

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 increase 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 has 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 stabilized. 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 (Fig. 1). Given that the 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 in maintaining current rates of yield improvement that are becoming 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. First, the biomass and yield of crops increased when they were grown under enriched atmospheric CO₂ concentrations which increased the photosynthetic rate (Ainsworth and Long, 2005). Secondly, the efficiency with which crops convert sunlight into biomass is generally greater for C₄ species compared with 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), to 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 and phenotypic), they need to be balanced with a framework to analyse and convert them 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 increase 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

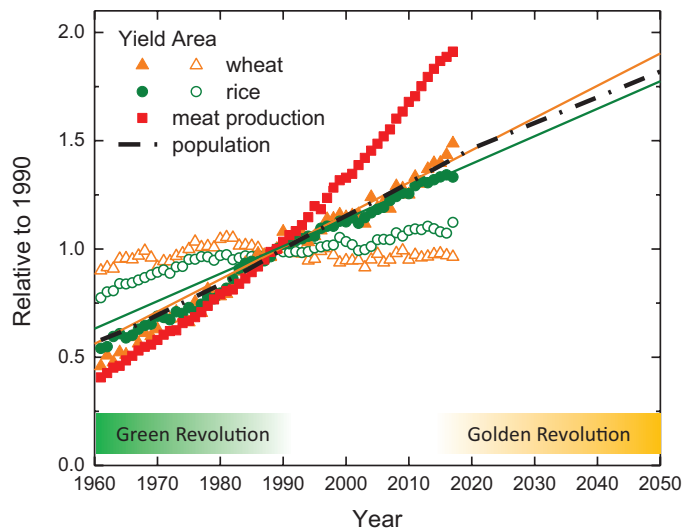


Fig. 1. Normalized changes in global wheat, rice, and meat production with respect to human population (data source <http://www.fao.org/faostat/en/#data/QC>). Data are normalized to 1 in 1990. 1960–1990 represents the Green Revolution, followed by a 30 year period of stability from 1990 to 2020, that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

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 life span. 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 (Lawson *et al.*, 2012; Adachi *et al.*, 2019; Silva-Perez *et al.*, 2020). However, there are a growing number of high-throughput phenotyping methods that relate to photosynthetic traits (Furbank *et al.*, 2019, 2020). These include hyperspectral reflectance (Yendrek *et al.*, 2017; Silva-Perez *et al.*, 2018; Lu *et al.*, 2019; Meacham-Hensold *et al.*, 2020), light-induced fluorescence transients, LIFT (Keller *et al.*, 2019; Osmond *et al.*, 2019), 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 such as plant height (Hu *et al.*, 2018) and canopy structure (Liu *et al.*, 2019). The ability to measure photosynthetic traits more rapidly will most probably lead to the identification of underlying markers

and genes that could be incorporated into ongoing breeding programmes 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 minimizing 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 result 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 led 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 and 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 *et al.*, 2020) and could provide a novel regulatory target for coordinating sink 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 *et 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 (Shen *et al.*, 2019; South *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 into a C₃ cereal (Ermakova *et 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. Clustered regularly interspaced palindromic repeats (CRISPR)/CRISPR-associated protein 9 (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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