



Improving photosynthesis and yield potential in cereal crops by targeted genetic manipulation: Prospects, progress and challenges



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ABSTRACT

Since the ground breaking work of Norman Borlaug in the 1960s produced large increases in yields of our major cereal crops, we have seen a gradual decline in annual yield progress. The genetic potential of the yield components harvest index and grain number, which were targeted in the “green revolution” and subsequently by cereal breeders have largely been optimised in our two largest global cereal crops, rice and wheat. Physiologists and breeders are turning to the biomass portion of the yield equation and in particular radiation use efficiency, as a means to push the yield potential barrier. Consequently, in the last decade a large effort has been initiated to identify targets to improve photosynthetic performance both using non-transgenic Phenomics approaches and transgenic technologies. Efficiency of light interception, harvesting and energy utilisation have been targeted but most efforts have so far focussed on improving photosynthetic capacity and efficiency in photosynthetic carbon metabolism in rice, wheat and model plants. Here the targets for improving light harvesting and carbon fixation are reviewed, the progress thus far evaluated and the likelihood of success of these activities in improving crop yields discussed in the context of modelling and scaling from the leaf to the canopy.

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1. Introduction

Large increases in global rice and wheat production, which later came to be known as the Green Revolution, began in Mexico in the late 1950s, spread to Asia during the 1960s and 1970s, and then continued in China in the 1980s and 1990s. The benefits of this quantum leap in cereal production were to reduce prices of wheat and rice grain by more than 75% and over a 40-year period the proportion of the globe in famine declined from about 60% in 1960 to 17% in 2000 (Borlaug, 2007). While the fruits of the green revolution have sustained global demand for many years, annual increases in cereal grain yield from wheat and rice arising from genetic progress in breeding have now dropped below 1% (Brisson et al., 2010; Sheehy and Mitchell, 2011). Global population growth estimates indicate that by 2050 we will face the daunting

prospect of feeding 9 billion people and even over the next 20 years, demand for cereal grain is likely to increase by 50% (FAO, 2005, 2010; Borlaug, 2007; Rosegrant and Agcaoili, 2010). To meet these burgeoning demands, quantum improvements in cereal grain yield are required and a coordinated effort to increase both genetic gain and efficiency of agronomic practices to reduce the “yield gap” is required (see Leegood et al., 2010).

A number of studies have been carried out in wheat to assess the yield components which had been targeted in the “Green Revolution” to produce the dramatic gains seen after introduction of the dwarfing genes to wheat and rice (Parry et al., 2011). A large part of the progress in yield potential achieved during this time resulted from improvements in harvest index and grain number (i.e. carbon partitioning) rather than biomass (see Austin, 1980; Fischer and Edmeades, 2010). However, there is evidence that this yield progress was also accompanied by higher photosynthetic rates on a leaf area basis and cooler canopies (Fischer et al., 1998). Regardless of whether photosynthetic performance has tracked selection pressure on other traits, to date cereal breeding programs have not generally focussed on increasing yield via biomass improvement or radiation use efficiency (Evans, 2012; Reynolds et al., 2011). It is becoming apparent in both wheat and rice that yield

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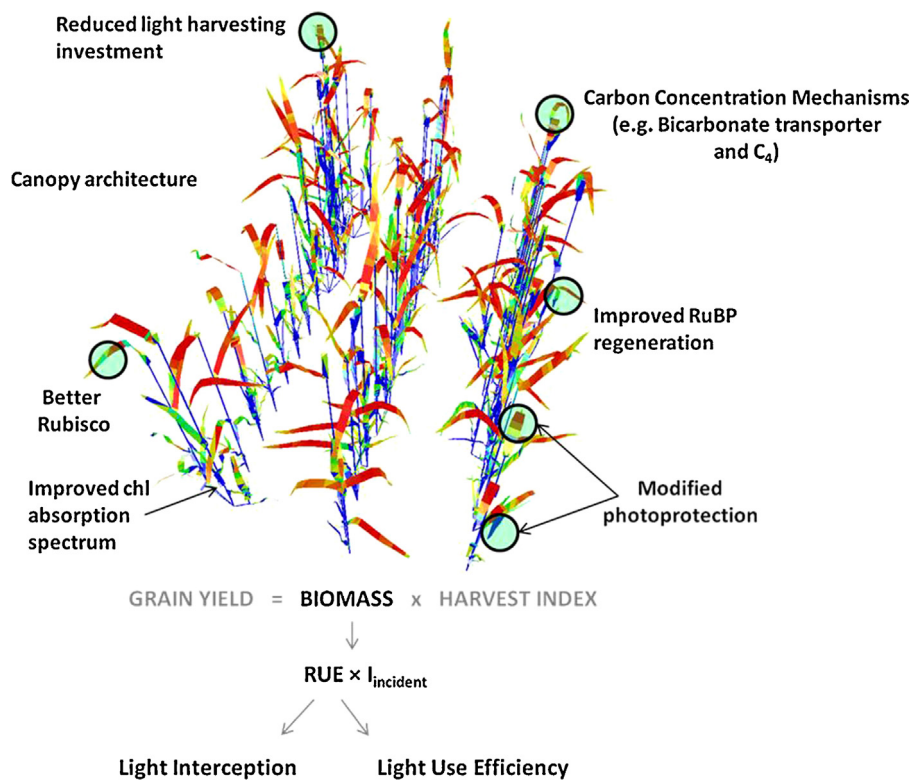


Fig. 1. A simulated wheat canopy with sunlit (red), shaded (blue) and intermediate leaves (yellow) labelled with the engineering strategy most appropriate for photosynthetic improvement in these canopy conditions. Improved light absorption through modification of leaf chlorophyll absorption spectrum and canopy architecture would contribute to the light interception component of the yield equation (shown at the bottom of the figure) while the majority of other strategies affect light use efficiency at the leaf level.

progress through improvements in harvest index has been largely exhausted and that further improvements must come from the biomass portion of the yield equation (i.e. from improved radiation use efficiency and photosynthetic performance; see Sheehy and Mitchell, 2011; Parry et al., 2011).

Fig. 1 summarises the physiological components of the yield and biomass equation, i.e. light interception and canopy level radiation use efficiency, and attempts to delineate in which part of the canopy these traits would have maximum impact. Most of these traits would be amenable to manipulation either by traditional/Phenomics screening based breeding approaches or candidate gene approaches using recombinant DNA technology. Light interception of the crop is of pivotal importance in harvesting incoming radiation post canopy closure in cereal crops, as evidenced by a strong breeding focus on erectness in the current elite and winter wheat breeding ideotypes. With increasing erectness in plant type, distribution of photosynthetic machinery between leaves from the top to the base of the canopy must also change to accommodate improved penetration of light, but so far, modelling of canopy level photosynthesis in response to these parameters of architecture and leaf level biochemistry have not advanced rapidly (see Sheehy and Mitchell, 2015; De Pury and Farquhar, 1997; text below). The most intensively studied processes determining radiation use efficiency have been almost exclusively measured at the leaf level. The biophysics of light harvesting, photosynthetic electron transport and the biochemical steps in C_3 photosynthesis are well understood and the steps controlling photosynthetic flux have been elucidated (reviewed in Zhu et al., 2010 and Evans, 2012). In many cases, candidate genes have been cloned and research has either demonstrated potential benefits in transgenic model plants or in some cases preliminary results have been presented in cereal crop species. The potential benefits of improved RUE on yield are evidenced by the positive effects of

elevated CO_2 on crop plant yield potential (Ainsworth and Long, 2005), comparisons of the yield of C_4 compared with C_3 crops (see Sheehy et al., 2007; Parry et al., 2011; Reynolds et al., 2012) and have been modelled at the leaf level for many crops and for rice at the canopy level in this issue (Sheehy and Mitchell, 2015).

This review details potential approaches to targeted genetic manipulation of canopy light interception and utilisation, and at the leaf level, follows potential routes to improvement along the path from light harvesting and chloroplast electron transport to carbon fixation and related biochemical processes.

1.1. Canopy architecture and leaf erectness

It has been shown that leaf erectness is an important trait in breeding for radiation use efficiency and there has been considerable success in breeding for more erect canopies in both rice and wheat (Yunusa et al., 1993; Sinclair and Muchow, 1999; Foulkes et al., 2009). The available genetic variation in this trait raises the question of the requirement to engineer erectness. However, parameters for optimal canopy leaf angular distribution may shift as the canopy develops, with more prostrate leaves pre-canopy closure being useful in moisture conservation while in later growth stages, erectness of upper leaves may be crucial for light penetration. Canopy erectness has also been difficult to quantitatively measure making precision phenotyping challenging until the recent advent of canopy digitisation tools (Sirault et al., 2013; Deery et al., 2014). In rice, genes controlling leaf angle have recently been elucidated and manipulated (Zhao et al., 2012) and QTLs identified in wheat (Isidro et al., 2012 and references therein). In rice, the *lc-1d* locus (Zhao et al., 2012) encodes OsGH3-1, an indole-3-acetic acid (IAA) amido synthetase thought to act through IAA metabolism and brassinosteroid signalling. In the case of gain of function mutants in OsGH3-1 in rice, the leaf inclination phenotype appears to result

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