The case for improving crop carbon sink strength or plasticity for a CO2-rich future

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

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9

10 **Highlights**

11 ➢ Large variation for yield response to increasing [CO₂] exists among current C3 cereal cultivars

12 ➢ Poor response is due to acclimation caused by carbon sink and nitrogen limitation

13 ➢ Low acclimation in wild crop relatives is due to undesirable plasticity and competition traits

14 ➢ Quantitative ideotype concepts are needed for optimal sink capacity and plasticity traits

15 ➢ Ideotype engineering may use the trehalose-6 phosphate feast/famine system

16 **Abstract**

17 Atmospheric CO₂ concentration [CO₂] has increased from 260-280 $\mu mol\ mol^{-1}$ (level during crop

18 domestication up to the industrial revolution) to currently 400 and will reach 550 $\mu mol\ mol^{-1}$ by

19 2050. C3 crops are expected to benefit from elevated [CO₂] (e-CO₂) thanks to photosynthesis

20 responsiveness to [CO₂] but this may require greater sink capacity. We review recent literature on

21 crop e-CO₂ responses, related source-sink interactions, how abiotic stresses potentially interact, and

22 prospects to improve e-CO₂ response *via* breeding or genetic engineering. Several lines of evidence

23 suggest that e-CO₂ responsiveness is related either to sink intrinsic capacity or adaptive plasticity, e.g.

24 involving enhanced branching. Wild relatives and old cultivars mostly showed lower photosynthetic

25 rates, less downward acclimation of photosynthesis to e-CO₂ and responded strongly to e-CO₂ due to

26 greater phenotypic plasticity. While reverting to such archaic traits would be an inappropriate

27 strategy for breeding, we argue that substantial enhancement of vegetative sink vigor, inflorescence

28 size and/or number and root sinks will be necessary to fully benefit from e-CO₂. Potential ideotype

29 features based on enhanced sinks are discussed. The generic 'feast-famine' sugar signaling pathway

30 may be suited to engineer sink strength tissue- and stage-specifically and help validate ideotype

31 concepts. Finally, we argue that models better accounting for acclimation to e-CO₂ are needed to

32 predict which trait combinations should be targeted by breeders for a CO₂-rich world.

35   **Introduction**

36   Anthropogenic climate change since the beginning of the industrial revolution has adversely affected

37   global yields of annual crops (Ray *et al.*, 2019), whereby CO_2 fertilization benefits were more than

38   offset by yield-reducing climatic factors (Iizumi *et al.*, 2018). As global warming accelerates in the

39   future, the effects of yield-reducing stresses will dominate and increasingly impact production (Zhao

40   *et al.*, 2017). Potential global arable land area is projected to increase as higher northern latitudes

41   warm (Zabel *et al.*, 2014), but current agricultural prime land is shrinking due to degradation and

42   competition with other economic activities (Döös, 2002). Meanwhile, global demand for food is

43   projected to increase by 69% from 2010 to 2050 (Pardey *et al.*, 2014). Thus, there is an objective

44   need to increase crop yields, whereas the changing climate tends to decrease them. Past

45   achievements in yield increase essentially relied on increased harvest index and light interception

46   through architectural changes. Further increasing harvest index of high-yielding cultivars would incur

47   excessive lodging risks (Shah *et al.*, 2019), and gains must now be achieved through increased

48   biomass resulting from greater radiation use efficiency and photosynthesis (Fischer and Edmaedes,

49   2010).

50   Potential breakthroughs were recently reported on the engineering of C_3-type plants having

51   increased photosynthetic potential, namely by reducing the photorespiratory loss (tobacco: South *et*

52   *al.*, 2019; rice: Shen *et al.*, 2019) [The reported 40% biomass increase observed in tobacco, however,

53   was questioned by Fischer (2019) on methodology grounds]. An alternative or complementary

54   approach to enhancing the assimilate source system directly is to stimulate it indirectly by

55   strengthening sinks (Ainsworth and Bush, 2011; Ruiz-Vera *et al.*, 2017). Under current atmospheric

56   CO_2 concentrations, which are about 50% higher that the pre-industrial levels (400 $\mu mol\ mol^{-1}$ vs 270-

57   280 $\mu mol\ mol^{-1}$; Rubino *et al.*, 2019), C3 crop growth and yield may frequently be sink limited (Borras

58   *et al.*, 2004; Ziska *et al.*, 2004; Ludewig and Sonnewald, 2016). Therefore, C3 crops may not be able

59   to efficiently use the higher CO_2 concentration expected to be present in the atmosphere in the

60   coming decades if sink capacity is not increased to maintain balanced source-sink relationships

61   (Sonnewald and Fernie, 2018). This is the rationale for our present review.

62   Several reviews (Paul and Foyer, 2001; Lawlor and Paul, 2014; Ludewig and Sonnewald, 2016; Paul *et*

63   *al.,* 2019) and opinion papers (Paul *et al*., 2017; Sonnewald and Fernie, 2019) have discussed the

64   potential of increasing crop productivity by enhancing sink strength. In these reviews, the targeted

65   sinks are most often reproductive and thus directly grain-yield related. However, all growth depends

66   on sinks, including that related to tillering and root growth. Stimulating them could not only release

67   breaks due to downregulation of photosynthesis but also provide additional gains in terms of

68   drought avoidance (Griffiths and Paul, 2017; Fromm, 2019) or soil carbon sequestration *via* roots

69   (Suseela *et al*., 2017). Recent studies showed that sink enhancement by molecular engineering, e.g.

70   using the T6P (Triose-6-Phosphate) feast-famine system, increased both the productivity of the

71   targeted sink organ and crop photosynthesis (Oszwald *et al*., 2018), thereby boosting overall crop

72   biomass production (Nuccio *et al*., 2015). The stimulation of specific sinks does more than simply re-

73   direct (partition) assimilates within the plant. There is growing evidence that the whole-plant level

74   source-sink relationships are affected, stimulating leaf photosynthesis (source) through the rapid

75   removal of photosynthate from their sites of production (Fabre *et al*., 2019). This may involve long

76   distance signaling between sources and sinks through sucrose gradients that then translate locally

77   into T6P signals (Griffiths *et al*., 2016a). Understanding source-sink signaling and interactions has

78   important implications for future crop breeding and engineering, particularly to draw maximal

79   benefits for crops and agro-ecosystems from the globally rising atmospheric CO_2 concentration.

80

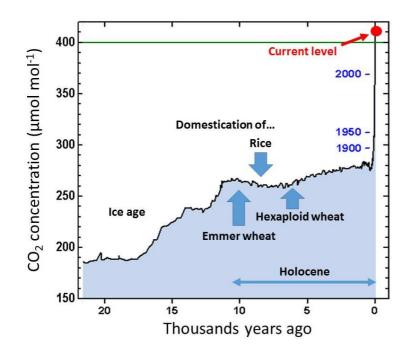81   **Fig. 1. Dynamics of atmospheric CO_2 concentration during the past 20,000 years. The current warm**

82   **period (Holocene) had 260-280 μmol mol^{-1} CO_2 (pre-industrial levels) and was conducive to**

83   **development of civilization and domestication of crops. The recent increase in [CO_2] to >400 μmol**

84   **mol^{-1} is anthropogenic. (Adapted from www.co2.earth)**

85

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 $\mu mol\ mol^{-1}$; Fig. 1) and

120   current level (ca. 400 $\mu mol\ mol^{-1}$), and even at projected levels for 2050 (>550 $\mu mol\ mol^{-1}$) as the

121   saturating intercellular CO_2 level is above 600 $\mu mol\ mol^{-1}$ (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

280   effects on crop growth are not necessarily caused by resource limitations such as nutrients or water.

281   Poorter *et al.* (2012) demonstrated in a meta-analysis that plants adjust growth to the accessible soil

282   volume, apparently through an unknown sensing mechanism. These findings underline the

283   importance of FACE experiments in this area of research. Controlled environments are suited to

284   investigate biological processes but are rarely predictive of crop behavior in the field (Ainsworth et

285   al., 2008a).

286

287   **Have domestication and selection history limited crop responsiveness to e-CO_2?**

288   Domestication of the major old-world cereals and subsequent selection/breeding processes, from ca.

289   10 millennia ago until the early 19th century, happened under low atmospheric CO_2 concentrations

290   compared to today's (260-280 µmol mol^{-1}; Fig. 1). Only during modern breeding were crops exposed

291   to the current, rapidly rising CO_2 levels. Although human crop selection never involved exposure to

292   increased CO_2 levels, it is likely that selection affected crop e-CO_2 response in some way because it

293   necessarily affected source-sink relationships and the phenotypic plasticity of sinks.

294   *Donald's ideotype and the aptitude of wild species for domestication*

295   Domestication shifts selection criteria from an individual's survival and reproduction (maximized

296   fitness frequently at the expense of neighbors; Weiner, 2019) to the productivity of a population of

297   genetically similar individuals. Crop plants thus tend to share resources more equitably with

298   neighbors, requiring some restraint on competitiveness ("Tragedy of the Commons"; Anten &

299   Vermeulen, 2016). Competitiveness would cause redundant vegetative growth and stand

300   heterogeneity. This concept is supported by Preece *et al.* (2018) who compared the phenotypic

301   plasticity among grass species, some being wild progenitors to modern cereals and others that did

302   not give rise to domestication. Plasticity was tested by growing plants in isolation or in a stand. The

303   crop progenitors were less plastic and more similar in biomass and tillering between treatments, as

304   compared to closely related species man did not domesticate.

305   The less aggressive gap-filling behavior of the crop progenitors, in terms of benefiting from open

306   spaces [*Hordeum vulgare* ssp. *spontaneum* (barley), *Triticum monococcum* ssp. *aegilopoides* (einkorn

307   wheat), *Triticum dicoccum* ssp. *Dicoccoides* (emmer wheat) and *Secale vavilovii* (progenitor of rye)]

308   appears to be a step in the direction of Donald's (1968) ideotype. This behavior necessarily involves a

309   smaller capacity to develop more or larger organs in response to the availability to additional spaces

310   (resources). This behavior is thus rooted in sink plasticity, particularly of vegetative organs, and is a

311   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^{-1}

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

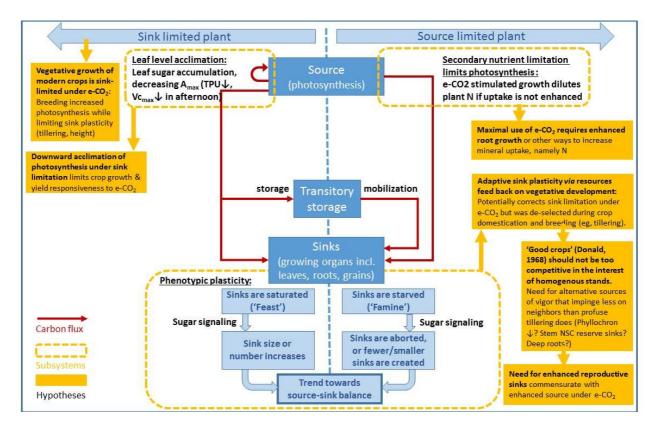373   functioning as active sinks (Slewinski, 2012), and enhanced root sinks may jointly enhance demand

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

377 systems might also enable the increased mineral uptake to support enhanced biomass. Combined

378 with enhanced reproductive sinks, such traits may increase biomass production under e-CO_2 while

379 maintaining the high harvest index already achieved in modern cultivars. More research is thus

380 needed to test if these traits, are as effective as tillering in controlling e-CO_2 acclimation. Our

381 hypotheses are summarized schematically in Fig. 2, projected onto the theoretical framework of sink-

382 source relationships and acclimation of photosynthesis to e-CO2.

383 If the hypotheses are valid, it will be useful to understand the gene networks and physiological

384 pathways controlling the number and size of sinks, both for the vegetative and reproductive

385 architecture of the plant. To predict improved ideotypes on this basis, appropriate crop models are

386 also needed.

387

388 **Fig. 2. Schematic diagram of source-sink interactions, downward acclimation of photosynthesis to**

389 **e-CO_2 and adaptive plasticity of sinks. Key hypotheses of this paper are inserted in yellow boxes.**

390

391 **Challenges in quantitative modelling to design ideotypes**

392 Donald's (1968) ideotype concept facilitated the use of quantitative physiological understanding in

393 crop breeding, i.e. design trait combinations that would enable high and stable yield in target ranges

394 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

524 trait) was predictive of e-CO$_2$ response of yield across different thermal regimes and for both modern

525 and wild rice lines, and may thus be used as a proxy. Other studies on rice (Kikuchi *et al.*, 2017) and

526 soybean (Kumagai *et al.*, 2015) support this idea. The local source-sink ratio in rice (flag leaf vs.

527 panicle size; Fabre *et al.*, 2020) may be another morphological proxy for e-CO$_2$ response potentially

528 scalable in breeding. Such morphological and developmental proxy traits should be validated for

529 large populations in FACE trials prior to any practical application in breeding. As discussed earlier,

530 there may be other sink traits increasing vegetative growth vigor and may thus relate to e-CO$_2$

531 response, as an alternative to tillering where it is not wanted. The search for scalable proxy traits in

532 breeding for e-CO$_2$ responsiveness has barely begun.

533 Several authors called for increased root/shoot ratio to improve adaptation to climate change

534 (review: Korres *et al.*, 2016). This may not only improve crop drought avoidance and enhance C

535 sequestration in the soil (Suseela *et al.*, 2017) but may also be essential to meet the increased

536 nutrient demand (Tausz *et al.*, 2013) and maintain grain quality (Hasegawa *et al.*, 2019) under e-CO$_2$.

537 Increased root/shoot ratio should translate into a greater soil volume accessed by roots to result in

538 greater nutrient uptake (Poorter *et al.*, 2012) – thus requiring sufficient soil depth and appropriate

539 cultural practices. As for the other sink traits, the challenge is to express these root traits in a plastic

540 (e-CO$_2$-responsive) fashion, requiring proxy traits that are easily used in selection. Where reliable

541 proxy traits cannot be found, molecular selection or engineering may be eventually more promising

542 because FACE experiments will probably always be too costly to host conventional breeding setups.

543

544 **Conclusion**

545 We found strong evidence for the potential to substantially increase crop photosynthesis, biomass

546 and yield by enhancing carbon sink capacity that would, in turn, stimulate carbon assimilation. This

547 would be particularly effective in annual C3 crops whose photosynthesis is sensitive to the recent

548 and anticipated rise of atmospheric [CO$_2$]. Much of the evidence provided concerns rice and wheat

549 but is likely extendable to other major C3-crops.

550 More research is needed to better understand what lies behind the strong cultivar differences

551 consistently observed in field e-CO$_2$ response. We raise the hypothesis that major processes

552 accounting for differences in acclimation are sink and N limitation. We have illustrated that some

553 equally high yielding cultivars are able or unable to adjust (increase) sink potential and N uptake.

554 Similarly, compensatory plasticity of tillering and inflorescence size as observed in plant spacing

555 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

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:

580   • of special interest

581   •• of outstanding interest

582

583

584   **References**

585   Acreche MM, Slafer GA. 2009. Grain weight response to increases in number of grains in wheat in a

586   Mediterranean area. *Field Crops Research* 98, 52-59.

587   Ainsworth EA, Bush DR. 2011. Carbohydrate export from the leaf: A highly regulated process and

588   target to enhance photosynthesis and productivity. *Plant Physiology* **155**, 64–69.

589   Ainsworth EA, Long SP. 2005. What have we learned from 15 years of free-air CO_2 enrichment

590   (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytol.* 165,

591   351–371. doi: 10.1111/j.1469-8137.2004.01224.x

592   Ainsworth EA, Rogers A, Nelson R, Long SP. 2004. Testing the source–sink hypothesis of down-

593   regulation of photosynthesis in elevated $[CO_2]$ in the field with single gene substitutions in

594   *Glycine max*. *Agric. Forest Meteorol.* 122, 85-94. Doi.org/10.1016/j.agrformet.2003.09.002

595   Ainsworth EA, Leakey ADB, Ort DR, Long SP. 2008a. FACE-ing the facts: inconsistencies and

596   interdependence among field, chamber and modelling $[CO_2]$ impacts on crop yield and food

597   supply. *New Phytologist* 179, 5-9.

598   Ainsworth EA, Rogers A, Leakey ADB. 2008b. Targets for Crop Biotechnology in a Future High-CO_2 and

599   High-O_3 World. *Plant Physiol.* 147, 13–19.

600   Allen LH, Kimball BA, Bunce JA, Yoshimoto M, Harazono Y, Baker, JT, Boote KJ, White JW, 2020.

601   Fluctuations of CO_2 in Free-Air CO_2 Enrichment (FACE) depress plant photosynthesis, growth,

602   and yield. *Agric. Forest Meteorol*. 284, 107899.

603   Anten NPR, Vermeulen,PJ. 2016. Tragedies and crops: understanding natural selection to improve

604   cropping systems. *Trends Ecol. Evol.* 31, 429-439. doi: 10.1016/j.tree.2016.02.010

605   Arp WJ. 1991. Effects of source-sink relations on photosynthetic acclimation to elevated CO_2. *Plant,*

606   *Cell and Environment* 14, 869-875.

607   Baumont M, Parent B, Manceau L, Brown H, Driever SM, Muller B, Martre P. 2019. Experimental and

608   modeling evidence of carbon limitation of leaf appearance rate for spring and winter wheat. *J.*

609   *Exp. Bot.* 70, 2449-2462.

610   Bloom AJ. 2015. The increasing importance of distinguishing among plant nitrogen sources. *Curr.*

611   *Opin. Plant Biol.* 25, 10–16. doi: 10.1016/j.pbi.2015.03.002

612   Borras L, Slafer GA, Otegui ME. 2004. Seed dry weight response to source–sink manipulations in

613   wheat, maize and soybean: a quantitative reappraisal. *Field Crops Research* 86, 131–146.

614   Bourgault M, James AT, Dreccer MF. 2016. Pot size matters revisited: does container size affect the
615   response to elevated CO_2 and our ability to detect genotypic variability in this response in
616   wheat? *Functional Plant Biology* 44, 52-61. doi.org/10.1071/FP16047

617   •Burnett AC, Rogers A, Rees M, Osborne CP. 2016. Carbon source–sink limitations differ between
618   two species with contrasting growth strategies. *Plant, Cell and Environment* 39, 2460–2472. **An**
619   **interesting comparison of a cultivated (sink limited) *vs* wild (source limited) barley at 180,**
620   **400 and 1500 μmol mol^{-1} [CO_2]. The wild acclimatizes less because it has more plastic sinks.**

621   •Cai C, Yin X, He S, Jiang W, S, C, Struik PC, Luo W, Li G, Xie Y, Xiong Y, Pan X. 2016. Responses of
622   wheat and rice to factorial combinations of ambient and elevated CO_2 and temperature in
623   FACE experiments. *Global Change Biology* 22: 856-874. **This is the most rigorous field study on**
624   **e-CO_2 x temperature interactions to our knowledge. It confirms a modest e-CO_2 alleviation of**
625   **heat stress but highlights the strong impact of heat.**

626   Cai C., Li G, Di L, Ding Y, Fu L, Guo X, Struik PC, Pan G, Chen W, Luo W, Yin X. 2019. The acclimation of
627   leaf photosynthesis of wheat and rice to seasonal temperature changes in T-FACE
628   environments. *Global Change Biology*, in press (DOI: 10.1111/gcb.14830).

629   •Caine RS, Yin X, Sloan J, Harrison EL, Mohammed U, Fulton T, Biswal AK, Dionora J, Chater CC, Coe
630   RA, Bandyopadhyay A, Murchie EH, Swarup R, Quick WP, Gray JE. 2019. Rice with reduced
631   stomatal density conserves water and has improved drought tolerance under future climate
632   conditions. New Phytol. 221, 371-384. doi: 10.1111/nph.15344 **The authors show that water**
633   **saving *via* lower stomatal density has negligible tradeoffs with photosynthetic rate under e-**
634   **CO_2 while helping to avoid drought. This may be an alternative strategy to make crops**
635   **benefit from rising [CO_2).**

636   Caizhe P, Ahammed GJ, Li X, Shi K. 2018. Elevated CO_2 improves photosynthesis under high
637   temperature by attenuating the functional limitations to energy fluxes, electron transport and
638   redox homeostasis in tomato leaves. *Front. Plant Sci.*, doi.org/10.3389/fpls.2018.01739

639   Chang T-G, Zhu X-G. 2017. Source–sink interaction: a century old concept under the light of modern
640   molecular systems biology *J. Exp. Bot.* 68, 4417–4431, https://doi.org/10.1093/jxb/erx002

641   Chen Y, Yuan L-P, Wang X-H, Zhang D-Y, Chen J, Deng Q-Y, Zhao B-R, Xu D-Q. 2007. Relationship
642   between grain yield and leaf photosynthetic rate in super hybrid rice. *Journal of plant*
643   *physiology and molecular biology* **33**, 235–243.

644   Clerget B, Dingkuhn M, Goze E, Rattunde HFW, Ney B. 2008. Variability of Phyllochron, Plastochron
645   and Rate of Increase in Height in Photoperiod-sensitive Sorghum Varieties. *Annals of Botany* **101,**
646   579-594.

647 Dingkuhn, M., F.W.T. Penning de Vries, S.K. De Datta, H.H. van Laar. 1991. Concepts for a new plant

648   type for direct seeded flooded tropical rice. In: Direct Seeded Flooded Rice in the Tropics.

649   International Rice Research Institute, P.O. Box 933, Manila, Philippines, 17-38.

650 Donald CM. 1968. The breeding of crop ideotypes. Euphytica **17**, 385-403.

651 Döös B. 2002. Population growth and loss of arable land. *Global Environmental Change* 12, 303-311.

652 Driever, S.M., Lawson, T., Andralojc, P.J., Raines, C.A. and Parry, M.A.J., 2014. Natural variation in

653   photosynthetic capacity, growth, and yield in 64 field-grown wheat genotypes. J. Exp. Bot. 65,

654   4959-4973.

655 •Fabre D, Yin X, Dingkuhn M, Clément-Vidal A, Roques S, Rouan L, Soutiras A, Luquet D. 2019. Is

656   triose phosphate utilization involved in the feedback inhibition of photosynthesis in rice under

657   conditions of sink limitation? *J. Exp. Bot.* **70**, 5773–5785. **The authors show that**

658   **photosynthesis downregulation under sink limitation mostly impacts in the afternoon. This**

659   **finding may change the way acclimation to e-CO_2 is modeled. Note also Sharkey's (2019)**

660   **follow-up paper to this study.**

661 •Fabre D, Dingkuhn M, Yin X, Clément-Vidal A, Roques S, Soutiras A, Luquet D. 2020. Genotypic

662   variation in morphological source and sink traits affects the response of rice photosynthesis

663   and growth to elevated atmospheric CO_2. *Plant Cell Envir.* doi: 10.1111/pce.13693 **The authors**

664   **describe a promising proxy trait for selecting for greater e-CO_2 response. Requires field**

665   **validation**.

666 Fatichi S, Leuzinger S, Körner C. 2013. Moving beyond photosynthesis: from carbon source to sink-

667   driven vegetation modeling. *New Phytologist* 201, 1086–1095.

668 Fischer RA, Edmaedes GO. 2010. Breeding and cereal yield progress. *Crop Sci*. 50, S-85–S-98. doi:

669   10.2135/cropsci2009.10.0564

670 Fischer RA. 2019. 40% increased growth with genetic engineering. *Science* 363, Issue 6422 (e-letter).

671 Fromm H. 2019. Root plasticity in the pursuit of water. Review. *Plants* 8, 236.

672   doi:10.3390/plants8070236

673 •Fitzgerald GJ, Tausz M, O'Leary G, Mollah MR, Tausz-Posch S, Seneweera S, Mock I, Löw M,

674   Partington DL, McNeill D, Norton RM. 2016. Elevated atmospheric [CO_2] can dramatically

675   increase wheat yields in semi-arid environments and buffer against heat waves. Global Change

676   Biology 22, 2269–2284. doi: 10.1111/gcb.13263 **A remarkable FACE multi-E (sites, years,**

677   **sowing dates, water regime) data resource for wheat informing on e-CO_2 interactions with**

678   **heat and water limitation.**

679 •Griffiths CA, Paul MJ, Foyer CH. 2016a. Metabolite transport and associated sugar signalling

680   systems. Review. *Biochimica et Biophysica Acta* 1857, 1715–1725. **A review integrating**

681   **metabolite transport and signaling at different scales, highlighting interesting paths to**

682   **improving yield and drought tolerance.**

683   Griffiths CA, Sagar R, Geng Y, Primavesi LF, Patel MK, Passarellis MK, Gilmore IS, Stevens RT, Buncj J,

684   Paul MJ, Davis BG. 2016b. Chemical intervention in plant sugar signalling increases yield and

685   resilience. Nature **540**, 574–578. doi:10.1038/nature20591

686   Griffiths CA, Paul MJ. 2017. Targeting carbon for crop yield and drought resilience. *Plant Science*,

687   Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK. DOI 10.1002/jsfa.8501

688   Gu J, Yin X, Zhang C, Wang H, Struik PC. 2014. Linking ecophysiological modelling with quantitative

689   genetics to support marker-assisted crop design for improved yields of rice (Oryza sativa)

690   under drought stress. *Ann. Bot*. 114, 499-511.

691   ••Hasegawa T, Sakai H, Tokida T, Nakamura H, Zhu C., Usui Y, Yoshimoto M, Fukuoka M, Wakatsuki

692   H, Katayanagi N, Matsunami T, Kaneta Y, Sato T, Takakai F, Sameshima R, Okada M, Mae T,

693   Makino A. 2013. Rice cultivar responses to elevated CO_2 at two free-air CO_2 enrichment (FACE)

694   sites in Japan. *Functional Plant Biology* **40**, 148-159. **A surprising diversity of cultivar yield**

695   **responses to e-CO_2, explained in part by sink traits, shows that breeding for e-CO_2 response**

696   **will not need archaic or weedy traits. Look also at the other papers of Hasegawa's group.**

697   Hasegawa T, Li T, Yin X, Zhu Y, Boote K, Baker J, Bregaglio S, Buis S, Confalonieri R, Fugice J, Fumoto T,

698   Gaydon D, Kumar SN, Lafarge T, III MM, Masutomi Y, Nakagawa H, Oriol P, Ruget F, Singh U,

699   Tang L, Tao F, Wakatsuki H, Wallach D, Wang Y, Wilson LT, Yang L, Yang Y, Yoshida H, Zhang Z,

700   Zhu J. 2017. Causes of variation among rice models in yield response to CO_2 examined with

701   free-air CO_2 enrichment and growth chamber experiments. *Nature Scientific Reports* 7, 14858.

702   DOI:10.1038/s41598-017-13582-y

703   •Hasegawa T, Sakai H, Tokida T, Usui Y, Nakamura I, Wakatsuki H, Chen CP, Ikawa H, Zhang G,

704   Nakano H, Matsushima MY, Hayashi K. 2019. A high-yielding rice cultivar "Takanari" shows no

705   N constraints on CO_2 fertilization. *Front. Plant Sci.*, https://doi.org/10.3389/fpls.2019.00361

706   **The authors present a high-yielding variety that overcomes both sink- and N-limitation under**

707   **e-CO2 through trait plasticity. This benefits both yield and grain quality.**

708   # Haworth M, Hoshika Y, Killi D. 2016. Has

709   # the impact of rising CO_2 on plants been

710   # exaggerated by meta-analysis of free air

CO₂ enrichment studies? *Front. Plant Sci.*, doi.org/10.3389/fpls.2016.01153

Huang G, Liang W, Sturrock CJ, Pandey BK, Giri J, Mairhofer S, Wang D, Muller L, Tan H, York LM, Yang J, Song Y, Kim Y-J, Quiao Y, Xu J, Kepinski S, Bennett MJ, Zhang D. 2018. Rice actin binding protein RMD controls crown root angle in response to external phosphate. Nat. Com. 9, 2346.

Huber SC, Huber JL. 1992. Role of sucrose-phosphate synthase in sucrose metabolism in leaves. *Plant Physiol.* **99**, 1275–1278.

Hufford MB, Xu X, van Heerwaardeb J, Pyhajarvi T, Chia J-M, Cartwright RA, Elshire RJ, Glaubiyz JC, Guill KE, Kaeppler SM, Lai J, Morrel PL, Shannon LM, Song C, Springer NM, Swanson-Wagner RA, Tiffin P, Wang J, Zhang G, Doebley J, McMullen MD, Ware D, Buckler ES, Yang S, Ross-Ibarra J. 2012. Comparative population genomics of maize domestication and improvement. *Nature Genetics* doi10.1038/ng.2309

Iglesias DJ, Lliso I, Tadeo FR, Talon M. 2002. Regulation of photosynthesis through source: sink imbalance in citrus is mediated by carbohydrate content in leaves. *Physiologia Plantarum* **116**, 563–572.

Iizumi T, Shiogama H, Imada Y, Hanasaki N, Takikawa H, Nishimori M. 2018. Crop production losses associated with anthropogenic climate change for 1981–2010 compared with preindustrial levels. *Int J Climatol.* 38, 5405–5417.

IPCC. 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

IPCC. 2016. Field CB *et al.* (eds*.),* Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: AR5 WG2 A, Global and Sectoral Aspects. Contribution of Working Group II (WG2) to the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC), Cambridge University Press. Archived from the original on 28 April 2016*.*

Isopp H, Frehner M, Long SP, Nösberger J. 2000. Sucrose-phosphate synthase responds differently to source-sink relations and to photosynthetic rates: *Lolium perenne* L. growing at elevated p_{CO2} in the field. *Plant, Cell and Environment* 23, 597-607.

Julia C., **Dingkuhn M**. 2013. Predicting temperature induced sterility of rice spikelets requires simulation of crop-generated microclimate. *European Journal of Agronomy* **49**, 50-60.

741 Kadam NN, Jagadish KSV, Struik PC, van der Linden GC, Yin X. 2019. Incorporating genome-wide
742   association into eco-physiological simulation to identify markers for improving rice yields. *J.*
743   *Exp. Bot.* 70, 2575-2586.

744 Kant S, Seneweera S, Rodin J, Materne M, Burch D, Rothstein SJ, Spangenberg G. 2012. Improving
745   yield potential in crops under elevated CO_2: Integrating the photosynthetic and nitrogen
746   utilization efficiencies. *Front. Plant Sci.* **3**.

747 Kikuchi S, Bheemanahalli R, Jagadish KSV, Kumagai E, Masuya Y, Kuroda E, Raghavan C, Dingkuhn M,
748   Shimono AA, Shimono H. 2017. Genome-wide association mapping for phenotypic plasticity in
749   rice. *Plant Cell Environ.*40, 1565_1575*.* DOI: 10.1111/pce.12955

750 Kim HY, Lieffering M, Kobayashi K, Okada M and Miura S., 2003, Seasonal changes in the effects of
751   elevated CO2 on rice at three levels of nitrogen supply: a free air CO2 enrichment (FACE)
752   experiment. *Global Change Biology* 9, 826-837.

753 Kirschbaum MUF. 2011. Does Enhanced Photosynthesis Enhance Growth? Lessons Learned from CO2
754   Enrichment Studies. *Plant Physiology* 155, 117–124.

755 Korres NE, Norsworthy JK, Tehranchian P, Gitsopoulos TK, Loka DA, Oosterhuis DM, Gealy DR, Moss
756   SR, Burgos NR, Miller MR, Palhano MP. 2016. Cultivars to face climate change effects on
757   crops and weeds: a review. *Agronomy for Sustainable Development*, Springer Verlag/EDP
758   Sciences/INRA 16, 36 (1), pp.12. HAL Id: hal-01532407. https://hal.archives-ouvertes.fr/hal-
759   01532407

760 ••Kumagai E, Aoki N, Masuya Y, Shimono H. 2015. Phenotypic Plasticity Conditions the Response of
761   Soybean Seed Yield to Elevated Atmospheric CO_2 Concentration*. Plant Physiol*. 169, 2021–
762   2029. **This is probably the strongest published evidence so far that compensatory growth**
763   **plasticity under differential crop spacing is predictive of e-CO₂ response. Similar: Kikuchi *et***
764   ***al*. (2017).**

765 •Kumar U, Laza MR, Soulie J-C, Pasco R, Mendez KVS, Dingkuhn M. 2016. Phenotypic plasticity of
766   irrigated rice: Sequential path analysis of yield components and simulation with the SAMARA
767   crop model. *Field Crops Res.* **193**, 164-177. **Hierarchical developmental plasticity of**
768   **sequentially formed yield components is modelled here at crop scale. Approach potentially**
769   **applicable to e-CO₂ response and underlying traits.**

770 Kumar U, Laza MR, Soulie J-C, Pasco R, Mendez KVS, Dingkuhn M**.** 2017. Analysis and simulation of
771   phenotypic plasticity for traits contributing to yield potential in twelve rice genotypes. *Field*
772   *Crops Res.* **202**, 94-107.

773 Lawlor DW, Paul MJ. 2014. Source/sink interactions underpin crop yield: the case for trehalose 6-
774   phosphate/SnRK1 in improvement of wheat. Review. *Front. Plant Sci.*
775   doi.org/10.3389/fpls.2014.00418

Legros S., Mialet-Serra I., Clement-Vidal A., Caliman J.P., Siregar F., Fabre D., Dingkuhn M. 2009a. Phenology, growth and physiological adjustments of oil palm (*Elaeis guineensis* Jacq.) to sink limitation induced by fruit pruning. *Annals of Botany* **104**, 1183-1194.

Legros S., Mialet-Serra I., Clement-Vidal A., Caliman J.P., Siregar F., Fabre D., Dingkuhn M. 2009b. Role of transitory carbon reserves during adjustment to climate variability and sink-source imbalances in oil palm (*Elaeis guineensis* Jacq.). *Tree Physiology* **29**, 1199-1211.

Li T, Hasegawa T, Yin X, Zhu Y, Boote K, Adam M, Bregaglio S, Buis S, Confalonieri R, Fumoto T, Gaydon D, Marcaida M 3rd, Nakagawa H, Oriol P, Ruane AC, Ruget F, Singh B, Singh U, Tang L, Tao F, Wilkens P, Yoshida H, Zhang Z, Bouman B. 2015. Uncertainties in predicting rice yield by current crop models under a wide range of climatic conditions. *Global Change Biology* **21**, 1328–1341.

Ludewig F, Sonnewald U. 2016. Demand for food as driver for plant sink development. *J. Plant Physiol.* **203**, 110–115.

•Lv C, Huang Y, Sun W, Yu L, Zhu J. 2020. Response of rice yield and yield components to elevated [CO_2]: A synthesis of updated data from FACE experiments. *Europ. J. Agron.* 112, 125961 **Based on a formidable data resource from FACE trials in China, the authors describe rice sub-species differences in e-CO_2 response. They are in part explained by sink trait plasticity.**

Makino A. 2003. Rubisco and nitrogen relationships in rice: Leaf photosynthesis and plant growth. *Soil Sci. Plant Nutr.* **49**, 319–327.

Maphosa L, Fitzgerald GJ, Panozzo J, Partington D, Walker C, Kant S. 2019. Genotypic response of wheat under semi-arid conditions showed no specific responsive traits when grown under elevated CO_2. Plant Prod. Sci. **22**, Issue 3

Matsui T, Namuco OS, Ziska LH and Horie T. 1997. Effects of high temperature and CO2 concentration on spikelet sterility in indica rice. Field Crops Res., 213-219.

•McClain AM, Sharkey TD. 2019. Triose phosphate utilization and beyond: from photosynthesis to end product synthesis. *J. Exp. Bot.* **70**, 1755–1766. **This paper elucidates regulatory processes that help avoid damage to the photosynthetic system under sink limitation.**

Mohammed U, Caine RS, Atkinson JA, Harrison EL, Wells D, Chater CC, Gray JE, Swarup R, Murchie EH. 2019. Rice plants overexpressing *OsEPF1* show reduced stomatal density and increased root cortical aerenchyma formation. *Nature* Scientific Reports **9**, 5584.

Muller B, Martre P. 2019. Plant and Crop Simulation Models: Powerful Tools to Link Physiology, Genetics, and Phenomics. *J. Exp. Bot.* 70, 2339-2344.

•Muller B, Pantin F, Génard M, Turc O, Freixes S, Piques M, Gibon Y. 2011. Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and

810 growth in sink organs. *J. Exp. Bot.* 62, 1715–1729. **The uncoupling of growth from**

811 **photosynthesis under drought described here may in part explain a poor e-CO₂ response**

812 **under drought (Fitzgerald *et al.*, 2016) and the strong impact under drought of T6P sink**

813 **boosting (Nuccio *et al.*, 2015).**

814 Myers SS, Zanobetti A, Kloog I, Huybers P, Leakey ADB, Bloom AJ, Carlisle E, Dietterich LH, Fitzgerald

815 G, Hasegawa T, Holbrook NM, Nelson RL, Ottman MJ, Raboy V, Sajai H, Sartor KA, Schwartz J,

816 Seneweera S, Tausz M,Usui Y. 2014. Increasing CO2 threatens human nutrition. *Nature* 510,

817 139–142. doi: 10.1038/nature13179

818 Nackley LL, Jeong JH, Oki LR, Kim S-H. 2016. Photosynthetic acclimation, biomass allocation, and

819 water use efficiency of garlic in response to carbon dioxide enrichment and nitrogen

820 fertilization. *J. Amer. SOC. Hort. Sci.* 141, 373–380.

821 •Nuccio ML, Wu J, Mowers R, Zhou H-P, Meghji M, Primavesi LF, Paul MJ, Chen X, Gao Y, Haque E,

822 Basu SS, Lagrimini LM. *2015.* Expression of trehalose-6-phosphate phosphatase in maize ears

823 improves yield in well-watered and drought conditions. *Nat Biotechnol 33, 862–869.* **Sink**

824 **boosting *via* T6P modification increases yield even more under drought than well-watered**

825 **conditions in the field.**

826 ••Oszvald M, Primavesi LF, Griffiths CA, Cohn C, Basu, SS, Nuccio ML, Paul MJ. 2018. Trehalose 6-

827 phosphate in maize reproductive tissue regulates assimilate partitioning and photosynthesis.

828 *Plant Physiol.* doi: 10.1104/pp.17.01673 **This paper establishes that boosting sinks *via* T6P**

829 **modification stimulates photosynthesis by feedback. The regulatory processes and gene**

830 **networks involved are elucidated.**

831 Pan C, Ahammed GJ, Li X, Shi K. 2018. Elevated CO₂ improves photosynthesis under high temperature

832 by attenuating the functional limitations to energy fluxes, electron transport and redox

833 homeostasis in tomato leaves. Front Plant Sci. 9, 1739. doi: 10.3389/fpls.2018.01739

834 **Pardey PG, Beddow JM, Hurley TM, Beatty TKM, Eidman VR. 2014.** A Bounds Analysis of World Food

835 Futures: Global Agriculture Through to 2050**.** *Austr. J. Agric. Res. Econ*., 571-589**.**

836 https://doi.org/10.1111/1467-8489.12072

837 Parent, B, Tardieu F. 2014. Can Current Crop Models Be Used in the Phenotyping Era for Predicting

838 the Genetic Variability of Yield of Plants Subjected to Drought or High Temperature? *J. Exp.*

839 *Bot.* **65,** 6179-6189.

840 Paul MJ, Foyer CH. 2001. Sink regulation of photosynthesis. *J. Exp. Bot.* **52**, 1383–1400.

841 Paul MJ, Pellny TK. 2003. Carbon metabolite feedback regulation of leaf photosynthesis and

842 development. *J. Exp. Bot.* **54**, 539–547.

843 •Paul MJ, Oszvald M, Jesus C, Rajulu C, Griffiths CA. 2017. Increasing crop yield and resilience with

844 trehalose 6-phosphate: targeting a feast–famine mechanism in cereals for better source–sink

845 optimization. *J. Exp. Bot*. 68, 4455–4462. doi.org/10.1093/jxb/erx083. **The authors**

846 **demonstrate the broad applicability of T6P based sink boosting (maize, wheat, rice) and**

847 **propose a vision for using it in the future.**

848 Paul MJ, Watson A, Griffiths CA**. 2019.** Linking fundamental science to crop improvement through

849 understanding source and sink traits and their integration for yield enhancement. *J. Exp. Bot.*,

850 erz480, https://doi.org/10.1093/jxb/erz480

851 Poorter H, Bühler J, Van Dusschoten D, Climent J, Postma JA. 2012. Pot size matters: a meta-analysis

852 of the effects of rooting volume on plant growth. *Functional Plant Biology* 39, 839–850.

853 Posch BC, Kariyawasam BC, Bramley H, Coast O, Richards RA, Reynolds MP, Trethowan R, Atkin OK.

854 2019. Exploring high temperature responses of photosynthesis and respiration to improve heat

855 tolerance in wheat. Review. *J. Exp. Bot*. 70, 5051–5069. doi.org/10.1093/jxb/erz257

856 •Preece C, Clamp NF, Warham G, Charles M, Rees M, Jones G, Osborne CP. 2018. Cereal progenitors

857 differ in stand harvest characteristics from related wild grasses. *Journal of Ecology,* DOI:

858 10.1111/1365-2745.12905 **Results suggest (implicitly) that the initial choice of species for**

859 **domestication already followed Donald's (1968) crop ideotype principle of restrained**

860 **plasticity. Consider this data in conjunction with Burnett et al. (2016) and Zhang et al. (1999).**

861 Ray DK, West PC, Clak M, Gerber JS, Prishchepov AV, Chatterjee S. 2019. Climate change has likely

862 already affected global food production. *PLOS ONE*, doi.org/10.1371/journal.pone.0217148

863 Rogers A, Ainsworth EA. 2006. The Response of Foliar Carbohydrates to Elevated [CO_2]. In: Nösberger

864 J, Long S, Norby R, Stitt M, Blum H (Eds.). Managed Ecosystems and CO2: Case Studies,

865 Processes, and Perspectives. DOI: 10.1007/3-540-31237-4, pp.293-308.

866 Rubino M, Etheridge DM, Thornton DP, Howden R, Allison CE, Francey RJ, Langenfelds RL, Steele LP,

867 Trudinger CM, Spencer DA, Curran MAJ, van Ommen TD, Smith AM. 2019. Revised records of

868 atmospheric trace gases CO_2, CH_4, N_2O, and $\delta_{13}C$-CO_2 over the last 2000 years from Law Dome,

869 Antarctica. *Earth Syst. Sci. Data* 11, 473–492

870 Ruiz-Vera UM, De Souza AP, Long SP, Ort DR. 2017. The role of sink strength and nitrogen availability

871 in the down-regulation of photosynthetic capacity in field-grown *Nicotiana tabacum* L. at

872 elevated CO_2 concentration. *Front. Plant Sci.* **8**.

873 Sage RF, Sharkey TD, Seemann JR. 1989. Acclimation of photosynthesis to elevated CO_2 in five C3

874 species. *Plant Physiol.* **89**, 590–596.

875 Sakai H, Hasegawa T, Kobayashi K. 2006. Enhancement of rice canopy carbon gain by elevated CO2 is

876 sensitive to growth stage and leaf nitrogen concentration. *New Phytologist* 170, 321-332.

877 •**Sakai** H, **Tokida** T, **Usui** Y, **Nakamura** H, **Hasegawa**

878 T. 2019. Yield responses to elevated CO_2 concentration among Japanese rice cultivars released

since 1882. *Plant Prod. Sci. 22*, doi.org/10.1080/1343943X.2019.1626255

The authors find that not the age of the cultivar but its capacity to adjust its N uptake may determine yield response to e-CO₂.

Schluepmann H, Pellny T, van Dijken A, Smeekens S, Paul MJ. 2003. Trehalose 6-phosphate is indispensable for carbohydrate utilisation and growth in Arabidopsis thaliana. *Proc. Nat. Acad. Sci.* 100, 6849-6854.

Setter TL, Conocono EA, Egdane JA, Kropff MJ. 1995. Possibility of increasing yield potential of rice by reducing panicle height in the canopy. I. Effects of panicles on light interception and canopy photosynthesis. *Austrian Journal of Plant Physiolpgy* 22, 441-451.

Shah L, Yahya M, Mehar S, Shah A, Nadeem M, Ali A, Ali A, Wang J, Riaz JW, Rehman S, Wu W, Khan RM, Abbas A, Riaz A, Anis GB, Si H, Jiang H, Ma C. 2019. Improving lodging resistance: Using wheat and rice as classical examples. Review. *Int. J. Mol. Sci.* 20, 4211. doi:10.3390/ijms20174211

Sharkey TD. 2019. Is triose phosphate utilization important for understanding photosynthesis? *J. Exp. Bot.* **70**, 5521–5525.

Sharkey TD, Berry JA, Sage RF. 1988. Regulation of photosynthetic electron-transport in *Phaseolus vulgaris* L., as determined by room-temperature chlorophyll a fluorescence. *Planta* **176**, 415–424.

Shen B-R, Wang L-M, Lin XL, Yao Z, Xu H-W, Zhu C-H, Teng H-Y, Cui L-L, Liu E-E, Zhang J-J, He Z-H, Peng X-X. 2019. Engineering a new chloroplastic photorespiratory bypass to increase photosynthetic efficiency and productivity in rice. *Molecular Plant* 12, 199-214.

Smith MR, Myers SS. 2018. Impact of anthropogenic CO_2 emissions on global human nutrition, *Nature Climate Change*, doi:10.1038/s41558-018-0253-3

Sonnewald U, Fernie AR. 2018. Next-generation strategies for understanding and influencing source–sink relations in crop plants. *Current Opinion in Plant Biology* **43**, 63–70.

Shimono H, Okada M, Inoue M, Nakamura H. 2019. Diurnal and seasonal variations in stomatal conductance of rice at elevated

atmospheric CO_2 under open-air conditions. *Plant Cell Envir.* 33, 322-31.

Slewinski TL. 2012. Non-structural carbohydrate partitioning in grass stems: a target to increase yield stability, stress tolerance, and biofuel production. *J. Exp. Bot.* 63, 4647–4670. doi.org/10.1093/jxb/ers124

South PF, Cavanagh AP, Liu HW, Ort DR. 2019. Synthetic glycolate metabolism pathways stimulate crop growth and productivity in the field. *Science* 363, 6422, eaat9077. DOI: 10.1126/science.aat9077

Suseela V, Tharayil N, Pendall E, Rao AM. 2017. Warming and elevated CO_2 alter the suberin chemistry in roots of photosynthetically divergent grass species. *AoB PLANTS* 9, plx041, https://doi.org/10.1093/aobpla/plx041

Tang L, Ma W, Noor MA, Li L, Hou H, Zhang X, Zhao M. 2018. Density resistance evaluation of maize varieties through new *"Density–Yield Model"* and quantification of varietal response to gradual planting density pressure. *Nature Sci. Rep.* **8,** 17281. doi:10.1038/s41598-018-35275-w

Tausz M, Posch S, Norton RM, Fitzgerald GJ, Nicolas ME, Seneweera S. 2013. Understanding crop physiology to select breeding targets and improve crop management under increasing atmospheric CO_2 concentrations. *Envir. Exp. Bot*., DOI: 10.1016/j.envexpbot.2011.12.005

Tausz-Posch S, Norton RM, Seneweera S, Fitzgerald GJ, Tausz M. 2012. Will intra-specific differences in transpiration efficiency in wheat be maintained in a high CO_2 world? A FACE study. *Physiologia Plantarum* 148, 232–245.

Tausz-Posch S, Dempsey RW, Seneweera S, Norton RM, Fitzgerald G, Tausz M. 2015. Does a freely tillering wheat cultivar benefit more from elevated CO_2 than a restricted tillering cultivar in a water-limited environment? *Europ. J. Agron.* 64, 21–28.

•Uddin S, Löw M, Parvin S, Fitzgerald GJ, Tausz-Posch S, Armstrong R, O'Leary G, Tausz M. 2018. Elevated [CO_2] mitigates the effect of surface drought by stimulating root growth to access sub-soil water. *PLOS1*, https://doi.org/10.1371/journal.pone.0198928 **The role of root sinks and root growth in e-CO_2 response is under-studied. This paper reports root growth stimulation contributing to drought avoidance.**

Usuda H, Shimogawara K. 1998. The effects of increased atmospheric carbon dioxide on growth, carbohydrates, and photosynthesis in radish, *Raphanus sativus. Plant Cell Physiol.* 39, 1-7.

938   Von Caemmerer S, Farquhar GD. 1981. Some relationships between the biochemistry of
939   photosynthesis and the gas exchange of leaves. *Planta* 153, 376-387.

940   Weber APM, Bar-Even A. 2019. Update: Improving the efficiency of photosynthetic carbon reactions.
941   *Plant Physiol.* **179**, 803–812.

942   Weiner J. 2019. Looking in the wrong direction for higher-yield crop genotypes. *Trends in Plant*
943   *Science* 24, 927-933.

944   •White A, Rogers A, Rees M, Osborne CP. 2016. How can we make plants grow faster? A source–sink
945   perspective on growth rate. Review. *J. Exp. Bot.* 67, 31–45. doi:10.1093/jxb/erv447 **This review**
946   **is significant as it calls for the integration of N in the C-centric debate on source-sink**
947   **optimization.**

948   Yang JT, Preiser AL, Li Z, Weise SE, Sharkey TD. 2016. Triose phosphate use limitation of
949   photosynthesis: short-term and long-term effects. *Planta* **243**, 687–698.

950   Yin X. 2013. Improving ecophysiological simulation models to predict the impact of elevated
951   atmospheric CO2 concentration on crop productivity. Ann. Bot. 112, 465-475.

952   Yin X, Schapendonk AHCM, Struik PC. 2019. Exploring the optimum nitrogen partitioning to predict
953   the acclimation of C_3 leaf photosynthesis to varying growth conditions. J. Exp. Bot. 70, 2435-
954   2447.

955   Yoshimoto M, Fukuoka M, Hasegawa T, Utsumi M, Ishigooka Y, Kuwagata T. 2011. Integrated
956   micrometeorology model for panicle and canopy tempera-ture (IM2PACT) for rice heat stress
957   studies under climate change. *J. Agric. Meteorol*. 67, 233–247.

958   Yuan LP. 2017. Progress in super-hybrid rice breeding. *The Crop Journal* 5, 100-102.

959   Zabel F, Putzenlechner B, Mauser W. 2014. Global Agricultural Land Resources – A High Resolution
960   Suitability Evaluation and Its Perspectives until 2100 under Climate Change Conditions. *PLOS*
961   *ONE* 9 (9), e107522.

962   Zhang Y, Primavesi LF, Jhurreea D, Mitchell R, Powers S, Schluepmann H, Delatte T, Wingler A, Paul
963   MJ. 2009. Inhibition of Snf1-related protein kinase (SnRK1) activity and regulation of metabolic
964   pathways by trehalose 6-phosphate. *Plant Physiol.* 149, 1860-1871.

965   Zhao C, Liu B, Piao S, Wang X, Lobell DB, Huang Y, Huang M, Yao Y, Bassu S, Ciais P, Durand J-L, Elliott
966   J, Ewert F, Janssens IA, Li T, Lin E, Liu Q, Martre P, Müller C, Peng S, Peñuelas J, Ruane AC,
967   Wallach D, Wang T, Wu D, Liu Z, Zhu Z, Asseng S. 2017. Temperature increase reduces global
968   yields of major crops in four independent estimates. *PNAS* 114 (35),
969   www.pnas.org/cgi/doi/10.1073/pnas.1701762114

970   Zheng Y, Li F, Hao L, Yu J, Guo L, Zhou H, Ma C, Zhang X, Xu M. 2019. Elevated CO_2 concentration
971   induces photosynthetic down-regulation with changes in leaf structure, non-structural

972   carbohydrates and nitrogen content of soybean. *BMC Plant Biology* 19, 255.

973   https://doi.org/10.1186/s12870-019-1788-9

974 Zhu C, Zhu J, Cao J, Jiang Q, Liu G, Ziska LH. 2014. Biochemical and molecular characteristics of leaf

975   photosynthesis and relative seed yield of two contrasting rice cultivars in response to elevated

976   [CO2]. *J. Exp. Bot.* **65**, 6049–6056.

977 Ziska L, Morris CF, Goins EW. 2004. Quantitative and qualitative evaluation of selected wheat

978   varieties released since 1903 to increasing atmospheric carbon dioxide: can yield sensitivity to

979   carbon dioxide be a factor in wheat performance? *Global Change Biology* 10, 1810–1819. doi:

980   10.1111/j.1365-2486.2004.00840.x

981 •Ziska LH, Tomecek MB, Gealy DR. 2013. Assessment of cultivated and wild, weedy rice lines to

982   concurrent changes in CO_2 concentration and air temperature: determining traits for enhanced

983   seed yield with increasing atmospheric CO_2. *Functional Plant Biology* **41**, 236-243.

984   https://doi.org/10.1071/FP13155. **Evidence that early tillering response to e-CO2 is predictive**

985   **of yield response, indicating that vegetative-stage sink plasticity contributes to it.**

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