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The Case for Improving Crop Carbon Sink Strength or Plasticity for a CO₂-Rich Future

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Highlights

- Large variation for yield response to increasing [CO₂] exists among current C3 cereal cultivars
- Poor response is due to acclimation caused by carbon sink and nitrogen limitation
- Low acclimation in wild crop relatives is due to undesirable plasticity and competition traits
- Quantitative ideotype concepts are needed for optimal sink capacity and plasticity traits
- Ideotype engineering may use the trehalose-6 phosphate feast/famine system

Abstract

Atmospheric CO₂ concentration [CO₂] has increased from 260-280 µmol mol⁻¹ (level during crop
domestication up to the industrial revolution) to currently 400 and will reach 550 µmol mol⁻¹ by
2050. C3 crops are expected to benefit from elevated [CO₂] (e-CO₂) thanks to photosynthesis
responsiveness to [CO₂] but this may require greater sink capacity. We review recent literature on
crop e-CO₂ responses, related source-sink interactions, how abiotic stresses potentially interact, and
prospects to improve e-CO₂ response via breeding or genetic engineering. Several lines of evidence
suggest that e-CO₂ responsiveness is related either to sink intrinsic capacity or adaptive plasticity, e.g.
involving enhanced branching. Wild relatives and old cultivars mostly showed lower photosynthetic
rates, less downward acclimation of photosynthesis to e-CO₂ and responded strongly to e-CO₂ due to
greater phenotypic plasticity. While reverting to such archaic traits would be an inappropriate
strategy for breeding, we argue that substantial enhancement of vegetative sink vigor, inflorescence
size and/or number and root sinks will be necessary to fully benefit from e-CO₂. Potential ideotype
features based on enhanced sinks are discussed. The generic ‘feast-famine’ sugar signaling pathway
may be suited to engineer sink strength tissue- and stage-specifically and help validate ideotype
concepts. Finally, we argue that models better accounting for acclimation to e-CO₂ are needed to
predict which trait combinations should be targeted by breeders for a CO₂-rich world.

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Introduction

Anthropogenic climate change since the beginning of the industrial revolution has adversely affected global yields of annual crops (Ray et al., 2019), whereby CO$_2$ fertilization benefits were more than offset by yield-reducing climatic factors (Iizumi et al., 2018). As global warming accelerates in the future, the effects of yield-reducing stresses will dominate and increasingly impact production (Zhao et al., 2017). Potential global arable land area is projected to increase as higher northern latitudes warm (Zabel et al., 2014), but current agricultural prime land is shrinking due to degradation and competition with other economic activities (Döös, 2002). Meanwhile, global demand for food is projected to increase by 69% from 2010 to 2050 (Pardey et al., 2014). Thus, there is an objective need to increase crop yields, whereas the changing climate tends to decrease them. Past achievements in yield increase essentially relied on increased harvest index and light interception through architectural changes. Further increasing harvest index of high-yielding cultivars would incur excessive lodging risks (Shah et al., 2019), and gains must now be achieved through increased biomass resulting from greater radiation use efficiency and photosynthesis (Fischer and Edmaedes, 2010).

Potential breakthroughs were recently reported on the engineering of C$_3$-type plants having increased photosynthetic potential, namely by reducing the photorespiratory loss (tobacco: South et al., 2019; rice: Shen et al., 2019) [The reported 40% biomass increase observed in tobacco, however, was questioned by Fischer (2019) on methodology grounds]. An alternative or complementary approach to enhancing the assimilate source system directly is to stimulate it indirectly by strengthening sinks (Ainsworth and Bush, 2011; Ruiz-Vera et al., 2017). Under current atmospheric CO$_2$ concentrations, which are about 50% higher that the pre-industrial levels (400 µmol mol$^{-1}$ vs 270-280 µmol mol$^{-1}$; Rubino et al., 2019), C3 crop growth and yield may frequently be sink limited (Borras et al., 2004; Ziska et al., 2004; Ludewig and Sonnewald, 2016). Therefore, C3 crops may not be able to efficiently use the higher CO$_2$ concentration expected to be present in the atmosphere in the coming decades if sink capacity is not increased to maintain balanced source-sink relationships (Sonnewald and Fernie, 2018). This is the rationale for our present review.

Several reviews (Paul and Foyer, 2001; Lawlor and Paul, 2014; Ludewig and Sonnewald, 2016; Paul et al., 2019) and opinion papers (Paul et al., 2017; Sonnewald and Fernie, 2019) have discussed the potential of increasing crop productivity by enhancing sink strength. In these reviews, the targeted sinks are most often reproductive and thus directly grain-yield related. However, all growth depends...
on sinks, including that related to tillering and root growth. Stimulating them could not only release
breaks due to downregulation of photosynthesis but also provide additional gains in terms of
drought avoidance (Griffiths and Paul, 2017; Fromm, 2019) or soil carbon sequestration via roots
(Suseela et al., 2017). Recent studies showed that sink enhancement by molecular engineering, e.g.
using the T6P (Triose-6-Phosphate) feast-famine system, increased both the productivity of the
targeted sink organ and crop photosynthesis (Oszwald et al., 2018), thereby boosting overall crop
biomass production (Nuccio et al., 2015). The stimulation of specific sinks does more than simply re-
direct (partition) assimilates within the plant. There is growing evidence that the whole-plant level
source-sink relationships are affected, stimulating leaf photosynthesis (source) through the rapid
removal of photosynthate from their sites of production (Fabre et al., 2019). This may involve long
distance signaling between sources and sinks through sucrose gradients that then translate locally
into T6P signals (Griffiths et al., 2016a). Understanding source-sink signaling and interactions has
important implications for future crop breeding and engineering, particularly to draw maximal
benefits for crops and agro-ecosystems from the globally rising atmospheric CO$_2$ concentration.

Fig. 1. Dynamics of atmospheric CO$_2$ concentration during the past 20,000 years. The current warm
period (Holocene) had 260-280 µmol mol$^{-1}$ CO$_2$ (pre-industrial levels) and was conducive to
development of civilization and domestication of crops. The recent increase in [CO$_2$] to >400 µmol
mol$^{-1}$ is anthropogenic. (Adapted from www.co2.earth)
Prior to the industrial revolution, atmospheric CO$_2$ concentrations were relatively stable for about 10,000 years at around 260 to 280 µmol mol$^{-1}$ (Fig. 1). The domestication and gradual improvement through selection of our main old-world cereal crops occurred during this period. This was followed during the last 150 years or so by an anthropogenic, exponential increase of [CO$_2$] which stands today at over 400 µmol mol$^{-1}$ and is expected to reach 550 µmol mol$^{-1}$ by 2050 (IPCC, 2014 & 2016; Smith & Myers, 2018). Our crops are thus exposed to a carbon resource that will soon be twice as abundant as it was when these species were domesticated as crops. FACE experiments (Free-Air CO$_2$ Enrichment: Ainsworth and Long, 2005; Fitzgerald et al., 2016; Hasegawa et al., 2017; Lv et al., 2020) have demonstrated the large potential for yield stimulation in C3-species under e-CO$_2$ in a large diversity of situations. However, there is large genotypic and experiment-to-experiment variation and meta analyses may carry a positive bias (Haworth et al., 2016). On the other hand, a negative bias may be caused by the effect of [CO$_2$] fluctuations in FACE setups which are much larger than natural fluctuations, suggesting that real-world stimulation by e-CO$_2$ on growth and photosynthesis is larger than observed in FACE trials (Allen et al. 2020). Are our current C3-crops able to fully exploit the potential provided by the increasing atmospheric [CO$_2$]?

In line with this question, there is growing evidence that large genotypic variation in e-CO$_2$ response exists, suggesting that there is scope for improvement through breeding. Moreover, this variation seems to be associated with source-sink relationships (e.g., Ainsworth et al. 2004; Hasegawa et al., 2013; Ruiz-Vera et al., 2017; Lv et al., 2020) prompting the need to better understand how sink strength feeds backward on photosynthesis. Such results also call for revisiting crop models which typically assume leaf photosynthesis to be driven only by genotype, external resources (light, CO$_2$, water), leaf nutritional status and stress factors, but not the plant capacity to remove assimilates from the source and use them in sink organs (Chang and Zhu, 2017).

Our purpose is therefore to review the evidence of acclimation of photosynthesis response of C3 crops to e-CO$_2$ concentration, to examine the causes of “downward acclimation” (Tausz et al., 2013), the interactions with some abiotic stresses, the main causes of cultivar differences in e-CO$_2$ response and how they may be related to domestication and breeding history, the design of crop ideotypes with the help of improved crop models, and the possibilities to engineer them experimentally. We will terminate with perspectives for improved breeding approaches.

High sink potential and sink plasticity improve e-CO2 response in C3-crops

Sink limitation of photosynthesis
It is well known that C₃ photosynthesis in the absence of physiological stresses is limited by the atmospheric CO₂ concentration, both at the pre-industrial level (ca. 270-280 µmol mol⁻¹; Fig. 1) and current level (ca. 400 µmol mol⁻¹), and even at projected levels for 2050 (>550 µmol mol⁻¹) as the saturating intercellular CO₂ level is above 600 µmol mol⁻¹ (von Caemmerer & Farquhar, 1982). If leaf photosynthetic rates were only determined by the constitutive properties of the photosynthetic apparatus and the environment it operates in (assuming the absence of stresses), the light- and CO₂-saturated rate (Amax) would be a constant system property. However, Amax changes with plant acclimation after plants are exposed to e-CO₂ for several weeks (Sage et al., 1989), and it also declines during the day, the degree of this decline depending on source-sink relationships (Fabre et al., 2019). Sink limitation feeds back on the photosynthetic rate as assimilates are not exported to sink organs at the rate at which they are produced. Consequently, e-CO₂ driven stimulation of the source (photosynthesis), or conversely sink pruning, reduces Amax and causes the diurnal decline of leaf photosynthesis, which in turn limits crop growth (Fabre et al., 2019).

Downward acclimation of photosynthesis to e-CO₂ is a commonly reported in C3 species (e.g., Tausz et al., 2013). A strong acclimation was observed in garlic, resulting in the absence of yield any gains from e-CO₂ (Nackley et al., 2016). In some cases, acclimation effects are absent like in radish (Usuda and Shimogawara, 1998), probably because the tuber has virtually unlimited carbon storage capacity. In addition to changes in photosynthetic parameters, acclimation can cause structural changes in the leaf (Zheng et al., 2019).

A decline of photosynthesis under sink limitation, as observed for rice under sink pruning (Fabre et al., 2019) has been attributed to end-product accumulation in photosynthetic tissues (Paul and Pellny 2003). Excess assimilates can negatively feedback on photosynthetic rate (Huber and Huber 1992; Iglesias et al., 2002; Li et al. 2015; Yang et al., 2016), possibly via leaf Triose phosphate utilization (TPU) capacity (Paul and Foyer 2001; Fabre et al. 2019). To avoid physiological damage, photosynthetic processes need to be down-regulated to avoid outright TPU limitation, probably involving co-adjustment of Vₖₘₐₓ (maximum carboxylation rate of Rubisco) and TPU parameters (Sharkey et al., 1988; Sage et al., 1989; McClain and Sharkey 2019; Fabre et al. 2019; Sharkey 2019).

Kirschbaum (2011) concluded in a review of crop responses to e-CO₂ that acclimation in most cases wipes out much of the potential gains in growth, largely due to the plants’ inability to use additional assimilates. Fatichi et al. (2013) went as far as calling for vegetation models to be sink and not source driven.

Greater sink potential enhances the yield response of crops to e-CO₂
Although it is not clear if TPU ever becomes rate-limiting for $C_3$ photosynthesis in a natural range of environments, inhibitory feedbacks clearly occur when sink activity does not match photosynthetic potential (Sharkey, 2019). Conversely, engineered enhancement of grain sinks can stimulate photosynthetic rate (and eventually increase grain yield), as demonstrated by Oszvald et al. (2018) using the T6P regulatory system, even in the case of the C4-crop maize (see section on T6P below).

Fabre et al. (2020) demonstrated that constitutive morphological differences in rice affecting source and sink capacity, namely flag leaf area and panicle size, are aligned with genotypic differences in photosynthetic responses to e-CO$_2$. Genotypes having large flag leaves and small panicles (and thus high local source/sink ratio) showed no increase in A$_\text{max}$ after a 15-d exposure to e-CO$_2$. A$_\text{max}$ increased substantially, however, when genotypes having low local source-sink ratio (small flag leaves, large panicle) were exposed to e-CO$_2$. The positive response of A$_\text{max}$ to e-CO$_2$ after acclimation in high-sink cultivars translated into greater yield gain (although the use of potted plants in growth chambers warrants caution here). Consistent with this, it was suggested that increasing A$_\text{max}$ of the flag leaf is important to improve rice yield potential particularly for e-CO$_2$ environments (Chen et al., 2007). A strong sink capacity may thus be necessary for increased A$_\text{max}$ to be expressed.

One would expect from these findings that genotypic differences in sink capacity might translate into crop yield response to atmospheric CO$_2$ concentration. This has been demonstrated by Hasegawa et al. (2013) for rice in FACE experiments in Japan: Genotypic yield response to e-CO$_2$ (200 µmol mol$^{-1}$ above ambient) ranging between +3% and +36% among 8 cvs. was observed in a single-site experiment and between +4% and 25% among 4 cvs. in a multi-site experiment. Effects were correlated with the spikelet number per unit ground area observed in the ambient (low) CO$_2$ concentration treatment. All genotypes were high-yielding types and the yield gain was mainly due to the number of fertile tillers. In FACE experiments in China, Lv at al. (2020) observed large genetic-group effects on the yield response to e-CO$_2$ (600 µmol mol$^{-1}$). Japonica inbred cvs. responded the least (+13.5%), indica inbred cvs. intermediate (+22.6%) and F1 hybrids the most (+32.8%), based on a large sample of 120 genotypes. The authors concluded that these genotype differences reflect different magnitudes of photosynthetic acclimation, with hybrids showing the least acclimation. The low e-CO$_2$ response (or strong acclimation, as presumed by the authors) of japonica types was mainly explained by their smaller capacity to adjust spikelet number per panicle (a sink trait) to the greater carbon source. A FACE treatment applying e-CO$_2$ only at post-heading stages benefitted yield of indica rice (+24%) more than japonica rice (+13%), indicating that the latter were probably more sink limited. The large body of experimental data from rice FACE trials in Japan and China combined indicate strong differences in e-CO$_2$ response among modern, high-yielding cultivars. The FACE trials
show that sink traits strongly affect genotypic e-CO$_2$ response, further supported by phytotron studies (Fabre et al., 2019 & 2020).

Greater sink plasticity enhances the response of crops to e-CO$_2$

A cereal crop’s sink capacity, in terms of the product of spikelet number per ground area and potential kernel weight, is a complex and plastic trait. Its components (tillering, tiller mortality, tiller fertility, inflorescence size and potential kernel weight) respond to external resources and show strong compensatory plasticity in rice, a cereal having small plasticity for kernel weight but large plasticity for tiller number and spikelet number per panicle (Kumar et al., 2016 & 2017). Modern maize cvs., by contrast do not tiller but “prolific” genotypes can compensate for wide spacing by increasing ear number per plant (Tang et al., 2018). Modern wheat cvs. tiller less than traditional ones, but highly plastic ear size and kernel weight provide adaptability to resource levels (Acreche & Slafer, 2009). One could therefore expect that a genotype’s adaptive or compensatory sink plasticity contributes to e-CO$_2$ response, in addition to the effects of constitutive differences in sink capacity.

Kikuchi et al. (2017) investigated this hypothesis for two rice diversity panels, using the response of tillering and spikelet number per panicle to plant population density as a measure of the phenotypic plasticity of sinks. Genome-wide association studies (GWAS) then provided quantitative trait loci (QTLs) for the plasticity traits, and a subset of genotypes carrying positive- or negative-effect alleles was subjected to e-CO$_2$ in a FACE experiment. The authors report greater growth and yield responses to e-CO$_2$ in the more plastic genotypes, thus validating the original hypothesis. Similarly, Kumagei et al. (2015) demonstrated that soybean genotypes exhibiting greater biomass and yield response to e-CO$_2$ also exhibited greater compensatory plasticity when subjected to differential planting densities. Genotypic differences in both e-CO$_2$ response and planting density response were very large, and both responses were positively correlated across genotypes. Consistent with this, Zhu et al. (2014) compared two rice cultivars differing in physiological and yield e-CO$_2$ responses. The poorly responding cultivar showed strong down regulation of photosynthesis (acclimation) whereas the more e-CO$_2$ responsive cultivar avoided acclimation through adaptive plasticity of sink capacity.

The combined results of Kumagei et al. (2015) and Kikuchi et al. (2017) make a strong case for a crop’s gap-filling capacity to be an enabling factor for biomass and yield gains under e-CO$_2$ conditions, for two annual crop species (rice and soybean) that are quite distant from each other biologically and phylogenetically. The gap-filling capacity, or ability to aggressively colonize resources through plasticity, can thereby be interpreted as the potential to opportunistically enhance existing sinks, or to generate new sinks through branching (e.g., tillering). The adaptive sink plasticity of the e-
CO₂ responsive rice cultivar described by Zhu et al. (2014) resulted in a greater ratio of spikelet number vs. flag leaf area (local sink-source ratio), driven by branching within the panicle.

**Effects of other resource factors and stresses on crop e-CO₂ response**

*Water and temperature interactions*

The crop water status seems to be an important factor interacting with the growth/yield response to e-CO₂. Indeed, under water deficit conditions, growth is more affected than photosynthesis, leading to carbohydrate accumulation in various plant parts (Muller et al. 2011) and this may impact photosynthesis response. Consistent with this, Fitzgerald et al. (2016) observed a +37% gain in wheat yield under e-CO₂ for an irrigated crop, but only +13% under water-limited conditions. Similarly, Tausz-Posch et al. (2015) found no superior e-CO₂ response in high- vs low-tillering wheat genotypes and suggested this to be due to the water-limited conditions in the FACE experiment.

A major effect of e-CO₂ is the partial stomatal closure which in turn may affect water status, and favor droughted plants. In principle, this effect should be dominating in C4 species where e-CO₂ is not expected to directly affect photosynthesis. Consistent with this, e-CO₂ stimulated photosynthesis and growth of maize under drought conditions, but not under well-watered conditions (Leakey et al., 2006). Drought can thus have opposing effects on e-CO₂ response, an indirect stimulation through stomatal regulation and a negative effect due to carbohydrate accumulation. According to Tausz-Posch et al. (2012), wheat genotypes having greater transpiration efficiency (TE) maintain this trait under e-CO₂, whereby e-CO₂ increased TE for all genotypes as expected.

The reduction of transpiration rate under e-CO₂ is large for irrigated rice (Shimono et al., 2019). Stomatal response to e-CO₂ thereby reduces transpirational cooling and thus can cause significant warming of the canopy (Yoshimoto et al., 2011). In fact, as an alternative to selecting genotypes that use e-CO₂ conditions for greater yield potential, breeders might consider selecting for lower water use while forfeiting potential increases in yield. Low stomatal density in rice was shown to conserve soil water (Caine et al., 2019). Interestingly, lower stomatal conductance as a trait in rice was reported to be associated with increased density of root aerenchyma, needed in anaerobic rice to supply the root with O₂ (Mohammed et al., 2019).

These observations demonstrate the numerous tradeoffs associated with changes in stomatal conductance, as a constitutive trait or induced by e-CO₂, or both: yield potential, drought avoidance, canopy temperature, and specifically for rice, the O₂ supply to roots. Fitzgerald et al. (2016) also reported a synergy between heat and e-CO₂ effects on wheat yield, observed at FACE trials located at
thermally different sites. Elevated temperatures and [CO$_2$] synergistically affect photosynthesis within temperature ranges the plants are adapted to (Caizhe et al., 2018; for tomato: Pan et al., 2018; wheat: Posch et al., 2019 (review)). However, increased canopy temperature can severely reduce cereal biomass and yield. Cai et al. (2016 & 2019) used factorial combinations of two temperature and two CO$_2$ levels in FACE experiments to study tradeoffs between the two factors for rice and wheat. In both crops, large yield reductions caused by a 1.5-2.0 °C temperature increase could not be fully offset by the yield gain caused by 500 µmol mol$^{-1}$ CO$_2$.

**Nitrogen interactions**

Growth stimulation by e-CO$_2$ causes significant dilution of mineral nutrients in the plant in the absence of concomitant increase of nutrient uptake. The resulting N deficiency can cause reallocation of N from Rubisco, which is the largest nitrogen pool in the plant (Makino, 2003; Kant et al., 2012; Weber and Bar-Even, 2019). A wheat crop grown in a CO$_2$ FACE experiment produced 30% higher grain yield under e-CO$_2$ but had 10% lower N concentration in grain (Maphosa et al., 2019). The decrease in N concentration, however, was not different between strong and weak responders to e-CO$_2$.

Myers et al. (2014) warned that nutrient limitation in crops under the influence of e-CO$_2$ will not only limit productivity but also the quality of human nutrition. Bloom et al. (2015) called for crop management and improvement strategies to enhance nutrient uptake commensurate with the increased yield potential. There may in fact be a substantial margin to genetically improve nutrient uptake along with the growth stimulation by e-CO$_2$. Hasegawa et al. (2019) investigated a rice variety (Takanari) that substantially increased N uptake and maintained grain quality as its yield was increased by 18% under e-CO$_2$ in a FACE experiment (3-year and 3 N-level average), whereas a common check variety showed grain quality degradation and no yield gains. These results demonstrate that yield gains under e-CO$_2$ are not only a matter of source-sink relationships but also depend on the adaptive plasticity of nutrient uptake. Consistent with this idea, Sakai et al. (2019) reported that strong genotypic differences in the yield response to e-CO2 among rice cultivars released over the past century in Japan were correlated with their ability to take up additional N.

Root growth stimulation upon e-CO$_2$ as shown in many cases (e.g., wheat: Uddin et al., 2018) may contribute, in a feedforward loop, to additional soil N and water acquisition needed under e-CO$_2$.

**Soil-volume interactions**

Arp (1991) and Bourgault et al. (2016) cautioned against extrapolating genotypic differences in e-CO$_2$ response from pot to field experiments. They demonstrated that the available soil volume per plant interacted with the growth response to [CO$_2$] and changed genotypic response patterns. Soil volume
effects on crop growth are not necessarily caused by resource limitations such as nutrients or water. Poorter et al. (2012) demonstrated in a meta-analysis that plants adjust growth to the accessible soil volume, apparently through an unknown sensing mechanism. These findings underline the importance of FACE experiments in this area of research. Controlled environments are suited to investigate biological processes but are rarely predictive of crop behavior in the field (Ainsworth et al., 2008a).

Have domestication and selection history limited crop responsiveness to e-CO$_2$?

Domestication of the major old-world cereals and subsequent selection/breeding processes, from ca. 10 millennia ago until the early 19$^{th}$ century, happened under low atmospheric CO$_2$ concentrations compared to today’s (260-280 µmol mol$^{-1}$; Fig. 1). Only during modern breeding were crops exposed to the current, rapidly rising CO$_2$ levels. Although human crop selection never involved exposure to increased CO$_2$ levels, it is likely that selection affected crop e-CO$_2$ response in some way because it necessarily affected source-sink relationships and the phenotypic plasticity of sinks.

Donald’s ideotype and the aptitude of wild species for domestication

Domestication shifts selection criteria from an individual’s survival and reproduction (maximized fitness frequently at the expense of neighbors; Weiner, 2019) to the productivity of a population of genetically similar individuals. Crop plants thus tend to share resources more equitably with neighbors, requiring some restraint on competitiveness (“Tragedy of the Commons”; Anten & Vermeulen, 2016). Competitiveness would cause redundant vegetative growth and stand heterogeneity. This concept is supported by Preece et al. (2018) who compared the phenotypic plasticity among grass species, some being wild progenitors to modern cereals and others that did not give rise to domestication. Plasticity was tested by growing plants in isolation or in a stand. The crop progenitors were less plastic and more similar in biomass and tillering between treatments, as compared to closely related species man did not domesticate.

The less aggressive gap-filling behavior of the crop progenitors, in terms of benefiting from open spaces [Hordeum vulgare ssp. spontaneum (barley), Triticum monococcum ssp. aegilopoides (einkorn wheat), Triticum dicoccum ssp. Dicoccoides (emmer wheat) and Secale vavilovii (progenitor of rye)] appears to be a step in the direction of Donald’s (1968) ideotype. This behavior necessarily involves a smaller capacity to develop more or larger organs in response to the availability to additional spaces (resources). This behavior is thus rooted in sink plasticity, particularly of vegetative organs, and is a developmental phenomenon.
Sink limitations in modern crops

A frequently reported but somewhat controversial view is that cereal crops are sink limited during vegetative growth and source limited during grain filling. Definitions of sink limitation and proxies used to evaluate it vary widely (Review: White et al., 2016) probably contributing to conflicting conclusions. Accumulation of non-structural carbohydrate (NSC) in leaves (and probably, in all tissues not specialized on storage) is a reliable indicator for sink limitation (Rogers & Ainsworth, 2006). Examples for the genericity of this proxy are found in several studies on a variety of species such as rice (Fabre et al., 2019 & 2020), tomato (Li et al., 2015), soybean (Rogers & Ainsworth, 2006) and oil palm (Legros et al., 2009ab).

Burnett et al. (2016) compared an annual cultivated barley with a perennial wild barley subjected to continuous 180, 400 and 1500 μmol mol⁻¹ CO₂ treatments in growth chambers over 61 days. The wild plants had lower photosynthetic rates than the cultivated ones under ambient [CO₂] but showed a greater positive response of photosynthesis, tillering, root-shoot weight ratio and biomass to increased [CO₂]. The cultivated species accumulated more NSC in vegetative organs than the wild barley in root and shoot at ambient [CO₂]. The authors conclude that the cultivated species was sink limited and the wild species source limited during vegetative development.

For wheat, the comparison of old and recent cultivars (released in 1903, 1921, 1965 and 1996) in growth chambers at 293, 385 and 715 μmol mol⁻¹ [CO₂] showed a clear trend towards smaller yield responses to e-CO₂ in modern cultivars (Ziska et al., 2004). Larger responses (and probably, smaller acclimation effects) in old cultivars were attributed to their greater tillering plasticity, enabling a better sink adjustment to the carbon resource. Of course, responses may be different in field-grown canopies involving intraspecific plant competition.

Too little information is available to judge if C3-type cereal cultivars are generally more sink limited than their ancestors. Borras et al. (2004) found modern wheat to be sink-limited during grain filling in most situations. By contrast, Acreche and Slafer (2008) compared Mediterranean wheat varieties released between 1940 and 2005 and found that the older ones were strongly sink limited. Recent cultivars had more balanced sink-source relationships as breeding had increased grain number. Sakai et al. (2019) studied the yield response of old and recent rice varieties to e-CO₂ in FACE experiments. They observed the strongest e-CO₂ response in older varieties but data were insufficient to establish a historical trend. Genotypic differences in e-CO₂ response were correlated with the genotypic ability to take up additional N to support the CO₂-stimulated growth. Similarly, a FACE study on Lolium perenne (Isopp et al., 2000) demonstrated a strong sink-limitation and accumulation of NSC in
response to e-CO$_2$ when N resources were limiting. These source-sink imbalances largely disappeared 344 in a high-N treatment, indicating the important role of N resources in e-CO$_2$ response. 345

We conclude that although there is insufficient evidence to support that modern varieties generally 346 lack sink capacity under e-CO$_2$ conditions during yield formation, evidence is accumulating that their 347 restrained sink plasticity during vegetative development, probably necessary to be good crops in 348 Donald’s sense, limits their overall growth response to e-CO$_2$. This may explain the positive 349 association between gap filling capacity (largely by tillering) in widely spaced crops and yield 350 response to e-CO$_2$ for cultivated rice (Kikuchi et al., 2017), and the observation that early variation in 351 rice tillering is positively correlated with the e-CO$_2$ response of yield (Ziska et al., 2013). Sink 352 limitation during vegetative development in modern cultivars under high ambient [CO$_2$] therefore 353 merits more attention in crop improvement because it limits the potential biomass gain.

Consequences for crop ideotypes better using e-CO$_2$

Crop ideotypes making better use of e-CO$_2$ need to minimize downward acclimation of 356 photosynthesis while maintaining the high potential photosynthetic rates of modern cultivars. They 357 should also satisfy Donald’s (1968) paradigm of restrained intraspecific competitiveness enabling 358 homogenous crop stands and avoiding redundant vegetative growth. It is thus not useful to revert to 359 archaic plasticity traits that breeders have de-selected even if they effectively reduce downward e- 360 CO$_2$ acclimation of photosynthesis. However, the principle of enhancing sinks to enable 361 photosynthetic rates unimpeded by acclimation under e-CO$_2$ conditions remains valid. The 362 magnitude of the required sink adjustments is substantial as [CO$_2$] in 2050 will be more than twice 363 the [CO$_2$] experienced during domestication and selection in pre-industrial times (260-280 µmol mol$^{-1}$), and 70 % higher than levels during the green revolution (ca. 320 µmol mol$^{-1}$). It is unclear to what 366 extent recent breeding has unwittingly achieved adaptation to current CO$_2$ levels (e.g. by increasing 367 grain number), as there is an astonishing diversity in e-CO$_2$ response among modern crop varieties 368 that is not fully understood.

Sink limitation during vegetative development might be corrected through increased, sink-driven 369 early vigor. Profuse tillering, although sometimes predictive of e-CO$_2$ response (Ziska et al., 2013; 370 Kikuchi et al., 2017) may not be the only way to achieve it. We hypothesize that increased leaf 371 number (Clerget et al., 2008), larger leaves and leaf sheaths, increased NSC reserve pools in the stem 372 functioning as active sinks (Slewinski, 2012), and enhanced root sinks may jointly enhance demand 373 for assimilate while avoiding the invasive weedy behavior associated with profuse tillering, which is 374 usually followed by high tiller mortality. Erect leaves, small tiller angle and small seminal root angle 375 (favoring deep roots; Huang et al., 2018) may control unwanted competitiveness. More vigorous root
systems might also enable the increased mineral uptake to support enhanced biomass. Combined with enhanced reproductive sinks, such traits may increase biomass production under e-CO$_2$, while maintaining the high harvest index already achieved in modern cultivars. More research is thus needed to test if these traits, are as effective as tillering in controlling e-CO$_2$ acclimation. Our hypotheses are summarized schematically in Fig. 2, projected onto the theoretical framework of sink-source relationships and acclimation of photosynthesis to e-CO$_2$.

If the hypotheses are valid, it will be useful to understand the gene networks and physiological pathways controlling the number and size of sinks, both for the vegetative and reproductive architecture of the plant. To predict improved ideotypes on this basis, appropriate crop models are also needed.

Fig. 2. Schematic diagram of source-sink interactions, downward acclimation of photosynthesis to e-CO$_2$ and adaptive plasticity of sinks. Key hypotheses of this paper are inserted in yellow boxes.

Challenges in quantitative modelling to design ideotypes

Donald’s (1968) ideotype concept facilitated the use of quantitative physiological understanding in crop breeding, i.e. design trait combinations that would enable high and stable yield in target ranges of environments. An example of using a crop model was the rice plant type with reduced panicle

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height combined with erect long uppermost-leaves (Setter et al., 1995). Dingkuhn et al. (1991) predicted a rice ideotype for high, direct-seeded stand densities on the basis of modified tillering and partitioning patterns. Both ideotypes influenced the successful development of Super Hybrid Rice in China (Yuan, 2017). Ideotyping may be extended to incorporate effects of major QTLs which can then be pyramided by marker-assisted selection (Gu et al., 2014; Kadam et al. 2019). Potentially, ideotypes can also be molecularly engineered as we will discuss further down. Whatever the genetic pathways used to build e-CO$_2$ efficient ideotypes, improved models are needed to orientate strategies towards relevant targets. They should able to predict observed genotypic differences for yield under variable [CO$_2$] conditions but also to cross-evaluate hypotheses. They should also integrate source-sink relationships across several biological and temporal scales.

At the leaf level and a time scale of minutes, sink limitation is characterised by TPU (Sharkey et al., 1988; McClain & Sharkey, 2019). At the whole-plant level and a time scale of hours, sink limitation is often indicated by sugar accumulation and the diurnal decline of $A_{max}$ (Fabre et al., 2019). Over days to weeks, sink limitation may build up and contribute to photosynthetic downward acclimation under e-CO$_2$ (e.g. Sage et al., 1989; Sakai et al. 2006). Over the whole crop cycle, competition for resources, compensatory growth responses and turnover of source and sink organs modify source-sink (Kim et al., 2003). Nitrogen and other mineral resources are key at this scale.

Presently, the general acclimation of both leaf and canopy photosynthesis to e-CO$_2$ can be modelled to some extent as an emergent property via a whole-plant feedforward mechanism, i.e. e-CO$_2$ increases carbon accumulation that dilutes plant nitrogen and causes more leaf senescence (Yin, 2013). Such a simple mechanism can avoid the overestimation by many crop models of the fertilisation effect of e-CO$_2$ on crop yield that was observed by Ainsworth et al. (2008a).

In addition to e-CO2 acclimation, the photosynthetic acclimation to other abiotic factors may involve mechanisms other than plant carbon/nitrogen status (Yin et al. 2019). For example, drought decouples growth from photosynthesis (Muller et al. 2011) and this uncoupling is diversely accounted for by models. Indeed some can be categorized as source-driven with drought induced leaf area adjustments being the consequence of reduction of photosynthesis whereas others are based on independent formalisms of photosynthesis and growth response to drought (Parent & Tardieu 2014, Muller & Martre 2019).

Another example of uncoupling of responses is provided by Matsui et al. (1997) who showed that at air temperatures above 30°C, filled spikelet fraction of rice was reduced under e-CO$_2$, a trend that is opposite to the interaction between CO$_2$ and temperature on photosynthesis. Reduced spikelet fertility was explained by reduced transpirational cooling (Julia & Dingkuhn, 2013) under e-CO$_2$, the
higher panicle temperature increasing pollen sterility. Modeling of crop response to e-CO$_2$ thus should also consider the heat balance and crop-generated microclimate.

Increased photosynthesis usually increases yield as seen in FACE trials, but genotypic variation in photosynthesis per se often does not correlate with yield (Driever et al., 2014; Gu et al., 2014). Are feedbacks from non-photosynthetic processes behind genotypic crop responses to e-CO$_2$? As discussed earlier, this may largely be the case, and acclimation of photosynthesis ultimately is an emergent response to complex carbon source-sink, developmental and nutrient dynamics at the crop level, involving adaptive phenotypic plasticity at several scales. To predict it and translate it into yield variation, a crop model would thus require skills to connect leaf level photosynthetic processes with the plasticity of developmental and morphological dynamics of the crop (sources, sinks and transitory storage), as well as nutritional dynamics (e.g., nitrogen) and to some extent the crop-generated microclimate. Parameterization of such a model will be a major challenge, both in terms of data requirements (phenotyping) and estimation of parameters that cannot be measured directly (e.g., reaction norms of developmental processes). A recent study showed that differences in phenology (phyllochron) during development and as a function of environmental (temperature, light) variation could be fully accounted for by intercepted radiation thereby offering a very simple mean to incorporate this behavior in a modeling algorithm (Baumont et al., 2019).

Building such a model should be a step-wise, iterative endeavor involving experimental research. Once proven valid for a reasonable range of conditions and genetic diversity, the model could be used to design ideotypes for future climatic conditions but also to inform biological engineering targets.

**T6P signaling, a lever to modify source-sink relations and engineer e-CO$_2$ responsive ideotypes?**

We are today technically equipped and sufficiently knowledgeable to genetically modify crop plants to express specific sink enhancements as warranted by an improved adaptation to e-CO$_2$ or by future crop production objectives in general. This approach, even if it may not necessarily provide societally acceptable cultivars for production, will increasingly be central to proving causative hypotheses and to develop and validate ideotypes for new or improved crops. We will focus here on the T6P feast-famine signaling system because of its omnipresence in higher plants, its regulatory involvement in all sinks, and the demonstrated feasibility of modifying it.

*Mechanics of the T6P system*
Trehalose-6-Phosphate (T6P) is a signal of sucrose concentration in plant tissues communicating the availability of C for growth and development. Plants have an absolute requirement for T6P signals to regulate sucrose utilization in physiological processes (Schluepmann et al. 2003). T6P inhibits SnRK1 (Zhang et al. 2009), a kinase related to the SNF1/AMPK protein kinases which are activated under starvation by AMP (adenosine monophosphate) to conserve ATP and C resources.

Inhibition of SnRK1 by T6P promotes the opposite of the starvation response, a so-called feast response. T6P-inhibited SnRK1 de-represses anabolism and represses catabolism enabling growth, development and biosynthetic processes to proceed. In plants and crops both feast and famine responses are necessary in different cells at different times and environmental conditions for growth and adaptation. The balance between survival and productivity has been shifted in crops towards the allocation of more C towards seed production with an increase in numbers and size of grain at the expense of stems. Both stems and seeds are sinks for C, but it is not known how increased harvest index has affected the overall plant source-sink dynamic. Seed sinks may be more easily perturbed by environmental stress than allocation of C to stem reserves, hence modern crops may become sink limited more readily, particularly under e-CO$_2$ and where stresses inhibit seed numbers and size. It may be expected that domestication and breeding of crops has exerted selection pressure on the T6P synthases (TPS) and phosphatases (TPP) of the T6P pathway. Accordingly, Hufford et al. (2012) listed both TPSs and TPPs as domestication improvement genes in maize.

Current and prospective use of T6P system for sink enhancement and ideotype engineering

As the T6P pathway regulates both feast and famine responses it can be a target to enhance productivity (feast) and the anabolic processes associated with it that support organ numbers and size; and at the same time to improve resilience (famine) processes to conserve grain numbers during stresses such as drought.

Oszvald et al. (2018) showed that through overexpression of a TPP gene in maize, primarily in phloem of florets, conservation of grain numbers was promoted during drought. Probably, the reduction of T6P promoted sucrose transport into developing grain as a famine response, preventing abortion due to lack of sucrose. Seven SWEET genes were upregulated in the transformed plants. Nuccio et al. (2015) reported for the same plant materials a significant increase in grain yield and biomass in the field due to TPP overexpression, for well-watered plants and more strongly under drought. Interestingly, enhanced grain number through expression of the TPP gene was associated with increased photosynthetic longevity of source leaves (Oszvald et al., 2018) suggesting that T6P through the stimulation of sink may also regulate the source as part of a source-sink homeostatic
mechanism. This offers clues as to how to increase photosynthesis to support stronger sinks through better source-sink relations.

Griffiths et al. (2016b) experimentally enhanced T6P through chemical intervention in A. thaliana and wheat plants, 10 days after anthesis, by spraying a plant-permeable T6P ‘signalling-precursor’ causing sunlight-triggered release of T6P in planta. The treatment increased grain size through promotion of feast processes.

For rising atmospheric [CO₂], the stimulation of both grain number and size via the T6P pathway may enable the sink enhancements necessary to maximize photosynthesis under e-CO₂ and sustain sink activity under abiotic stresses in C3 crops. Both examples (Nuccio et al., 2015 and Oszvald et al., 2018; Griffiths et al. 2016b) show that there is room to optimize the T6P pathway for grain numbers and size and hence this may be a promising target for breeding if natural, functional polymorphisms for the respective genes can be identified.

In terms of enabling the tailored engineering of crop ideotypes expressing sink modifications in specific organs and developmental stages, further research should adapt T6P gene transformation to various crop species and develop constructs (genome editing approaches) targeting the size and number of specific organs, developmental stages and environmental triggers for gene expression. This would constitute genetic engineering toolbox for the experimental creation of different source-sink and assimilate partitioning ideotypes.

Ways forward in crop breeding

Effective breeding for improved e-CO₂ response at a high quantity and quality level of yield in C3 crops will require (1) appropriate ideotype concepts and adaptive physiological traits to guide selection; (2) improved models better accounting for e-CO₂ acclimation, capable of predicting the yield benefits of the targeted traits in variable environments; and (3) scalable phenotyping and selection tools. None of those are currently available. However, avenues can be envisaged.

For most high-yielding crops, the general approach would be to increase biomass production while maintaining the high harvest index and increasing nutrient uptake commensurate with the stimulated growth (Ainsworth et al., 2008b). Tausz et al. (2013) called for traits that would help avoiding “downward acclimation” of photosynthesis by adjusting the source-sink balance not only during grain filling (seed number and size) but throughout crop development (tillering or branching, NSC storage in vegetative organs). Moving towards this direction clearly requires proxies that can be used to characterize the plant material preferably at early stages and at high throughput. For instance, Ziska et al. (2013) reported that the tillering response to e-CO₂ in juvenile rice (a plasticity
trait) was predictive of e-CO$_2$ response of yield across different thermal regimes and for both modern and wild rice lines, and may thus be used as a proxy. Other studies on rice (Kikuchi et al., 2017) and soybean (Kumagai et al., 2015) support this idea. The local source-sink ratio in rice (flag leaf vs. panicle size; Fabre et al., 2020) may be another morphological proxy for e-CO$_2$ response potentially scalable in breeding. Such morphological and developmental proxy traits should be validated for large populations in FACE trials prior to any practical application in breeding. As discussed earlier, there may be other sink traits increasing vegetative growth vigor and may thus relate to e-CO$_2$ response, as an alternative to tillering where it is not wanted. The search for scalable proxy traits in breeding for e-CO$_2$ responsiveness has barely begun. Several authors called for increased root/shoot ratio to improve adaptation to climate change (review: Korres et al., 2016). This may not only improve crop drought avoidance and enhance C sequestration in the soil (Suseela et al., 2017) but may also be essential to meet the increased nutrient demand (Tausz et al., 2013) and maintain grain quality (Hasegawa et al., 2019) under e-CO$_2$. Increased root/shoot ratio should translate into a greater soil volume accessed by roots to result in greater nutrient uptake (Poorter et al., 2012) – thus requiring sufficient soil depth and appropriate cultural practices. As for the other sink traits, the challenge is to express these root traits in a plastic (e-CO$_2$-responsive) fashion, requiring proxy traits that are easily used in selection. Where reliable proxy traits cannot be found, molecular selection or engineering may be eventually more promising because FACE experiments will probably always be too costly to host conventional breeding setups.

**Conclusion**

We found strong evidence for the potential to substantially increase crop photosynthesis, biomass and yield by enhancing carbon sink capacity that would, in turn, stimulate carbon assimilation. This would be particularly effective in annual C$_3$ crops whose photosynthesis is sensitive to the recent and anticipated rise of atmospheric [CO$_2$]. Much of the evidence provided concerns rice and wheat but is likely extendable to other major C$_3$-crops. More research is needed to better understand what lies behind the strong cultivar differences consistently observed in field e-CO$_2$ response. We raise the hypothesis that major processes accounting for differences in acclimation are sink and N limitation. We have illustrated that some equally high yielding cultivars are able or unable to adjust (increase) sink potential and N uptake. Similarly, compensatory plasticity of tillering and inflorescence size as observed in plant spacing experiments seem to contribute to the ability to minimize e-CO$_2$ acclimation.
Wild crop relatives and very old cultivars tend to respond better than most modern crops to e-CO$_2$ due to aggressive gap filling behavior and competitiveness, but on the basis of lower photosynthetic rates. Adopting such archaic traits in breeding would sacrifice essential features of a good crop. Instead, a more constitutively expressed and targeted sink enhancement may be a better strategy. This calls for quantitative modeling to design ideotypes and methodologies to validate them. The appropriate predictive models should consider how acclimation to e-CO$_2$ will interact with stresses such as drought and heat.

It may be possible to genetically engineer experimental ideotypes that express desirable patterns of sink enhancement, by using organ-specific, T6P-based, ‘feast-famine’, sugar signaling. This approach can in principle be applied to any C3 crop, and the engineered ideotypes can be validated in FACE e-CO$_2$ field environments. There are also opportunities to breed in more conventional ways for improved crop response to e-CO$_2$ but this will hinge on the availability of valid and easily measurable proxy traits.

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Conflict of interest statement

Nothing declared.

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