthesis contribution to grain filling increased from 10% to 35% among 10 Argentinian wheat varieties released between 1920 and 2008. By designing panicle chambers, [Chang \*et al.\*, \(2020\)](#) measured panicle photosynthetic rates in seven rice cultivars. They represented 20–38% of rates of the corresponding flag leaves. Similarly, [Molero and Reynolds \(2020\)](#) used a custom-made chamber to measure 45 genetically diverse spring wheat genotypes, and showed a variation of 2.8-fold for spike photosynthetic rate. By covering the spikes, they further estimated that the contribution of spike photosynthesis to grain weight was 30–40% in 196 wheat lines. [Jiang \*et al.\*, \(2006\)](#) showed that spike/ear photosynthesis is not only a highly proximal source for grain filling but can also offset the very high local carbon demand for dark respiration. Thus, strategies to increase canopy photosynthesis should consider inflorescence photosynthesis. This is especially relevant if the presence of  $C_4$ -type photosynthesis in developing wheat grains is real ([Rangan \*et al.\*, 2016](#); contested by [Busch and Farquhar, 2016](#)). Significant spike photosynthetic rates also reduce the need to lower panicle height in favour of canopy top-leaf photosynthesis ([Setter \*et al.\*, 1995](#)), as this trait invites humidity-loving pathogens.

## Molecular mapping of photosynthesis-related traits

The natural variations reviewed above represent only phenotypic trait variations. Genetic variations are smaller because of (i) measurement errors; (ii) confounding environmental variation; and (iii) possible differences in nodes of physiological and genetic control. Of the genetic variation, mainly additive effects are utilized in inbred breeding, only dominant alleles can be exploited in hybrid breeding, and complex gene interaction components (epistasis) are difficult to use ([Kearsey and Pooni, 1996](#)). To support breeding, it is important to map QTL for traits, providing information on the effect and putative function of loci, and markers as selection tools. This is mostly achieved with bi-parental populations for linkage analysis or association panels for GWAS (genome-wide association study). Here, we review the mapping of the aforementioned photosynthesis-related traits but present them in groups.

### Radiation-use efficiency and crop photosynthesis traits

[Yin \*et al.\*, \(2003\)](#) reported that the dwarfing allele of the major gene *denso* (also designated as *sdw1*) on chromosome (chr.) 3 decreased RUE in a recombinant inbred line (RIL) population of barley. More recently, [Molero \*et al.\*, \(2019\)](#)

used GWAS for 150 elite spring wheat genotypes including landraces and synthetically derived lines. They identified 94 single nucleotide polymorphisms (SNP) associated with RUE and biomass at various stages that explained 7–17% of the phenotypic variation. Common SNP markers were identified for grain yield, final biomass, and RUE on chr.5A and chr.7A. Landraces and synthetic derivative lines had higher RUE but lower harvest index (HI), suggesting that RUE has not been improved by breeding. Building on [Molero \*et al.\*, \(2019\)](#), [Joynson \*et al.\*, \(2021\)](#) conducted high-throughput hyperspectral reflectance phenotyping to map wheat photosynthetic capacity, demonstrating that GWAS for photosynthesis traits is feasible in the field ([Silva-Perez \*et al.\*, 2020](#)).

Genetic mapping studies mostly focus only on photosynthesis at a specific stage. To study the effects of photosynthesis on crop productivity, [Honda \*et al.\*, \(2021\)](#) phenotyped photosynthetic rate and crop growth rate (CGR) of 76 Koshihikari×Takanari rice chromosome segment substitution lines (CSSLs) during the growing season, and CGR was phenotyped based on biomass sampled at two stages. Cumulative photosynthetic rate during the post-heading phase predicted the CGR during that period well. However, importantly, sustaining high photosynthesis levels was more crucial for CGR than the maximal level, which is usually observed around flowering and followed by a decline. Thus, sustaining high photosynthesis (e.g. via green leaf area duration), rather than maximal rates, is important for increasing CGR and biomass. A genomic region on chr.3 was found to enhance both biomass at harvest and photosynthesis sustenance.

### Leaf photosynthesis and its underlying parameters

[Barbour \*et al.\*, \(2016\)](#) mapped leaf  $A_{\max}$ ,  $g_s$ , and  $g_m$  on 150 doubled-haploid wheat lines, whereby  $A_{\max}$  varied from 22.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$  to 35.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $g_s$  from 0.50  $\text{mol m}^{-2} \text{s}^{-1}$  to 1.30  $\text{mol m}^{-2} \text{s}^{-1}$ , and  $g_m$  from 0.27  $\text{mol m}^{-2} \text{s}^{-1} \text{bar}^{-1}$  to 0.94  $\text{mol m}^{-2} \text{s}^{-1} \text{bar}^{-1}$ . However, only two QTL were identified for  $A_{\max}$ , each explaining 5–7% of phenotypic variation; there were two QTL for  $g_s$ , each explaining 5%; and one for  $g_m$ , explaining 9% of variation.

[Adachi \*et al.\*, \(2011a\)](#) mapped three QTL for rice flag-leaf  $A_{\max}$  on chr.5, 8, and 11 from a Habataki×Sasanishiki cross and attributed the higher  $A_{\max}$  (Habataki alleles) to higher SLN and  $g_s$ . [Adachi \*et al.\*, \(2011b\)](#) confirmed the  $A_{\max}$  allele on chr.8 from Habataki in a Habataki×Koshihikari cross and reported another QTL on chr.4. Each QTL explained 6–9% of  $A_{\max}$  phenotypic variation. The high SLN and  $g_s$  putatively responsible for high  $A_{\max}$  were associated with increased root surface area and hydraulic conductivity, hinting at underlying traits promoting nitrogen uptake. Among backcrossed inbred lines derived from a third cross between Takanari and Koshihikari, two rice lines were identified that had 20–50% higher  $A_{\max}$

than the parental rates (Adachi *et al.*, 2013). In addition to SLN, high  $g_m$  underlined the high  $A_{max}$  of the lines, due to their higher density and more developed lobes of mesophyll cells. Thus, Tanaka *et al.* (2014) considered SLN,  $g_s$ , and  $g_m$  as the main factors for increasing rice  $A_{max}$ , as confirmed by near-isogenic lines for these QTL (Adachi *et al.*, 2014). This differs from the results of Barbour *et al.* (2016) in wheat, where the loci for  $A_{max}$ ,  $g_s$ , and  $g_m$  were independent. Using CSSLs, Adachi *et al.* (2019) were able to detect several more  $A_{max}$  QTL, each explaining 8–18% of phenotypic variations. Pyramiding these QTL alleles increased  $A_{max}$  consistently, and some alleles increased biomass and grain yield. Takai *et al.* (2013) identified the *NAL1* (*Narrow leaf1*) gene underlying one QTL on chr.4. The flowering-date gene *DTH8/Ghd8/LHD1* (Dai *et al.*, 2012) was underlying the  $A_{max}$ -increasing QTL on chr.8 (Adachi *et al.*, 2017).

For rice, another systematic study was conducted involving modelling, using 96 introgression lines. Initially, 1–3 QTL were detected for  $A_{max}$ ,  $g_s$ , and PSII quantum efficiency, each explaining 4–22% of phenotypic variation (Gu *et al.*, 2012a). The two parents and 11 lines were then selected to measure CO<sub>2</sub>- and light-response curves (Gu *et al.*, 2012b), allowing parameterization of a combined conductance-photosynthesis model of Farquhar *et al.* (1980). Photosynthesis was thus dissected into components  $g_s$ ,  $g_m$ ,  $V_{cmax}$ ,  $J_{max}$ ,  $\kappa_{2LL}$  (conversion efficiency of incident light to electron transport), and  $R_d$  (day respiration). Seven loci significantly affected these model parameters. Each parameter was controlled by 1–3 loci, and most loci controlled several parameters. Assuming additivity, ideotypes were designed, combining positive-effect alleles for the parameters (Gu *et al.*, 2014a). The best combination was projected to improve photosynthesis by ~20% compared with the best of the 13 lines investigated by Gu *et al.* (2012b). Scaled up to crop level by using the crop model GECROS (Yin and van Laar, 2005), a 25% genetic variation in photosynthesis of 25% gave a theoretical increase in biomass of 22–29%.  $\kappa_{2LL}$  was predicted to contribute most to variation in biomass, being more effective than  $g_s$  and  $g_m$  within the range of observed variation.

Among the Farquhar *et al.* (1980) model parameters,  $R_d$  is hard to measure on a large population and is commonly assumed to correlate with leaf respiration in the dark ( $R_{dk}$ ). Qu *et al.* (2020) observed  $R_{dk}$  on 206 rice accessions grown under both indoor and field conditions.  $R_{dk}$  positively correlated with leaf thickness and [CHL]. GWAS identified an overlapped genomic region on chr.3 for  $R_{dk}$  in both environments. A single SNP in the promoter region of the *LRK1* (leucine-rich repeat receptor kinase) gene was strongly correlated with the mean annual temperature of the regions where accessions were collected.

### Source-sink traits

The realization that sink capacity co-controls leaf photosynthetic rates via feedback becomes increasingly relevant for

improving crop productivity as [CO<sub>2</sub>] rises (Dingkuhn *et al.*, 2020). Because genotypic sink traits strongly affect elevated CO<sub>2</sub> response (Hasegawa *et al.*, 2013; Fabre *et al.*, 2020), traits well known to breeders will be seen in a new light, such as tiller, phytomere, and floret initiation rates (organogenetic vigour) and inflorescence size.

For reproductive stage sink-source relationships, Wang *et al.* (2020) conducted GWAS for 272 rice accessions, finding 70 QTL influencing 11 traits. Overall, 5–9 QTL were found per trait, each explaining 7–20% of trait phenotypic variation. The *NAL2* (*Narrow leaf2*) gene was found to control a typical sink trait, panicle number per plant, agreeing with *NAL2* and *NAL3* encoding the OsWOX3A transcription factor that is broadly involved in organ development (Cho *et al.*, 2013). Another generic mechanism for sink enhancement is T6P-mediated sugar signalling (Dingkuhn *et al.*, 2020). Lyra *et al.* (2021) indicated that beyond proven options for engineered T6P-based sink enhancement, much natural, functionally effective genetic variation in key genes *TPS* and *TPP* exists in wheat waiting to be mined for breeding.

Source-sink trait analyses rarely consider photosynthesis of the inflorescence. Molero *et al.* (2014) identified markers associated with spike photosynthesis contribution to grain yield in a RIL population of wheat. Three QTL were detected that explained 10–24% of the variation in the contribution, highlighting the potential for improving spike photosynthesis.

### Other morpho-physiological traits

Canopy photosynthesis ( $A_{canopy}$ ) is a complex trait integrating many physiological and morphological components. Leaf angle is particularly important and has been a pivotal trait for Green Revolution breeding. The role of the rice semi-dwarfing (*SD1*) gene in reducing height, changing leaf angle, and increasing tillering is history and requires no review here. In sorghum, Truong *et al.* (2015) identified 2–4 loci, explaining 12–38% of phenotypic variation in leaf angle in each of two RIL populations. Alleles of the gene *dwarf-3* were shown to change leaf inclination by up to 34°. Li *et al.* (2015) phenotyped three connected RIL maize populations (538 RILs) for leaf angle. Seventeen identified QTL together explained ~60% of phenotypic variance. Also for maize, Lu *et al.* (2018) conducted GWAS with 80 inbred lines. Twenty-two SNPs were detected for leaf angle, with five each explaining 5–22% of the phenotypic variation.

Stay-green can maintain high  $A_{canopy}$  during grain filling. To map stay-green, Chapman *et al.* (2021) developed RIL populations segregating for the timing of senescence in wheat. They found two independent loci of 4.8 Mb and 16.7 Mb in size encompassing 56 and 142 genes. Combining association analysis with variant effect prediction, they identified effective SNPs in the locus of *NAM-1*, a gene associated with grain

protein content. This provides a molecular basis for the earlier discussed ‘nitrogen remobilization’.

Stay-green also depends on leaf [CHL], which in turn determines leaf photon absorptance and affects canopy  $k_L$ . Wang *et al.* (2015) conducted GWAS for [CHL] using a collection of 529 diverse rice accessions. A total of 46 loci were identified. Three F<sub>2</sub> mapping populations with parents selected from the panel were developed to validate the major GWAS signals, each providing 1–2 QTL that explained 10–20% of phenotypic variation. *Ghd7* (*Grain number, plant height, and heading date7*), being a major regulator of nitrogen uptake (Wang *et al.*, 2021), was a major underlying gene for [CHL] at heading stage. Enhanced expression of *Ghd7* decreased [CHL]. On another locus, *NAL1*—the gene involved in cell division and auxin-mediated expansion—was identified (Lin *et al.*, 2019).

For early vigour, Yin *et al.* (1999) reported several QTL for early-stage SLA in a barley RIL population, together explaining >40% of phenotypic variation. Zhang *et al.* (2017) phenotyped four traits including seedling shoot length in 132 rice RILs. They detected 10–28 QTL, each explaining up to 14% of phenotypic variation. Chen *et al.* (2019) used 744 rice accessions to detect QTL for tiller number, plant height, and above-ground dry weight at the seedling stage, detecting 42 QTL.

## Outlook

Our review shows large phenotypic variations (sometimes >2-fold) for steady-state photosynthesis traits. There are few QTL identified for photosynthesis traits *per se* such as  $A_{\max}$ , and these QTL accounted for a low percentage of phenotypic variations, typically <20%. In contrast, more QTL were reported for sink size (that feeds back on photosynthesis) or morphophysiological traits (that affect canopy productivity and duration), together explaining a much higher percentage of their phenotypic variation (typically >60%).

Measurement error (Gu *et al.*, 2012a) and the uncertainty in innate reasons for observed variability of photosynthesis (Fabre and Dingkuhn, 2022) might explain why its variation remains poorly explained. However, this does not mean that there is little opportunity to improve photosynthesis. Instead, breeding may have selected photosynthesis-related traits that probably partly contributed to recent yield progress (Fischer *et al.*, 2014). Our review showed that apart from some existing variation in the photosynthetic apparatus itself, much of the molecular basis of photosynthesis QTL resides in genes controlling nitrogen use, source–sink relations, leaf morphology, or senescence patterns. We thus hypothesized that some genotypic variation in  $A_{\max}$  (and its degree of heritability) might actually be due to variation in sink limitation. In addition, traits for both photosynthetic rate and its sustenance during grain filling are strongly related to nitrogen-related traits.

Given these considerations, we conducted an analysis using the crop model GECROS to evaluate how improving photosynthesis can enhance crop productivity (Box 2; Table 1). The model confirmed that the maximum benefit can be achieved from simultaneous improvement of other traits; in particular, proportionally increased root nitrogen uptake is required to significantly improve productivity. The model also showed that understudied electron transport parameters were much more effective than the commonly studied  $A_{\max}$ . This is because photosynthesis of most leaves at most hours in a canopy, even on sunny days, are light subsaturated (electron transport limited). This is corroborated by observations of Qu *et al.* (2017) and Taniyoshi *et al.* (2020) on the importance of  $A_{\text{low}}$  and supports views on optimizing photosynthetic light reactions (Yin and Struik, 2021; Walter and Kromdijk, 2022). Thus, improving photosynthesis is not merely a matter of increasing  $A_{\max}$  but should improve multiple parameters synergistically, allowing for high canopy photosynthesis and duration.

Many mapping studies use diversity panels showing very large phenotypic trait variation. For breeding to improve yield, only the portions of variation beyond best-performing cultivars are useful. Our modelling suggests that many structural crop traits (such as stay-green or early vigour) have already been largely optimized by breeding, with limited scope for further improvement (Box 2), at least under current ambient [CO<sub>2</sub>]. However, natural variation in photosynthesis remains largely unexploited (Driever *et al.*, 2014; Gu *et al.* 2014b; Faralli and Lawson, 2020). In fact, as shown in this review, there are cases where dwarfing seems to have decreased photosynthesis or RUE (e.g. Yin *et al.*, 2003; Molero *et al.*, 2019; Mathan *et al.*, 2021). Thus, our view is somewhere between that of photosynthesis biologists and crop physiologists: improving the photosynthetic apparatus can contribute to yield improvement, namely regarding its electron transport components; but enabling traits such as root nutrient uptake and sink capacity must be co-selected by breeding. As stated in Box 2, the synergistic impact of exploiting natural variation of multiple components could match the impact of implementing the full mechanism of maize C<sub>4</sub> photosynthesis in C<sub>3</sub> crops.

We discussed little about photosynthesis under fluctuating light conditions. Acevedo-Siaca *et al.* (2020a, b) showed that genotypic variation in non-steady-state rice photosynthesis did not correlate with that under steady-state conditions, but exceeded it. However, Salter *et al.* (2020) identified a QTL for Rubisco activation rate under fluctuating light overlapping with a QTL for steady-state photosynthesis in barley. Taniyoshi *et al.* (2020) showed that the cumulative CO<sub>2</sub> fixation rate during the 10 min after the transition from low to high irradiance was not correlated with the rate at the high irradiance but significantly correlated with the rate at low light. The potential significance of such traits for crop improvement requires further study.

**Box 2. Modelling potential RUE and biomass gains from pyramiding photosynthetic traits**

We used the crop model GECROS (Yin and van Laar, 2005; Yin and Struik, 2017) to assess the potential of improving various traits for increasing crop productivity. The model version here was used by Yin and Struik (2017) and Kadam *et al.* (2019) but incorporates a multilayer module for computing canopy photosynthesis. We first assess the traits individually and then assess them in combination (Table 1). We used weather data of 1980–2010 at the International Rice Research Institute (IRRI), Philippines, for simulation. Baseline GECROS parameter values were taken from Yin and Struik (2017), predicting 31 year average above-ground biomass at 19.6 t ha<sup>-1</sup>, representing the best check rice cultivar observed at IRRI where nitrogen (N) uptake ( $N_{\text{umax}}$ ) is ~20 g N m<sup>-2</sup> for well-managed crops (Setter *et al.*, 1994). Considering typical phenotypic variations and percentages explained by identified QTL as reviewed in the main text, we assumed that each trait (model parameter) can be improved in a favourable direction by 20% (except  $\Phi_{2\text{LL}}$  whose maximum value is ~0.85, Björkman and Demmig, 1987) given that it is unknown how much a trait can be improved by breeding.

Modelled impact of trait improvement was mostly similar on RUE and biomass, but not identical due to pleiotropic effects simulated on light interception. Among six photosynthetic traits ( $V_{\text{cmax}}$ ,  $J_{\text{max}}$ ,  $\Phi_{2\text{LL}}$ ,  $g_s$ ,  $g_m$ , and TPU limitation removal), increasing  $V_{\text{cmax}}$  by 20% did not increase biomass. In contrast, improving electron transport parameters,  $J_{\text{max}}$  (+20%) and  $\Phi_{2\text{LL}}$  (+9%), had the greatest impact and increased biomass by 5% and 3%, respectively (Table 1). Improving CO<sub>2</sub> diffusion parameters ( $g_s$  and  $g_m$ ) by 20% and removing TPU limitation each increased biomass by ~1%. The greater importance of improving  $J_{\text{max}}$  versus  $V_{\text{cmax}}$  was reported previously (Gu *et al.*, 2014a; Yin and Struik, 2015), suggesting a possible overinvestment of N in Rubisco in existing cultivars. Improving  $V_{\text{cmax}}$  or removing TPU limitation only increases light-saturated  $A_{\text{max}}$  (see Equation 1), which is relevant for top leaves around noon on sunny days. In contrast, improving  $J_{\text{max}}$  not only increases  $A_{\text{max}}$  but also lifts up the entire light–response curve of electron transport, thus also increasing light subsaturated rates. This, especially if combined with improved  $\Phi_{2\text{LL}}$ , has a significant consequence on productivity of most leaves at any time of day and season. This is supported by Qu *et al.* (2017), reporting that genotypic variation in productivity was associated with  $A_{\text{low}}$  (photosynthesis under low light). Although a limited scope for improving  $\Phi_{\text{CO}_2}$  was previously suggested (Austin, 1989), there is evidence for large variation in chloroplast electron transport, with 4-fold differences reported for barley (Burkey, 1994). Furthermore, with  $J_{\text{max}}$ ,  $\Phi_{2\text{LL}}$ ,  $g_s$ , and  $g_m$  all improved and TPU limitation removed, combined effects were higher than the sum of the individual effects, increasing RUE and biomass by ~14% (Table 1).

In addition to the sink limitation at a biochemical level (the TPU limitation), there are feedback effects of morpho-physiological sinks (such as grain number and size) on photosynthesis (see the main text). However, further research is needed to model this feedback. Among five modelled canopy morpho-physiological traits, adjusting leaf angle and SLA for early vigour had no or slightly negative effects on biomass (Table 1). Improving  $k_{\text{N}}:k_{\text{L}}$ , stay-green by adjusting N remobilization, and improving non-leaf photosynthesis each increased biomass by 2–3%. Combined improvement of the latter three traits increased biomass by 6.7% (Table 1), slightly less than the sum of individual effects. Overall, improving these morpho-physiological traits had a smaller effect, compared with the combined improvement of photosynthetic parameters. Thus, these morpho-physiological traits are probably near optimal due to past breeding. Nevertheless, effects of combining photosynthetic and morpho-physiological traits seemed additive, together increasing biomass by ~19% (Table 1).

Improving photosynthetic traits may be combined with increasing N uptake. Higher leaf N content enables higher photosynthetic rates and can be associated with greater root surface area and conductivity (Hikosaka, 2010; Adachi *et al.*, 2011b). The causality between improved photosynthesis and root N uptake ability is unclear. Increasing  $N_{\text{umax}}$  by 20% increased simulated RUE by 10.7% and biomass by 14.6% (Table 1), in line with the importance of past breeding for more N input-responsive cultivars (Sinclair *et al.*, 2019). Increasing N uptake combined with either improved photosynthetic or morpho-physiological traits resulted in synergistic effects. When all these traits were improved, RUE and biomass increased by ~37% and 39%, respectively (Table 1). These values are similar to the projected impact of introducing the full crop C<sub>4</sub> mechanism into rice (Yin and Struik, 2017).

**Table 1.** Simulated advantage (%) in radiation use efficiency (RUE) and above-ground biomass (31 year average) as a result of improving individual traits or trait combinations over the baseline simulation

Trait type	Parameter <sup>a</sup>	Parameter values		Advantage over the baseline (%) <sup>b</sup>	
		Baseline	Improved	RUE	Biomass
Photosynthetic	1 $\chi_{V_{cmax}}$	75	90	0.2	0.0
	2 $\chi_{J_{max}}$	100	120	3.7	5.0
	3 $\Phi_{2LL}$	0.78	0.85	2.8	3.0
	4 $g_s$	Variable	1.2×baseline	0.8	1.0
	5 $\chi_{gm}$	0.125	0.150	0.8	1.0
	6 TPU limitation	Present	Removed <sup>c</sup>	1.1	1.3
Morpho-physiological	7 Leaf angle	65	52	-0.3	0.0
	8 $k_N:k_L$	0.80	0.96	2.4	2.5
	9 Stay-green <sup>d</sup>	Baseline	Improved	1.6	2.1
	10 SLA	0.030	0.036	-1.9	-1.8
	11 Non-leaf tissue <sup>e</sup>	Baseline	Improved	2.8	3.1
Nitrogen uptake <sup>f</sup>	12 $N_{umax}$	20	24	10.7	14.6
Trait combination	Photosynthetic traits 2–6			14.0	13.0
	Morpho-physiological traits 8, 9, and 11			6.9	6.7
	Traits 2–6, 8, 9, and 11			21.9	19.1
	Traits 2–6, plus 12 (i.e. $N_{umax}$ )			29.0	31.5
	Traits 8, 9, 11, plus 12 (i.e. $N_{umax}$ )			18.9	22.6
	Traits 2–6, 8, 9, 11, plus 12 (i.e. $N_{umax}$ )			37.2	39.1

<sup>a</sup> Parameter definition: (1)  $\chi_{V_{cmax}}$ , slope of  $V_{cmax}$  (maximum rate of carboxylation by Rubisco) versus leaf nitrogen ( $\mu\text{mol g}^{-1} \text{N s}^{-1}$ ); (2)  $\chi_{J_{max}}$ , slope of  $J_{max}$  (maximum rate of photosynthetic electron transport) versus leaf nitrogen ( $\mu\text{mol g}^{-1} \text{N s}^{-1}$ ); (3)  $\Phi_{2LL}$ , PSII electron transport efficiency under limiting light ( $\text{mol mol}^{-1}$ ); (4)  $g_s$ , stomatal conductance (which is variable, depending on light,  $\text{CO}_2$ , temperature, and vapour pressure); (5)  $\chi_{gm}$ , slope of  $g_m$  (mesophyll conductance) versus leaf nitrogen ( $\text{mol g}^{-1} \text{N s}^{-1} \text{bar}^{-1}$ ); (6) TPU (triose phosphate utilization)-limited photosynthetic rate, set in its simplest form as  $3T_p - R_d$  (Sharkey, 1985), which can be derived from Equation 1 with  $\alpha_s=0$ ; where  $R_d$  is day respiration, and  $T_p$  is the rate of TPU with  $\chi_{TP}$  (slope of  $T_p$  versus leaf nitrogen) being  $5 \mu\text{mol g}^{-1} \text{N s}^{-1}$  (Harley *et al.*, 1992); (7) leaf angle from the horizontal line at the early phase ( $^\circ$ ); (8) the leaf nitrogen to light extinction coefficient ratio (-); (9) stay-green coefficients in relation to grain demand for nitrogen (-); (10) specific leaf area (SLA) at the early phase ( $\text{m}^2 \text{g}^{-1}$ ); (11) coefficients for quantifying the photosynthesis contribution from non-leaf tissues (-); (12) season-long crop nitrogen uptake ( $\text{g N m}^{-2}$ ).

<sup>b</sup> Simulated 31 year average using the baseline parameter values (taken from Yin and Struik, 2017) was  $2.57 \text{ g (MJ PAR)}^{-1}$  for RUE and  $19.6 \text{ t ha}^{-1}$  for above-ground biomass.

<sup>c</sup> The removal of this TPU limitation was simply assumed to be the ‘improved’ form because of the lack of understanding of the whole-plant physiology to fully represent the extent of sink feedbacks on source.

<sup>d</sup> Stay-green traits are modelled in GECROS in relation to nitrogen remobilization from vegetative organs in support of grain filling. Therefore, parameters were changed by 20% to allow slower remobilization, thereby, improving stay-green status.

<sup>e</sup> In the GECROS model, green surface area index (GAI) includes leaf and green non-leaf tissue areas. Here, parameters were changed by 20% to allow more non-leaf tissue areas.

<sup>f</sup> Nitrogen uptake ( $N_{umax}$ ) is not an input parameter but a simulated output in the default GECROS model. Here we set  $N_{umax}$  as a controlled crop variable, so as to separate the impact of improving photosynthetic or morpho-physiological traits from that of increasing nitrogen uptake on crop productivity (see Box 2). For this simulation, the dynamics of crop N uptake were assumed to follow a sigmoid pattern, with  $N_{umax}$  (default value= $20 \text{ g N m}^{-2}$ ) as the total N uptake during the growing season (Setter *et al.*, 1994). A 20% increase scenario was to increase  $N_{umax}$  by 20% but with the uptake proportion for each specific day unaltered.

## Author contributions

XY and PCS: conceptualization; XY: conducting the simulation; XY: writing initial draft with input from JG and PCS; MD: contributed the discussion on the source–sink relationship and improved the review structure; all authors participated in the revising process.

## Conflict of interest

The authors declare no conflict of interest.

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## References

- Acevedo-Siaca LG, Coe R, Quick WP, Long SP. 2020a. Variation between rice accessions in photosynthetic induction in flag leaves and underlying mechanisms. *Journal of Experimental Botany* **72**, 1282–1294.
- Acevedo-Siaca LG, Coe R, Quick WP, Long SP. 2021. Evaluating natural variation, heritability, and genetic advance of photosynthetic traits in rice (*Oryza sativa*). *Plant Breeding* **140**, 745–757.
- Acevedo-Siaca LG, Coe R, Wang Y, Kromdijk J, Quick WP, Long SP. 2020b. Variation in photosynthetic induction between rice accessions and its potential for improving productivity. *New Phytologist* **227**, 1097–1108.
- Adachi S, Baptista LZ, Sueyoshi T, Murata K, Yamamoto T, Ebitani T, Ookawa T, Hirasawa T. 2014. Introgression of two chromosome regions

- for leaf photosynthesis from an indica rice into the genetic background of a *japonica* rice. *Journal of Experimental Botany* **65**, 2049–2056.
- Adachi S, Nakae T, Uchida M, et al.** 2013. The mesophyll anatomy enhancing CO<sub>2</sub> diffusion is a key trait for improving rice photosynthesis. *Journal of Experimental Botany* **64**, 1061–1072.
- Adachi S, Nito N, Kondo M, Yamamoto T, Arai-Sanoh Y, Ando T, Ookawa T, Yano M, Hirasawa T.** 2011a. Identification of chromosomal regions controlling the leaf photosynthetic rate in rice by using a progeny from *Japonica* and high-yielding *Indica* varieties. *Plant Production Science* **14**, 118–127.
- Adachi S, Tsuru Y, Nito N, Murata K, Yamamoto T, Ebitani T, Ookawa T, Hirasawa T.** 2011b. Identification and characterization of genomic regions on chromosomes 4 and 8 that control the rate of photosynthesis in rice leaves. *Journal of Experimental Botany* **62**, 1927–1938.
- Adachi S, Yamamoto T, Nakae T, et al.** 2019. Genetic architecture of leaf photosynthesis in rice revealed by different types of reciprocal mapping populations. *Journal of Experimental Botany* **70**, 5131–5144.
- Adachi S, Yoshikawa K, Yamanouchi U, Tanabata T, Sun J, Ookawa T, Yamamoto T, Sage RF, Hirasawa T, Yonemaru J.** 2017. Fine mapping of carbon assimilation rate 8, a quantitative trait locus for flag leaf nitrogen content, stomatal conductance and photosynthesis in rice. *Frontiers in Plant Science* **8**, 60.
- Amthor JS.** 2010. From sunlight to phytomass: on the potential efficiency of converting solar radiation to phyto-energy. *New Phytologist* **188**, 939–959.
- Araus JL, Sanchez-Bragado R, Vicente R.** 2021. Improving crop yield and resilience through optimization of photosynthesis: panacea or pipe dream? *Journal of Experimental Botany* **72**, 3936–3955.
- Atkinson RR, Mockford EJ, Bennett C, Christin PA, Spriggs EL, Freckleton RP, Thompson K, Rees M, Osborne CP.** 2016. C<sub>4</sub> photosynthesis boosts growth by altering physiology, allocation and size. *Nature Plants* **2**, 16038.
- Austin RB.** 1989. Genetic variation in photosynthesis. *Journal of Agricultural Science, Cambridge* **112**, 287–294.
- Barbour MM, Warren CR, Farquhar GD, Forrester G, Brown H.** 2010. Variability in mesophyll conductance between barley genotypes, and effects on transpiration efficiency and carbon isotope discrimination. *Plant, Cell & Environment* **33**, 1176–1185.
- Barbour MM, Bachmann S, Bansal U, Bariana H, Sharp P.** 2016. Genetic control of mesophyll conductance in common wheat. *New Phytologist* **209**, 461–465.
- Barraclough PB, Lopez-Bellido R, Hawkesford MJ.** 2014. Genotypic variation in the uptake, partitioning and remobilisation of nitrogen during grain-filling in wheat. *Field Crops Research* **156**, 242–248.
- Bertheloot J, Martre P, Andrieu B.** 2008. Dynamics of light and nitrogen distribution during grain filling within wheat canopy. *Plant Physiology* **148**, 1707–1720.
- Biscoe PV, Gallagher JN, Littleton EJ, Monteith JL, Scott RK.** 1975. Barley and its environment. IV. Sources of assimilate for the grain. *Journal of Applied Ecology* **12**, 295–318.
- Björkman O, Demmig B.** 1987. Photon yield of O<sub>2</sub> evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. *Planta* **170**, 489–504.
- Bogard M, Allard V, Brancourt-Hulmel M, Heumez E, Machet JM, Jeuffroy MH, Gate P, Martre P, Le Gouis J.** 2010. Deviation from the grain protein concentration–grain yield negative relationship is highly correlated to post-anthesis N uptake in winter wheat. *Journal of Experimental Botany* **61**, 4303–4312.
- Boote KJ, Tollenaar M.** 1994. Modeling genetic yield potential. In: Boote KJ, Bennett JM, Sinclair TR, Paulsen GM, eds. *Physiology and determination of crop yield*. Madison, WI: ASA, CSSA, and SSSA, 533–565.
- Borrell A, Hammer G, van Oosterom E.** 2001. Stay-green: a consequence of the balance between supply and demand for nitrogen during grain filling? *Annals of Applied Biology* **138**, 91–95.
- Bunce J.** 2016. Variation among soybean cultivars in mesophyll conductance and leaf water use efficiency. *Plants* **5**, 44.
- Burkey KO.** 1994. Genetic variation of photosynthetic electron transport in barley: identification of plastocyanin as a potential limiting factor. *Plant Science* **97**, 177–187.
- Busch FA, Farquhar GD.** 2016. Poor evidence for C<sub>4</sub> photosynthesis in the wheat grain. *Plant Physiology* **172**, 1357.
- Busch FA, Sage RF, Farquhar GD.** 2018. Plants increase CO<sub>2</sub> uptake by assimilating nitrogen via the photorespiratory pathway. *Nature Plants* **4**, 46–54.
- Carmo-Silva E, Andralojc PJ, Scales JC, Driever SM, Mead A, Lawson T, Raines CA, Parry MAJ.** 2017. Phenotyping of field-grown wheat in the UK highlights contribution of light response of photosynthesis and flag leaf longevity to grain yield. *Journal of Experimental Botany* **68**, 3473–3486.
- Chang TG, Song QF, Zhao HL, Chang S, Xin C, Qu M, Zhu XG.** 2020. An *in situ* approach to characterizing photosynthetic gas exchange of rice panicle. *Plant Methods* **16**, 92.
- Chapman EA, Orford S, Lage J, Griffiths S.** 2021. Delaying or delivering: identification of novel NAM-1 alleles that delay senescence to extend wheat grain fill duration. *Journal of Experimental Botany* **72**, 7710–7728.
- Chen K, Zhang Q, Wang CC, Liu ZX, Jiang YJ, Zhai LY, Zheng TQ, Xu JL, Li ZK.** 2019. Genetic dissection of seedling vigour in a diverse panel from the 3,000 Rice (*Oryza sativa* L.) Genome Project. *Scientific Reports* **9**, 4804.
- Cho SH, Yoo SC, Zhang H, Pandeya D, Koh HJ, Hwang JY, Kim GT, Paek NC.** 2013. The rice narrow leaf2 and narrow leaf3 loci encode WUSCHEL-related homeobox 3A (OsWOX3A) and function in leaf, spikelet, tiller and lateral root development. *New Phytologist* **198**, 1071–1084.
- Czyczyło-Mysza I, Tyrka M, Marcińska I, Skrzypek E, Karbarz M, Dziurka M, Hura T, Dziurka K, Quarrie SA.** 2013. Quantitative trait loci for leaf chlorophyll fluorescence parameters, chlorophyll and carotenoid contents in relation to biomass and yield in bread wheat and their chromosome deletion bin assignments. *Molecular Breeding* **32**, 189–210.
- Dai X, Ding Y, Tan L, et al.** 2012. LHD1, an allele of DTH8/Ghd8, controls late heading date in common wild rice (*Oryza rufipogon*). *Journal of Integrative Plant Biology* **54**, 790–799.
- Dingkuhn M, Johnson DE, Sow A, Audebert AY.** 1999. Relationship between upland rice canopy characteristics and weed competitiveness. *Field Crops Research* **61**, 79–95.
- Dingkuhn M, Luquet D, Fabre D, Muller B, Yin X, Paul MJ.** 2020. The case for improving crop carbon sink strength or plasticity for a CO<sub>2</sub>-rich future. *Current Opinion in Plant Biology* **56**, 259–272.
- Dingkuhn M, Penning De Vries FWT, De Datta SK, Van Laar HH.** 1991. Concepts for a new plant type for direct seeded flooded tropical rice. In: *Direct seeded flooded rice in the tropics—Selected papers from the International Rice Research Conference*. Los Baños, Philippines: International Rice Research Institute, 17–38.
- Dingkuhn M, Tivet F, Siband P-L, Asch F, Audebert A, Sow A.** 2001. Varietal differences in specific leaf area: a common physiological determinant of tillering ability and early growth vigor? In: Peng S, Hardy B, eds. *Rice research for food security and poverty alleviation*. Metro Manila: IRRI, 95–108.
- Dreccer MF, van Oijen M, Schapendonk AHCM, Pot CS, Rabbinge R.** 2000. Dynamics of vertical leaf nitrogen distribution in a vegetative wheat canopy: impact on canopy photosynthesis. *Annals of Botany* **86**, 821–831.
- Driever SM, Lawson T, Andralojc PJ, Raines CA, Parry MA.** 2014. Natural variation in photosynthetic capacity, growth, and yield in 64 field-grown wheat genotypes. *Journal of Experimental Botany* **65**, 4959–4973.
- Driever SM, Simkin AJ, Alotaibi S, Fisk SJ, Magwick PJ, Spark CA, Jones HD, Lawson T, Parry MAJ, Raines CA.** 2017. Increased SBPase activity improves photosynthesis and grain yield in wheat grown in greenhouse conditions. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160384.
- Evans JR.** 1993. Photosynthetic acclimation and nitrogen partitioning within a lucerne canopy. I. Canopy characteristics. *Australian Journal of Plant Physiology* **20**, 55–67.

- Fabre D, Dingkuhn M.** 2022. Why is rice  $A_{\max}$  (at saturating  $\text{CO}_2$ ) more heritable than  $A_{\text{sat}}$  (at ambient  $\text{CO}_2$ )? A commentary on Acevedo-Siaca *et al.* (2021). *Plant Breeding* doi: [10.1111/pbr.13000](https://doi.org/10.1111/pbr.13000).
- Fabre D, Dingkuhn M, Yin X, Clément-Vidal A, Roques S, Soutiras A, Luquet D.** 2020. Genotypic variation in source and sink traits affects the response of photosynthesis and growth to elevated atmospheric  $\text{CO}_2$ . *Plant, Cell & Environment* **43**, 579–593.
- Fabre D, Yin X, Dingkuhn M, Clément-Vidal A, Roques S, Rouan L, Soutiras A, Luquet D.** 2019. Is triose phosphate utilization involved in the feedback inhibition of photosynthesis in rice under conditions of sink limitation? *Journal of Experimental Botany* **70**, 5773–5785.
- Faralli M, Lawson T.** 2020. Natural genetic variation in photosynthesis: an untapped resource to increase crop yield potential? *The Plant Journal* **101**, 518–528.
- Farquhar GD, von Caemmerer S, Berry JA.** 1980. A biochemical model of photosynthetic  $\text{CO}_2$  assimilation in leaves of  $\text{C}_3$  species. *Planta* **149**, 78–90.
- Fischer RA, Byerlee D, Edmeades GO.** 2014. Crop yields and global food security: will yield increase continue to feed the world? ACIAR Monograph No. 158. Canberra: Australian Centre for International Agricultural Research.
- Fischer RA, Rees D, Sayre KD, Lu ZM, Condon AG, Larque-Saavedra A.** 1998. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Science* **38**, 1467–1475.
- Flexas J.** 2016. Genetic improvement of leaf photosynthesis and intrinsic water use efficiency in  $\text{C}_3$  plants: why so much little success? *Plant Science* **251**, 155–161.
- Flexas J, Niinemets U, Gallé A, et al.** 2013. Diffusional conductances to  $\text{CO}_2$  as a target for increasing photosynthesis and photosynthetic water-use efficiency. *Photosynthesis Research* **117**, 45–59.
- Flood PJ, Harbinson J, Aarts MG.** 2011. Natural genetic variation in plant photosynthesis. *Trends in Plant Science* **16**, 327–335.
- Furbank RT, Sharwood R, Estavillo GM, Silva-Perez V, Condon AG.** 2020. Photons to food: genetic improvement of cereal crop photosynthesis. *Journal of Experimental Botany* **71**, 2226–2238.
- Gaju O, Allard V, Martre P, Le Gouis J, Moreau D, Bogard M, Hubbart S, Foulkes MJ.** 2014. Nitrogen partitioning and remobilization in relation to leaf senescence, grain yield and grain nitrogen concentration in wheat cultivars. *Field Crops Research* **155**, 213–223.
- Gao B, Hu S, Jing L, Niu X, Wang Y, Zhu J, Wang Y, Yang L.** 2021. Alterations in source–sink relations affect rice yield response to elevated  $\text{CO}_2$ : a free-air  $\text{CO}_2$  enrichment study. *Frontiers in Plant Science* **12**, 700159.
- Giuliani R, Koteyeva N, Voznesenskaya E, Evans MA, Cousins AB, Edwards GE.** 2013. Coordination of leaf photosynthesis, transpiration, and structural traits in rice and wild relatives (genus *Oryza*). *Plant Physiology* **162**, 1632–1651.
- Giunta F, Motzo R, Deidda M.** 2002. SPAD readings and associated leaf traits in durum wheat, barley and triticale cultivars. *Euphytica* **125**, 197–205.
- Goudriaan J.** 1995. Optimization of nitrogen distribution and of leaf area index for maximum canopy photosynthesis rate. In: Thiyagarajan TM, ten Berge HFM, Woperies MCS, eds. *Nitrogen management studies in irrigated rice*. Los Baños, Philippines: IRRI, 85–97.
- Gu J, Yin X, Stomph TJ, Wang H, Struik PC.** 2012b. Physiological basis of genetic variation in leaf photosynthesis among rice (*Oryza sativa* L.) introgression lines under drought and well-watered conditions. *Journal of Experimental Botany* **63**, 5137–5153.
- Gu J, Yin X, Stomph TJ, Struik PC.** 2014a. Can exploiting natural genetic variation in leaf photosynthesis contribute to increasing rice productivity? A simulation analysis. *Plant, Cell & Environment* **37**, 22–34.
- Gu J, Yin X, Struik PC, Stomph TJ, Wang H.** 2012a. Using chromosome introgression lines to map quantitative trait loci for photosynthesis parameters in rice (*Oryza sativa* L.) leaves under drought and well-watered field conditions. *Journal of Experimental Botany* **63**, 455–469.
- Gu J, Yin X, Zhang C, Wang H, Struik PC.** 2014b. Linking ecophysiological modelling with quantitative genetics to support marker-assisted crop design for improved yields of rice (*Oryza sativa*) under drought stress. *Annals of Botany* **114**, 499–511.
- Gu J, Zhou Z, Li Z, Chen Y, Wang Z, Zhang H.** 2017. Rice (*Oryza sativa* L.) with reduced chlorophyll content exhibit higher photosynthetic rate and efficiency, improved canopy light distribution, and greater yields than normally pigmented plants. *Field Crops Research* **200**, 58–70.
- Harley PC, Thomas RB, Reynolds JF, Strain BR.** 1992. Modelling photosynthesis of cotton grown in elevated  $\text{CO}_2$ . *Plant, Cell & Environment* **15**, 271–282.
- Hasegawa T, Sakai H, Tokida T, et al.** 2013. Rice cultivar responses to elevated  $\text{CO}_2$  at two free-air  $\text{CO}_2$  enrichment (FACE) sites in Japan. *Functional Plant Biology* **40**, 148–159.
- Hebbbar KB, Rane J, Ramana S, Panwar NR, Ajay S, Rao AS, Prasad PVV.** 2014. Natural variation in the regulation of leaf senescence and relation to N and root traits in wheat. *Plant and Soil* **378**, 99–112.
- Hedden P.** 2003. The genes of the green revolution. *Trends in Genetics* **19**, 5–9.
- Hikosaka K.** 2010. Mechanisms underlying interspecific variation in photosynthetic capacity across wild plant species. *Plant Biotechnology* **27**, 223–229.
- Hikosaka K, Anten NP, Borjigidai A, et al.** 2016. A meta-analysis of leaf nitrogen distribution within plant canopies. *Annals of Botany* **118**, 239–247.
- Honda S, Ohkubo S, San NS, Nakkasame A, Tomisawa K, Katsura K, Ookawa T, Nagano AJ, Adachi S.** 2021. Maintaining higher leaf photosynthesis after heading stage could promote biomass accumulation in rice. *Scientific Reports* **11**, 7579.
- Horton P.** 2000. Prospects for crop improvement through the genetic manipulation of photosynthesis: morphological and biochemical aspects of light capture. *Journal of Experimental Botany* **51**, 475–485.
- Jahan E, Amthor JS, Farquhar GD, Trethowan R, Barbour MM.** 2014. Variation in mesophyll conductance among Australian wheat genotypes. *Functional Plant Biology* **41**, 568–580.
- Jahn CE, Mckay JK, Mauleon R, Stephens J, McNally KL, Bush DR, Leung H, Leach JE.** 2011. Genetic variation in biomass traits among 20 diverse rice varieties. *Plant Physiology* **155**, 157–168.
- Jaikumar NS, Stutz SS, Fernandes SB, Leakey ADB, Bernacchi CJ, Brown PJ, Long SP.** 2021. Can improved canopy light transmission ameliorate loss of photosynthetic efficiency in the shade? An investigation of natural variation in *Sorghum bicolor*. *Journal of Experimental Botany* **72**, 4965–4980.
- Jiang Q, Roche D, Durham S, Hole D.** 2006. Awn contribution to gas exchanges of barley ears. *Photosynthetica* **44**, 536–541.
- Jin J, Liu X, Wang G, Mi L, Shen Z, Chen X, Herbert SJ.** 2010. Agronomic and physiological contributions to the yield improvement of soybean cultivars released from 1950 to 2006 in Northeast China. *Field Crops Research* **115**, 116–123.
- Joynson R, Molero G, Coombes B, Gardiner LJ, Rivera-Amado C, Piñera-Chávez FJ, Evans JR, Furbank RT, Reynolds MP, Hall A.** 2021. Uncovering candidate genes involved in photosynthetic capacity using unexplored genetic variation in spring wheat. *Plant Biotechnology Journal* **19**, 1537–1552.
- Kadam NN, Jagadish SVK, Struik PC, van der Linden CG, Yin X.** 2019. Incorporating genome-wide association into eco-physiological simulation to identify markers for improving rice yields. *Journal of Experimental Botany* **70**, 2575–2586.
- Kearsey MJ, Pooni HS.** 1996. *The genetical analysis of quantitative traits*. London: Chapman & Hall.
- Kikuchi S, Bheemanahalli R, Jagadish KSV, Kumagai E, Masuya Y, Kuroda E, Raghavan C, Dingkuhn M, Abe A, Shimono H.** 2017. Genome-wide association mapping for phenotypic plasticity in rice. *Plant, Cell & Environment* **40**, 1565–1575.
- Koester RP, Nohl BM, Diers BW, Ainsworth EA.** 2016. Has photosynthetic capacity increased with 80 years of soybean breeding? An examination of historical soybean cultivars. *Plant, Cell & Environment* **39**, 1058–1067.

- Koester RP, Skoneczka JA, Cary TR, Diers BW, Ainsworth EA.** 2014. Historical gains in soybean (*Glycine max* Merr.) seed yield are driven by linear increases in light interception, energy conversion, and partitioning efficiencies. *Journal of Experimental Botany* **65**, 3311–3321.
- Kromdijk J, Glowacka K, Leonelli L, Gabilly ST, Iwai M, Niyogi KK, Long SP.** 2016. Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science* **354**, 857–861.
- Li C, Li Y, Shi Y, Song Y, Zhang D, Buckler ES, Zhang Z, Wang T, Li Y.** 2015. Genetic control of the leaf angle and leaf orientation value as revealed by ultra-high density maps in three connected maize populations. *PLoS One* **10**, e0121624.
- Lin L, Zhao Y, Liu F, Chen Q, Qi J.** 2019. Narrow leaf 1 (NAL1) regulates leaf shape by affecting cell expansion in rice (*Oryza sativa* L.). *Biochemical and Biophysical Research Communications* **516**, 957–962.
- Long SP, Marshall-Colon A, Zhu XG.** 2015. Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. *Cell* **161**, 56–66.
- López-Calcagno PE, Brown KL, Simkin AJ, Fisk SJ, Vialet-Chabrand S, Lawson T, Raines CA.** 2020. Stimulating photosynthetic processes increases productivity and water-use efficiency in the field. *Nature Plants* **6**, 1054–1063.
- Lu S, Zhang M, Zhang Z, Wang Z, Wu N, Song Y, Wan P.** 2018. Screening and verification of genes associated with leaf angle and leaf orientation value in inbred maize lines. *PLoS One* **13**, e0208386.
- Lv C, Huang Y, Sun W, Yu L, Zhu J.** 2020. Response of rice yield and yield components to elevated [CO<sub>2</sub>]: a synthesis of updated data from FACE experiments. *European Journal of Agronomy* **112**, 125961.
- Lyra DH, Griffiths CA, Watson A, Joynson R, Molero G, Igna AA, Hassani-Pak K, Reynolds MP, Hall A, Paul MJ.** 2021. Gene-based mapping of trehalose biosynthetic pathway genes reveals association with source- and sink-related yield traits in a spring wheat panel. *Food and Energy Security* **10**, e292.
- Mathan J, Singh A, Jathar V, Ranjan A.** 2021. High photosynthesis rate in two wild rice species is driven by leaf anatomy mediating high Rubisco activity and electron transport rate. *Journal of Experimental Botany* **72**, 7119–7135.
- Maydup ML, Antonietta M, Guamet JJ, Tambussi EA.** 2012. The contribution of green parts of the ear to grain filling in old and modern cultivars of bread wheat (*Triticum aestivum* L.): evidence for genetic gains over the past century. *Field Crops Research* **134**, 208–215.
- McAusland L, Vialet-Chabrand S, Jauregui I, et al.** 2020. Variation in key leaf photosynthetic traits across wheat wild relatives is accession dependent not species dependent. *New Phytologist* **228**, 1767–1780.
- Meena RK, Reddy KS, Gautam R, Maddela S, Reddy AR, Gudipalli P.** 2021. Improved photosynthetic characteristics correlated with enhanced biomass in a heterotic F1 hybrid of maize (*Zea mays* L.). *Photosynthesis Research* **147**, 253–267.
- Mifflin B.** 2000. Crop improvement in the 21st century. *Journal of Experimental Botany* **51**, 1–8.
- Molero G, Joynson R, Pinera-Chavez FJ, Gardiner LJ, Rivera-Amado C, Hall A, Reynolds MP.** 2019. Elucidating the genetic basis of biomass accumulation and radiation use efficiency in spring wheat and its role in yield potential. *Plant Biotechnology Journal* **17**, 1276–1288.
- Molero G, Reynolds MP.** 2020. Spike photosynthesis measured at high throughput indicates genetic variation independent of flag leaf photosynthesis. *Field Crops Research* **255**, 107866.
- Molero G, Sukumaran S, Reynolds MP.** 2014. Spike photosynthesis contribution to grain yield and identification of molecular markers: a potential trait for breeding programs? Proceedings of the Conference of 4th Wheat Yield Consortium, CIMMYT, Cd. Obregon, Sonora, Mexico.
- Monaghan JM, Snape JW, Chojecki AJS, Kettlewell PS.** 2001. The use of grain protein deviation for identifying wheat cultivars with high grain protein concentration and yield. *Euphytica* **122**, 309–317.
- Moreau D, Allard V, Gaju O, Le Gouis J, Foulkes MJ, Martre P.** 2012. Acclimation of leaf nitrogen to vertical light gradient at anthesis in wheat is a whole-plant process that scales with the size of the canopy. *Plant Physiology* **160**, 1479–1490.
- Mu X, Chen Q, Chen F, Yuan L, Mi G.** 2018. Dynamic remobilization of leaf nitrogen components in relation to photosynthetic rate during grain filling in maize. *Plant Physiology and Biochemistry* **129**, 27–34.
- Nunes-Nesi A, Nascimento Vde L, de Oliveira Silva FM, Zsögön A, Araújo WL, Sulpice R.** 2016. Natural genetic variation for morphological and molecular determinants of plant growth and yield. *Journal of Experimental Botany* **67**, 2989–3001.
- Ort DR, Zhu X-G, Melis A.** 2011. Optimizing antenna size to maximize photosynthetic efficiency. *Plant Physiology* **155**, 79–85.
- Ort DR, Merchant SS, Alric J, et al.** 2015. Redesigning photosynthesis to sustainably meet global food and bioenergy demand. Proceedings of the National Academy of Sciences, USA **112**, 8529–8536.
- Ouyang W, Struik PC, Yin X, Yang J.** 2017. Stomatal conductance, mesophyll conductance, and transpiration efficiency in relation to leaf anatomy in rice and wheat genotypes under drought. *Journal of Experimental Botany* **68**, 5191–5205.
- Ouyang W, Yin X, Yang J, Struik PC.** 2021. Roles of canopy architecture and nitrogen distribution in the better performance of an aerobic than a lowland rice cultivar under water deficit. *Field Crops Research* **271**, 108257.
- Paul MJ, Driscoll SP, Lawlor DW.** 1992. Sink-regulation of photosynthesis in relation to temperature in sunflower and rape. *Journal of Experimental Botany* **43**, 147–153.
- Pearcy RW, Ehleringer J.** 1984. Comparative ecophysiology of C<sub>3</sub> and C<sub>4</sub> plants. *Plant, Cell & Environment* **7**, 1–13.
- Penning de Vries FWT, Jansen DM, ten Berge HFM, Bakema A.** 1989. Simulation of ecophysiological processes of growth in several annual crops. Los Baños, Philippines: IRRI, and Wageningen, Netherlands: Pudoc.
- Peng S, Garcia FV, Laza RC, Cassman KG.** 1993. Adjustment for specific leaf weight improves chlorophyll meter's estimate of rice leaf nitrogen concentration. *Agronomy Journal* **85**, 987–990.
- Qu M, Essemine J, Li M, Chang S, Chang T, Chen G-Y, Zhu X-G.** 2020. Genome-wide association study unravels LRK1 as a dark respiration regulator in rice (*Oryza sativa* L.). *International Journal of Molecular Sciences* **21**, 4930.
- Qu M, Zheng G, Hamdani S, Essemine J, Song Q, Wang H, Chu C, Sirault X, Zhu XG.** 2017. Leaf photosynthetic parameters related to biomass accumulation in a global rice diversity survey. *Plant Physiology* **175**, 248–258.
- Rangan P, Furtado A, Henry RJ.** 2016. New evidence for grain specific C<sub>4</sub> photosynthesis in wheat. *Scientific Reports* **6**, 31721.
- Richards RA.** 2000. Selectable traits to increase crop photosynthesis and yield of grain crops. *Journal of Experimental Botany* **51**, 447–458.
- Sadras VO, Lawson C, Montoro A.** 2012. Photosynthetic traits in Australian wheat varieties released between 1958 and 2007. *Field Crops Research* **134**, 19–29.
- Salter WT, Li S, Dracatos PM, Barbour MM.** 2020. Identification of quantitative trait loci for dynamic and steady-state photosynthetic traits in a barley mapping population. *AoB Plants* **12**, plaa063.
- Sands PJ.** 1995. Modelling canopy production. II. From single-leaf photosynthetic parameters to daily canopy photosynthesis. *Australian Journal of Plant Physiology* **22**, 603–614.
- Scafaro AP, Von Caemmerer S, Evans JR, Atwell BJ.** 2011. Temperature response of mesophyll conductance in cultivated and wild *Oryza* species with contrasting mesophyll cell wall thickness. *Plant, Cell & Environment* **34**, 1999–2008.
- Setter TL, Conocono EA, Egdane JA, Kropff MJ.** 1995. Possibility of increasing yield potential of rice by reducing panicle height in the canopy. I. Effects of panicles on light interception and canopy photosynthesis. *Australian Journal of Plant Physiology* **22**, 441–451.
- Setter TL, Peng S, Kirk GJD, Virmani SS, Kropff MJ, Cassman KG.** 1994. Physiological considerations and hybrid rice. In: Cassman KG, ed. Breaking the yield barrier. Proceedings of a workshop on rice yield potential in favorable environments. Los Baños, Philippines: IRRI, 39–62.
- Shao L, Liu Z, Li H, et al.** 2021. The impact of global dimming on crop yields is determined by the source-sink imbalance of carbon during grain filling. *Global Change Biology* **27**, 689–708.



- Sharkey TD.** 1985. Photosynthesis in intact leaves of C<sub>3</sub> plants: physics, physiology and rate limitations. *The Botanical Review* **51**: 53–105.
- Sharkey TD.** 2019. Is triose phosphate utilization important for understanding photosynthesis? *Journal of Experimental Botany* **70**, 5521–5525.
- Shen BR, Wang LM, Lin XL, et al.** 2019. Engineering a new chloroplastic photorespiratory bypass to increase photosynthetic efficiency and productivity in rice. *Molecular Plant* **12**, 199–214.
- Shrestha A, Buckley TN, Lockhart EL, Barbour MM.** 2018. The response of mesophyll conductance to short- and long-term environmental conditions in chickpea genotypes. *AoB Plants* **10**, ply073.
- Silva-Pérez V, De Faveri J, Molero G, Deery DM, Condon AG, Reynolds MP, Evans JR, Furbank RT.** 2020. Genetic variation for photosynthetic capacity and efficiency in spring wheat. *Journal of Experimental Botany* **71**, 2299–2311.
- Simkin AJ, McAusland L, Lawson T, Raines CA.** 2017. Overexpression of the RieskeFeS protein increases electron transport rates and biomass yield. *Plant Physiology* **175**, 134–145.
- Sinclair TR, de Wit CT.** 1976. Analysis of the carbon and nitrogen limitations to soybean yield. *Agronomy Journal* **68**, 319–324.
- Sinclair TR, Rufty TW, Lewis RS.** 2019. Increasing photosynthesis: unlikely solution for world food problem. *Trends in Plant Science* **24**, 1032–1039.
- South PF, Cavanagh AP, Liu HW, Ort DR.** 2019. Synthetic glycolate metabolism pathways stimulate crop growth and productivity in the field. *Science* **363**, eat9077.
- Takai T, Adachi S, Taguchi-Shiobara F, et al.** 2013. A natural variant of NAL1, selected in high-yield rice breeding programs, pleiotropically increases photosynthesis rate. *Scientific Reports* **3**, 2149.
- Tambussi EA, Maydup ML, Carrión CA, Guiamet JJ, Araus JL.** 2021. Ear photosynthesis in C<sub>3</sub> cereals and its contribution to grain yield: methodologies, controversies, and perspectives. *Journal of Experimental Botany* **72**, 3956–3970.
- Tanaka Y, Kumagai E, Tazoe Y, Adachi S, Homma K.** 2014. Leaf photosynthesis and its genetic improvement from the perspective of energy flow and CO<sub>2</sub> diffusion. *Plant Production Science* **17**, 111–123.
- Taniyoshi K, Tanaka Y, Shiraiwa T.** 2020. Genetic variation in the photosynthetic induction response in rice (*Oryza sativa* L.). *Plant Production Science* **23**, 513–521.
- Thomas H, Howarth CJ.** 2000. Five ways to stay green. *Journal of Experimental Botany* **51**, 329–337.
- Tomeo NJ, Rosenthal DM.** 2017. Variable mesophyll conductance among soybean cultivars sets a tradeoff between photosynthesis and water-use efficiency. *Plant Physiology* **174**, 241–257.
- Truong SK, McCormick RF, Rooney WL, Mullet JE.** 2015. Harnessing genetic variation in leaf angle to increase productivity of *Sorghum bicolor*. *Genetics* **201**, 1229–1238.
- von Caemmerer S, Quick WP, Furbank RT.** 2012. The development of C<sub>4</sub> rice: current progress and future challenges. *Science* **336**, 1671–1672.
- Walker BJ, Drewry DT, Slattery RA, VanLoocke A, Cho YB, Ort DR.** 2018. Chlorophyll can be reduced in crop canopies with little penalty to photosynthesis. *Plant Physiology* **176**, 1215–1232.
- Walter J, Kromdijk J.** 2022. Here comes the sun: how optimization of photosynthetic light reactions can boost crop yields. *Journal of Integrative Plant Biology* **64**, 564–591.
- Wang Q, Su Q, Nian J, et al.** 2021. The Ghd7 transcription factor represses ARE1 expression to enhance nitrogen utilization and grain yield in rice. *Molecular Plant* **14**, 1012–1023.
- Wang Q, Xie W, Xing H, et al.** 2015. Genetic architecture of natural variation in rice chlorophyll content revealed by a genome-wide association study. *Molecular Plant* **8**, 946–957.
- Wang Y, Pang Y, Chen K, Zhai L, Shen C, Wang S, Xu J.** 2020. Genetic bases of source-, sink-, and yield-related traits revealed by genome-wide association study in Xian rice. *The Crop Journal* **8**, 119–131.
- Wei H, Meng T, Li X, Dai Q, Zhang H, Yin X.** 2018. Sink–source relationship during rice grain filling is associated with grain nitrogen concentration. *Field Crops Research* **215**, 23–38.
- Ye M, Peng SB, Li Y.** 2019. Intraspecific variation in photosynthetic nitrogen-use efficiency is positively related to photosynthetic rate in rice (*Oryza sativa* L.) plants. *Photosynthetica* **57**, 311–319.
- Yin X, Busch FA, Struik PC, Sharkey TD.** 2021. Evolution of a biochemical model of steady-state photosynthesis. *Plant, Cell & Environment* **44**, 2811–2837.
- Yin X, Harbinson J, Struik PC.** 2006. Mathematical review of literature to assess alternative electron transports and interphotosystem excitation partitioning of steady-state C<sub>3</sub> photosynthesis under limiting light. *Plant, Cell & Environment* **29**, 1771–1782.
- Yin X, Kropff MJ, Stam P.** 1999. The role of ecophysiological models in QTL analysis: the example of specific leaf area in barley. *Heredity* **82**, 415–421.
- Yin X, Stam P, Kropff MJ, Schapendonk AHCM.** 2003. Crop modeling, QTL mapping, and their complementary role in plant breeding. *Agronomy Journal* **95**, 90–98.
- Yin X, Struik PC.** 2015. Constraints to the potential efficiency of converting solar radiation into phytoenergy in annual crops: from leaf biochemistry to canopy physiology and crop ecology. *Journal of Experimental Botany* **66**, 6535–6549.
- Yin X, Struik PC.** 2017. Can increased leaf photosynthesis be converted into higher crop mass production? A simulation study for rice using the crop model GECROS. *Journal of Experimental Botany* **68**, 2345–2360.
- Yin X, Struik PC.** 2021. Exploiting differences in the energy budget among C<sub>4</sub> subtypes to improve crop productivity. *New Phytologist* **229**, 2400–2409.
- Yin X, van Laar HH.** 2005. Crop systems dynamics: an ecophysiological simulation model for genotype-by-environment interactions. Wageningen, The Netherlands: Wageningen Academic Publishers.
- Yiotis C, McElwain JC, Osborne BA.** 2021. Enhancing the productivity of ryegrass at elevated CO<sub>2</sub> is dependent on tillering and leaf area development rather than leaf-level photosynthesis. *Journal of Experimental Botany* **72**, 1962–1977.
- Yoon DK, Ishiyama K, Suganami M, et al.** 2020. Transgenic rice overproducing Rubisco exhibits increased yields with improved nitrogen-use efficiency in an experimental paddy field. *Nature Food* **1**, 134–139.
- Zhang A, Liu C, Chen G, et al.** 2017. Genetic analysis for rice seedling vigor and fine mapping of a major QTL qSSL1b for seedling shoot length. *Breeding Science* **67**, 307–315.
- Zhu G, Ren Z, Liu Y, Lu F, Gu L, Shi Y, Liu J, Zhou G, Nimir NEA, Mohapatra PK.** 2020. Optimization of leaf properties and plant phenotype through yield-based genetic improvement of rice over a period of seventy years in the Yangtze River Basin of China. *Food and Energy Security* **9**, e223.