

eXtra Botany

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From green to gold: agricultural revolution for food security

Fifty years ago, Norman Borlaug was awarded the Nobel Peace Prize in recognition of his efforts to raise cereal production. The changes, which became known as the 'Green Revolution', included the introduction of dwarfing genes that enabled dramatic increases in yield through the use of fertilizer and irrigation, coupled with disease resistance. Since the human population continued to rise dramatically, maintaining a constant per capita cereal production has required a continual increase in global cereal production. Now a Golden Revolution in agriculture is needed to sustainably feed the future population and meet their rising expectations.

Production is the combination of the area farmed and the yield. Between 1960 and 1990, global per capita production of wheat and rice increased by 40% and then stabilised. The area farmed for wheat has been virtually constant over the last 50 years, while there has been a 25% increase in the area dedicated to growing rice (Figure 1). Given that population has doubled since 1970, the increases in cereal production to meet the rising demand are mainly due to continual improvements in yield rather than expansion of agricultural land. Yields of wheat and rice have both been increasing linearly over the last 30 years. If we extrapolate these trends to 2050, then together they would match food requirements of the forecast population of 9.7 billion. However, rising standards of living are also resulting in a dramatic increase in meat consumption and current rates of cereal yield improvement are inadequate to satisfy this additional demand for animal feed (Ray et al. 2013). We thus face tremendous challenges maintaining current rates of yield improvement that are getting progressively harder to achieve, while also increasing production to feed more animals. A lower and more sustainable bar could be set by convincing people to alter their diet for the sake of their own and the planet's health (Willett et al. 2019) and reducing global population. Of great concern is that yield increases need to continue despite climate change that is generally predicted to be detrimental to agriculture (Pachauri and Meyer 2014).

The introduction of dwarfing genes into cereals enabled substantial increases in grain yield due to a reallocation of plant biomass from stems to grain. As the opportunities to further increase harvest index (the ratio of grain to plant biomass) are becoming limited, attention has changed and now focuses on how to increase the biomass of a crop. Biomass accumulates as a result of photosynthesis that requires light interception, water, CO₂ and nutrient uptake. If the photosynthetic process could be manipulated, could this be translated into increased biomass production? There are two lines of evidence supporting the idea that increasing photosynthesis could translate into greater biomass and yield. Firstly, the biomass and yield of crops increased when they were grown under enriched atmospheric CO₂ concentrations which increased photosynthetic rate (Ainsworth and Long 2005). Secondly, the efficiency with which crops convert sunlight into biomass is generally greater for C₄ species compared to C₃ species due to the suppression of photorespiration, the process in which Rubisco catalyses the 'wasteful' oxygenase reaction (Sheehy et al. 2007). On the other hand, it has been argued that yield is not closely related to photosynthetic rate. Studies vary between no relationship (Driever et al. 2014), one that varies with nutrient conditions (Gaju et al. 2016) or when measurements were taken (Reynolds et al. 2000), while others support a strong relationship (Fischer et al. 1998). These conflicting reports often depend on the type of measurements taken, on which part of the plants and at what point in the growing season (Faralli and Lawson 2020). Other reports

have suggested that if carbon input does not limit the rate of crop growth, increased nutrient accumulation perhaps should be the primary target (Sinclair et al. 2019). There are many factors that result in a gap between potential yield and farmers yield (Fischer et al. 2014) and therefore it is clear that future increases in yield are likely to involve a variety of targets and hopefully these can be combined to multiply their effectiveness. Given the length of time it takes to engineer a trait and create a plant that can be assessed, the use of crop simulation models provides a useful way to compare the potential benefits of a given trait or combination of traits (Wu et al. 2019). While we are able to generate increasingly big data (molecular, phenotypic), it needs to be balanced with a framework to analyse and convert it into useful information (Sadras 2019).

Improving the efficiency in the use of resources: light, water and nutrients

The easiest way to increase yield has been to increase the supply of resources available to the crop. Longer crop duration or more rapid canopy closure increases the potential amount of sunlight intercepted. Irrigation can avoid crop growth being limited by water stress and the supply of fertilizer can satisfy the need for greater nutrient uptake required to increase biomass. However, the next and harder challenge is whether we can improve the efficiency with which plants convert these resources into biomass.

Light: Photosynthesis converts sunlight into the fundamental units needed for plant growth. However, it is not a simple process to link photosynthetic rate of a given piece of leaf through to plant or crop growth, or yield. Actual photosynthesis achieved by a crop will depend on the photosynthetic capacity, development of the plant and the seasonal weather and is an integration over the whole plant area and lifespan. Traditional methods for measuring photosynthesis are relatively slow which has limited our ability to fully examine and exploit the natural genetic variation that is known to exist in photosynthetic processes (Silva-Perez and al. 2020; Adachi et al. 2019; Lawson et al. 2012). However, there are a growing number of high throughput phenotyping methods that relate to photosynthetic traits (Furbank et al. 2019; Furbank et al. 2020). These include hyperspectral reflectance (Yendrek et al. 2017; Silva-Perez et al. 2018; Lu et al. 2019; Meacham-Hensold and al. 2020), light induced fluorescence transients, LIFT (Keller et al. 2019; Osmond et al. 2019; Grolí and al. 2020) and solar induced fluorescence, SIF (Camino et al. 2019). The beauty of these methods is that they can be deployed in the field to measure large numbers of plants, thereby providing a rapid, non-destructive measure of photosynthesis on plants in their growth environment. Other methods can determine important crop traits like plant height (Hu et al. 2018) and canopy structure (Liu et al. 2019). The ability to measure photosynthetic traits more rapidly will most likely lead to the identification of underlying markers and genes that could be incorporated into on-going breeding programs for improved photosynthesis and productivity (Faralli and Lawson 2020).

Water: In many regions, water availability poses the greatest limit to crop yield and is threatened by climate change altering rainfall and the finite availability of water for agriculture. Rather than just focus on the exchange of water for CO₂ during photosynthesis, Condon (2020) takes a step back to consider the whole picture. Of the water captured by an area of soil from rainfall or irrigation that is not lost in runoff and deep drainage, some evaporates directly from the soil rather than via transpiration. Direct soil evaporation is effectively a lost opportunity for photosynthesis and minimising this fraction leads to greater biomass production for a given amount of soil water. There are various ways in which this can be achieved, ranging from early vigour where germinating seedlings expand leaf area to cover the soil more rapidly, to growing deeper roots to gain access to

water deep in the soil profile which can be particularly valuable late in a dry season. At the leaf level, altering transpiration efficiency can be achieved by targeting stomatal or photosynthetic physiology.

Stomata respond to numerous internal and external signals that results in a complex web of controls and responses. In the dynamic natural light environment where clouds and leaf movement result in rapid fluctuations in the light intensity reaching a leaf, stomata are continually altering aperture in order to balance CO₂ uptake for photosynthesis with water loss for evaporative cooling and nutrient uptake. Matthews et al. (2020) discuss the separate roles that red and blue light play in regulating stomatal aperture. They propose that altering the stomatal blue light response could result in improved transpiration efficiency that is not at the expense of photosynthetic performance. Increasing the rapidity of stomatal opening to increasing irradiance could reduce CO₂ diffusional constraints on photosynthesis (Lawson et al. 2012). Kimura et al. (2020) used Arabidopsis mutants with higher stomatal conductance and the Patrol (proton ATPase translocation control 1) overexpressing line with faster stomatal opening to confirm increased photosynthesis with rapid stomatal behaviour. An alternative route for manipulating stomatal conductance has been to alter stomatal density via mutating the development of stomatal complexes. Manipulating the expression of the epidermal patterning factor gene in wheat lead to the development of fewer stomata per unit leaf area and an increase in transpiration efficiency (Dunn et al. 2019). However, further work is needed to fine-tune the effect so that growth and yield are not adversely affected. The importance of dynamic stomatal behaviour and the ability to assess stomatal dynamics in a high throughput manner is provided by Violet-Chabrand & Lawson (2020), who illustrate a simplified energy balance approach for determining stomatal conductance by remotely monitoring canopy temperature (Deery et al. 2019; Violet-Chabrand and Lawson 2020).

Nitrogen: To sustain high yields, the nutrients removed in the harvested product must be replaced and this has led to an increasing use of fertilizers. Unfortunately, the synthesis of nitrogenous fertilizers is an energy demanding process that directly contributes to greenhouse emissions and escape to the environment of nitrogen fertilizer can cause eutrophication and environmental damage. There is still room for improvement as recently demonstrated by the discovery and manipulation of a nitrogen responsive gene that alters tillering in rice (Wu et al. 2020). While nitrogen can be captured from the atmosphere by legumes through their symbiotic association with bacteria, this option is unavailable to cereals. However, progress is being made to engineer nitrogen fixation directly into a plant without the need for a symbiotic partner (Allen et al. 2017). Thus, rather than creating a root nodule to house the bacterial partner, it may be feasible to introduce the metabolic capability for dinitrogen reduction directly into the plant.

Alternative sinks for photosynthesis

Although photosynthesis is the starting point for carbon gain by plants, it does not always follow that growth is limited by the rate of photosynthesis. Ultimately, the fixed carbon has to be translocated into the grain or harvestable part of the crop and the ability of that sink to process the carbon can be the rate limiting step. A key regulatory molecule, trehalose 6 phosphate, has been found to be important in the process of moving carbon from leaves to the grain (Paul 2020) and could provide a novel regulatory target for coordinating sinks demand with source strength. Alternative end products, such as lipids, have been introduced into plants that normally would not contain this as a major constituent, through the use of metabolic engineering to produce oil as a significant storage product (Vanhercke et al. 2017; Beechey-Gradwell et al. 2020). Such alternative

sinks may result in greater photosynthesis by providing additional storage pools that reduce feedback inhibition as well as providing a novel way to increase the nutritional value of fodder (Paul and Eastmond 2020).

Synthetic Biology

Genetically modified crop plants provide a targeted approach to manipulating and improving plant performance. They have been grown in many countries, yet their introduction was and remains controversial in many communities. While the introduction of herbicide resistant varieties has proven very popular with technologically advanced farmers as well as small scale farmers, the consumer has not always been convinced of their benefit. As the technology advances, new opportunities emerge, but it is important that the broader societal impact is considered to enable rapid acceptance (Kohli and al. 2020).

The need to develop novel pathways for crop improvement, the potential to speed up the introduction of desirable traits through genetic engineering and the rapid development of new engineering/editing approaches is opening up a rich and diverse front that offers many exciting opportunities. Zhu et al. (2020) provide a summary of candidate genes/traits that were contemplated and discussed at the International Symposium on Synthetic Biology in Photosynthesis Research held in Shanghai in 2018. A diversity of protein complexes have evolved that capture sunlight and transfer the energy to chemical intermediates for photosynthesis and there is speculation as to whether we could engineer alternative combinations that enhance efficiency for improved plant performance (Leister 2019). Manipulation of the dynamic responsiveness of photoprotection led to improved growth of tobacco plants in the field (Kromdijk et al. 2016). The same approach is being applied to cereal crops and the results are eagerly awaited. Many targets have been identified in the carbon fixation reactions of photosynthesis that could be synthetically manipulated to increase photosynthesis. These potential targets range from known enzymes such as Rubisco, to postulating additional novel metabolic pathways (Weber and Bar-Even 2019). The bifunctional nature of the Rubisco enzyme that catalyses a reaction between oxygen and ribulose biphosphate is an unfortunate and apparently unavoidable reaction. Plants must deal with the 2 carbon product of the oxygenase reaction through a complex pathway called photorespiration which is considered wasteful and reduces photosynthetic efficiency by about 25% in C3 plants. Alternative photorespiratory pathways have been proposed (Maurino and Peterhansel 2010) and engineered (South et al. 2019; Shen et al. 2019), that re-route the C2 pathway and reduce the losses associated with the oxygenase reaction. The C4 photosynthetic pathway, in which photorespiration is greatly reduced due to the employment of a carbon concentrating mechanism, has evolved independently nearly 70 times (Sage et al. 2011) and an alternative to engineering the photorespiratory pathway is to introduce the C4 pathway in to a C3 cereal (Ermakova and al. 2020).

Transforming nuclear genes has been possible for decades and for some species it has been possible to transform genes in the chloroplast (Whitney and Sharwood 2008). Now, a method has emerged that allows mitochondrial genes to be altered (Kazama et al. 2019), so it is theoretically possible that we can engineer changes into any parts of an organism's genome. CRISPR Cas9 is being used to manipulate diverse targets, such as improving seed dormancy (Abe et al. 2019) or introducing semi dwarf habit to elite rice landraces (Hu et al. 2019). The simultaneous development of these methods along with our increasing understanding of metabolic processes and the identification of new breeding targets add new options with which to improve cereal crops.

Conclusion

We have highlighted current technological advances in the field of plant science and novel and emerging approaches to re-engineer crops that could potentially lead to innovations in agriculture that benefit food security. This area of research could not be more exciting for scientists and not be more relevant for humankind given the challenge we face to increase yield. To feed the future global population in a sustainable way without occupying more arable land and in the face of unprecedented changes in global climate, will draw on diverse, creative skills and innovative approaches and require combining these efforts at all levels in order to achieve a Golden Revolution in agriculture.

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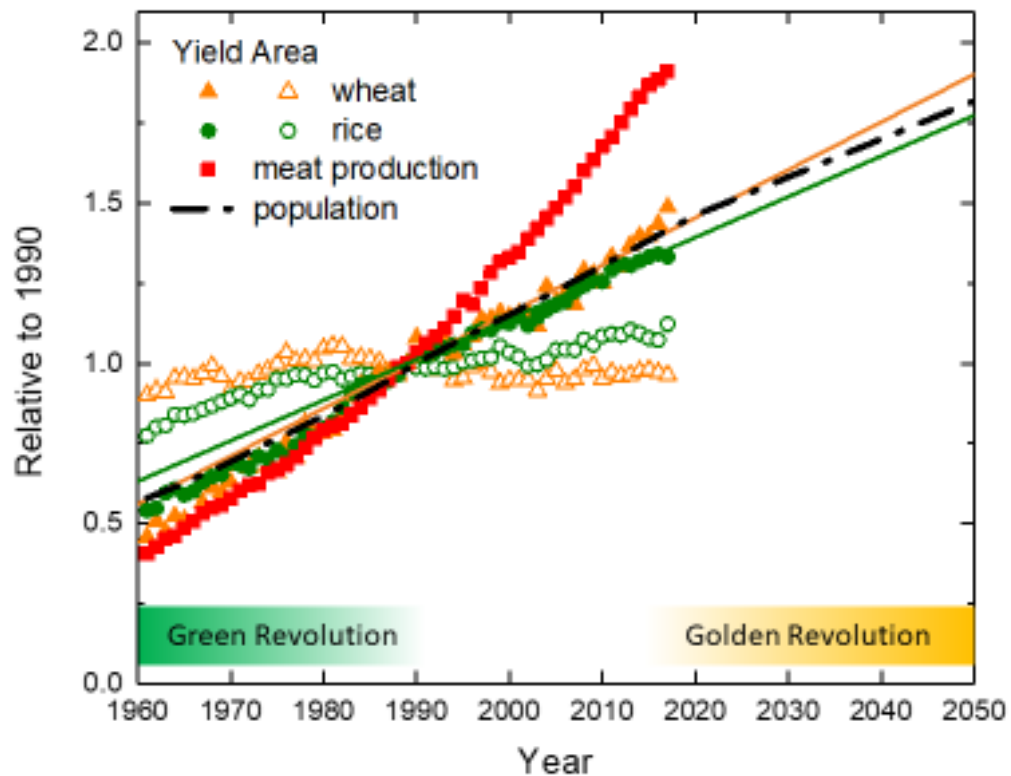


Figure 1. Normalised changes in global wheat, rice and meat production with respect to human population (source data <http://www.fao.org/faostat/en/#data/QC>). Data normalised to 1 in 1990. 1960-1990 represents the Green Revolution, followed by a 30 year period of stability from 1990-2020, that is extrapolated forwards to predict production in 2050, or backwards to show gains associated with the Green Revolution. Black dashed line is global population. Open symbols are global areas under wheat or rice production. Closed symbols are global wheat and rice yields per area and meat represents the global sum of beef, pig, sheep, goat and chicken production.

References

- Abe F, Haque E, Hisano H, Tanaka T, Kamiya Y, Mikami M, Kawaura K, Endo M, Onishi K, Hayashi T, Sato K (2019) Genome-Edited Triple-Recessive Mutation Alters Seed Dormancy in Wheat. *Cell Reports* 28 (5):1362-1369.e1364. doi:10.1016/j.celrep.2019.06.090
- Adachi S, Yamamoto T, Nakae T, Yamashita M, Uchida M, Karimata R, Ichihara N, Soda K, Ochiai T, Ao R, Otsuka C, Nakano R, Takai T, Ikka T, Kondou K, Ueda T, Ookawa T, Hirasawa T (2019) Genetic architecture of leaf photosynthesis in rice revealed by different types of reciprocal mapping populations. *Journal of Experimental Botany* 70 (19):5131-5144. doi:10.1093/jxb/erz303
- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytologist* 165 (2):351-371
- Allen RS, Tilbrook K, Warden AC, Campbell PC, Rolland V, Singh SP, Wood CC (2017) Expression of 16 Nitrogenase Proteins within the Plant Mitochondrial Matrix. *Frontiers in Plant Science* 8:1-14. doi:10.3389/fpls.2017.00287
- Beechey-Gradwell Z, al. e (2020) Storing carbon in leaf lipids. *JOURNAL OF EXPERIMENTAL BOTANY*
- Camino C, Gonzalez-Dugo V, Hernandez P, Zarco-Tejada PJ (2019) Radiative transfer Vcmax estimation from hyperspectral imagery and SIF retrievals to assess photosynthetic performance in rainfed and irrigated plant phenotyping trials. *Remote Sens Environ* 231. doi:10.1016/j.rse.2019.05.005
- Condon A (2020) Drying times. *Journal of experimental botany*
- Deery DM, Rebetzke GJ, Jimenez-Berni JA, Bovill WD, James RA, Condon AG, Furbank RT, Chapman SC, Fischer RA (2019) Evaluation of the Phenotypic Repeatability of Canopy Temperature in Wheat Using Continuous-Terrestrial and Airborne Measurements. *Frontiers in Plant Science* 10 (875). doi:10.3389/fpls.2019.00875
- Driever SM, Lawson T, Andralojc PJ, Raines CA, Parry MAJ (2014) Natural variation in photosynthetic capacity, growth, and yield in 64 field-grown wheat genotypes. *Journal of Experimental Botany*. doi:10.1093/jxb/eru253
- Dunn J, Hunt L, Afsharinafar M, Al Meselmani M, Mitchell A, Howells R, Wallington E, Fleming AJ, Gray JE (2019) Reduced stomatal density in bread wheat leads to increased water-use efficiency. *Journal of Experimental Botany* 70 (18):4737-4747. doi:10.1093/jxb/erz248
- Ermakova M, al. e (2020) On the road to C₄ rice. *The Plant Journal*
- Faralli M, Lawson T (2020) Natural genetic variation in photosynthesis: an untapped resource to increase crop yield potential? *Plant J* 101 (3):518-528. doi:10.1111/tpj.14568
- Fischer RA, Rees D, Sayre KD, Lu ZM, Condon AG, Saavedra AL (1998) Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Science* 38 (6):1467-1475
- Fischer T, Byerlee D, Edmeades G (2014) Crop yields and global food security. *ACIAR*,
- Furbank R, Sharwood R, Estavillo G, Silva-Perez V, Condon A (2020) Photons to food. *Journal of experimental botany*
- Furbank RT, Jimenez-Berni JA, George-Jaeggli B, Potgieter AB, Deery DM (2019) Field crop phenomics: enabling breeding for radiation use efficiency and biomass in cereal crops. *New Phytologist* 223 (4):1714-1727. doi:10.1111/nph.15817
- Gaju O, DeSilva J, Carvalho P, Hawkesford MJ, Griffiths S, Greenland A, Foulkes MJ (2016) Leaf photosynthesis and associations with grain yield, biomass and nitrogen-use efficiency in landraces, synthetic-derived lines and cultivars in wheat. *Field Crops Research* 193:1-15. doi:<http://doi.org/10.1016/j.fcr.2016.04.018>
- Groli E, al. e (2020) Chlorophyll fluorescence under daylight. *Journal of experimental Botany*
- Hu PC, Chapman SC, Wang XM, Potgieter A, Duan T, Jordan D, Guo Y, Zheng BY (2018) Estimation of plant height using a high throughput phenotyping platform based on unmanned aerial

- vehicle and self-calibration: Example for sorghum breeding. *Eur J Agron* 95:24-32. doi:10.1016/j.eja.2018.02.004
- Hu XM, Cui YT, Dong GJ, Feng AH, Wang DY, Zhao CY, Zhang Y, Hu J, Zeng DL, Guo LB, Qian Q (2019) Using CRISPR-Cas9 to generate semi-dwarf rice lines in elite landraces. *Scientific Reports* 9. doi:10.1038/s41598-019-55757-9
- Kazama T, Okuno M, Watari Y, Yanase S, Koizuka C, Tsuruta Y, Sugaya H, Toyoda A, Itoh T, Tsutsumi N, Toriyama K, Koizuka N, Arimura S-i (2019) Curing cytoplasmic male sterility via TALEN-mediated mitochondrial genome editing. *Nature Plants* 5 (7):722-730. doi:10.1038/s41477-019-0459-z
- Keller B, Matsubara S, Rascher U, Pieruschka R, Steier A, Kraska T, Muller O (2019) Genotype Specific Photosynthesis x Environment Interactions Captured by Automated Fluorescence Canopy Scans Over Two Fluctuating Growing Seasons. *Frontiers in Plant Science* 10 (1482). doi:10.3389/fpls.2019.01482
- Kimura H, Hashimoto-Sugimoto M, Iba K, Terashima I, Yamori W. 2010. Improved stomatal opening enhances photosynthetic rate and biomass production in fluctuating light. *Journal of Experimental Botany* 71, xxxx-xxxx.
- Kohli A, al. e (2020) Photosynthesis research: A model to bridge fundamental science. *Journal of experimental Botany*
- Kromdijk J, Głowacka K, Leonelli L, Gabilly ST, Iwai M, Niyogi KK, Long SP (2016) Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science* 354 (6314):857-861. doi:10.1126/science.aai8878
- Lawson T, Kramer DM, Raines CA (2012) Improving yield by exploiting mechanisms underlying natural variation of photosynthesis. *Current Opinion in Biotechnology* 23 (2):215-220. doi:10.1016/j.copbio.2011.12.012
- Leister D (2019) Genetic Engineering, Synthetic Biology and the Light Reactions of Photosynthesis. *Plant Physiology* 179 (3):778-793. doi:10.1104/pp.18.00360
- Liu S, Martre P, Buis S, Abichou M, Andrieu B, Baret F (2019) Estimation of Plant and Canopy Architectural Traits Using the Digital Plant Phenotyping Platform. *Plant Physiology* 181 (3):881-890. doi:10.1104/pp.19.00554
- Lu N, Wang W, Zhang Q, Li D, Yao X, Tian Y, Zhu Y, Cao W, Baret F, Liu S, Cheng T (2019) Estimation of Nitrogen Nutrition Status in Winter Wheat From Unmanned Aerial Vehicle Based Multi-Angular Multispectral Imagery. *Frontiers in Plant Science* 10 (1601). doi:10.3389/fpls.2019.01601
- Matthews J, Violet-Chabrand S, Lawson T (2020) Role of blue and red light in stomatal dynamic behaviour. *Journal of experimental Botany*
- Maurino VG, Peterhansel C (2010) Photorespiration: current status and approaches for metabolic engineering. *Current Opinion in Plant Biology* 13 (3):249-256. doi:10.1016/j.pbi.2010.01.006
- Meacham-Hensold K, al. e (2020) Plot level rapid screening for photosynthetic parameters. *Journal of experimental botany*
- Osmond B, Chow WS, Pogson BJ, Robinson SA (2019) Probing functional and optical cross-sections of PSII in leaves during state transitions using fast repetition rate light induced fluorescence transients. *Functional Plant Biology* 46 (6):567-583. doi:<https://doi.org/10.1071/FP18054>
- Pachauri RK, Meyer LA (2014) 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 IPCC, Geneva, Switzerland
- Paul M (2020) Linking fundamental science to crop improvement through understanding source and sink. *Journal of experimental botany*
- Paul M, Eastmond P (2020) Turning sugar into oil: making photosynthesis blind to feedback inhibition. *Journal of Experimental Botany*
- Ray DK, Mueller ND, West PC, Foley JA (2013) Yield Trends Are Insufficient to Double Global Crop Production by 2050. *Plos One* 8 (6). doi:10.1371/journal.pone.0066428

- Reynolds MP, van Ginkel M, Ribaut JM (2000) Avenues for genetic modification of radiation use efficiency in wheat. *Journal of Experimental Botany* 51:459-473
- Sadras VO (2019) Effective Phenotyping Applications Require Matching Trait and Platform and More Attention to Theory. *Frontiers in Plant Science* 10 (1339). doi:10.3389/fpls.2019.01339
- Sage RF, Christin P-A, Edwards EJ (2011) The C₄ plant lineages of planet Earth. *Journal of Experimental Botany* 62 (9):3155-3169. doi:10.1093/jxb/err048
- Sheehy JE, Ferrer AB, Mitchell PL, Elmido-Mabilangan A, Pablico P, Dionora MJA (2007) How the rice crop works and why it needs a new engine. In: Sheehy JE, Mitchell PL, Hardy B (eds) *Charting new pathways to C₄ rice*. International Rice Research Institute, Los Banos, Philippines, pp 3-26
- Shen BR, Wang LM, Lin XL, Yao Z, Xu HW, Zhu CH, Teng HY, Cui LL, Liu EE, Zhang JJ, He ZH, Peng XX (2019) Engineering a New Chloroplastic Photorespiratory Bypass to Increase Photosynthetic Efficiency and Productivity in Rice. *Mol Plant* 12 (2):199-214. doi:10.1016/j.molp.2018.11.013
- Silva-Perez V, al. e (2020) Genetic variation for photosynthetic capacity. *Journal of experimental botany*
- Silva-Perez V, Molero G, Serbin SP, Condon AG, Reynolds MP, Furbank RT, Evans JR (2018) Hyperspectral reflectance as a tool to measure biochemical and physiological traits in wheat. *Journal of Experimental Botany* 69 (3):483-496. doi:10.1093/jxb/erx421
- Sinclair TR, Rufty TW, Lewis RS (2019) Increasing Photosynthesis: Unlikely Solution For World Food Problem. *Trends in Plant Science* 24 (11):1032-1039. doi:10.1016/j.tplants.2019.07.008
- 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
- Vanhercke T, Divi UK, El Tahchy A, Liu Q, Mitchell M, Taylor MC, Eastmond PJ, Bryant F, Mechanicos A, Blundell C, Zhi Y, Belide S, Shrestha P, Zhou X-R, Ral J-P, White RG, Green A, Singh SP, Petrie JR (2017) Step changes in leaf oil accumulation via iterative metabolic engineering. *Metabolic Engineering* 39:237-246. doi:<https://doi.org/10.1016/j.ymben.2016.12.007>
- Violet-Chabrand S, Lawson T (2020) Thermography methods to assess stomatal behaviour in dynamic environment. *Journal of experimental botany*
- Weber APM, Bar-Even A (2019) Update: Improving the Efficiency of Photosynthetic Carbon Reactions. *Plant Physiology* 179 (3):803-812. doi:10.1104/pp.18.01521
- Whitney SM, Sharwood RE (2008) Construction of a tobacco master line to improve Rubisco engineering in chloroplasts. *Journal of Experimental Botany* 59 (7):1909-1921. doi:10.1093/jxb/erm311
- Willett W, Rockstrom J, Loken B (2019) Food in the Anthropocene: the EAT-Lancet Commission on healthy diets from sustainable food systems (vol 393, pg 447, 2018). *Lancet* 393 (10191):2590-2590
- Wu A, Hammer GL, Doherty A, von Caemmerer S, Farquhar GD (2019) Quantifying impacts of enhancing photosynthesis on crop yield. *Nature Plants* 5 (4):380-388. doi:10.1038/s41477-019-0398-8
- Wu K, Wang S, Song W, Zhang J, Wang Y, Liu Q, Yu J, Ye Y, Li S, Chen J, Zhao Y, Wang J, Wu X, Wang M, Zhang Y, Liu B, Wu Y, Harberd NP, Fu X (2020) Enhanced sustainable green revolution yield via nitrogen-responsive chromatin modulation in rice. *Science* 367 (6478):eaaz2046. doi:10.1126/science.aaz2046
- Yendrek CR, Tomaz T, Montes CM, Cao Y, Morse AM, Brown PJ, McIntyre LM, Leakey ADB, Ainsworth EA (2017) High-Throughput Phenotyping of Maize Leaf Physiological and Biochemical Traits Using Hyperspectral Reflectance. *Plant Physiology* 173 (1):614-626. doi:10.1104/pp.16.01447
- Zac Beechey-Gradwell, Luke Cooney, Somrutai Winichayakul, Mitchell Andrews, Shen Hea, Tracey Crowther, Nick Roberts Storing carbon in leaf lipid sinks enhanced perennial ryegrass carbon

capture especially under high N and elevated CO₂. 2020. *Journal of Experimental Botany* 71, xxxx-xxxx.

Zhu X-G, al. e (2020) A wish list for synthetic biology in photosynthetic research. *Journal of experimental botany*