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Review

Research review

Enhancing crop yields through improvements in the efficiency of photosynthesis and respiration

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Summary

The rate with which crop yields per hectare increase each year is plateauing at the same time that human population growth and other factors increase food demand. Increasing yield potential (Y_p) of crops is vital to address these challenges. In this review, we explore a component of Y_p that has yet to be optimised – that being improvements in the efficiency with which light energy is converted into biomass (ϵ_c) via modifications to CO_2 fixed per unit quantum of light (α), efficiency of respiratory ATP production (ϵ_{prod}) and efficiency of ATP use (ϵ_{use}). For α, targets include changes in photoprotective machinery, ribulose bisphosphate carboxylase/oxygenase kinetics and photorespiratory pathways. There is also potential for ϵ_{prod} to be increased via targeted changes to the expression of the alternative oxidase and mitochondrial uncoupling pathways. Similarly, there are possibilities to improve ϵ_{use} via changes to the ATP costs of phloem loading, nutrient uptake, futile cycles and/or protein/membrane turnover. Recently developed high-throughput measurements of respiration can serve as a proxy for the cumulative energy cost of these processes. There are thus exciting opportunities to use our growing knowledge of factors influencing the efficiency of photosynthesis and respiration to create a step-change in yield potential of globally important crops.

Introduction

Anthropogenic carbon emissions since the Industrial Revolution have led to sustained global warming, with 2020 tying 2016 as the hottest year on record, at 1.25°C above preindustrial times (Voosen, 2021). How climate change affects our natural and managed systems is of major concern, particularly the effect of warming on major agricultural crop production. To keep pace with increasing crop demand for human and animal consumption – which will potentially double between 2010 and 2050 (van Dijk *et al.*, 2021) – and to minimise the demand for arable land, grain yields per hectare need to increase by 2.4% each year. Yet, for the period 1989–2008, actual annual increases fell markedly short of this figure, being 1.6%, 1.0%, 0.9% and 1.3% for maize, rice, wheat and soybean, respectively (Ray *et al.*, 2013). Therefore, it is imperative that we improve major crop yields (Smith, 2013). This goal can be achieved through increasing both yield resilience in suboptimal

conditions (Munns & Gilliham, 2015; Rivero *et al.*, 2022) and yield potential, discussed herein.

To date, increases in crop yields have been driven by Green Revolution cultivars – that lent themselves to more intensive irrigation, fertilisation and mechanisation – and continued selective breeding (Tilman, 1998; Crespo-Herrera *et al.*, 2018). These strategies doubled wheat yield and tripled that of maize between 1961 and 2000 – outcomes that were achieved with only a 30% increase in cultivated land area (World Bank, 2007; Hazell, 2009). Global wheat production grew from 222 Mt in 1961 to 585 Mt in 2000 and then to 735 Mt as of 2018. However, in recent years, yield per hectare has plateaued and further investment in the current strategies may be ineffective at further boosting yield (Tester & Langridge, 2010; Mózner *et al.*, 2012; Iizumi *et al.*, 2017). To avoid farming more land and using more fertilisers, it is essential that new pathways are found to boost crop yields. Improving yield potential (Y_p) is one such opportunity.

Breaking Y_p into components allows assessment of targeted multiplicative improvements. Y_p is the product of several underlying components:

$$Y_p = Q \times \epsilon_i \times \epsilon_c \times \epsilon_p \quad \text{Eqn 1}$$

where Q is the cumulative incident solar radiation (MJ m^{-2}) throughout the growing season; ϵ_p is the partitioning efficiency (commonly referred to as harvest index), the proportion of biomass allocated to harvested product; ϵ_i is the efficiency with which the plant intercepts/absorbs radiation; and ϵ_c is the efficiency with which the intercepted radiation is converted into biomass (Monteith, 1977; Long *et al.*, 2015) (see Box 1 for a mathematical expansion of ϵ_c, and Fig. 1 for examples of factors that influence each underlying component of Y_p). In theory, an increase in any of these factors would increase overall Y_p. However, not every term of the equation holds promise for a significant improvement in future years (Loomis & Amthor, 1999).

Both ϵ_p and ϵ_i have improved greatly since the Green Revolution through selective breeding, approaching 0.6 and 0.8–0.9, respectively (Zhu *et al.*, 2010). Increasing crop yields throughout the second half of the 20th century came with a concomitant increase in harvest index, attributable to biomass allocation patterns and dwarf genes that resulted in shorter stems that could support more grain (Sinclair, 1998). Meanwhile, because higher ϵ_i increases the amount of incident solar radiation available for photosynthesis, improvements in canopy architecture and responses to light have been targets for selection. In many field-grown crops, plants with leaves perpendicular to incoming light will intercept most of the solar radiation at the uppermost layer of the canopy, shading lower levels and preventing them from achieving light-saturated levels of photosynthesis (Campbell & Ogren, 1990; Ort & Long, 2003). Structuring canopies such that leaves higher in the canopy arrange themselves at steeper angles allows for deeper penetration of solar radiation, potentially doubling ϵ_i at peak irradiance or low latitudes. Through selective breeding during the Green Revolution, ϵ_i was increased through reductions in plant stature and lodging.

By comparison, there are still many untapped opportunities for improvements in the underlying factors that influence the efficiency with which solar radiation is converted into biomass (i.e. ϵ_c). Currently, the maximum observed value of ϵ_c lies at *c.* 0.024, yet the ϵ_c for C_3 crops has a theoretical maximum efficiency of 0.046–0.051 (Monteith, 1977; Long *et al.*, 2006; Zhu *et al.*, 2010). Given this gap, ϵ_c values could be strategically targeted as they provide one of the best options for future improvement (Fig. 2). To enable this, opportunities to increase the efficiency of the biochemical processes underpinning ϵ_c urgently need to be identified and prioritised.

Steps to improve the efficiency of net photosynthetic CO_2 fixation

One way of improving ϵ_c is to increase the efficiency of photosynthesis (Eqn B3). But how might this be achieved? Ultimately, improvements are needed in the ability of plants to convert absorbed light energy into products (ATP and NADPH) needed to drive CO_2 fixation by ribulose bisphosphate carboxylase/oxygenase (Rubisco) and in minimising carbon loss through processes such as photorespiration, while protecting the system from photoinhibition. Here, we discuss attributes that influence the efficiency of photosynthesis and strategies being employed to improve net photosynthesis.

Making better use of intercepted light and improving carboxylation efficiency

The variable nature of light availability across space and time in the plant canopy requires consideration of biochemical responses to these fluctuations. Incoming solar radiation above saturating rates can cause photooxidative damage to light-harvesting complexes (Havaux & Niyogi, 1999; Baroli & Niyogi, 2000). Photoprotective mechanisms can decrease the quantum yield of photosystem II, accounting for *c.* 15% decrease in daily canopy carbon uptake, and even higher values under stress conditions (Long *et al.*, 1994; Zhu *et al.*, 2004). Photosynthetic induction, the ramp-up of photosynthetic activity after exposure to light, can delay a leaf from reaching optimal photosynthetic rates under given conditions on the scale of minutes (Retkute *et al.*, 2015; Soleh *et al.*, 2017). Modulating these responses could improve net photosynthetic performance in certain situations (Murchie & Niyogi, 2011). The issue of induction is related to canopy structure because lower canopy layers are more reliant on intermittent light interception for photosynthesis. For example, total canopy photosynthesis could increase up to 17% with increased light penetration to the lower canopy in rice (Burgess *et al.*, 2016). Additionally, the delay of photosynthetic induction ramping up to full capacity can cause a > 20% loss of potential carbon assimilation in wheat (Taylor & Long, 2017), which could potentially be ameliorated through overexpression or amino acid substitutions in Rubisco activase (Yamori *et al.*, 2012; Carmo-Silva & Salvucci, 2013). Because leaf N is not necessarily distributed to maximise photosynthesis, optimising nitrogen distribution throughout the canopy is another strategy for increased photosynthesis, particularly at key growth

Box 1 Meeting agricultural demand for a growing population requires us to consider the components of yield

Improving the efficiency of these components will boost realised yield to keep pace with that demand. Yield potential $\left(\frac{g\ \text{yield}}{m^2\ \text{ground area}}\right)$ can be thought of as a function of incident solar radiation $\left(Q, \frac{J\ \text{light incoming}}{m^2\ \text{ground area}}\right)$, efficiency of radiation interception and absorption $\left(\epsilon_i, \frac{J\ \text{light absorbed}}{J\ \text{light incoming}}\right)$, efficiency of converting intercepted radiation to biomass $\left(\epsilon_c, \frac{g\ \text{plant biomass}}{J\ \text{light absorbed}}\right)$ and partitioning efficiency $\left(\epsilon_p, \frac{g\ \text{yield}}{g\ \text{plant}}\right)$. These factors are related by the following equation,

$$Y_p = Q \times \epsilon_i \times \epsilon_c \times \epsilon_p. \quad \text{Eqn B1}$$

Currently, the maximum observed value of ϵ_c lies *c*. 0.024 (Monteith, 1977). Yet, the ϵ_c for C_3 crops has a theoretical efficiency of 0.046–0.051 (Long *et al*., 2006; Zhu *et al*., 2010). With current ϵ_c values being only half of their theoretical maximum, there is clearly scope for improvement. Here, improvements in the efficiency of biochemical processes underpinning ϵ_c are urgently needed. To understand ways of improving ϵ_c, we can mathematically consider which factors contribute to variation in ϵ_c. One way of achieving this is to define ϵ_c according to:

$$\epsilon_c = \frac{\text{biomass}}{Q_{\text{absorbed}}} = \frac{CO_2\ \text{fixed}}{Q_{\text{absorbed}}} \times \frac{g\ \text{plant}}{g\ CO_2\ \text{fixed}}, \quad \text{Eqn B2}$$

where ϵ_c (and thus the biomass produced per joule of light absorbed) is the product of how much CO_2 is fixed by photosynthesis per joule of light, multiplied by the amount of plant mass per unit of CO_2 fixed by photosynthesis. Eqn B2 shows that ϵ_c could be improved through targeting aspects of photosynthetic biochemistry to improve the amount of CO_2 fixed per unit quantum of light. Put another way:

$$\alpha = \frac{CO_2\ \text{fixed}}{Q_{\text{absorbed}}}. \quad \text{Eqn B3}$$

It also shows that ϵ_c can be improved via changes in the efficiency with which plants accumulate biomass per unit of CO_2 fixed:

$$\epsilon_{\text{biosynthesis}} = \frac{g\ \text{plant}}{g\ CO_2\ \text{fixed}}. \quad \text{Eqn B4}$$

Bringing Eqns B3 and B4 together, we see that ϵ_c is related to α and $\epsilon_{\text{biosynthesis}}$ according to:

$$\epsilon_c = \alpha \times \epsilon_{\text{biosynthesis}}, \quad \text{Eqn B5}$$

where $\epsilon_{\text{biosynthesis}}$ is dependent on the efficiency of ATP production (hereon termed ϵ_{prod}; i.e. how much substrate must be consumed for a certain ATP yield) and the efficiency of ATP use (ϵ_{use}), with the latter being the ATP yield necessary to drive processes of biosynthesis, transport and cellular maintenance. Bringing these factors together, we see that:

$$\epsilon_{\text{biosynthesis}} = \epsilon_{\text{prod}} \times \epsilon_{\text{use}}, \quad \text{Eqn B6}$$

and therefore:

$$\epsilon_c = \alpha \times \epsilon_{\text{prod}} \times \epsilon_{\text{use}}. \quad \text{Eqn B7}$$

These equations thus show that improvements in ϵ_c could be achieved through α, ϵ_{prod} and ϵ_{use}. In subsequent sections, we discuss strategies available for improvement in these components of ϵ_c.

stages (Johnson *et al*., 2010; Moreau *et al*., 2012). Potential strategies to improve induction of photosynthesis include speeding up the rate at which proteins are activated in the photosynthetic electron transport system, increasing carbon fixation capacity via increases in concentrations in Rubisco and Rubisco activase, and improving CO_2 supply via increases in stomatal and mesophyll conductance (Yamori, 2021). Increasing nonphotochemical quenching (NPQ) relaxation under fluctuating light conditions could also be beneficial, in order to increase the efficiency of light energy use under light-limiting conditions (Yamori, 2021). A recent example is the study by De Souza *et al*. (2022) for soybean; they reported that the overexpression of genes linked to NPQ relaxation (*AtVDE*, *AtPsbS* and *AtZEP*) improved photosynthetic efficiency of soybean under fluctuating light over 2 yr in field trials. Yield may also be improved, as shown by the 24% higher soybean yields of five independent transgenic lines at the Urbana site in 2020. While further work is needed across multiple sites and years, the work of De Souza *et al*. (2022) does highlight opportunities to improve yield potential via targeting photosynthetic properties such as NPQ relaxation.

Another approach to improve photosynthesis is via targeting the biochemical properties of Rubisco. As a central protein in the Calvin cycle, Rubisco's biochemical properties play a large role in defining photosynthetic performance. Variations in Rubisco's

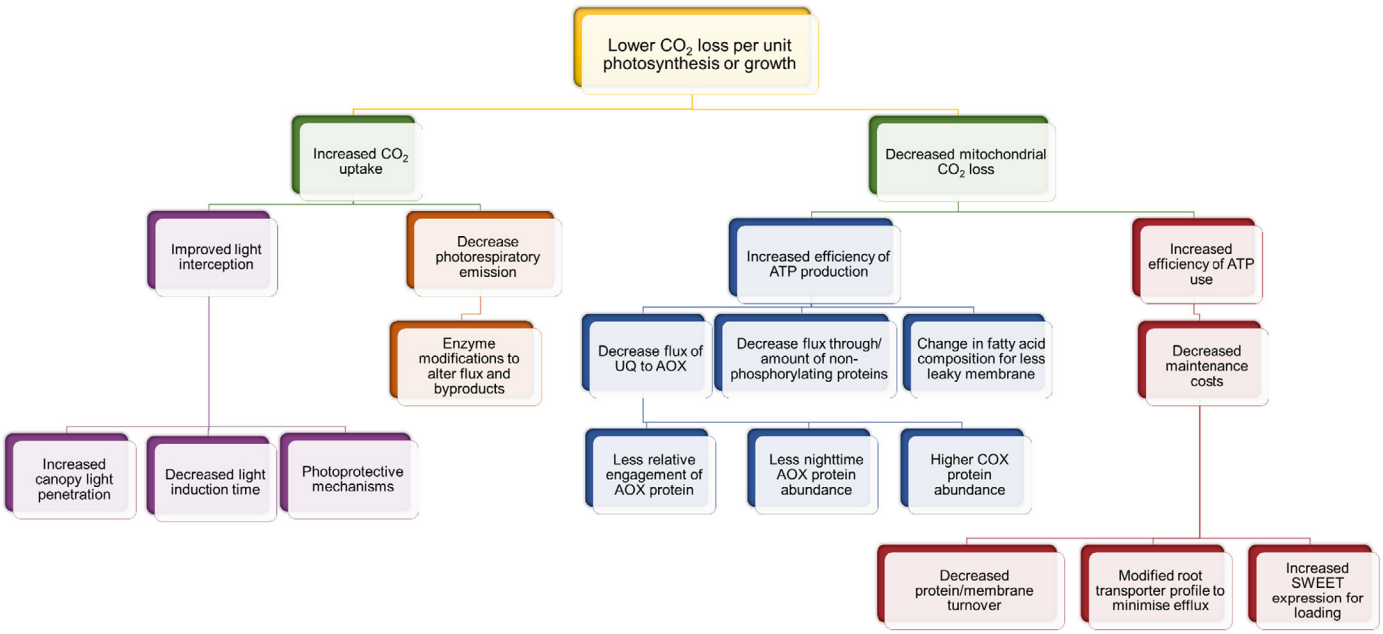

Fig. 1 Logic flow of improvements to the carbon economy of plants in order to increase yield potential. Minimising the ratio of respiration to either photosynthesis (R : P) or growth (R : RGR) increases the amount of photo assimilate available for yield (yellow). This goal can be achieved in two ways (green): by shrinking the numerator (decreased mitochondrial CO_2 loss) or by increasing the denominator (more CO_2 uptake). To date, increases in yield potential have been in part due to improvements in ϵ_i (violet). Further improvements will require improving ϵ_c through modifying the photorespiratory pathway (α; orange), increased ϵ_{prod} (blue) or increased ϵ_{use} (red). AOX, alternative oxidase; COX, cytochrome *c* oxidase; SWEET, Sugars Will Eventually be Exported Transporter; UQ, ubiquinone pool.

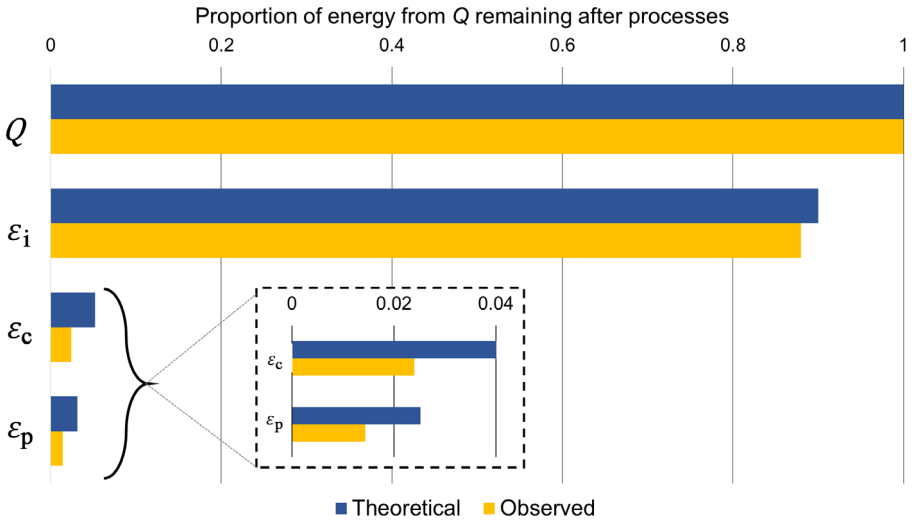

Fig. 2 Theoretical efficiencies of yield potential factors. Yield potential can be improved by increasing any of its factors – ϵ_i, ϵ_c and ϵ_p. However, only ϵ_c shows appreciable difference between its observed and theoretical efficiency and therefore stands as the best target for improvement. Energy remaining after ϵ_c processes is in the form of biomass, and a doubling would hypothetically flow downstream and double energy remaining during ϵ_p, that is yield. Q, incoming solar radiation for growing season.

structure, catalytic activity and interactions with other proteins (such as Rubisco activase) present both opportunities and limitations for engineering improvements in photosynthesis (Whitney *et al.*, 2011; Conlan & Whitney, 2018). Collaborations such as the Realizing Increased Photosynthetic Efficiency project (https://ripe.illinois.edu/) highlight the role of strategies such as introducing novel Rubisco types (Prins *et al.*, 2016), selecting for shorter photosynthetic induction (Acevedo-Siaca *et al.*, 2020) and improving stomatal CO_2 response of mesophyll conductance of CO_2 (Bailey-Serres *et al.*, 2019). Hyperspectral reflectance has also shown promising correlations to related traits, such as the maximum catalytic activity of Rubisco (V_{cmax}) and maximum rate of photosynthetic electron transport (J_{max}) (Silva-Perez *et al.*, 2018; Fu *et al.*, 2020). Focusing on such traits, and using emerging high-throughput, nondestructive methods of quantifying photosynthetic traits, provides opportunities to breed for increased α and through it, improve ϵ_c.

Modifications to photorespiratory pathways to reduce CO_2 loss

Another route to improving the efficiency of net photosynthesis is via modifications to photorespiration – the pathway through which the oxygenation reaction by Rubisco consumes RuBP to form 3-

PGA and 2-phosphoglycolate (2PG), the latter being converted to glycolate. The 2PG inhibits triose-phosphate isomerase and disrupts the Calvin cycle, emphasising the need not only to minimise Rubisco oxygenation, but also to efficiently metabolise 2PG once produced. This is achieved, in part, via the export of glycolate to the peroxisome where it is converted to glyoxylate and then glycine (resulting in the release of H_2O_2), with glycine being exported to mitochondria where it is decarboxylated by glycine decarboxylase (GDC) to yield serine, NH_3, NAD(H) and CO_2. Together, these reactions mean that photorespiration reduces the efficiency of net photosynthesis (and thus α and ϵ_c). Because of this, minimising Rubisco oxygenation and associated rates of photorespiratory CO_2 release are potential targets for improving yield potential. Importantly, any strategy to modify photorespiration needs to regulate the production and metabolism of toxic intermediates, the loss of nitrogen as volatile NH_3, and also consider the current role of photorespiration in wider amino acid biosynthesis and metabolism (Novitskaya *et al.*, 2002; Abadie & Tcherkez, 2019).

From a carbon metabolism perspective, photorespiration represents an energetically expensive process, either as an opportunity cost during Rubisco oxygenation (every O_2 bound to Rubisco represents a potential CO_2 that did not bind), or as CO_2 release during glycine decarboxylation. Rubisco oxygenation will be influenced by the relative specificity of Rubisco ($S_{c/o}$), leaf temperature and the intercellular and intracellular concentrations of CO_2 (Parry *et al.*, 2013), with the subsequent rate of photorespiratory CO_2 release varying depending on which metabolic intermediates are shuttled to other pathways (Peterhansel *et al.*, 2010; Busch, 2020). Reassimilation of photorespiratory CO_2 by Rubisco will also influence the extent to which photorespiration reduces α and ϵ_c (Sage & Sage, 2009).

Because of its potential to reduce the efficiency of net photosynthesis, many researchers have investigated the effect of mutations to different points in the photorespiratory pathway over the past 30 yr. These studies have revealed a wide range of 'photorespiratory phenotypes' that vary depending on the site of disruption to photorespiratory pathway and the environmental conditions in which plants are grown (e.g. see table 2 in Timm & Bauwe (2013) for a list of mutants and associated phenotypes). In many cases, knockout of key steps in the photorespiratory pathway is deleterious and potentially lethal. For example, in *Arabidopsis thaliana*, the most severe phenotypes show conditional lethality in GDC double knockout mutants (*gldp1* × *gldp2*) and serine hydroxymethyltransferase double knockout mutants (*shm1* × *shm2*) (Engel *et al.*, 2007, 2011). Other deletions result in a milder photorespiratory phenotype because of functional redundancy with other members in the gene family (Timm & Bauwe, 2013) and/or because of the plasticity of phenotypic response in photorespiratory mutants (Peterhansel *et al.*, 2013; Walker *et al.*, 2016). In any case, the available mutant studies highlight that fully knocking out the entire photorespiratory pathway is not a viable strategy and that photorespiratory modifications (to reduce photorespiratory CO_2 release) must consider reducing flux through the pathway, while regulating production and metabolism of toxic intermediates.

A range of studies provide examples of how modifications of photorespiration can increase biomass production (see Fig. 3), including: increasing CO_2 concentration around Rubisco (to reduce the rate of oxygenation) based on the modelled introduction of cyanobacterial carboxysomes; changing associations between chloroplasts and mitochondria; and engineering photorespiratory bypasses (Sage & Sage, 2009; Price *et al.*, 2013; Xin *et al.*, 2015; Betti *et al.*, 2016; Batista-Silva *et al.*, 2020). One example is the expression of CO_2 permeable aquaporins to improve membrane CO_2 conductance (Groszmann *et al.*, 2017; Zhao *et al.*, 2017; Ermakova *et al.*, 2021) and reabsorb emitted CO_2 in the chloroplast. Another example of the latter is recent work by South *et al.* (2019) who detail three alternative photorespiratory pathways (APs) in *Nicotiana tabacum*, two of which led to increased biomass and one which increased light-use efficiency. AP1 plants (with *Escherichia coli* glycolate oxidase genes targeted to the chloroplast) exhibited a 13% increase in plant dry mass. AP3 plants (with replaced malate synthase and glycolate oxidase) exhibited an 18% increase in the absence of an RNAi construct that reduced PLGG1 expression and 24% biomass increase with the RNAi construct – as well as increased glyoxylate and pyruvate, increased photosynthetic rate, increased chloroplastic CO_2 concentration and decreased serine and glycerate. These findings highlight the potential and viability of modifications to the photorespiratory pathway to improve plant growth.

Modifying respiratory metabolism to improve yield

Net photosynthesis determines the upper bounds of the plant carbon budget; however, understanding the fate of fixed carbon is just as important to ultimately improving Y_p. Photoassimilate from the Calvin cycle is stored or exported to sink tissues, where it can be respired to produce ATP, carbon skeletons and reductants. Between 30 and 60% of daily fixed carbon ends up being respired (Amthor *et al.*, 2019). The ultimate goal is to improve the efficiency of ATP synthesis and use, reducing the proportion of daily fixed carbon that is respired and improving yield through enhanced ϵ_c. This could be accomplished through improvements in $\epsilon_{biosynthesis}$ (Eqns B4 and B6). Knowing that respiration is a key component in determining available carbon for growth in a plant's carbon budget, we first explore the components of $\epsilon_{biosynthesis}$ (i.e. processes that influence the efficiency of ATP production and consumption).

Improving the efficiency of ATP production

To improve $\epsilon_{biosynthesis}$, one option is to consider ϵ_{prod} – the efficiency with which ATP and other respiratory products are made (Eqn B7). During oxidative phosphorylation, high-energy electrons generated during glycolysis and from the tricarboxylic acid (TCA) cycle are transported through a series of complexes along the inner mitochondrial membrane (IMM) to the terminal electron acceptor, oxygen. The flow of electrons through Complexes I (NAD(H) dehydrogenase), III (cytochrome bc_1 complex) and IV (cytochrome *c* oxidase, COX) is coupled to the pumping of protons across the IMM to create the electrochemical gradient that drives generation of ATP by Complex V (ATP synthase). Importantly, the plant IMM also contains rotenone-resistant dehydrogenases

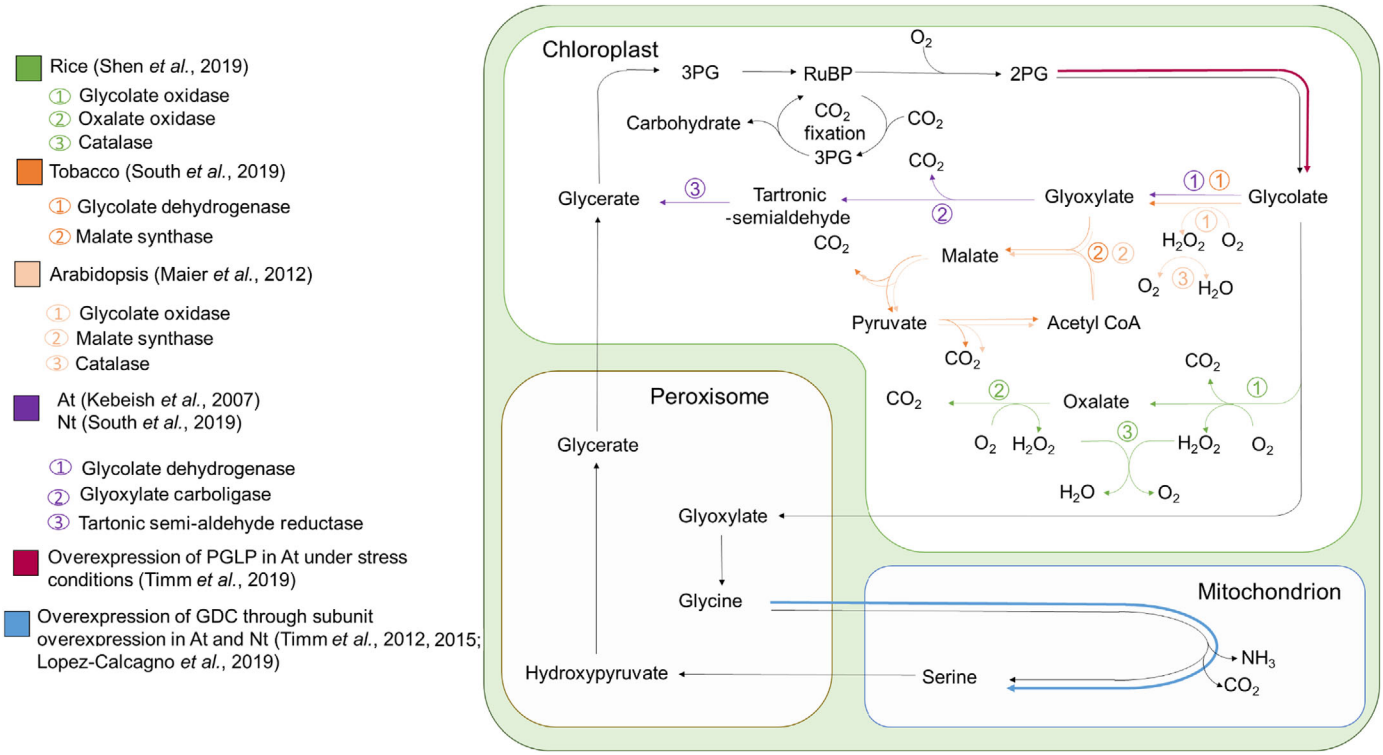

Fig. 3 Photorespiratory modifications can minimise carbon loss. Ribulose 1,5-bisphosphate (RuBP) oxygenation by Rubisco results in the photorespiratory pathway (black) being engaged to process 2-phosphoglycolate (2PG) back into the Calvin cycle via the peroxisome and mitochondria. Changes to the pathway (coloured) represent improved efficiency of photosynthesis by modifying enzyme activity or abundance, colocalising CO_2 release to the site of Rubisco and/or modified flux through a branch of the pathway (thick, coloured lines). 3PG, 3-phosphoglycerate; Acetyl CoA, acetyl coenzyme A.

(alternative DHs) that reduce the ubiquinone pool without utilising Complex I (Rasmusson *et al.*, 2004) and the cyanide-resistant alternative oxidase (AOX) that diverts the flow of electrons from the ubiquinone pool directly to O_2 (McIntosh, 1994; Vanlerberghe & McIntosh, 1997; Berthold *et al.*, 2000). The alternative DHs and AOX pathway reduce the efficiency of ATP production per mol substrate because electrons bypass either Complex I, or both Complex III/IV, respectively, resulting in a decrease in the number of protons pumped across the membrane such that the amount of ATP per unit of CO_2 released and/or O_2 consumed decreases. Similarly, dissipation of the electrochemical gradient also occurs when protons are transported through the IMM-located uncoupling proteins (UCPs) or mechanosensitive ion channels and results in reduced ATP yield, with energy being dissipated as heat (Sweetlove *et al.*, 2006; Lee *et al.*, 2016). Because of this, ϵ_{prod} has the potential to be inversely related to engagement of the AOX pathway and/or other nonphosphorylating/uncoupling pathways (Fig. 4). While we lack examples of where engagement of these pathways are linked to changes in ϵ_{prod}, low activity of them could – in theory – contribute to increased ϵ_{prod} and ultimately Y_p.

One challenge for improving ϵ_{prod} through targeting the AOX and/or other nonphosphorylating/uncoupling pathways is the fact that nonphosphorylating and uncoupling pathways broadly increase stress resistance. For example, AOX transcripts increase under stressed conditions such as the presence of inhibitors of mitochondrial electron transport chain (Saisho *et al.*, 1997; Polidoros *et al.*, 2005), chilling temperatures (Djajanegara *et al.*, 2002) and oxidative stress (Yukioka *et al.*, 1998). Loss of AOX makes plants susceptible to stress (Giraud *et al.*, 2008; Demircan *et al.*, 2020), and overexpression can improve plant stress tolerance (Dahal *et al.*, 2015; Gong *et al.*, 2020). Changes in UCP and NDH expression have similar effects (Taylor *et al.*, 2005; Arcuri *et al.*, 2021). Increases in the abundance of nonphosphorylating and uncoupling pathways enable plants to maintain flux through glycolysis and the TCA cycle under conditions of low ATP demand (i.e. enabling flexibility in the ATP yield and depending on demand). This flexibility comes with the trade-off of decreased efficiency in ATP production, and a decrease in ϵ_{prod} means that more assimilated carbon must be consumed to produce ATP. However, suboptimal ATP yield is counteracted by increased stress tolerance and blunt excision of these pathways may do more harm than good, as the aforementioned mutant phenotypes show.

Assuming in specific scenarios that changes in ϵ_{prod} could help increase $\epsilon_{biosynthesis}$, how might future studies incorporate screens for genotypic variability in ϵ_{prod} into breeding strategies? One approach is to quantify the relative engagement of these pathways *in vivo*. In the case of terminal oxidases, COX and AOX exhibit differential isotope discrimination when consuming O_2 (Guy *et al.*, 1987; Cheah *et al.*, 2014). When placed in a closed system, the ratios of ^{16}O and ^{18}O change through time; when coupled to measurements of overall O_2 uptake, rates of COX and AOX can be calculated. While such an approach could be used to screen divergent genotypes of crops, the method is currently low

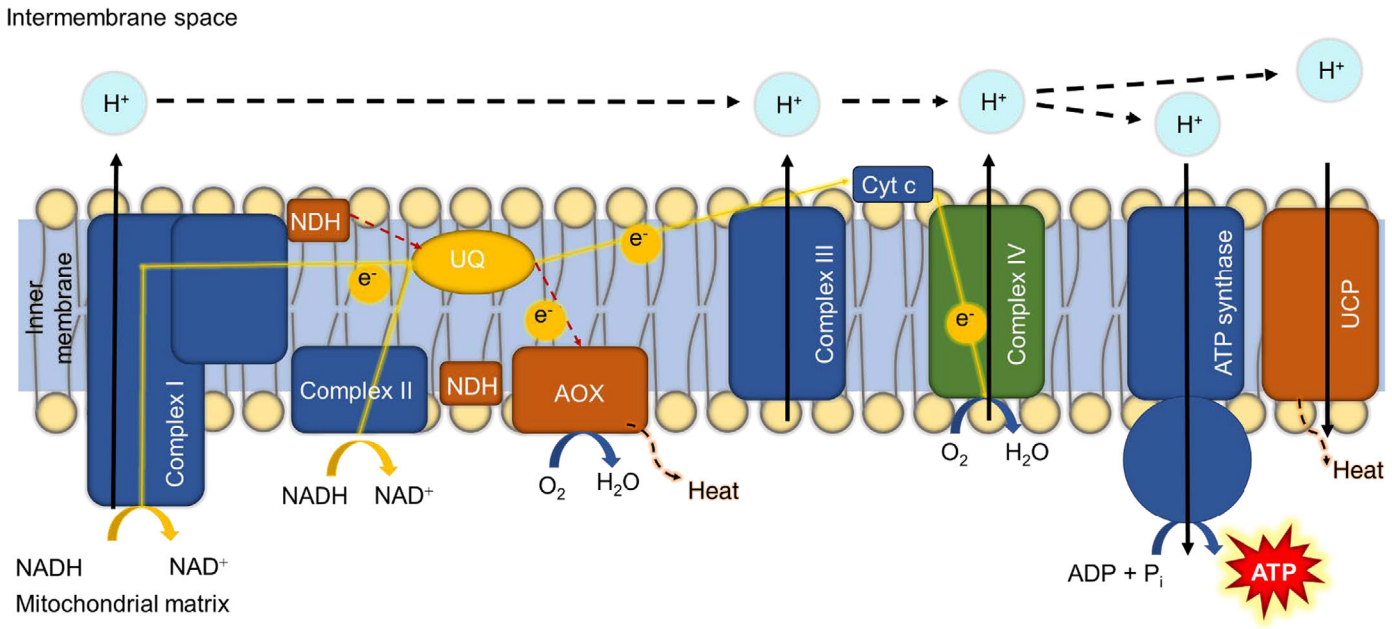

Fig. 4 Efficiency of ATP production decreases with increasing alternative oxidase (AOX) engagement. Electrons flow (yellow arrows) from Complex I and Complex II to ubiquinone pool (UQ). From UQ, electrons can be transported through Complex III to Complex IV as terminal oxidase. Complexes I, III and IV concurrently pump protons into the intermembrane space (dotted black lines) as they transfer electrons. Those protons drive ATP synthase and ATP production. However, electron flux through the alternative oxidase (dotted red lines) diverts electrons from Complexes III and IV and does not contribute to building proton gradient. Stoichiometrically, the AOX pathway is less efficient at ATP production than the COX pathway because significantly fewer electrons are pumped into the intermembrane space. Therefore, we hypothesise that to a first order, ϵ_{prod} will increase as either: (1) a higher proportion of electron flux passes through the COX pathway; or (2) AOX protein abundance decreases. Additionally, the presence of nonphosphorylating alternative dehydrogenases and uncoupling proteins reduce the ubiquinone pool but produce heat instead of ATP, also lowering ϵ_{prod}. ADP, adenosine diphosphate; Cyt c, cytochrome c; e^-, electrons; H^+, protons; NDH, nonphosphorylating alternative dehydrogenases; P_i, inorganic phosphate; UCP, uncoupling proteins.

throughput and requires sustained use of high-sensitivity mass spectrometers; thus, as currently available, the oxygen isotope discrimination method is unlikely to provide the rapid screening required by the crop breeding industry. Similarly, we lack methods to rapidly screen for variability in *in vivo* proton translocation via uncoupling pathways or the use of alternative NDHs. Thus, new approaches will need to be developed that enable *in vivo* rates through any or all of these alternative pathways in high-throughput measurements as part of screens of diverse germplasm. An alternative approach could be to employ a synthetic biology approach to modify their engagement. For example, Amthor *et al.* (2019) suggested engineering a light-specific AOX to replace constitutive expression, minimising AOX flux in the dark and improving ϵ_{prod}. A dual-track approach – using screens of diversity panels and a synthetic biology approach – would allow us to take advantage of natural variation in engagement of alternative pathways and engineered variation. Finally, further efforts need to be made to adapt the genetically-encoded biosensors developed for live monitoring of photosynthetic redox and energy status in chloroplasts (Müller-Schüssele *et al.*, 2021) to the monitoring of respiratory energetics in mitochondria.

Increasing the efficiency that energy is used

Improvements to $\epsilon_{biosynthesis}$ can also be accomplished through changes to the efficiency by which respiratory energy is used (i.e. ϵ_{use}) for biosynthetic, maintenance and active transport. Cellular respiration not only provides the energy required for metabolic reactions, but also creates the carbon skeletons necessary for biosynthesis and regulates the cellular redox environment in which these reactions to take place (Plaxton & Podestá, 2006; Millar *et al.*, 2011; O'Leary *et al.*, 2019). Changes in the efficiency of processes that use products of respiration can thus influence ϵ_{use}, with consequences for $\epsilon_{biosynthesis}$, ϵ_c and Y_p.

Biosynthesis costs of plant tissues are generally invariant Could ϵ_{use} be improved via screening for variation in the energy costs of synthesising new tissues? The energy demand associated with biosynthesis depends on two factors: (1) the ATP costs of making individual chemical constituents; and (2) the relative abundance of individual chemicals in plant tissues (De Vries *et al.*, 1983; Lambers & Rychter, 1989). Beyond acquisition (described later), minerals have no construction cost, and organic acids, total nonstructural carbon and total structural carbon are relatively cheap to produce (0.91, 1.09 and 1.22 g glucose g^{-1} dry mass, respectively). Meanwhile, the costs of synthesis are higher for lignin, protein, soluble phenolics and lipids (2.12, 2.48, 2.60 and 3.03 g glucose g^{-1}, respectively), and key components of energy organelles. Theoretically, differences in the chemical makeup of different tissues could mean that some tissues are cheaper to produce than others. However, in studies that have quantified the construction costs of plant tissues in a range of contrasting plant species,

relatively minor differences have been observed. For example, Poorter & Villar (1994) found only small differences in the construction costs for different functional types: a 6% difference between herbaceous and woody plants (1.45 to 1.54 g glucose g^{-1}, respectively) and a 4% difference between deciduous angiosperms and evergreens (1.52 and 1.58 g glucose g^{-1}, respectively). Additionally, environmental-limiting conditions ((CO_2), light and nutrients) have a minimal impact (≤10%) on construction costs. Underpinning the uniformity of construction costs is the fact that there are often trade-offs in the abundance of energetically expensive compounds. For example, fast-growing species are protein-rich, whereas slow-growing species contain high concentrations of lignin, with both compounds being energetically expensive to construct (Poorter & Villar, 1994), with there being a general trade-off between inexpensive and expensive constituents in both slow- and fast-growing species (Lambers *et al.*, 2008). Given these observations, targeting the efficiency of biosynthesis is unlikely to be the best strategy for improving ϵ_{use}. Rather, improvements are likely to come through a focus on the efficiency with which respiratory energy is used by processes of cellular maintenance and/or ion transport.

Improvements through targeting the energy costs of maintenance processes Perhaps of greater significance in determining whether a particular plant has low or high ϵ_{use} are the energy costs associated with *maintenance* of mature tissues (e.g. protein turnover and maintenance of solute gradients across membranes), which can consume 30–60% of daily fixed carbon (Penning de Vries, 1975; Amthor, 2000), with high costs being associated with slow growth rates (Lambers *et al.*, 2008). More recently, Amthor *et al.* (2019) outlined the opportunity to reduce energy costs of maintenance processes, including decreasing protein and membrane turnover, relocating and/or rescheduling metabolic activities, suppressing futile cycles in metabolism and reducing ion transport costs. As such, there is potential for ϵ_{use} to be improved through screening for variation in the energy costs of these processes and/or genetic manipulation of the underlying components of each process (Jacoby *et al.*, 2016; Amthor *et al.*, 2019).

Plants employ a diverse assortment of proteins for daily growth, metabolism and function, as well as in response to dynamic stimuli. The plant proteome is responsive to abiotic and developmental factors as well as carbon and nitrogen economy (Kosová *et al.*, 2011). Total protein content in a plant is not constant and changes in response to environmental factors such as salinity (Doganlar *et al.*, 2010; Jouyban, 2012), drought (Akhzari & Pessarakli, 2016) and heat stress (Giri *et al.*, 2017) to name a few. Protein abundance depends on the rate of protein synthesis (k_s) and degradation (k_d) (Li *et al.*, 2017; Ross *et al.*, 2021). As Li *et al.* (2017) note, these two processes are often combined to loosely define protein turnover, the process by which degradation of existing proteins and replacement with newly synthesised proteins modify the proteome. For a given time period, Ross *et al.* (2021) define total protein produced simply as the integral of k_s, whereas total protein degraded is expressed as an exponential decay function, with k_d as the rate constant. By relating protein abundance to rates, the authors find that k_d controls turnover under steady-state conditions, including after changes in k_s, as only k_d controls protein half-lives (see Ross *et al.*, 2021).

What do we know about the relationship between protein turnover and its associated ATP costs? Reflecting the factors mentioned earlier, it is clear that plants have evolved a complex system to regulate protein synthesis and degradation, allowing metabolism to dynamically adjust to changes in the type and abundance of proteins needed in different environments and growth stages (Vierstra, 2009; Marshall & Vierstra, 2018). Protein synthesis can be controlled at the transcriptional, post-transcriptional and translational levels, whereas degradation is dependent on post-translational regulation related to protein location and function, local environment and protein–protein interactions (Hinkson & Elias, 2011; Nelson & Millar, 2015; Huang *et al.*, 2020). The balance between synthesis and degradation dictates maintenance costs of protein turnover, either through differences in specific ATP cost of turnover or the absolute amount of turnover occurring.

While protein turnover can help plants adjust to new environments, it is energetically expensive. Each day, *c.* 6% of all proteins are replaced, with 6–10 mol ATP being consumed per mol peptide bonds undergoing turnover and 0.9–1.6 CO_2 per amino acid (Noguchi *et al.*, 2001; Nelson *et al.*, 2014; Ishihara *et al.*, 2015). Bouma *et al.* (1994) estimated that protein turnover in bean leaves accounted for 17–21% of darkened mature leaf respiration (*c.* 2.3 nmol CO_2 g^{-1} s^{-1}). In a review of previous research, Noguchi *et al.* (2001) reported that protein turnover consumes 3.5–60% of total ATP produced. In their own experiment, Noguchi *et al.* (2001) found protein turnover consumed 15.9–23.8% and 40.8–61.3% of total ATP produced in shaded and sunlit leaves, respectively. Quigg & Beardall (2003) reported that the proportion of maintenance respiration is attributable to protein turnover in higher plants, ranging from *Dactylis glomerata* roots (7%) to *Hordeum vulgare* full-grown leaves (30–60%). In wheat, protein turnover consumes approximately a third of total respiratory energy (Zagdańska, 1995). In Arabidopsis, 25–40% of ATP is used for protein turnover, depending on the age and growth rate of leaves, and this overall cost has been broken down to specific costs of maintaining different kinds of cellular organelles, metabolic pathways and enzymes (Li *et al.*, 2017). Specific proteins also play disproportionately large roles in turnover costs. For example, thiazole synthase (THI4) turnover can account for 2–10% of total maintenance respiration (Amthor *et al.*, 2019). Thus, while there is clearly considerable variability in the estimated ATP costs associated with protein turnover, what is clear is that reducing the costs of turnover could be a target for improving ϵ_{use}, particularly when designing plants for future, warmer climates. This is because turnover costs are likely to increase under conditions of environmental stress (e.g. heat, salinity and hypoxia) that accelerate the turnover of proteins, thereby consuming more of the ATP budget (Hachiya *et al.*, 2007; Edwards *et al.*, 2012).

Bearing in mind the goal of maximising ϵ_{use}, are there correlations between whole-plant growth and protein turnover? In *Arabidopsis*, larger (higher growth rate and rosette biomass) accessions reduced ribosome abundance at night, whereas smaller accessions maintained end-of-day levels of ribosomes (Ishihara

et al., 2017). Smaller accessions also had rates of protein synthesis up to 30% higher than the estimated rate required for growth, and up to 25% of the observed difference in relative growth rate could be tied to increased ATP costs of protein turnover. Gibon *et al.* (2009) found a tight correlation between growth, starch metabolism and protein content in *Arabidopsis* grown under different photoperiods, although they observed protein *amount*, not turnover rate. There are currently few studies in this space, but it should be considered a priority for further study, considering the substantial proportion of ATP use devoted to protein turnover.

Other substantive energy demands are phospholipid membrane turnover (*c.* 0.7 nmol $CO_2\ g^{-1}\ s^{-1}$) (Penning de Vries, 1975) and maintenance of ion gradients within cells; for the latter, Penning de Vries (1975) estimated that the total cost of maintaining intracellular ion gradients was *c.* 4.6 nmol $CO_2\ g^{-1}\ s^{-1}$ in some leaves, that is over 50% of respiratory rate. Lipids (a large part of membrane composition) are expensive to produce, costing nearly 3 g of glucose to produce 1 g of lipid (De Vries *et al.*, 1974) To our knowledge, little work exists on the specific construction costs or turnover rates of plant membranes. Prior studies show that whole-plant cell membranes can be fully turned over in 200 min (Warren & Glick, 1968; Steer, 1988). However, Hao & Maxfield (2000) found membrane turnover rates as low as 5–10 min in Chinese hamster ovarian cells. This large difference between very distinct cell types suggests more work remains to address gaps in how membrane turnover is supported by maintenance respiration. Similarly, considering protein turnover, improved measurement techniques will allow for fine-resolution, context-specific descriptions of synthesis and degradation rates, k_s and k_d, respectively (Nelson *et al.*, 2014; Ross *et al.*, 2021), across the multitude of subcellular and ambient environments experienced, allowing greater specificity of turnover characterisation. Variation in energy demands associated with maintenance can, therefore, have a substantive impact on ϵ_{use} of leaves. From the context of increasing ϵ_{use} and ultimately Y_P, minimising the energy costs associated with protein turnover, while maintaining adequate function, would present an opportunity to decrease the maintenance respiration costs incurred (Amthor *et al.*, 2019).

Lowering the energy costs of phloem loading A further factor that influences the demand for respiratory ATP is nocturnal carbohydrate export from mature leaves. Once synthesised in photosynthetic source leaves, sucrose (Suc), the main assimilate in most seed plants, needs to be loaded into the phloem for translocation towards nonphotosynthetic sink organs where Suc is unloaded. This source-to-sink allocation of assimilate plays critical roles in determining how biomass is translated into crop yield (Ruan, 2014; Fernie *et al.*, 2020). Opportunities exist to increase source-to-sink phloem translocation efficiency with no or little additional ATP cost as elaborated later.

In most species, phloem loading takes place either via the apoplast across plasma membranes or via the symplast through plasmodesmata (PD) at the interface of phloem parenchyma and the companion cell–sieve element (CC–SE) complex in developed leaves. The latter pathway also includes Suc moving from mesophyll and bundle sheath cells through PD into specialised CCs called intermediary cells, where Suc is synthesised into a raffinose family oligosaccharide for loading into the SE, the so-called polymer trap model. This pathway has been observed in *Cucurbita* genus and some trees (Fu *et al.*, 2011; Zhang & Turgeon, 2018). In apoplasmic phloem loading, the uptake of Suc into CCs is typically mediated by H^+- Suc symporters energised by plasma membrane-bound ATPase, while efflux of Suc from phloem parenchyma is facilitated by the energy-independent clade III Sugars will Eventually be Exported transporter (SWEET). Knockout of clade III SWEETs significantly reduced phloem loading, leading to a severe growth phenotype in a range of species such as Arabidopsis (Chen *et al.*, 2012) and maize (Bezrutczyk *et al.*, 2018). These findings indicate a major role of SWEETs in controlling Suc efflux for subsequent uptake into the CC–SE. It is therefore plausible that enhancing Suc efflux by increasing clade III SWEET expression or activity could improve phloem loading of Suc with no direct energy cost (and thus improve ϵ_{use}).

In parallel to apoplasmic loading, Suc may also be loaded into CC–SE symplasmically via PD (Braun *et al.*, 2014; Bezrutczyk *et al.*, 2018). In this case, phloem loading may be improved through increasing PD conductance by modifying sterol homeostasis or callose turnover or other PD-associated proteins (Zhang *et al.*, 2017; Fernie *et al.*, 2020). To this end, β-1,3 glucan synthase and β-1,3 glucanase are the two enzymes synthesising and degrading callose, respectively (Ruan, 2007; Zhang *et al.*, 2017). Thus, the knockout of η-1,3 glucan synthase could block callose synthesis at the PD neck region, while overexpressing β-1,3 glucanase could degrade callose at the PD neck region. Such changes would have the effect of 'opening up' or increasing PD conductance for symplasmic loading (potentially increasing ϵ_{use}).

The SWEETs also play an important role in unloading of Suc into sinks. Interestingly, clade III SWEETs could be bound and inactivated by SP6A, a homologue of FT and phloem-mobile tuberigen in potato tubers, which switches the apoplasmic unloading route into symplasmic unloading, triggering tubulisation (Abelenda *et al.*, 2019). This shows potential to optimise phloem unloading for yield gain such as tuber formation via manipulating SWEET activity. On the contrary, PD appears to impose major restrictions on the delivery of assimilates to meristematic sinks such as shoot or root apex and ovules (Ruan, 2012). In this context, computational modelling has identified inefficient delivery of carbon as a cause of floral and seed abortion on the secondary and tertiary branches of rice panicles (Seki *et al.*, 2015), likely due to low PD conductance in those high-order branches (Fernie *et al.*, 2020). Collectively, the above analyses indicate potential scope and avenues for improving phloem loading and unloading for growth and yield gain in an energy-efficient manner, with positive implications for ϵ_{use}.

Reducing the energy costs associated with root nutrient uptake Uptake of nutrients from the soil into roots is another major energy cost, with 50–60% of root respiratory ATP being used to support ion uptake (Poorter *et al.*, 1991). Importantly, the specific energy costs of ion uptake differ among species adapted to contrasting environments, with more respiratory ATP being needed to take up a given amount of nitrate in inherently slow-

growing species than their fast-growing counterparts, when plants are provided with high nutrient supply (Poorter *et al.*, 1991). The differences in the specific costs of ion uptake reflect the fact that: (1) there is an efflux of ions (e.g. nitrate) from roots, resulting in a reduction in the net rate of ion uptake; and (2) the extent of efflux is relatively greater in inherently slow-growing species than in fast-growing species (Scheurwater *et al.*, 1998, 1999). Such differences suggest that we may be able to increase ϵ_{use} via understanding the mechanistic basis for these differences.

Roots collect water and nutrients from the surrounding soil matrix, not only through bulk flow passive transport but also through active transport facilitated by transporter proteins. Active transport impacts ϵ_{use} by using ATP to transport nutrients across membranes, against a concentration gradient, to be assimilated by roots or transported to shoots (Xu *et al.*, 2012). In the case of nitrate, this movement is undertaken by nitrate transporter 1 (NRT1)/peptide transporter gene superfamily (NPF) that encodes transporters throughout the plant that allow its movement from root to shoot and ultimately nitrate reduction (Campbell, 1999; Plett *et al.*, 2010; Zhang *et al.*, 2020). However, as outlined earlier, nitrogen efflux from roots is common (Segonzac *et al.*, 2007; Xu *et al.*, 2012) and can contribute to high rates of respiration in slower growing plants as the ratio of nitrate influx to net nitrate uptake increases (Scheurwater *et al.*, 1998). Ideally, ϵ_{use} would be maximised through maintaining high rates of net nitrate uptake and assimilation per ATP used. This could be achieved through increased influx, decreased efflux or more rapid translocation to the shoot. Strategies including suppressed expression of nitrate efflux transporters such as NAXT1 (Segonzac *et al.*, 2007) or other anion channels (Teakle & Tyerman, 2010; Wege *et al.*, 2017), targeted overexpression of influx transporters with high NO_3^- selectivity (Fan *et al.*, 2016), increasing structural barriers to impede leakage in roots such as suberised hypodermal or endodermal layers (Barberon, 2017) and relocation of nitrate assimilation from roots to shoots have been proposed to increase biomass gains from lower respiration rates (Amthor *et al.*, 2019). Microbiome interactions, for example with arbuscular mycorrhizal fungi, also aid with nutrient uptake and growth promotion (Pascale *et al.*, 2020). Griffiths *et al.* (2021) studied hydroponically-grown *Zea mays* and found genotypic variation in specific root ion uptake rates, which were heritable and positively correlated with specific root respiration rates. Variation between two rice subspecies in their *NRT1.1B* transporter showed increased nitrate uptake and transport to shoots, as well as upregulation expression of root and shoot nitrate reductase genes (Hu *et al.*, 2015). As Griffiths & York (2020) point out, the extent of genetic variation in transporter traits such as energy costs of active transport is not yet well-characterised. Thus, variations in uptake kinetics exist and present another target for improved ϵ_{use}.

Linking respiration rates to photosynthesis, growth and yield

The earlier sections have shown that there is potential for variability in both ϵ_{prod} and ϵ_{use} to occur in nature, with consequences for $\epsilon_{biosynthesis}$ and ϵ_c. Amthor *et al.* (2019) estimated that a 10% reduction in the energy costs of maintenance could increase biomass accumulation by 6%, and a 20% maintenance respiration reduction could lead to gains up to 14%. This provides a rationale for screening genotypic variability in ϵ_{prod} and/or ϵ_{use} and therefore possibly identifying genotypes with improved yield. However, to be useful, such an approach needs an array of high-throughput methods capable of large-scale phenotyping of ϵ_{prod} (e.g. rapid assays of nonphosphorylating or uncoupling pathway engagement) and/or ϵ_{use} (e.g. measurements of the ratio of net to gross nitrate uptake and associated rates of root respiratory ATP production). However, such high-throughput tools are not available.

Consequently, we need to consider new ways of assessing variation in $\epsilon_{biosynthesis}$. Here, one option is to screen for variation in the relationship between plant respiration and photosynthesis (i.e. what fraction of daily fixed carbon is respired rather than conserved in plant biomass). Another is to look for variability in the relationship between respiration and relative growth rate (i.e. screen for genotypes that achieve high growth rates while also having low rates of respiration).

What evidence is there that rates of plant respiration vary among genotypes that differ in productivity? Here, insights can be drawn from the eco-physiology literature which has shown that inherently fast-growing species respire a lower fraction of daily fixed carbon than their slow-growing counterparts (Poorter *et al.*, 1990; Lambers & Poorter, 1992; Loveys *et al.*, 2002). Rates of whole-plant respiration are also *relatively* similar among species that differ markedly in relative growth rates, with high growth rates of some species being achieved without concomitant proportional increases in respiration rates. Such studies point to variation in $\epsilon_{biosynthesis}$ being an outcome of evolution, with $\epsilon_{biosynthesis}$ being highest in fast-growing species adapted to resource-rich, favourable habitats, and lowest in species adapted to resource-poor, unfavourable habitats.

Further evidence of the possible link between $\epsilon_{biosynthesis}$, biomass accumulation and yield comes from the work done on *Lolium perenne* (perennial ryegrass) in the 1980s. In a series of papers by Wilson, Jones and Robson, up to 13% increases in biomass accumulation and up to 40% increases in annual yield (in repeated years) were observed in plants grown under high-density conditions and selected for lower rates of mature leaf respiration (Wilson, 1975, 1982; Robson, 1982a,b; Wilson & Jones, 1982). In Wilson (1982), slow-respiring and fast-respiring progeny were produced by pair-crossing parents within either a slow- or fast-respiring cultivar. Additionally, progeny with low rates of mature leaf respiration were found to have higher net assimilation rate, relative growth rate, dry weight at harvest and leaf area index. Another study comparing selected fast- and slow-respiring ryegrass cultivars found the slow-respiring cultivar to have higher shoot and root mass at each harvest point (Day *et al.*, 1985). More recently, selection across multiple generations of lines with low respiration rates has been shown to be associated with higher yields in canola (Hauben *et al.*, 2009). Thus, there is some evidence that screening for variability in plant respiration rates may enable genotypes with higher ϵ_c to be identified, with future work needing to use screens to ultimately identify what genes are responsible for variability in $\epsilon_{biosynthesis}$.

The link between respiration, growth and yield is not, however, always consistent. For example, in perennial ryegrass, the relationship between low rates of mature leaf respiration and improved biomass accumulation disappeared when plants were grown in low-density swards (Kraus *et al.*, 1993), a result that was supported by a later study (Kraus & Lambers, 2001). Similarly, there is evidence that the growth of pea plants is linked to the efficiency of the respiratory system in some studies (Musgrave *et al.*, 1986) but not others (Obenland *et al.*, 1988). Thus, future efforts to explore the link between respiration, growth and yield will need to ensure that this relationship holds over a wide range of industry-relevant planting regimes.

One of the challenges facing work designed to link respiratory rates to photosynthesis, biomass accumulation and yield is the need to screen large numbers of plants for variability in traits of interest and to establish the genetic basis of variability in $\epsilon_{biosynthesis}$. In the past, assays of photosynthesis and respiration were painstakingly slow, limiting our ability to screen large numbers of plants. Similarly, growth analysis required repeated destructive harvesting of plants. However, in recent years, methods have been developed that enable each of these parameters to be quantified in high throughput. Growth analyses are now possible using light detection and ranging technology to quantify aboveground biomass in field experiments (Jimenez-Berni *et al.*, 2018; Furbank *et al.*, 2019; Walter *et al.*, 2019; Jin *et al.*, 2020). For respiration, a breakthrough was the development of a high-throughput, robotic fluorophore method for measuring respiratory O_2 uptake (Scafaro *et al.*, 2017). This method has provided the opportunity to screen hundreds of plant samples per day and has revealed that there is substantial variation in leaf respiration rates among genotypes of individual species, both in wheat (Scafaro *et al.*, 2017) and Arabidopsis (O'Leary *et al.*, 2017). Subsequent work has also shown that we can use hyperspectral reflectance signatures to predict variability in leaf respiration rates of laboratory and field-grown wheat (Coast *et al.*, 2019), further increasing our ability to screen respiration rates in field trials; similarly, hyperspectral reflectance can be used to predict photosynthetic capacity in wheat (Silva-Perez *et al.*, 2018). There is now an opportunity to use these methods to screen diversity panels and recombinant inbred line populations for variations in leaf respiration, photosynthesis and growth, and to identify quantitative trait loci for traits associated with high $\epsilon_{biosynthesis}$.

To fully exploit the potential for screens of variability in respiration rates to be used in strategies to improve $\epsilon_{biosynthesis}$, consideration needs to be given, not just to screening variations in leaf respiration (R_{leaf}), but also R_{stem} and R_{root}. An understanding of the fraction of whole-plant biomass allocated to leaves (LMF), stems (SMF) and roots (RMF), with rates of whole-plant respiration (R_{total}) being calculated according to:

$$R_{total} = (R_{leaf} \times LMF) + (R_{stem} \times SMF) + (R_{root} \times RMF) \quad \text{Eqn 2}$$

The challenge going forward will be developing high throughput, (ideally) nondestructive ways of estimating stem and root respiration, and the patterns of biomass allocation above and belowground.

How would a warmer world temperature affect ϵ_c?

Given that the world is warming, it is important to understand how rising temperatures affect ϵ_c. Noting that $\epsilon_c = \alpha \times \epsilon_{prod} \times \epsilon_{use}$ (Eqn B7), any temperature-dependent change in the factors and processes previously discussed would likewise influence ϵ_c. On a short-term timescale, increasing temperature past the photosynthetic optimum will decrease photosynthetic efficiency by decreased Rubisco carboxylation, damage thylakoid membranes and induce changes to vapour pressure deficit that result in stomatal closure (Mathur *et al.*, 2014; Dusenge *et al.*, 2019). At the same time, respiration, along with photorespiration and reactive oxygen species, is stimulated by increasing temperatures (Tjoelker *et al.*, 2001; Mundim *et al.*, 2020). Importantly, the initial imposition of heat likely results in an increasing proportion of respiratory ATP being used to support maintenance processes instead of growth (Gibon *et al.*, 2009; Scafaro *et al.*, 2021). Rapid increases in temperature result in membranes becoming more fluid and therefore leaky (Allakhverdiev *et al.*, 2008), decreasing ϵ_{use} as a result of more ATP being needed to maintain ion gradients across membranes and decreasing ϵ_{prod} as protons leak across the IMM (Divakaruni & Brand, 2011). Heat also increases the rate of protein turnover and associated demand for respiratory ATP, lowering ϵ_{use}. More severe temperature increases can denature proteins, deactivating enzymes and elevating the cost of maintenance chaperone and heat shock proteins, further lowering ϵ_{use} (Wang *et al.*, 2004). Such factors – combined with knowledge of the mechanisms via which plants adjust membrane fluidity (via alterations in the degree of saturation of fatty acids) and stabilise proteins (e.g. via synthesis of heat shock proteins), as well as thermally acclimate photosynthesis and respiration (Smith & Keenan, 2020) – will need to be considered in work targeting higher ϵ_c in crops developed to cope with more frequent and severe heat waves.

Considering abiotic stress more broadly, the complex, interacting nature of many of the components affecting energy efficiency in plants requires a multivariate investigative approach. Screening for trait variation in ϵ_{prod} and ϵ_{use} and isolation of genetic candidates via GWAS or QTL – while being an approach that can enhance classical breeding approaches – is complicated by the high degree of environmental sensitivity of ϵ_{prod}- and ϵ_{use}-related traits (O'Leary *et al.*, 2019; Scafaro *et al.*, 2021). As such, the experimental design used to screen trait ϵ_{prod} and ϵ_{use} variation needs to be done in ways that enable the roles of genetics and adverse environments to be clearly identified.

A further option to improve ϵ_{prod} and ϵ_{use} is to combine the above trait screens with additional approaches that harness the potential of genetic engineering. For example, modern genetic engineering techniques will permit the introduction of low-cost alleles that maintain stress responsiveness by targeting modifications to specific tissues only under permissive conditions, or by editing regulatory elements of promoters to better tune expression under such

Table 1 Summary of targets and opportunities for increasing yield potential.

ϵ_c component	Process	Target	Cost	Opportunity
α	Light and dark reactions of photosynthesis	Photoprotection and photoinhibition	15–20% loss of potential CO_2 fixation	Optimise photoprotective systems at the molecular *and* canopy level to avoid drop in quantum yield due to photoinhibition (Murchie *et al*., 2015) and increase the speed that NPQ relaxes following shift from sun to shade (de Souza *et al*., 2022).
		Photosynthetic induction	21% loss of potential CO_2 capture in wheat when induction is slow	Screen for natural variation in induction rate (Taylor & Long, 2017) – for example in amino acid substitutions and overexpression of Rca – to speed induction of photosynthesis following illumination.
	Carboxylation	Rubisco properties	Competitive inhibition, slow turnover, inactivation resulting in lower carboxylation rates	Study structure and catalytic properties of Rubisco (as in RIPE) to ultimately improve enzyme CO_2 fixing efficiency.
	Photorespiration	Oxygenation	Low Rubisco specificity to CO_2 leading to reduced net CO_2 uptake and increased H_2O_2 formation	Increase local CO_2 concentration – for example introducing cyanobacterial carboxysomes (Price *et al*., 2013; Long *et al*., 2021) which can lead to reduced photorespiration. Target *Escherichia coli* glycolate oxidase to chloroplast (Kebeish *et al*., 2007) to convert glycolate into glycerate and reduce photorespiratory carbon flux to peroxisome and mitochondria. Replace glycolate oxidase with *Chlamydo reinhardtii* glycolate dehydrogenase (Maier *et al*., 2012) to eliminate photorespiratory CO_2 release.
ϵ_{prod}	Mitochondrial electron transport and dissipation of the proton motive force	Alternative dehydrogenases and UCP	Reduce ubiquinone pool without engaging ATP synthase	Knockout of UCP (Sweetlove *et al*., 2006) lead to photorespiratory defects and decreased expression of type A NAD(H) dehydrogenases and AtNDB1 (Wallström *et al*., 2014) which resulted in delayed growth, knockdown of AtNDB4 resulted in better or unaltered growth under standard and stress growth conditions (Smith *et al*., 2011), while knockout of AtNDB2 lead to susceptibility to environmental stress (Sweetman *et al*., 2019). Therefore, a strategy for improvement will need to be tissue specific or timed to avoid these detriments.
		Alternative oxidase pathway	Flux through AOX does not pump protons into IMM	Replace constitutive AOX isoform with a diel-scheduled isoform (such as with a light-specific promoter region) to increase ϵ_{prod} at night (Amthor *et al*., 2019).
ϵ_{use}	Growth	Construction costs	Expensive constituents (lignin, protein, lipids) cost > 2 g glucose g^{-1} to construct	Employ Fourier transform (near-) infrared spectroscopy for high-throughput screening for variation of chemical composition in tissues (Collins *et al*., 2014).
		Membrane composition	Lipids in membranes are expensive to synthesise and leaky membranes can reduce efficiency of cellular processes	Engineer DNA nanostructures to mimic transmembrane proteins, regulate liposomes, modify membrane morphology and mediate membrane interface chemistry (Feng *et al*., 2021).
	Maintenance	Protein turnover	Large proportion of maintenance respiration	Slowing protein turnover may translate to higher growth rate and biomass (Jacoby *et al*., 2016), for example by modifying synthesis of THI4, a high-turnover protein (Hanson *et al*., 2018).
		Metabolic futile cycles	Inefficient energy use with no net gain in useful product	Minimising enzymatic sucrose degradation and resynthesis (especially that paired with active transport), or F6P/F16BP cycling under specific developmental or stress conditions (Amthor *et al*., 2019).
		Phloem loading	Active transport costs ATP	Upregulate SWEET/SUC/WAKL proteins to increase phloem loading, biomass and yield (Xu *et al*., 2020).

Table 1 (Continued)

ϵ_c component	Process	Target	Cost	Opportunity
				Replace hydrolase with phosphorylase to avoid ATP-dependent hexokinase phosphorylation (Marques *et al*., 2018).
		Nutrient uptake and translocation	ATP cost of ion uptake	Quantify unexplored genetic variation in transporter profile (Griffiths *et al*., 2021) to select for optimised traits of interest.
			High efflux of ions necessitates reassimilation	Suppress expression of efflux transporters such as NAXT1 and overexpress selective influx transporters (Segonzac *et al*., 2007; Fan *et al*., 2016) to reduce futile cycling of nutrients.

AOX, alternative oxidase; F16BP, fructose 1,6-biphosphate; F6P, fructose 6-phosphate; IMM, mitochondrial intermembrane matrix; NPQ, nonphotochemical quenching; Rca, Rubisco activase; RIPE, Realizing Increased Photosynthetic Efficiency; SUC, sucrose transporter; SWEET, Sugars Will Eventually be Exported Transporter; UCP, uncoupling proteins; WAKL, wall-associated kinase-like gene.

conditions (Zhang *et al*., 2018). The generation of a range of cis-regulatory element edits provides the opportunity to produce a wide range of expression levels of endogenous genes, producing a broader range of potential trait variation than can be seen in natural populations (Rodriguez-Leal *et al*., 2017; Liu *et al*., 2021). Because of this, trait stacking (i.e. incorporation of multiple genetic modifications into a single variety of a crop) via transgenesis has enormous potential to speed up the process of crop improvement compared with approaches that relay on traditional breeding approaches. Trait stacking has proven successful in improving crop resistance/tolerance to biotic stresses (Dormatey *et al*., 2020) where a binary response – immune or susceptible – can be easily assessed; with improvements in high-throughput phenotyping methods, the same is likely to be true for assessing the outcomes of stacking of traits that contribute to improved ϵ_c. While 'trait stacking' will not always deliver overall positive outcomes for plant metabolism and biomass accumulation – with balance between positive vs negative likely to depend on developmental stage, environment and management practices – there is clearly potential to create crop lines with marked improvements in ϵ_c through exploring the effect of multiple changes in energy-related traits.

Conclusions

As outlined earlier, annual increases in crop production are well behind that needed to meet future global demand for food, with new ways needed to improve yield potential (Y_p). Our review has highlighted opportunities to increase Y_p using a range of approaches – summarised in Table 1 – that target photosynthesis and respiration to improve the efficiency with which light energy is converted into biomass (ϵ_c). For photosynthesis, this includes changes in the properties of Rubisco and photosynthetic induction rates to increase carbon fixation (Table 1). Minimising photorespiratory carbon loss through metabolic engineering to increase carboxylation rates while still allowing oxygenation at a reduced but viable rate also shows promise (Table 1). Similarly, reducing the percentage of daily fixed carbon that is released through respiration could improve $\epsilon_{biosynthesis}$ – with there being potential to improve the efficiency of ATP synthesis (i.e. ϵ_{prod}) and/or ATP use (i.e. ϵ_{use}) to improve ϵ_c (Table 1). When such changes are brought together through a 'trait stacking' approach, there is potential to create additive or even multiplicative improvements to ϵ_c, and through it, a step change in Y_p.

Key to exploiting the potential to improve yields through increases in efficiency of photosynthesis and respiration will be the development of high-throughput assays that quantify components of ϵ_c. We suggest prioritising high-throughput and digital phenotyping of these components through hyperspectral and automated fluorophore systems and associated growth. The ability to phenotype variation in the balance between respiration, photosynthesis and growth across many plants would provide opportunities to exploit genetic variation in α and $\epsilon_{biosynthesis}$ – and through them ϵ_c and Y_p. Collectively, a focus on these strategies will inform breeding programmes targeting the increases in annual yield necessary to keep pace with increasing demand for food, reduce the amount of land used for agriculture, limit the demand for inorganic fertilisers and restrict greenhouse gas emissions from the agriculture sector.

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Author contributions

AG, OG and OKA initiated the review. AG and OKA wrote the manuscript. AFB, SAB, JRE, RTF, MG, AHM, BJP, MPR, Y-LR, NLT and SDT provided substantial contributions to the editing and revision of the manuscript.

Competing interests

None declared.

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