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The Case for Improving Crop Carbon Sink Strength or Plasticity for a CO_2-Rich Future

Michael Dingkuhn[1]*, Delphine Luquet[1], Denis Fabre[1], Bertrand Muller[2], Xinyou Yin[3], Matthew J. Paul[4]

[1]CIRAD, UMR 108 AGAP, F-34398 Montpellier, France
[2]INRA, UMR 759 LEPSE, Institut de Biologie Intégrative des Plantes, F-34060 Montpellier, France
[3]Centre for Crop Systems Analysis, Dept. Plant Sciences, Wageningen University & Research, Wageningen, The Netherlands
[4]Plant Science, Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, United Kingdom
*Corresponding author <michael.dingkuhn@cirad.fr>

Highlights

- Large variation for yield response to increasing [CO_2] 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 CO_2 concentration [CO_2] 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 [CO_2] (e-CO_2) thanks to photosynthesis responsiveness to [CO_2] but this may require greater sink capacity. We review recent literature on crop e-CO_2 responses, related source-sink interactions, how abiotic stresses potentially interact, and prospects to improve e-CO_2 response *via* breeding or genetic engineering. Several lines of evidence suggest that e-CO_2 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-CO_2 and responded strongly to e-CO_2 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-CO_2. 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-CO_2 are needed to predict which trait combinations should be targeted by breeders for a CO_2-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 a*l., 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.

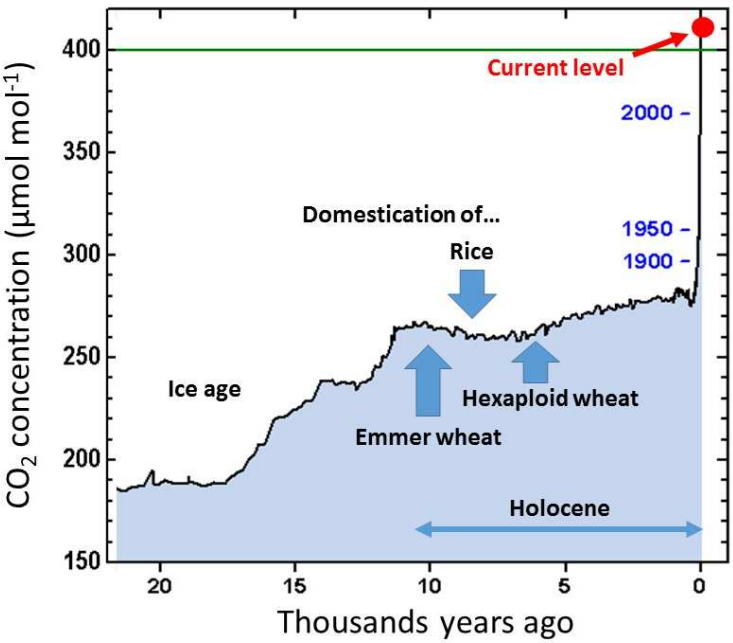

Fig. 1. Dynamics of atmospheric CO_2 concentration during the past 20,000 years. The current warm period (Holocene) had 260-280 µmol mol^{-1} CO_2 (pre-industrial levels) and was conducive to development of civilization and domestication of crops. The recent increase in [CO_2] to >400 µmol mol^{-1} is anthropogenic. (Adapted from www.co2.earth)

86 Prior to the industrial revolution, atmospheric CO_2 concentrations were relatively stable for about
87 10,000 years at around 260 to 280 µmol mol^{-1} (Fig. 1). The domestication and gradual improvement
88 through selection of our main old-world cereal crops occurred during this period. This was followed
89 during the last 150 years or so by an anthropogenic, exponential increase of [CO_2] which stands today
90 at over 400 µmol mol^{-1} and is expected to reach 550 µmol mol^{-1} by 2050 (IPCC, 2014 & 2016; Smith &
91 Myers, 2018). Our crops are thus exposed to a carbon resource that will soon be twice as abundant
92 as it was when these species were domesticated as crops. FACE experiments (Free-Air CO_2
93 Enrichment: Ainsworth and Long, 2005; Fitzgerald *et al*., 2016; Hasegawa *et al*., 2017; Lv *et al*., 2020)
94 have demonstrated the large potential for yield stimulation in C3-species under e-CO_2 in a large
95 diversity of situations. However, there is large genotypic and experiment-to-experiment variation
96 and meta analyses may carry a positive bias (Haworth *et al*., 2016). On the other hand, a negative
97 bias may be caused by the effect of [CO_2] fluctuations in FACE setups which are much larger than
98 natural fluctuations, suggesting that real-world stimulation by e-CO_2 on growth and photosynthesis is
99 larger than observed in FACE trials (Allen *et al.* 2020). Are our current C3-crops able to fully exploit
100 the potential provided by the increasing atmospheric [CO_2]?

101 In line with this question, there is growing evidence that large genotypic variation in e-CO_2 response
102 exists, suggesting that there is scope for improvement through breeding. Moreover, this variation
103 seems to be associated with source-sink relationships (e.g., Ainsworth *et al*. 2004; Hasegawa *et al*.,
104 2013; Ruiz-Vera *et al*., 2017; Lv *et al*., 2020) prompting the need to better understand how sink
105 strength feeds backward on photosynthesis. Such results also call for revisiting crop models which
106 typically assume leaf photosynthesis to be driven only by genotype, external resources (light, CO_2,
107 water), leaf nutritional status and stress factors, but not the plant capacity to remove assimilates
108 from the source and use them in sink organs (Chang and Zhu, 2017).

109 Our purpose is therefore to review the evidence of acclimation of photosynthesis response of C3
110 crops to e-CO_2 concentration, to examine the causes of "downward acclimation" (Tausz *et al*., 2013),
111 the interactions with some abiotic stresses, the main causes of cultivar differences in e-CO_2 response
112 and how they may be related to domestication and breeding history, the design of crop ideotypes
113 with the help of improved crop models, and the possibilities to engineer them experimentally. We
114 will terminate with perspectives for improved breeding approaches.

115

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

117 *Sink limitation of photosynthesis*

118 It is well known that C_3 photosynthesis in the absence of physiological stresses is limited by the
119 atmospheric CO_2 concentration, both at the pre-industrial level (ca. 270-280 μmol mol^{-1}; Fig. 1) and
120 current level (ca. 400 μmol mol^{-1}), and even at projected levels for 2050 (>550 μmol mol^{-1}) as the
121 saturating intercellular CO_2 level is above 600 μmol mol^{-1} (von Caemmerer & Farquhar, 1982). If leaf
122 photosynthetic rates were only determined by the constitutive properties of the photosynthetic
123 apparatus and the environment it operates in (assuming the absence of stresses), the light- and CO_2-
124 saturated rate (Amax) would be a constant system property. However, Amax changes with plant
125 acclimation after plants are exposed to e-CO_2 for several weeks (Sage *et al*., 1989), and it also
126 declines during the day, the degree of this decline depending on source-sink relationships (Fabre *et*
127 *al*., 2019). Sink limitation feeds back on the photosynthetic rate as assimilates are not exported to
128 sink organs at the rate at which they are produced. Consequently, e-CO_2 driven stimulation of the
129 source (photosynthesis), or conversely sink pruning, reduces Amax and causes the diurnal decline of
130 leaf photosynthesis, which in turn limits crop growth (Fabre *et al.*, 2019).

131 Downward acclimation of photosynthesisto e-CO_2 is a commonly reported in C3 species (e.g., Tausz
132 *et al*., 2013). A strong acclimation was observed in garlic, resulting in the absence of yield any gains
133 from e-CO_2 (Nackley *et al*., 2016). In some cases, acclimation effects are absent like in radish (Usuda
134 and Shimogawara, 1998), probably because the tuber has virtually unlimited carbon storage capacity.
135 In addition to changes in photosynthetic parameters, acclimation can cause structural changes in the
136 leaf (Zheng *et al*., 2019).

137 A decline of photosynthesis under sink limitation, as observed for rice under sink pruning (Fabre *et al*.
138 (2019) has been attributed to end-product accumulation in photosynthetic tissues (Paul and Pellny
139 2003). Excess assimilates can negatively feedback on photosynthetic rate (Huber and Huber 1992;
140 Iglesias *et al*., 2002; Li *et al.* 2015; Yang *et al*., 2016), possibly *via* leaf Triose phosphate utilization
141 (TPU) capacity (Paul and Foyer 2001; Fabre *et al.* 2019). To avoid physiological damage,
142 photosynthetic processes need to be down-regulated to avoid outright TPU limitation, probably
143 involving co-adjustment of V_{cmax} (maximum carboxylation rate of Rubisco) and TPU parameters
144 (Sharkey *et al*., 1988; Sage *et al*., 1989; McClain and Sharkey 2019; Fabre *et al.* 2019; Sharkey 2019).

145 Kirschbaum (2011) concluded in a review of crop responses to e-CO_2 that acclimation in most cases
146 wipes out much of the potential gains in growth, largely due to the plants' inability to use additional
147 assimilates. Fatichi *et al*. (2013) went as far as calling for vegetation models to be sink and not source
148 driven.

149 *Greater sink potential enhances the yield response of crops to e-CO_2*

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

155 Fabre *et al.* (2020) demonstrated that constitutive morphological differences in rice affecting source
156 and sink capacity, namely flag leaf area and panicle size, are aligned with genotypic differences in
157 photosynthetic responses to e-CO_2. Genotypes having large flag leaves and small panicles (and thus
158 high local source/sink ratio) showed no increase in Amax after a 15-d exposure to e-CO_2. Amax
159 increased substantially, however, when genotypes having low local source-sink ratio (small flag
160 leaves, large panicle) were exposed to e-CO_2. The positive response of Amax to e-CO_2 after
161 acclimation in high-sink cultivars translated into greater yield gain (although the use of potted plants
162 in growth chambers warrants caution here). Consistent with this, it was suggested that increasing
163 Amax of the flag leaf is important to improve rice yield potential particularly for e-CO_2 environments
164 (Chen *et al.,* 2007). A strong sink capacity may thus be necessary for increased Amax to be expressed.

165 One would expect from these findings that genotypic differences in sink capacity might translate into
166 crop yield response to atmospheric CO_2 concentration. This has been demonstrated by Hasegawa *et*
167 *al.* (2013) for rice in FACE experiments in Japan: Genotypic yield response to e-CO_2 (200 μmol mol^{-1}
168 above ambient) ranging between +3% and +36% among 8 cvs. was observed in a single-site
169 experiment and between +4% and 25% among 4 cvs. in a multi-site experiment. Effects were
170 correlated with the spikelet number per unit ground area observed in the ambient (low) CO_2
171 concentration treatment. All genotypes were high-yielding types and the yield gain was mainly due
172 to the number of fertile tillers. In FACE experiments in China, Lv at al. (2020) observed large genetic-
173 group effects on the yield response to e-CO_2 (600 μmol mol^{-1}). Japonica inbred cvs. responded the
174 least (+13.5%), indica inbred cvs. intermediate (+22.6%) and F1 hybrids the most (+32.8%), based on
175 a large sample of 120 genotypes. The authors concluded that these genotype differences reflect
176 different magnitudes of photosynthetic acclimation, with hybrids showing the least acclimation. The
177 low e-CO_2 response (or strong acclimation, as presumed by the authors) of japonica types was mainly
178 explained by their smaller capacity to adjust spikelet number per panicle (a sink trait) to the greater
179 carbon source. A FACE treatment applying e-CO_2 only at post-heading stages benefitted yield of
180 indica rice (+24%) more than japonica rice (+13%), indicating that the latter were probably more sink
181 limited. The large body of experimental data from rice FACE trials in Japan and China combined
182 indicate strong differences in e-CO_2 response among modern, high-yielding cultivars. The FACE trials

183 show that sink traits strongly affect genotypic e-CO_2 response, further supported by phytotron
184 studies (Fabre *et al*., 2019 & 2020).

185 *Greater sink plasticity enhances the response of crops to e-CO2*

186 A cereal crop's sink capacity, in terms of the product of spikelet number per ground area and
187 potential kernel weight, is a complex and plastic trait. Its components (tillering, tiller mortality, tiller
188 fertility, inflorescence size and potential kernel weight) respond to external resources and show
189 strong compensatory plasticity in rice, a cereal having small plasticity for kernel weight but large
190 plasticity for tiller number and spikelet number per panicle (Kumar *et al.*, 2016 & 2017). Modern
191 maize cvs., by contrast do not tiller but "prolific" genotypes can compensate for wide spacing by
192 increasing ear number per plant (Tang *et al.*, 2018). Modern wheat cvs. tiller less than traditional
193 ones, but highly plastic ear size and kernel weight provide adaptability to resource levels (Acreche &
194 Slafer, 2009). One could therefore expect that a genotype's adaptive or compensatory sink plasticity
195 contributes to e-CO_2 response, in addition to the effects of constitutive differences in sink capacity.

196 Kikuchi *et al.* (2017) investigated this hypothesis for two rice diversity panels, using the response of
197 tillering and spikelet number per panicle to plant population density as a measure of the phenotypic
198 plasticity of sinks. Genome-wide association studies (GWAS) then provided quantitative trait loci
199 (QTLs) for the plasticity traits, and a subset of genotypes carrying positive- or negative-effect alleles
200 was subjected to e-CO_2 in a FACE experiment. The authors report greater growth and yield responses
201 to e-CO_2 in the more plastic genotypes, thus validating the original hypothesis. Similarly, Kumagei *et*
202 *al.* (2015) demonstrated that soybean genotypes exhibiting greater biomass and yield response to e-
203 CO_2 also exhibited greater compensatory plasticity when subjected to differential planting densities.
204 Genotypic differences in both e-CO_2 response and planting density response were very large, and
205 both responses were positively correlated across genotypes. Consistent with this, Zhu *et al.* (2014)
206 compared two rice cultivars differing in physiological and yield e-CO_2 responses. The poorly
207 responding cultivar showed strong down regulation of photosynthesis (acclimation) whereas the
208 more e-CO_2 responsive cultivar avoided acclimation through adaptive plasticity of sink capacity.

209 The combined results of Kumagei *et al.* (2015) and Kikuchi *et al.* (2017) make a strong case for a
210 crop's gap-filling capacity to be an enabling factor for biomass and yield gains under e-CO_2
211 conditions, for two annual crop species (rice and soybean) that are quite distant from each other
212 biologically and phylogenetically. The gap-filling capacity, or ability to aggressively colonize resources
213 through plasticity, can thereby be interpreted as the potential to opportunistically enhance existing
214 sinks, or to generate new sinks through branching (e.g., tillering). The adaptive sink plasticity of the e-

215 CO_2 responsive rice cultivar described by Zhu *et al.* (2014) resulted in a greater ratio of spikelet
216 number *vs*. flag leaf area (local sink-source ratio), driven by branching within the panicle.

217

218 **Effects of other resource factors and stresses on crop e-CO_2 response**

219 *Water and temperature interactions*

220 The crop water status seems to be an important factor interacting with the growth/yield response to
221 e-CO_2. Indeed, under water deficit conditions, growth is more affected than photosynthesis, leading
222 to carbohydrate accumulation in various plant parts (Muller *et al*. 2011) and this may impact
223 photosynthesis response. Consistent with this, Fitzgerald *et al*. (2016) observed a +37% gain in wheat
224 yield under e-CO_2 for an irrigated crop, but only +13% under water-limited conditions. Similarly,
225 Tausz-Posch *et al*. (2015) found no superior e-CO_2 response in high- vs low-tillering wheat genotypes
226 and suggested this to be due to the water-limited conditions in the FACE experiment.

227 A major effect of e-CO_2 is the partial stomatal closure which in turn may affect water status, and
228 favor droughted plants. In principle, this effect should be dominating in C4 species where e-CO_2 is not
229 expected to directly affect photosynthesis. Consistent with this, e-CO_2 stimulated photosynthesis and
230 growth of maize under drought conditions, but not under well-watered conditions (Leakey *et al*.,
231 2006). Drought can thus have opposing effects on e-CO_2 response, an indirect stimulation through
232 stomatal regulation and a negative effect due to carbohydrate accumulation. According to Tausz-
233 Posch *et al*. (2012), wheat genotypes having greater transpiration efficiency (TE) maintain this trait
234 under e-CO_2, whereby e-CO_2 increased TE for all genotypes as expected.

235 The reduction of transpiration rate under e-CO_2 is large for irrigated rice (Shimono *et al.,* 2019).
236 Stomatal response to e-CO_2 thereby reduces transpirational cooling and thus can cause significant
237 warming of the canopy (Yoshimoto *et al.*, 2011). In fact, as an alternative to selecting genotypes that
238 use e-CO_2 conditions for greater yield potential, breeders might consider selecting for lower water
239 use while forfeiting potential increases in yield. Low stomatal density in rice was shown to conserve
240 soil water (Caine *et al.*, 2019). Interestingly, lower stomatal conductance as a trait in rice was
241 reported to be associated with increased density of root aerenchyma, needed in anaerobic rice to
242 supply the root with O_2 (Mohammed *et al.*, 2019).

243 These observations demonstrate the numerous tradeoffs associated with changes in stomatal
244 conductance, as a constitutive trait or induced by e-CO_2, or both: yield potential, drought avoidance,
245 canopy temperature, and specifically for rice, the O_2 supply to roots. Fitzgerald *et al.* (2016) also
246 reported a synergy between heat and e-CO_2 effects on wheat yield, observed at FACE trials located at

247 thermally different sites. Elevated temperatures and [CO_2] synergistically affect photosynthesis
248 within temperature ranges the plants are adapted to (Caizhe *et al.*, 2018; for tomato: Pan *et al.*,
249 2018; wheat: Posch *et al.*, 2019 (review)). However, increased canopy temperature can severely
250 reduce cereal biomass and yield. Cai *et al.* (2016 & 2019) used factorial combinations of two
251 temperature and two CO_2 levels in FACE experiments to study tradeoffs between the two factors for
252 rice and wheat. In both crops, large yield reductions caused by a 1.5-2.0 °C temperature increase
253 could not be fully offset by the yield gain caused by 500 µmol mol^{-1} CO_2.

254 *Nitrogen interactions*

255 Growth stimulation by e-CO2 causes significant dilution of mineral nutrients in the plant in the
256 absence of concomitant increase of nutrient uptake. The resulting N deficiency can cause
257 reallocation of N from Rubisco, which is the largest nitrogen pool in the plant (Makino, 2003; Kant *et*
258 *al.,* 2012; Weber and Bar-Even, 2019). A wheat crop grown in a CO_2 FACE experiment produced 30%
259 higher grain yield under e-CO_2 but had 10% lower N concentration in grain (Maphosa *et al.*, 2019).
260 The decrease in N concentration, however, was not different between strong and weak responders
261 to e-CO_2.

262 Myers *et al.* (2014) warned that nutrient limitation in crops under the influence of e-CO_2 will not only
263 limit productivity but also the quality of human nutrition. Bloom *et al.* (2015) called for crop
264 management and improvement strategies to enhance nutrient uptake commensurate with the
265 increased yield potential. There may in fact be a substantial margin to genetically improve nutrient
266 uptake along with the growth stimulation by e-CO_2. Hasegawa *et al.* (2019) investigated a rice variety
267 (*Takanari*) that substantially increased N uptake and maintained grain quality as its yield was
268 increased by 18% under e-CO_2 in a FACE experiment (3-year and 3 N-level average), whereas a
269 common check variety showed grain quality degradation and no yield gains. These results
270 demonstrate that yield gains under e-CO_2 are not only a matter of source-sink relationships but also
271 depend on the adaptive plasticity of nutrient uptake. Consistent with this idea, Sakai *et al.* (2019)
272 reported that strong genotypic differences in the yield response to e-CO2 among rice cultivars
273 released over the past century in Japan were correlated with their ability to take up additional N.
274 Root growth stimulation upon e-CO_2 as shown in many cases (e.g., wheat: Uddin *et al*., 2018) may
275 contribute, in a feedforward loop, to additional soil N and water acquisition needed under e-CO_2.

276 *Soil-volume interactions*

277 Arp (1991) and Bourgault *et al.* (2016) cautioned against extrapolating genotypic differences in e-CO_2
278 response from pot to field experiments. They demonstrated that the available soil volume per plant
279 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 19th 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.

312 *Sink limitations in modern crops*

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

321 Burnett *et al.* (2016) compared an annual cultivated barley with a perennial wild barley subjected to
322 continuous 180, 400 and 1500 μmol mol^{-1} CO_2 treatments in growth chambers over 61 days. The wild
323 plants had lower photosynthetic rates than the cultivated ones under ambient [CO_2] but showed a
324 greater positive response of photosynthesis, tillering, root-shoot weight ratio and biomass to
325 increased [CO_2]. The cultivated species accumulated more NSC in vegetative organs than the wild
326 barley in root and shoot at ambient [CO_2]. The authors conclude that the cultivated species was sink
327 limited and the wild species source limited during vegetative development.

328 For wheat, the comparison of old and recent cultivars (released in 1903, 1921, 1965 and 1996) in
329 growth chambers at 293, 385 and 715 μmol mol^{-1} [CO_2] showed a clear trend towards smaller yield
330 responses to e-CO_2 in modern cultivars (Ziska *et al.*, 2004). Larger responses (and probably, smaller
331 acclimation effects) in old cultivars were attributed to their greater tillering plasticity, enabling a
332 better sink adjustment to the carbon resource. Of course, responses may be different in field-grown
333 canopies involving intraspecific plant competition.

334 Too little information is available to judge if C3-type cereal cultivars are generally more sink limited
335 than their ancestors. Borras *et al.* (2004) found modern wheat to be sink-limited during grain filling in
336 most situations. By contrast, Acreche and Slafer (2008) compared Mediterranean wheat varieties
337 released between 1940 and 2005 and found that the older ones were strongly sink limited. Recent
338 cultivars had more balanced sink-source relationships as breeding had increased grain number. Sakai
339 *et al.* (2019) studied the yield response of old and recent rice varieties to e-CO_2 in FACE experiments.
340 They observed the strongest e-CO_2 response in older varieties but data were insufficient to establish
341 a historical trend. Genotypic differences in e-CO_2 response were correlated with the genotypic ability
342 to take up additional N to support the CO_2-stimulated growth. Similarly, a FACE study on *Lolium*
343 *perenne* (Isopp *et al.*, 2000) demonstrated a strong sink-limitation and accumulation of NSC in

344 response to e-CO_2 when N resources were limiting. These source-sink imbalances largely disappeared
345 in a high-N treatment, indicating the important role of N resources in e-CO_2 response.

346 We conclude that although there is insufficient evidence to support that modern varieties generally
347 lack sink capacity under e-CO_2 conditions during yield formation, evidence is accumulating that their
348 restrained sink plasticity during vegetative development, probably necessary to be good crops in
349 Donald's sense, limits their overall growth response to e-CO_2. This may explain the positive
350 association between gap filling capacity (largely by tillering) in widely spaced crops and yield
351 response to e-CO_2 for cultivated rice (Kikuchi *et al*., 2017), and the observation that early variation in
352 rice tillering is positively correlated with the e-CO_2 response of yield (Ziska *et al*., 2013). Sink
353 limitation during vegetative development in modern cultivars under high ambient [CO_2] therefore
354 merits more attention in crop improvement because it limits the potential biomass gain.

355 *Consequences for crop ideotypes better using* e-CO_2

356 Crop ideotypes making better use of e-CO_2 need to minimize downward acclimation of
357 photosynthesis while maintaining the high potential photosynthetic rates of modern cultivars. They
358 should also satisfy Donald's (1968) paradigm of restrained intraspecific competitiveness enabling
359 homogenous crop stands and avoiding redundant vegetative growth. It is thus not useful to revert to
360 archaic plasticity traits that breeders have de-selected even if they effectively reduce downward e-
361 CO_2 acclimation of photosynthesis. However, the principle of enhancing sinks to enable
362 photosynthetic rates unimpeded by acclimation under e-CO_2 conditions remains valid. The
363 magnitude of the required sink adjustments is substantial as [CO_2] in 2050 will be more than twice
364 the [CO_2] experienced during domestication and selection in pre-industrial times (260-280 μmol mol^{-}
365 ^{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.

369 Sink limitation during vegetative development might be corrected through increased, sink-driven
370 early vigor. Profuse tillering, although sometimes predictive of e-CO_2 response (Ziska *et al*., 2013;
371 Kikuchi *et al*., 2017) may not be the only way to achieve it. We hypothesize that increased leaf
372 number (Clerget *et al*., 2008), larger leaves and leaf sheaths, increased NSC reserve pools in the stem
373 functioning as active sinks (Slewinski, 2012), and enhanced root sinks may jointly enhance demand
374 for assimilate while avoiding the invasive weedy behavior associated with profuse tillering, which is
375 usually followed by high tiller mortality. Erect leaves, small tiller angle and small seminal root angle
376 (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.

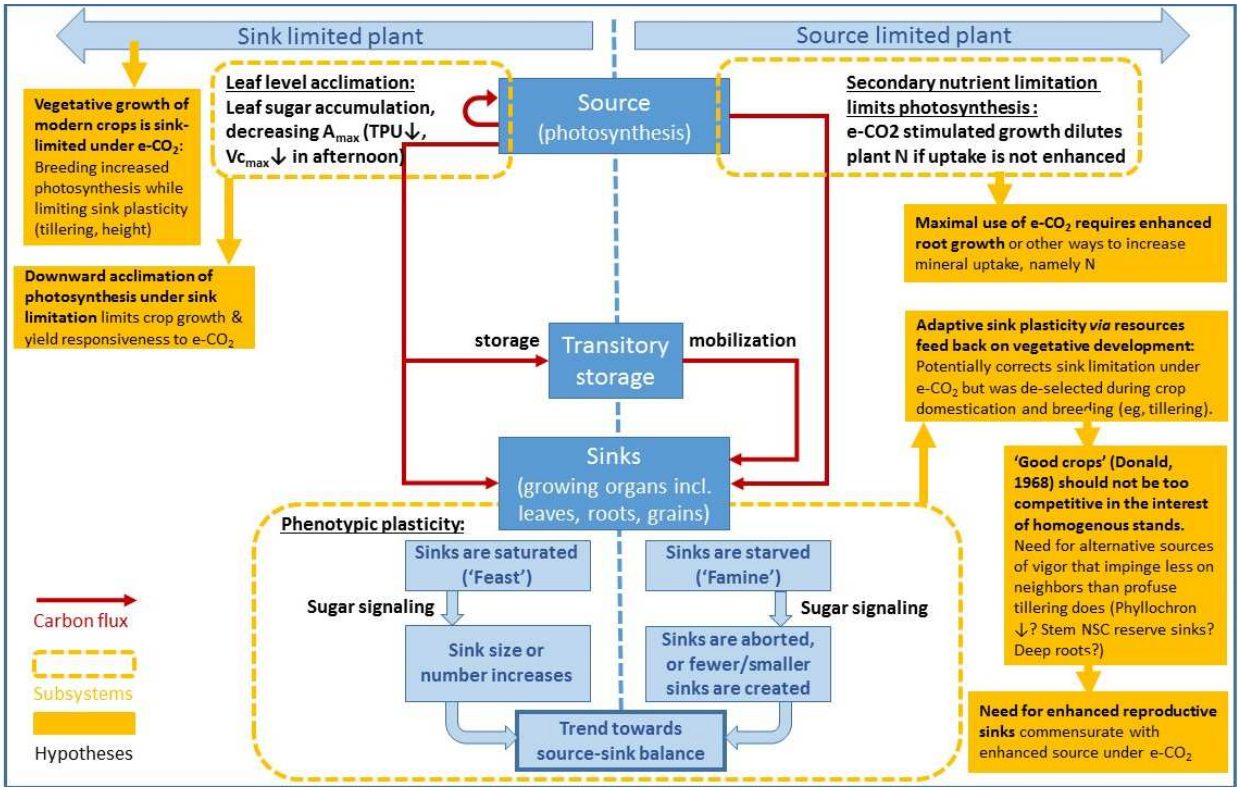

Fig. 2. Schematic diagram of source-sink interactions, downward acclimation of photosynthesis to e-CO_2 and adaptive plasticity of sinks. Key hypotheses of this paper are inserted in yellow boxes.

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

395 height combined with erect long uppermost-leaves (Setter *et al*., 1995). Dingkuhn *et al*. (1991)
396 predicted a rice ideotype for high, direct-seeded stand densities on the basis of modified tillering and
397 partitioning patterns. Both ideotypes influenced the successful development of Super Hybrid Rice in
398 China (Yuan, 2017). Ideotyping may be extended to incorporate effects of major QTLs which can then
399 be pyramided by marker-assisted selection (Gu *et al*., 2014; Kadam *et al*. 2019). Potentially,
400 ideotypes can also be molecularly engineered as we will discuss further down. Whatever the genetic
401 pathways used to build e-CO_2 efficient ideotypes, improved models are needed to orientate
402 strategies towards relevant targets. They should able to predict observed genotypic differences for
403 yield under variable [CO_2] conditions but also to cross-evaluate hypotheses. They should also
404 integrate source-sink relationships across several biological and temporal scales.

405 At the leaf level and a time scale of minutes, sink limitation is characterised by TPU (Sharkey *et al*.,
406 1988; McClain & Sharkey, 2019). At the whole-plant level and a time scale of hours, sink limitation is
407 often indicated by sugar accumulation and the diurnal decline of A_{max} (Fabre *et al*., 2019). Over days
408 to weeks, sink limitation may build up and contribute to photosynthetic downward acclimation under
409 e-CO_2 (e.g. Sage *et al.*, 1989; Sakai *et al*. 2006). Over the whole crop cycle, competition for resources,
410 compensatory growth responses and turnover of source and sink organs modify source-sink (Kim *et*
411 *al*., 2003). Nitrogen and other mineral resources are key at this scale.

412 Presently, the general acclimation of both leaf and canopy photosynthesis to e-CO_2 can be modelled
413 to some extent as an emergent property *via* a whole-plant feedforward mechanism, i.e. e-CO_2
414 increases carbon accumulation that dilutes plant nitrogen and causes more leaf senescence (Yin,
415 2013). Such a simple mechanism can avoid the overestimation by many crop models of the
416 fertilisation effect of e-CO_2 on crop yield that was observed by Ainsworth *et al*. (2008a).

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

424 Another example of uncoupling of responses is provided by Matsui *et al*. (1997) who showed that at
425 air temperatures above 30°C, filled spikelet fraction of rice was reduced under e-CO_2, a trend that is
426 opposite to the interaction between CO_2 and temperature on photosynthesis. Reduced spikelet
427 fertility was explained by reduced transpirational cooling (Julia & Dingkuhn, 2013) under e-CO_2, the

428 higher panicle temperature increasing pollen sterility. Modeling of crop response to e-CO_2 thus
429 should also consider the heat balance and crop-generated microclimate.

430 Increased photosynthesis usually increases yield as seen in FACE trials, but genotypic variation in
431 photosynthesis *per se* often does not correlate with yield (Driever *et al*., 2014; Gu *et al*., 2014). Are
432 feedbacks from non-photosynthetic processes behind genotypic crop responses to e-CO_2? As
433 discussed earlier, this may largely be the case, and acclimation of photosynthesis ultimately is an
434 emergent response to complex carbon source-sink, developmental and nutrient dynamics at the crop
435 level, involving adaptive phenotypic plasticity at several scales. To predict it and translate it into yield
436 variation, a crop model would thus require skills to connect leaf level photosynthetic processes with
437 the plasticity of developmental and morphological dynamics of the crop (sources, sinks and
438 transitory storage), as well as nutritional dynamics (e.g., nitrogen) and to some extent the crop-
439 generated microclimate. Parameterization of such a model will be a major challenge, both in terms of
440 data requirements (phenotyping) and estimation of parameters that cannot be measured directly
441 (e.g., reaction norms of developmental processes). A recent study showed that differences in
442 phenology (phyllochron) during development and as a function of environmental (temperature, light)
443 variation could be fully accounted for by intercepted radiation thereby offering a very simple mean
444 to incorporate this behavior in a modeling algorithm (Baumont et al., 2019).

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

449

450 **T6P signaling, a lever to modify source-sink relations and engineer e-CO_2 responsive ideotypes?**

451 We are today technically equipped and sufficiently knowledgeable to genetically modify crop plants
452 to express specific sink enhancements as warranted by an improved adaptation to e-CO_2 or by future
453 crop production objectives in general. This approach, even if it may not necessarily provide societally
454 acceptable cultivars for production, will increasingly be central to proving causative hypotheses and
455 to develop and validate ideotypes for new or improved crops. We will focus here on the T6P feast-
456 famine signaling system because of its omnipresence in higher plants, its regulatory involvement in
457 all sinks, and the demonstrated feasibility of modifying it.

458 *Mechanics of the T6P system*

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

464 Inhibition of SnRK1 by T6P promotes the opposite of the starvation response, a so-called feast
465 response. T6P-inhibited SnRK1 de-represses anabolism and represses catabolism enabling growth,
466 development and biosynthetic processes to proceed. In plants and crops both feast and famine
467 responses are necessary in different cells at different times and environmental conditions for growth
468 and adaptation. The balance between survival and productivity has been shifted in crops towards the
469 allocation of more C towards seed production with an increase in numbers and size of grain at the
470 expense of stems. Both stems and seeds are sinks for C, but it is not known how increased harvest
471 index has affected the overall plant source-sink dynamic. Seed sinks may be more easily perturbed by
472 environmental stress than allocation of C to stem reserves, hence modern crops may become sink
473 limited more readily, particularly under e-CO_2 and where stresses inhibit seed numbers and size. It
474 may be expected that domestication and breeding of crops has exerted selection pressure on the T6P
475 synthases (TPS) and phosphatases (TPP) of the T6P pathway. Accordingly, Hufford *et al.* (2012) listed
476 both TPSs and TPPs as domestication improvement genes in maize.

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

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

482 Oszvald *et al.* (2018) showed that through overexpression of a TPP gene in maize, primarily in phloem
483 of florets, conservation of grain numbers was promoted during drought. Probably, the reduction of
484 T6P promoted sucrose transport into developing grain as a famine response, preventing abortion due
485 to lack of sucrose. Seven SWEET genes were upregulated in the transformed plants. Nuccio *et al.*
486 (2015) reported for the same plant materials a significant increase in grain yield and biomass in the
487 field due to TPP overexpression, for well-watered plants and more strongly under drought.
488 Interestingly, enhanced grain number through expression of the TPP gene was associated with
489 increased photosynthetic longevity of source leaves (Oszvald *et al.*, 2018) suggesting that T6P
490 through the stimulation of sink may also regulate the source as part of a source-sink homeostatic

491 mechanism. This offers clues as to how to increase photosynthesis to support stronger sinks through
492 better source-sink relations.

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

497 For rising atmospheric [CO_2], the stimulation of both grain number and size *via* the T6P pathway may
498 enable the sink enhancements necessary to maximize photosynthesis under e-CO_2 and sustain sink
499 activity under abiotic stresses in C3 crops. Both examples (Nuccio *et al.*, 2015 and Oszvald *et al.*,
500 2018; Griffiths *et al.* 2016b) show that there is room to optimize the T6P pathway for grain numbers
501 and size and hence this may be a promising target for breeding if natural, functional polymorphisms
502 for the respective genes can be identified.

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

509

510 **Ways forward in crop breeding**

511 Effective breeding for improved e-CO_2 response at a high quantity and quality level of yield in C3
512 crops will require (1) appropriate ideotype concepts and adaptive physiological traits to guide
513 selection; (2) improved models better accounting for e-CO2 acclimation, capable of predicting the
514 yield benefits of the targeted traits in variable environments; and (3) scalable phenotyping and
515 selection tools. None of those are currently available. However, avenues can be envisaged.

516 For most high-yielding crops, the general approach would be to increase biomass production while
517 maintaining the high harvest index and increasing nutrient uptake commensurate with the
518 stimulated growth (Ainsworth *et al*., 2008b). Tausz *et al*. (2013) called for traits that would help
519 avoiding "downward acclimation" of photosynthesis by adjusting the source-sink balance not only
520 during grain filling (seed number and size) but throughout crop development (tillering or branching,
521 NSC storage in vegetative organs). Moving towards this direction clearly requires proxies that can be
522 used to characterize the plant material preferably at early stages and at high throughput. For
523 instance, Ziska *et al.* (2013) reported that the tillering response to e-CO_2 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 C3 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 C3-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.

556 Wild crop relatives and very old cultivars tend to respond better than most modern crops to e-CO_2
557 due to aggressive gap filling behavior and competitiveness, but on the basis of lower photosynthetic
558 rates. Adopting such archaic traits in breeding would sacrifice essential features of a good crop.
559 Instead, a more constitutively expressed and targeted sink enhancement may be a better strategy.
560 This calls for quantitative modeling to design ideotypes and methodologies to validate them. The
561 appropriate predictive models should consider how acclimation to e-CO_2 will interact with stresses
562 such as drought and heat.

563 It may be possible to genetically engineer experimental ideotypes that express desirable patterns of
564 sink enhancement, by using organ-specific, T6P-based, 'feast-famine', sugar signaling. This approach
565 can in principle be applied to any C3 crop, and the engineered ideotypes can be validated in FACE e-
566 CO_2 field environments. There are also opportunities to breed in more conventional ways for
567 improved crop response to e-CO_2 but this will hinge on the availability of valid and easily measurable
568 proxy traits.

569

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575

576 **Conflict of interest statement**

577 Nothing declared.

578 **References and recommended reading**

579 Papers of particular interest, published within the period of review, have been highlighted as:

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581 •• of outstanding interest

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