Review

Improving photosynthesis in agricultural environments

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There has been much recent interest in improving photosynthesis to increase crop yields. Here we evaluate strategies for increasing photosynthesis, focusing mainly on *Triticum aestivum* (bread wheat). We conclude that photosynthetic improvement needs to be viewed within a context of balancing feedbacks and resources (water, nitrogen) in an agricultural system with strategies required to best manage the source–sink dynamic during reproductive development to maximize radiation use efficiency (RUE). New genetic resources provide promise; genetic modifications (GM) of photosynthesis have not been sufficiently tested in field conditions. Trehalose 6-phosphate (T6P) chemical intervention increases photosynthesis and yield by activating grain filling sink strength. Technologies and breeding strategies that improve source and sink together currently provide the best prospects for improving crop photosynthesis and yield.

Higher crop photosynthesis for food security and carbon sequestration

Crop yields increased dramatically during the 20th century particularly as a consequence of The Green Revolution which tripled **yield potential** (see Glossary) for staple crops, wheat and rice [1,2]. Shorter stems led to greater carbon allocation to the developing spike, increasing spike dry weight at anthesis. This, in turn, improved spike fertility and yield through a higher **harvest index (HI)** [3]. Reduced plant height also decreased lodging risk, enabling the crop to better respond to fertilization and irrigation. With HI at or near a limit, there has been a major effort directed towards photosynthetic improvement to further increase crop yields, with leaf photosynthetic rate regarded in some assessments as 'the remaining major trait for crop improvement' [4]. In addition to improving food security, more photosynthesis and biomass accumulation can sequester carbon in soil in larger roots and crop residues, which may help mitigate climate change. Currently, it is estimated that plant breeding is increasing carbon soil inputs by 0.02 Mg C ha^{-1} year^{-1} and this could become greater with further interventions that increase photosynthesis, yield, and biomass [5]. More crop biomass would reverse the long decline in soil carbon caused by crop cultivation over the millennia, estimated as 133 Pg due to soil erosion, organic carbon mineralization, and removal in the harvested crop [6].

The focus on targeting photosynthesis for yield improvement has been controversial, as photosynthesis is regarded in many analyses as not limiting for agricultural yields and increasingly so as atmospheric CO_2 levels rise. Realized crop yield (as opposed to genetic yield potential) is co-limited by nitrogen and water, which are considered more of a constraint for crop productivity than carbon [7]. This is a view which had largely prevailed in crop improvement backed by analyses of yield gaps between potential yield and yield actually achieved [8]. Carbon accumulation in the absence of additional nitrogen does not increase yield [7] because of the requirement for nitrogen in grain and seeds. For bread wheat (*Triticum aestivum*) this is a particular issue as grain protein determines bread-making quality and market value. New higher yielding bread wheat varieties have required more nitrogen fertilizer to sustain quality [9]. In the case of water, Wu *et al.*

Highlights

Photosynthetic improvement must be viewed in the context of water and nitrogen constraints and the source–sink balance during reproductive development to maximize radiation use efficiency (RUE).

Genetic improvement of RUE to enhance source strength from stem extension to anthesis would increase spike fertility (by reducing floret mortality and grain abortion) and enhance sink capacity during grain filling, raising photosynthesis.

T6P signaling regulates source and sink and is a promising target for yield improvement. T6P signaling can be best modified with chemical methodology, increasing photosynthesis, improving yield potential and drought resilience, and tackling recalcitrant trade-offs.

Most genetic modification (GM) crops with improved photosynthesis lack full field testing. Targeting individual photosynthetic components offers limited room for improvement; whereas novel engineering such as of the malyl-CoA glycerate (McG) cycle may provide promise.

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pointed out the risks of crops with higher photosynthesis going into water limitation sooner because of more transpiration [10].

Complex traits, such as photosynthetic efficiency, that give competitive advantage to individual plants have likely been optimized by natural selection such that the potential for improvement by genetic engineering is very small [11]. For example, the photon yield of photosynthesis (mol CO_2 fixed per mol light absorbed, efficiency of light utilization) is very consistent across C3 and C4 species [12]. Despite prevailing arguments to the contrary, **Rubisco** has been described as almost perfectly optimized [13]. Natural selection of complex traits favoring individual plants does not necessarily translate to favorable expression in a crop stand of genetically uniform plants, a rarity in nature.

Models have traditionally linked photosynthesis as the driver of crop growth and yield [14]. Other models have placed emphasis on sinks being more dominant [15] as photosynthesis is regulated by the carbon demand from sink activity. Source or sink 'limitations' may, however, oversimplify complex biology where source and sink are balanced in a homeostatic system [16]. Despite a conclusion in wheat of source limitations pre-anthesis and sink limitations post-anthesis (Figure 1), many traits and processes do not neatly fit into source or sink categories, with many underpinning both [17]. By definition, 'adapted' cultivars balance carbon relationships so that neither source nor sink dominate but rather allow reproductive sinks to approximately match photosynthetic capacity.

After a major push to increase photosynthesis in crops over the last 15 years we critically assess progress for improved crop yield focusing on bread wheat. Our assessment is that photosynthetic improvement needs to be viewed within a context of balancing feedbacks and resources (water, nitrogen) in an agricultural system, with strategies required to best manage the **source–sink** dynamic during reproductive development to maximize RUE. Targeting individual photosynthetic components offers less room for improvement given these parameters have been optimized for fitness in the natural environment, whereas balancing source and sink for yield, less crucial for fitness, may not have been. Few **genetic modification (GM)** studies of photosynthesis have been validated over multiple years, locations, and relevant genetic backgrounds with farmer-realistic management. New breeding approaches that incorporate lost or novel germplasm plus chemical intervention that can activate multiple genes at once at key stages in an array of germplasm are providing the best immediate route for improvements in photosynthesis.

Have increased crop yields been associated with improved photosynthetic rate per unit leaf area?

A prevailing view has been that crop photosynthetic rate per unit leaf area has not increased through breeding improvement and that this justifies a targeted approach to increase photosynthetic rate [4,18]. Others would argue that because leaf photosynthetic rate is uncoupled from yield, it is not a good target for yield improvement [7]. Although this conclusion is made without knowing underground carbon accumulation or operational limitations of water, nitrogen, or soil-based factors. It has been argued that the photosynthetic mechanism is one of the best understood plant processes and hence its modification could be potentially straightforward to deliver quick wins [19,20]; however, this has not happened [21]. In the justification for targeting photosynthetic rates, Long *et al*. [4] cite Evans and Dunstone [22], who found a close relationship in 21 diploid, tetraploid, and hexaploid lines of wild progenitors and cultivated wheat, between the area of the largest leaf on the main stem and ear and individual grain weight coupled with a reduction in the rate of photosynthesis per unit leaf area [4,22]. This finding has been used to

Source Limited

Grain number/sink establishment:
- spike & spikelet architecture
- fertility

Overall plant and photosynthetic tissue development

Improvement of RUE and reproductive structure development

Sink Limited

Grain number/sink retention:
- Grain resource accumulation/metabolism
- flag leaf stay-green

Improvement of sink strength through T6P, linking sink to source.

Establish

Source **Sink**

Maintain

Yield

Co-limitation

Nitrogen Carbon Water

PRE-ANTHESIS

POST-ANTHESIS

Trends in Plant Science

Figure 1. Source–sink model for improving photosynthesis and yields in wheat. Strong source activity during early reproductive development establishes a strong reproductive sink which sustains photosynthesis during subsequent development and grain filling. Further enhancing sink strength post-anthesis through activation of the sucrose to starch pathway during early grain filling with trehalose 6-phosphate (T6P) increases photosynthetic rate of leaves during grain filling and yield. Targeting photosynthesis around reproductive development may minimize water loss associated with photosynthetic gas exchange compared with general upregulation of photosynthesis during the whole life cycle. Based on Lichthardt *et al*.; Reynolds *et al*.; Griffiths *et al*. [70,71,92]. Abbreviation: RUE, radiation use efficiency.

conclude that development of modern wheat has involved an increase in leaf size, with an accompanying decrease in photosynthetic rate per unit leaf area. However, the observed decrease in photosynthetic rate per unit leaf area may have been more than offset by greater radiation interception due to lower specific leaf weight. Thinner leaves increase total leaf area and, hence, light interception, even if photosynthetic rate per unit area declines. Thus, reduced leaf photosynthesis would not necessarily translate into lower overall crop photosynthesis. Further survey of the literature, however, finds many examples of breeding improvement of photosynthetic rate and leaf area together. Tian *et al.* [23], in 35 wheat varieties widely planted in the Yangtze River Basin from 1950 to 2005, show that the maximum rate of photosynthesis (photosynthetic capacity) was increased by between 2–5 µmol CO_2 m^{-2} s^{-1} (+10–66%) after anthesis combined with increases in leaf area, leaf area index, and duration of photosynthetically active leaf area [23]. However, if yield gains were driven primarily by enhanced photosynthesis, it would be expected that biomass would increase as well, which was not observed. It seems more plausible that higher leaf photosynthesis during grain filling may have been a consequence of increased sink strength,

rather than its cause. There is evidence of some relationship between photosynthetic rate and yield in winter wheat in the UK [24,25]. However, no consistent correlation was found between photosynthetic capacity of the flag leaf and grain yield when all cultivars were compared [24]. Active duration (stay-green) rather than the instantaneous photosynthetic rate best correlated with yield [25]. In spring wheat varieties in Australia and Mexico [26,27], there is evidence of increases in photosynthetic rate, which correlated most with stomatal conductance [26], although no yield data were presented in [27]. Hence, increases in photosynthesis with breeding improvement are widespread and complex at a whole plant level, and not always directly causal for yield, and at times may be sink-driven. In some cases, substantial boosts (10% and more) in photosynthesis are linked to chromatin/alleles from wild relatives [28]. To see if photosynthetic rate could be increased directly to increase yield, a large program has targeted leaf level processes through GM and we assess the progress of this.

GM of leaf photosynthetic rate

GM has been very successful and transformative in introducing traits of insect pest resistance and herbicide resistance in maize, soybean, and cotton. These traits rely on the modification of few genes with limited feedback interactions, which can confound GM of more complex traits [29]. Such GM crops increase yields and help reduce greenhouse gas emissions and support carbon sequestration in the soil by facilitating low tillage farming and reducing pesticide use [30,31]. For more complex traits that interact with carbon and energy homeostasis, a complex finely tuned whole plant process, there are many more considerations. If there is not a feedforward effect of photosynthesis on growth and filling of grain sinks, then feedbacks may limit source activity and the benefits of additional photosynthesis. For example, overexpression of Rubisco in sorghum (*Sorghum bicolor*) increases photosynthesis and vegetative biomass but decreases grain yield [32]. For simpler systems, synthetic biology is recreating carbon fixation (e.g., artificial leaf and in bacteria) [33,34]. A recent report shows a dramatic effect of engineering 'C2' photosynthesis [35]. The authors introduced an additional metabolic pathway, the malyl-CoA glycerate (McG) cycle into Arabidopsis (*Arabidopsis thaliana*). The plants converted glycolate produced by the oxygenation function of Rubisco into acetyl coenzyme A, which fed into endogenous lipid synthesis pathways. Plants with the McG cycle had increased lipids, seed yield, and overall biomass. If shown to work in crops, this could provide a breakthrough. Apart from this recent study, however, the intimate integration of photosynthesis with all major plant processes of growth and development in multicellular organisms make GM of photosynthesis in crops in a field environment a particular challenge. The highly ambitious attempt to transform rice to a C4 photosynthetic metabolism is a case in point [36]. Successful engineering of photosynthesis may require an intervention such as the McG cycle, to convert carbon into lipid, that avoids endogenous feedback mechanisms and does not require alteration and integration with leaf anatomy.

Milestones for modification of specific photosynthetic targets by GM have been detailed [20]. Ten years later, Araus *et al*. concluded that none had been met [21]. Khaipho-Burch *et al*. delivered a highly critical assessment of studies of GM targeting photosynthesis, stating that none were properly tested in a full agricultural context, as would happen with conventionally bred lines [37]. However, Vijayakumar *et al*. were more positive, stating that engineered increases in photosynthesis have recently been shown to substantially increase crop productivity under field conditions [38–43]. Vijayakumar *et al*. cited Nölke *et al*. [44], who demonstrated how expressing a transgenic polyprotein construct in potato led to increased productivity in terms of photosynthetic rate, as well as tuber yield and tuber dry matter content. Looking at the examples in Vijayakumar *et al*. [43] in depth, all were field studies except for Nölke *et al*., which was a greenhouse study [44]. Closer scrutiny of [39–41] shows tobacco was field tested. Tobacco is representative of C3 physiology and large canopies, however, lacks reproductive allocations suitable for studying

source–sink balance. Tobacco is not a crop that has been bred for seed or tuber production and is unrepresentative of food or feed crops. De Souza et al. [38] showed promising results in soybean expressing genes encoding proteins for fast recovery of photosynthesis after low light. However, some positive effects were achieved at a significance level of $P < 0.1$ and in one variety only in only one full trialing season (Table 1). Irrigation was used to establish the crop. While showing promise, the results of De Souza et al. [38] would need to be shown to be widely applicable in more genetic backgrounds and seasons in typical field environments without irrigation to establish the crop. Shen et al. showed promising results in rice from expressing a multigene photorespiratory bypass [45]. Grain yield was increased by +7% to +27% in the spring seeding season but reduced in the autumn season. Consistency would progress this finding.

For Rubisco improvement there is conceptual complexity from the view that Rubisco is an inefficient enzyme owing to its bifunctional nature and slow catalysis [46], to the opposite view that Rubisco is nearly perfectly optimized [13]. Contrary to popular wisdom, Rubisco may be slowly evolving for improved catalytic efficiency and CO_2 assimilation rather than being in a genetic *cul de sac* [47]. GM with superior Rubiscos to increase carboxylation over oxygenation has been proposed as a strategy, but would require correct assembly and regulation of new Rubisco after removal of native Rubisco, and potentially could disrupt the mobilization of nitrogen from Rubisco in leaves into grain sinks. Under stress conditions, oxygenation can dissipate excess light energy

Table 1. Increases of photosynthesis achieved by GM trialed in field conditions[a,b,c]

Crop	Transgene	Best observed increase in leaf photosynthetic rate	% yield increase per area of land (or per plant)	Years of full field trials	Irrigation used?	Limiting H_2O tested?	More than one variety tested?	Refs
Transcription factor								
Rice Wheat	GROWTH-REGULATING FACTOR 4	50%	Up to 73% per plant	1	Paddy	No	No	[53]
Rice	Maize GOLDEN-LIKE	Up to 48%	*30–40%*	3	Paddy	No	No	[51]
T6P pathway								
Maize	OsMads6-Tpp1	50%	*9–123%*	*>5*	*Rainfed and irrigated*	*Yes*	*Yes*	[29,75]
Rice	OsNAC23	10%	*13–17%*	1	Paddy	No	No	[80]
Brassica	BnTPS8	23%	*16–28%*	3	*Low and high rainfall*	*Yes*	No	[81]
Direct targeting of photosynthesis								
Rice	mEmBP1	33%	Up to 33% per plant	1	Paddy	No	No	[52]
Rice	Rubisco	16%	*Up to 20%*	*4*	Paddy	No	No	[42]
Rice	Photo respiratory bypass	Up to 20%	7–27% per plant in spring; decrease in the fall	3	Paddy	No	No	[45]
Sorghum	Rubisco	15%	Biomass increased; seed yield decreased	1	Yes	No	No	[32]
Soybean	Upregulation of VDE, PsbS, ZEP (VPZ)	Accelerated recovery from photoprotection	*Up to 33%*	1	Yes	No	No	[38]

[a]Food crops only. GM of photosynthesis has been achieved through direct targeting of the photosynthetic mechanism or its regulation.
[b]Italic emphasis means that requirements required for field testing new varieties have been met.
[c]Not in bold means further testing required, for example, to express yield per unit land area rather than per plant, to include more trialing years and include more varieties.

and maintain a metabolite pool to rapidly provide intermediates for the Calvin-Benson cycle when needed [48]. Prins *et al*. identified two superior Rubiscos amongst 25 genotypes which could direct mutagenesis strategies for Rubisco, if expression systems to test the effect of amino acid substitutions on Rubisco from monocots became available [49]. Alternatively, superior Rubiscos could be introgressed. Overexpression of native Rubisco increased photosynthesis and yield in paddy-grown rice [42]. Crucial to the success may have been the ready supply of nitrogen for additional Rubisco and grain growth. Additionally, water was not limiting in a paddy field setting; hence any cost of more transpiration from enhanced gas exchange did not impact in a fully hydrated environment. Increasing amounts of Rubisco may be less beneficial in water- [10] or nitrogen-limited conditions [7]. Recent results from elevating Rubisco in C4 crops sorghum and sugar cane show increased photosynthesis but no extra grain yield in field conditions [32]. **Gene editing (GE)** for Rubisco may generate structural changes to improve catalytic properties in favor of CO_2 [50]. GE has the benefit of precision and simplicity over GM approaches. New methods developed through engineering biology could overcome current technical limitations to potentially generate a paradigm shift if the complexity of photosynthetic regulation in crops becomes better understood. Incorporating the McG cycle [35], which deals with Rubisco oxygenation, by converting glycolate to lipid may be a way forward.

In other studies shown to increase yield in field conditions, in all cases paddy rice, success has been achieved by expressing transcription factors that regulate photosynthetic genes. Constitutive expression of nuclear-encoded GOLDEN2-LIKE (GLK) transcription factors enhance levels of chlorophylls and pigment-protein antenna complexes, improving light harvesting efficiency via photosystem II. Increased xanthophylls dissipated excess light, preventing photoinhibition [51]. Overexpression of transcription factor *mEmBP-1* in rice increased expression of genes encoding light reaction components and Calvin cycle, including Rubisco [52]. Another transcription factor, GROWTH-REGULATING FACTOR 4 (*OsGRF4*), promoted and integrated nitrogen assimilation, carbon fixation, and growth, antagonistically with DELLA; overexpression increased photosynthesis and yield in rice and wheat [53]. The success of all these cases may have been due to coordination of carbon and nitrogen metabolism combined with no water limitation (Table 1). However, except for the case of Rubisco expression in paddy rice [42] and expression of trehalose phosphate phosphatase (TPP) in maize [54] (Table 1), insufficient field testing has been performed for GM crops that target photosynthesis or regulators of photosynthesis. As pointed out by Khaipho-Burch *et al*. testing in a full agricultural context for any GM crop – elite lines, multiple years, normal spacing, irrigation only when it is the typical agricultural practice – needs to be performed as for any conventionally bred variety [37].

RUE
RUE is the efficiency with which plants convert intercepted solar radiation into biomass. General improvement of RUE in crop breeding has been underpinned by many traits such as altered stoichiometry of proteins related to dynamic photosynthesis and photoprotection mechanisms [55] being targeted by Kromdijk *et al*. and De Souza *et al*. [38,39]. Selection of upright leaves [56,57] and ideal plant architecture rice cultivars [58] distribute light more evenly through the canopy. From the late 1980s a focus on increasing crop biomass [59] has boosted spring wheat RUE [60] with genetic bases identified [61]. A challenge is to simplify laborious RUE determinations. **Hyperspectral imaging** sensors with a wide range of wavelengths have advanced the development of high-resolution spectroscopy techniques, increasing accuracy and the type of physiological property that can be retrieved [62–64]. In an association analysis, hyperspectral reflectance data linked quantum yield of photosynthesis with maximum activities of Rubisco and PEP carboxylase in elite maize and grain sorghum hybrids [65]. Optimization of stay-green to benefit canopy area and RUE is estimated to increase global wheat yield, especially under water stress where

faster leaf senescence is common [66,67]. Spike photosynthesis, a neglected trait, can intercept up to 40% of light incident on the canopy with significant genetic variation, which appears to be independent from leaf photosynthesis [68]. Similarly, light extinction coefficient as affected by N distribution in the crop canopy when assessed using hyperspectral reflectance data can improve prediction models of RUE [63]. In summary, improving RUE provides a major means to improving crop photosynthesis and yield as it can integrate many processes that positively affect photosynthesis and yield and enable coordination of source and sink.

Combining source and sink

Success in improving photosynthetic traits will depend on whether these changes effectively enhance sink strength; otherwise, the photosynthetic potential may not be fully realized or sustained. Crosses between high source lines and lines favoring sink variables such as fruiting efficiency, HI, grain number, and thousand-grain weight in wheat have improved yield and RUE across international yield trials [69]. Combining high source and sink to increase RUE may represent one of the most promising strategies to improve and realize photosynthesis capacity and yield potential. Yield gains can be boosted further if current knowledge gaps are filled, including respiration, stem reserves, root structure and function, how the former affects source–sink balance, and the role of hormones and sugar signals (see later) in coordinating these processes. New information would leverage extant knowledge and increase precision of models to inform hybridization and selection strategies [70]. However, there is still a complex interaction of factors that is incompletely understood.

During reproductive development, the source–sink interaction is pivotal for yield. Reproductive development places the highest demand on carbon supply. High photosynthesis pre-anthesis provides carbon for strong sink development of grain number and probably root capacity to keep photosynthesis active during grain filling [70]. Our thesis that source and sink are actively balanced during reproductive development in high yielding wheat is supported by a study over 3 years of 220 cultivars representing the breeding history of German wheat over 50 years [71]. Breeding progress has increased photosynthetic activity around anthesis, leading to higher grain number and, consequently, greater sink strength during grain filling – a prerequisite for yield gains derived from improved photosynthesis. The apparent coevolution of source and sink strength may reflect the source-limited establishment of post-anthesis sink capacity. For future breeding Lichthardt *et al.* suggest choosing parental lines with many grain numbers per spike and high photosynthetic activity around anthesis [71]. It is likely that targeting high photosynthesis during stem extension will also be beneficial as stem extension stage is very important for the determination of grain number [72]. The benefits of targeting photosynthesis to a discrete period around reproductive development and during grain filling are that water loss that can accompany elevated photosynthetic gas exchange will be restricted to this developmental period.

Genes and mechanisms that link source and sink together during reproductive development are not well characterized but could provide a basis for more targeted selection. Mechanisms are thought to involve hormones including cytokinin [73,74] and the sugar signaling mechanism mediated by **trehalose 6-phosphate (T6P)** [75]. T6P is a signal of **sucrose** availability and links sucrose transport from source to the grain sink by interacting with major protein kinase regulators, **SnRK1** [54,75,76] and TOR [77]. SWEETs in particular are regulated by T6P [75]; in wheat grain T6P also regulates sucrose transporters SUT [78]. Both SWEETs and SUT are likely to be regulated through SnRK1-mediated transcription. T6P is an inhibitor of SnRK1 [76]. T6P inhibition of SnRK1 stimulates the utilization of sucrose in growth and development and the synthesis of storage compounds such as starch (anabolism). The normal function of SnRK1 to conserve carbon and energy and to promote catabolism of reserves is inhibited by T6P. T6P has been shown to

activate TOR directly in combination with the inhibition of SnRK1 in the case of promoting lateral root growth [77]. Inhibition of SnRK1 and activation of TOR occur downstream of auxin repression of TPP transcription. Auxin repression of TPP transcription increases T6P levels. Elevated T6P then inhibits SnRK1 and activates TOR to promote root growth. Lyra *et al.* showed association of T6P pathway genes, trehalose phosphate synthases, (TPSs), and TPPs with reproductive traits such as spikelets per spike and spike fertility in the CIMMYT HiBAP wheat population [79]. Some of these genes were still undergoing positive selection, which may provide opportunity in yield improvement. Confirmation of likely success of an approach to modify T6P to increase source and sink together comes from studies where GM has resulted in large increases of yield >10% in crops in field conditions. Perturbing T6P by GM has increased yield in multiyear field trials in rice up to 17% [80], maize 9–123% depending on water availability [54,75], and in *Brassica* 27–70% depending on nitrogen supply [81] (Table 1). For these three examples, the mode of action of yield increase is T6P regulation of carbon fluxes and primary metabolism that affects both source and sink. In rice this was achieved through targeting a transcription factor NAC23 constitutively to decrease expression of a TPP gene to increase T6P. This increased photosynthetic rate, sucrose transport, and sink organ size. In maize, a MADS6 promoter was used to increase expression of a TPP gene in the phloem companion cells in florets and pith tissue of developing cobs, which decreased T6P levels and enhanced sucrose transport through SWEETs from pith tissue to kernels [75]. It appears that some SWEETs are repressed by T6P and others are induced, depending on cell type. In some cases, activation of SWEETS could represent a starvation response to correct a carbon deficit. Activation of sink strength also increased the rate of photosynthesis indirectly through enhanced sink strength. In *Brassica* overexpression of a class II TPS gene in leaves stimulated leaf metabolism, photosynthesis, and seed yield [81]. Class II TPSs are thought to be regulatory rather than catalytically active and may exert their effects through SnRK1 [82]. The modified crops in these three examples would need testing and backcrossing into other varieties for further validation.

Untapped genetic resources

Modern elite wheat has limited genetic variation, particularly in the D genome, due to historic genetic bottlenecks and intensive artificial selection by breeders [83,84]. In a major study of whole-genome resequencing of 827 Watkins landraces and 208 modern cultivars along with field evaluation, Cheng *et al.* concluded that modern cultivars are derived from just two of the seven ancestral groups of wheat [78]. The remaining five groups represent untapped genetic sources of landrace-specific alleles and haplotypes for breeding. CIMMYT is increasing genetic diversity using landraces and wild relatives [17,28,69,84,85]. Primary synthetics are being produced by hybridizing tetraploid durum wheat with *Aegilops tauschii*, the ancestral donor of the D genome, to recreate hexaploid bread wheat [86]. Landrace and synthetics have superior biomass in comparison with elite lines under heat [87] and drought [85,88]. Elite lines that include landrace or synthetic material in their background have been developed for drought, heat, and yield potential, including photosynthesis [28,61,69]. Encouragingly, for photosynthetic improvement, introgression of landraces into elite wheat germplasm may offer scope for raising flag leaf photosynthetic rate [89].
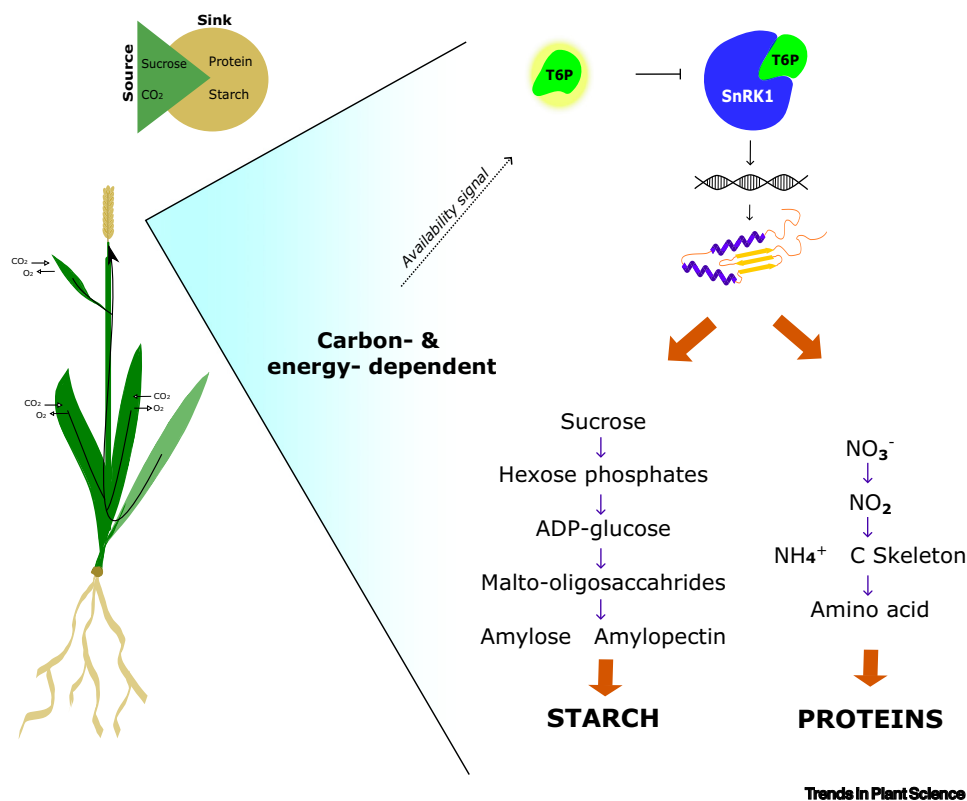
New technologies

Non-genetic technologies can overcome genetic complexity in crops, especially in wheat and issues of GM crop development costs and acceptance and offer a broader solution across crop groups, from arable to horticultural growing systems. With this in mind, a chemical strategy targeted the T6P sugar signal to regulate gene expression of starch synthesis [90]. Chemical application of T6P activates or 'primes' many genes at once through SnRK1 [91]. This is currently not possible in such a targeted way with current genetic methods. Beyond this, the benefits of a chemical approach are its immediate applicability to any crop, hence avoiding the need for

backcrossing into varieties suited to different locations as required for genetics. T6P compounds were synthesized incorporating a protecting group on the phosphate of T6P to create permeable T6P precursors that release T6P in planta in sunshine or bright light. After testing in a controlled environment [90], wheat photosynthesis and yield were increased in the field when T6P precursors were applied during early grain filling at 10 days after anthesis (DAA) [92]. T6P activated the whole sucrose to starch pathway and protein synthesis in grain. Enhanced sink strength in grain increased flag leaf photosynthesis. The results show that in addition to increasing source and sink activity pre-anthesis, as achieved through breeding [71], targeting the sink post-anthesis during grain filling is a viable approach to yield improvement (Figure 1). The same results are achieved whether the whole crop is sprayed, as would happen in the field, or if the spike only is targeted by spraying. It shows the mode of action is through upregulating metabolic pathways from sucrose import through to amylose and amylopectin synthesis in starch and nitrate reduction amino acid biosynthesis and aminoacyl-tRNA synthetases to protein synthesis in developing grain, likely achieved by T6P inhibition of SnRK1 [78]. Higher grain sink strength increases photosynthesis. Starch synthesis had been thought not limiting for grain yield [93].

Significantly, yield was increased irrespective of rainfall [92]. The short period of elevation of photosynthesis (10–20 DAA) in response to T6P treatment minimizes transpirational water loss associated with elevated photosynthetic gas exchange throughout growth [10]. Additionally, it may enable allocation of carbon to reproductive tissue rather than other competing vegetative sinks (which accompanied overexpression of Rubisco) if photosynthesis were stimulated during early growth [32]. The improvement of yield under wet years and dry years by effective targeting of sucrose allocation to grain filling indicates that yield potential and drought resilience can be addressed together rather than treated as separate traits as a generic strategy for combining yield and resilience.

In addition to combining yield potential and resilience, T6P precursor treatment dealt with two recalcitrant issues facing breeders – dilution of protein content in higher yielding grain and **trade-off** between grain size and number. As a metabolic regulator, T6P is able to activate both starch and protein synthesis, whereas breeding has favored starch synthesis over protein synthesis [92]. Improving carbon supply from the source may explain carbon and energy sufficiency for both enhanced starch and protein synthesis and increased grain size and number together, as there was less competition for carbon within the spike. Developmental regulators of grain size or number may increase grain size or number in a reciprocal manner without improving yield in many cases because developmental regulators may not link development with carbon supply [92]. Sucrose is the end product of photosynthesis and starting point for growth and T6P as sucrose signal may provide a means to link source and sink in a way not possible with developmental regulators. T6P enables yield to be improved per unit of nitrogen and water, hence sustainably, which is a major consideration (Figure 2).

The activation of the whole source to sink pathway cannot as yet be easily replicated by genetic means with current knowledge of source sink regulation or how to modify the T6P pathway or its downstream targets. Recent advances from T6P pathway gene-trait association studies may provide direction for genetic approaches [79]. T6P chemistry provides an immediate means to increase yield. If T6P stimulated yield by the average of 10.4% that we observed from field trials (wet and dry years at 10 DAA application), then the increase in global wheat yield average of 3.6 tons per hectare would be 0.37 tons per hectare (worth an extra $116 per hectare, wheat price in February 2023) amounting to $25.6 billion globally (221 million hectares grown in 2021). This will make the application cost effective and with further improvements in formulation and adjuvants, it may be possible to reduce application dose rate and/or exceed the current yield improvements.

Figure 2. Trehalose 6-phosphate (T6P) inhibits SnRK1 to activate starch and protein synthesis in wheat grain during grain filling (Griffiths *et al*. 2025 [92]). Enhanced sink strength through upregulation of pathways for starch and protein synthesis activates flag leaf photosynthesis. Grain size and grain number retention are increased with no dilution of grain protein. Yield is increased under abundant and low rainfall.

Another method based on sugar chemistry is the use of sugar-derived nanomaterials that promote light capture across photosystems. The carbon dots enhance electron transport in the thylakoid membranes, increasing photosynthesis because of their ability to exchange electrons when photoexcited [94] in a range of crops. Field trialing would show the full potential of this technology. Other nano technologies based around micronutrients have produced improvements in photosynthesis and yield, for example, one based around selenium [95]. Other biostimulants increase nutrient acquisition from soil and crop abiotic stress resilience [96]. The biostimulant field does appear to be burgeoning [96] and it will be interesting to see which applications stand the test of time in improving photosynthesis and yield in field conditions.

Concluding remarks and future perspectives

Ultimately how best to improve photosynthesis in crops has to be based around empirical evidence from agricultural conditions. Most progress has come through breeding, which may continue given recent progress in germplasm diversity and advances in phenotyping, especially for RUE [58,61,97]. The source–sink interrelationship, and ensuring that as much photosynthetic carbon flow ends up in grain rather than non-productively, is crucial. A new chemical method based on T6P increases photosynthesis and yield by >10% sustainably. To improve such a complex trait as photosynthesis genetically may require continued improvements in breeding and phenotyping to combine favorable genes for strong source and sink together. Additionally, technologies for pivotal source–sink regulators, such as that developed for T6P precursors or other

biostimulants for improved nutrient uptake and supply and abiotic stress resilience, may come into their own once technology is more fully developed. For GM of photosynthesis, much more testing in field conditions is required for validation of this approach. Genetic interventions such as engineering the McG cycle may provide a way forward (see Outstanding questions).

Declaration of interests

C.A.G. and M.J.P. are cofounders and shareholders of SugaROx, which holds rights to the commercial exploitation of DMNB-T6P. C.A.G. is a part-time employee of SugaROx. M.J.P. is a consultant for SugaROx. Patents have been filed on the use of DMNB-T6P on which C.A.G. and M.J.P. are named as inventors. No part of this study involved SugaROx. The remaining authors declare no competing interests.

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