

## Symposium on ‘Food supply and quality in a climate-changed world’

### Session 1

## Food security: increasing yield and improving resource use efficiency

Martin A. J. Parry\* and Malcolm J. Hawkesford

*Centre for Crop Genetic Improvement, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK*

Food production and security will be a major issue for supplying an increasing world population. The problem will almost certainly be exacerbated by climate change. There is a projected need to double food production by 2050. In recent times, the trend has been for incremental modest yield increases for most crops. There is an urgent need to develop integrated and sustainable approaches that will significantly increase both production per unit land area and the resource use efficiency of crops. This review considers some key processes involved in plant growth and development with some examples of ways in which molecular technology, plant breeding and genetics may increase the yield and resource use efficiency of wheat. The successful application of biotechnology to breeding is essential to provide the major increases in production required. However, each crop and each specific agricultural situation presents specific requirements and targets for optimisation. Some increases in production will come about as new varieties are developed which are able to produce satisfactory crops on marginal land presently not considered appropriate for arable crops. Other new varieties will be developed to increase both yield and resource use efficiency on the best land.

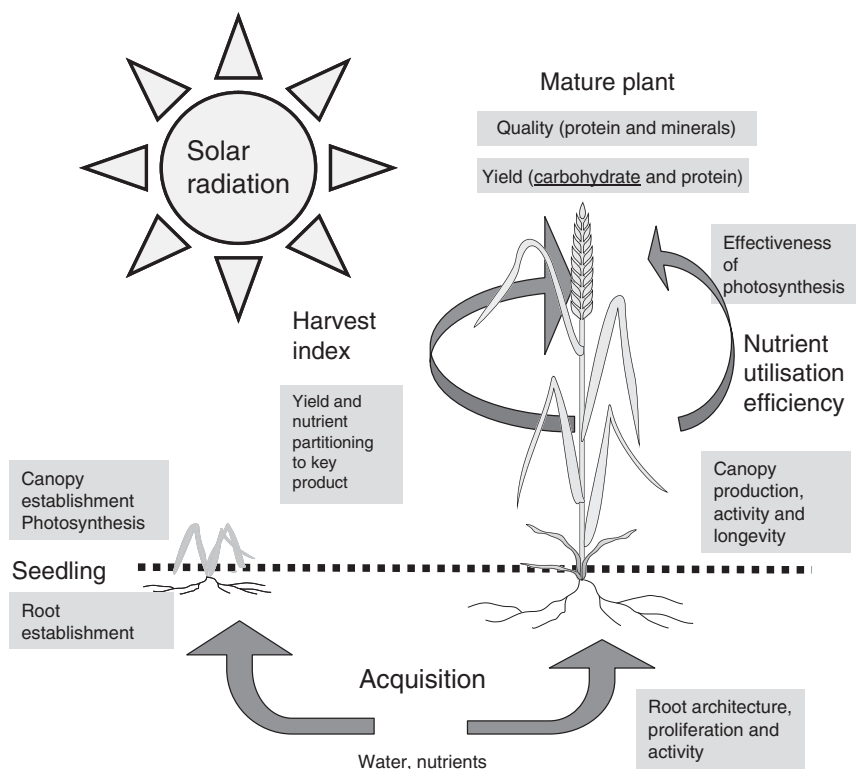
#### Drought: Salinity: Nutrition: Photosynthesis: Biotechnology

The concern for global food security results primarily from an imbalance between the supply and demand of the major food crops (wheat, rice and maize). Increasing production on a sustained basis is an essential component of ensuring food security; however, the wider issues of distribution and economics are also major challenges for the whole of society. Currently, at least 1 billion people are chronically malnourished and the situation is deteriorating; more people are hungrier now than at the start of the millennium. The United Nations Millennium Development Goal of substantially reducing the world's hungry by 2015 will not be met<sup>(1)</sup>. Reliable food production and distribution determine the availability of food, and both are key factors in achieving food security. The demand for food is driven by the increase in world population, an estimated 8.2–11 billion people by 2050, and by increasing affluence coupled with an accompanied desire to eat meat. A major problem is the worldwide distribution of food availability,

on the one hand resulting in poverty-stricken areas with major food shortages, while other areas have a problem of increasingly obese populations; part of a solution would be the achievement of equitable distribution. However, food production needs to increase 50% by 2030 and double by 2050 to meet projected demands. The projected increases in population appear to have been accepted as inevitable, but such increases are not sustainable and the viewpoint of acceptance of continued increases will need to be challenged to ensure future food security.

At the same time, that demand for food is increasing, production is progressively being limited by increased urbanisation, land degradation (erosion and salinisation), non-food uses of crops and cropland (e.g. bioenergy and leisure activities) and climate change. For example, in the UK, by 2015 more than a quarter of wheat grain may be destined for bioenergy production. Global climate change is projected to further decrease agricultural yields as a

**Abbreviations:** QTL, quantitative trait loci; Rubisco, ribulose 1,5 biphosphate carboxylase/oxygenase.  
**\*Corresponding author:** Professor Martin Parry, fax +44 1582763010, email martin.parry@bbsrc.ac.uk



**Fig. 1.** Key processes contributing to yield and effective use of resources in a grain crop (wheat).

consequence of increasing temperatures and altered patterns of and more erratic rainfall.

To ensure global food security, a new green revolution in agricultural productivity is needed to dramatically increase crop yields and the supply of food. This requires an integrated, multifaceted and sustainable approach that will increase both production per unit area, and, at the same time, optimise the resource use efficiency of crops. The successful and acceptable application of biotechnology to crop breeding will be essential to provide the required stepwise increases in production. In recent years, reserve stocks of grain have been very low; the stock to use ratio in 2008 was at the lowest level in 50 years<sup>(2)</sup> and thus the situation needs to be addressed urgently.

This review summarises the key processes involved in plant growth and development and gives some examples of ways in which molecular technology, plant breeding and genetics may increase the yield and resource use efficiency of wheat which is a staple food in many countries and globally supplies about 20% of the food energies to the world's population (see Fig. 1).

### Carbon

In photosynthesis, plants convert light energy into chemical energy (ATP and NADPH), which is used in the assimilation of atmospheric CO<sub>2</sub> and the formation of sugars that fuel growth and yield. Increasing photosynthesis has the potential to increase crop yields. Although wheat yields have increased, this was not due to an

increase in total biomass but rather due to an increase in harvest index (i.e. the proportion of the total biomass devoted to grain at harvest) and to improvements in agronomic practice including the use of fertilisers, herbicides and pesticides. The harvest index for wheat is thought to be approaching a ceiling and any further increase in yield will need to involve an increase in total biomass and therefore more photosynthesis<sup>(3)</sup>. CO<sub>2</sub> enrichment experiments clearly demonstrate that provided that other constraints do not become limiting, increasing photosynthesis will increase yields<sup>(4)</sup>. Thus, photosynthesis is a major target for improving crop productivity both via conventional breeding and biotechnology<sup>(5,6)</sup>.

Total crop photosynthesis is dependent on (1) the ability of the crop canopy to intercept and capture light, (2) the period over which the canopy can capture light and (3) the photosynthetic rate per unit leaf area. All three are potential targets for crop improvement, although wheat breeding has already optimised canopy architecture and there may be a few further obvious opportunities for improvement<sup>(7)</sup>.

The period over which the canopy can capture light and thus produce sugars for growth and yield may be extended by establishing early ground cover and/or by delaying senescence. Early ground cover may be determined by a number of diverse component traits (e.g. grain size and low-temperature tolerance). Alternatively, stay green phenotypes can delay senescence and extend the period for light capture. However, in some environments, extending the period over which the canopy can capture light could be detrimental if other resources (e.g. water or temperature) are limiting.

There is some evidence from work on historic wheat genotypes which suggests that improvements in photosynthesis per unit leaf area have already occurred<sup>(8,9)</sup>. However, in wheat (and other C<sub>3</sub> crops like rice), the enzyme that assimilates the CO<sub>2</sub>, ribulose 1,5 bisphosphate carboxylase/oxygenase (Rubisco), is not ideal for crop productivity: in addition to catalysing the productive carboxylation of CO<sub>2</sub>, Rubisco also catalyses a competing and wasteful reaction with O<sub>2</sub>. The extent of the wasteful reaction is dependent on the relative concentrations of CO<sub>2</sub> and O<sub>2</sub>. The oxygenase reaction is favoured by high temperatures and conditions that promote stomatal closure and thus a lowering of the CO<sub>2</sub> concentration within the leaf. The oxygenase reaction subsequently leads, in a mechanism called photorespiration, to the loss of previously fixed CO<sub>2</sub> and NH<sub>3</sub>, and uses energy in the process. Between 10 and 60% of potential carbon assimilation is lost in photorespiration depending on the environmental conditions<sup>(10)</sup>.

In C<sub>4</sub> plants, such as maize, the oxygenase reaction is greatly decreased. In C<sub>4</sub> plants, photosynthetic biochemistry is segregated into two cell types. The atmospheric CO<sub>2</sub> is initially fixed in the mesophyll cells, which are in contact with intercellular air spaces, into C<sub>4</sub> acids (malate or oxaloacetate) by a high-affinity enzyme. The C<sub>4</sub> acids are transported into gas tight bundle sheath cells where they are decarboxylated, and the CO<sub>2</sub> released is recaptured by Rubisco. This process ensures that the CO<sub>2</sub> concentration within the bundle sheath cells is high (10 × atmospheric levels) and that the oxygenase reaction of Rubisco is negligible<sup>(11,12)</sup>. C<sub>4</sub> photosynthesis has evolved independently more than 50 times<sup>(3)</sup> and introducing a CO<sub>2</sub> concentrating mechanism of this type into C<sub>3</sub> plants such as grain cereals could be advantageous<sup>(13)</sup>. However, C<sub>4</sub> photosynthesis is not advantageous in cool or light-limited environments, because the CO<sub>2</sub> concentrating mechanism diverts precious light energy away from the Calvin cycle. Although introducing the pathway requires complex anatomical and biochemical changes, a large multinational project is underway to introduce C<sub>4</sub> characteristics into rice by genetic transformation<sup>(11,14,15)</sup>. A similar approach is worthwhile for wheat.

Approaches to increase photosynthesis include:

1. Stay green phenotypes
2. Early vigour
3. Minimising stomatal and mesophyll resistance
4. Increasing photosynthetic capacity
5. Utilising best photosynthetic enzymes (C<sub>3</sub>/C<sub>4</sub>)
6. Minimising down regulation under stress
7. Decreasing photorespiratory losses

In some plants, a C<sub>4</sub> system operates within a single cell where the C<sub>4</sub>-like cycle is separated between the cytoplasm and the chloroplast, rather than between two different cell types<sup>(16)</sup>. Thus, so far, attempts to install a single cell C<sub>4</sub> mechanism into rice have not been successful<sup>(17)</sup>, and the leakage of CO<sub>2</sub> from the chloroplast may require a great diversion of energy to attain high CO<sub>2</sub> concentrations in the chloroplast. An alternate and simpler, and therefore potentially less technically challenging approach with

inherently lower energy costs than that of the C<sub>4</sub> pathway, would be introduced into C<sub>3</sub> crop plants, an inorganic CO<sub>2</sub> concentrating mechanism similar to that found in cyanobacteria and algae<sup>(18)</sup>. This may only necessitate the introduction of the well-characterised cyanobacterial bicarbonate pumps (BicA and SbtA) into the chloroplast envelope of terrestrial mesophyll cells.

A less elaborate approach would be to decrease the cost of photorespiration by increasing the probability that photorespiratory CO<sub>2</sub> is recaptured. This could be achieved by introducing genes encoding proteins that can short-circuit the normal photorespiratory cycle<sup>(19)</sup>. Some success appears to have been achieved in *Arabidopsis*<sup>(20)</sup>, but it will be important to prevent the accumulation of toxic intermediates which could occur if there was a high flux through the pathway.

Since Rubisco is the source of photorespiration and the catalytic properties of Rubisco are not optimal for current or projected environments, a direct approach to improve photosynthesis would be to replace the enzyme in wheat with another enzyme which had features more suited to high photosynthesis in current conditions<sup>(19,21,22)</sup>. Rubisco is also such a slow catalyst that very large amounts are required in leaves to attain high photosynthetic rates. In wheat, more than 25% of the leaf N is invested Rubisco. Despite this huge investment in Rubisco, at CO<sub>2</sub> concentrations less than ambient, net assimilation is generally limited by Rubisco amounts and kinetics, while at higher CO<sub>2</sub> concentrations, the limitation shifts to the regeneration of the Rubisco substrate, ribulose 1,5 bisphosphate<sup>(23)</sup>.

The weak affinity for CO<sub>2</sub>, and the competing reaction with oxygen, could be partially overcome by selecting for natural variants with greater affinity for CO<sub>2</sub> or higher carboxylase capacity, relative to the competing oxygenase activity, such that the specificity factor remains unchanged or increases. Rubisco from diverse sources has a wide range of kinetic constants and the replacement of the Rubisco in wheat with that from other species, with a higher catalytic rate or selectivity for CO<sub>2</sub> could be advantageous under some conditions. Such homologues already exist (e.g. in *Limonium*<sup>(24)</sup>) and could increase photosynthetic rates by 100% under some conditions<sup>(19)</sup>. However, although great progress has been made in introducing foreign Rubisco genes into model species, considerable technical advances, including the development of plastid transformation, are needed before this can be achieved in wheat or other cereals.

The balance between Rubisco and the other Calvin cycle enzymes is not optimised for wheat and other C<sub>3</sub> crops, even under current conditions<sup>(25)</sup>. Models suggest that increasing the amounts of some Calvin cycle enzymes involved in ribulose 1,5 bisphosphate regeneration would be advantageous<sup>(26)</sup>. This confirms experimental evidence that increasing the activity of one Calvin cycle enzyme, sedoheptulose-1,7-bisphosphatase relaxes the limitation to assimilation caused by ribulose 1,5 bisphosphate regeneration and increases both photosynthetic rate and biomass<sup>(27–31)</sup>. Under optimal conditions, increasing sedoheptulose-1,7-bisphosphatase activity in wheat should be advantageous and is easily testable.

Ensuring that the existing photosynthetic capacity is fully exploited could lead to significant increases in photosynthetic carbon assimilation. For example, at elevated temperatures photosynthetic rates are lower than models would predict. This is thought to result from the temperature-induced loss of Rubisco activity that is caused by the thermal inactivation of Rubisco activase. Species variation in the thermotolerances of Rubisco activases have been identified and new forms generated by directed evolution<sup>(32–34)</sup>. Their introduction into wheat plants could maintain Rubisco activity and therefore photosynthesis at elevated temperatures.

### Efficient utilisation of mineral resources for food security

Plant growth, including canopy production for efficient photosynthesis (see earlier) is dependent on adequate nutrition, and optimised fertiliser inputs are an essential component of efficient crop production. The efficient use of both N and P is of particular concern for food security and sustainable production, and are key targets for crop breeding programmes which have previously often been ignored. However, the problems of efficient use of fertiliser inputs depend on circumstance: sustainability of food production must be underpinned by acceptable energy and environmental costs of the fertiliser employed, and will require appropriately individually tailored nutrient use efficient germplasm targeted, respectively, for highly managed intensive crop production or for low-input systems.

Increasing yield without additional inputs of mineral fertilisers is by definition an improvement in nutrient use efficiency. However, yields must be sustainable to provide food security. In many cropping systems, inputs are minimal and yields are sustainable while production is low, a situation which may be appropriate given other physical limitations to production. Small fertiliser inputs, for example, organic manures, can have a huge impact on yield and positive benefits for food security. Furthermore, soil improvement as a consequence of the introduction of organic matter can have subsequent positive impacts on water retention and mineralisation and/or the availability of other nutrients such as P. However, inappropriate unbalanced use of fertilisers together with increased productivity may lead to ‘mining’ of other mineral nutrients from the soil and a lack of sustainability. If the net balance of dynamics is such that take-off exceeds inputs, then the resulting imbalance is clearly not sustainable. Ultimately sustainability may be compromised by limited fertiliser availability or by the economics of fertiliser supply.

In any agricultural system, the inefficient use of fertilisers, and particularly nitrogen, contributes to the carbon footprint of agriculture and therefore potentially to climate change. On the other hand, climate change impacts on crop development and growth with concomitant implications for timing and amounts of fertilisers<sup>(35)</sup>. It has been estimated that for grain crops, globally, N use efficiency may be as low as 33%<sup>(36)</sup>. While not all agricultural systems are subject to such losses, worldwide this represents a huge

waste of resources and a threat to food security due to the increased costs of fertiliser production and/or losses of non-renewable resources, which is specifically the case for phosphate (see below). Efficient utilisation requires both efficient capture and conversion into useable biomass: a crop plant will include vegetative and reproductive tissues and either may be croppable, although the major world staples are either reproductive tissues or storage organs (seeds, tubers etc.). Production of tissues such as the grain is dependent on the functioning (size, duration and activity) photosynthetic vegetative tissues (see previous section and later). Nutrient use efficiency may be defined in many ways; however, essentially there is a requirement for maximising outputs and not wasting inputs. In the case of many nutrients, the overall trait of efficiency is divided into two major components: efficient uptake (thus minimising fertiliser losses) and effective utilisation of the nutrients taken up to produce useful croppable biomass. In addition, post-harvest processing and utilisation will have a big contribution to the whole system nutrient budget. However, for the crop, uptake efficiency is primarily a set of root characteristics, principally architectural (density and depth of roots), but also related to function (uptake and translocation of resources). Prolific shallow roots may be required to capture applied fertiliser, particularly immobile species such as phosphate, and deeper roots are likely to be important for accessing water (see next section) and deeper N reserves. The second key trait involving efficient production of useable biomass will depend on canopy function (photosynthesis), architecture, longevity (as discussed above) and efficient remobilisation of nutrient from discarded/non-harvested material to the croppable biomass.

For the croppable biomass, both yield and quality are often desirable traits, and increasing one may not be compatible with the other, and therefore each needs to be targeted as appropriate for the market and end use. Increasing yield by improving photosynthesis and hence starch production, which is targeted to storage organs, without concomitant increased protein synthesis and/or essential nutrient uptake will lead to a dilution of the quality components. In wheat, as an example, at any given N input, grain yield is inversely proportional to grain percentage N<sup>(37)</sup>. Varieties that deviate from this rule<sup>(38)</sup> and have unusually high yield and grain N combinations are much sought after by breeders targeting bread-making varieties.

Sustainable agricultural production depends on many factors including, as discussed here, adequate supplies of water (see later), N and P. In addition, several other nutrients may limit productivity and are of importance to nutritional quality: K, S, Fe/Zn and other micronutrients are essential for healthy crops and may have important nutritional values (Zn/Fe/Se). Major projects are in place, such as HarvestPlus (funded by Gates, the World Bank and others) and Healthgrain (funded by the European Union), which are examining genetic variation for the ability to acquire mineral nutrients (particularly Fe and Zn) with the aim of introducing these key traits into key crop improvement programmes. Variations in Se availability for crops and the implications for the health of human subjects and livestock have been reviewed recently<sup>(39)</sup>. Generally, there

are either large reserves of appropriate raw materials for fertiliser production, or only relatively small quantities are required; however, economics and distribution problems result in shortages of these nutrients in many areas, worldwide. Partitioning of these nutritionally important elements between discarded and harvested crop fractions is again, as with overall biomass (harvest index) a major target for crop improvement and key genes which control remobilisation have been identified<sup>(40)</sup>.

N supply determines yield irrespective of the crop in question or the agricultural practice employed. N supply will determine the limit of vegetative growth, and in addition, other factors may limit productivity irrespective of nutrient availability, notably water availability and pest and diseases: optimising crops for efficient nutrient use requires the knowledge and management of these limiting factors. The importance of selecting varieties under reduced nutrient availability for low-input and organic systems has been highlighted<sup>(41)</sup>. Indeed a detrimental impact on yield and quality was observed with the supply of organic N compared to conventional fertilisers to modern bread-making varieties of wheat<sup>(42)</sup>, and furthermore, for modern varieties generally variety performance at low and high inputs are highly correlated<sup>(37)</sup>. However, selection has seldom been made at low inputs.

It is questionable as to whether yield can be increased greatly without supplying more N, as N determines vegetative growth, e.g. canopy and therefore sets the potential for photosynthate production. In addition, storage organs would require N, and in cases where protein content is an essential quality attribute, optimised N supply is even more essential. However, when carbohydrate is the major component of yield, increased photosynthesis without an increased canopy biomass (and hence the requirement of N for canopy production), will enable an increase in yield without a concomitant increased crop N requirement. Ideally, N in the canopy will be either remobilised to the harvested organ as a useful protein or may be recycled as manure for future crop production.

Industrially manufactured (Haber process) N fertiliser supply is in theory unlimited and only dependent on energy inputs; however, there are substantial economic and environmental costs associated with fixation, distribution and application. Additional consequences of excessive fertilisation and inefficient capture or management are the negative effects on rivers, lakes and coastal waters. High inputs, particularly of N will accelerate soil acidification<sup>(43)</sup>, adding pressure for appropriate and efficient fertiliser application. Crop improvement relating to both capture and use efficiency of N (conversion into biomass) are key targets for sustainable food security with minimised environmental impact. Minimising losses may also be achieved by enhancing natural processes of exudation of biological nitrification inhibitors<sup>(44)</sup>. The ultimate solution to the supply of N for world food supply will be the incorporation of the N-fixation trait of the Rhizobia/legume symbiosis in cereals; however, this remains a prospect for the distant future.

P is a non-renewable reserve and in the long term a systems approach to conservation will be required. Estimates vary as to global reserves, however, agricultural use

has reached a plateau or even decreased as management and regulation have controlled usage, while in some developed countries excess application still occurs. In many tropical countries, soil acidity places a severe restriction on P availability<sup>(45)</sup> and selection or engineering of appropriate P-efficient varieties may be the most appropriate solution to this problem. Traits including root exudation of organic acids or phosphates combined with root morphology are likely contributors to improved P use efficiency<sup>(46)</sup>. Management of both fertiliser application and soil properties affecting availability are also important. Much P is subsequently lost as recycling and reclamation, for example, from animal wastes or sewage, are often not employed.

It is necessary to combine genetic improvement with resource management: major inefficiencies for N or P use are not uniformly distributed geographically or across farming systems or crops. In many cases, education and effective management can massively improve nutrient use efficiency. However, once the agronomy is optimised, the major gains are then to be made from genetic improvement of the crops. Historical selection for yield improvement has effectively selected for nutrient use improvement, because the definition of efficiency has been rightly related to yield, and as already noted this has usually been at high inputs. Due to the selection based on yield alone, and because nutrient use efficiency is a complex trait, optimal performance in the subtraits which include efficient capture may not have been combined in current elite varieties, and essential alleles may have even been lost from modern variety gene pools.

In addition to traditional breeding methods and the selection of varieties for nutrient use efficiency, whether for yield and high nutrient use efficiency under intensive conditions, or for effective nutrient scavenging under nutrient-limited conditions, a complementary approach is the targeted identification of underpinning processes contributing to nutrient use efficiency, for example, and the constituent genes controlling these processes. These genes would be involved in nutrient acquisition as well as efficient utilisation of the nutrients taken up, including appropriate partitioning between harvested/non-harvested plant parts. A number of approaches are being followed, including traditional quantitative trait loci (QTL) analysis<sup>(47)</sup> and mapping of underpinning genes as well as target gene manipulation, with candidates identified either through biochemical or genetic approaches. Examples would be genes enhancing nutrient remobilisation from the canopy to the grain in wheat, albeit at the expense of yield<sup>(40)</sup> or the enhancement of N acquisition, possibly by alleviating negative feedback regulation, by a transgenic expression of genes affecting local N pools, such as alanine amino transferase<sup>(48,49)</sup>.

In summary, each crop and each specific agricultural situation will have specific requirements and targets for optimising nutrient use efficiency. Nutrient imbalances resulting in the huge gap between low input, but unsustainable agriculture in many developing countries compared to excess (and also unsustainable) inputs in many developed and rapidly growing economies<sup>(50)</sup> require different and unique approaches, combining both management

**Table 1.** The global average water productivity of various C<sub>3</sub> and C<sub>4</sub> cereals.<sup>(57)</sup>

Crop	Volume of water (m <sup>3</sup> ) required to produce 1 tonne of grain
Maize	909
Sorghum	2853
Millet	4596
Barley	1388
Wheat	1334
Rice	2291

and appropriate germplasm. In low-/no-input systems, increasing capture may exacerbate nutrient mining problems and not provide food security. In high-/excessive-input systems, both managed inputs and appropriate germplasm will contribute to maximum nutrient capture. The clear targets are early developing and extensive root systems. These may be combined with specific attributes to maximise biological availability (phosphorus) or minimise losses (nitrification), as described earlier. Example traits to optimise nutrient use in wheat were identified as root density to aid capture, stem storage, low leaf N, efficient remobilisation to grain and customised grain attributes (protein *v.* carbohydrate) suitable for specific markets<sup>(51)</sup>.

### Water

The availability of water is the major constraint on world crop productivity<sup>(52)</sup>. Global climate change is predicted to alter patterns of rainfall and the overall availability will decrease. By 2050, it is estimated that more than 65% of the global population will live where water is scarce<sup>(53)</sup>.

Since more than 80% of the available water is used for agricultural production<sup>(54)</sup>, there is little opportunity to use additional water for crop production, especially because as populations increase, the demand to use water for other activities also increases<sup>(55)</sup>.

A real and immediate challenge for agriculture is to increase crop production with less available water<sup>(56)</sup>. This requires an increased water productivity (i.e. the amount of water required per unit biomass production). Water is essential for plant growth and cell expansion, but often only 10% of the water available to crops is used productively in transpiration<sup>(54)</sup>. This means that there are significant opportunities to improve water productivity both by increasing the water allocated to transpiration and the efficiency with which transpired water produces biomass<sup>(53)</sup>. The amount of water required per unit of yield varies greatly from crop to crop. Although C<sub>4</sub> species like maize have inherently greater water use efficiency under well-watered conditions compared to C<sub>3</sub> crops such as wheat, this is not always reflected in these figures. The global average water productivities for various crops are shown in Table 1, but there is considerable variation in water productivity between individual crops growing in different regions<sup>(58)</sup>.

The constraint that water availability imposes on plant productivity is complex, because it is not constant and

varies within and between environments. Thus specific strategies to improve water productivity are often not applicable to all crops or all environments. For example, traits related to coleoptile length may not be valuable in an environment only subjected to terminal drought<sup>(59)</sup>.

The ability of a crop to yield well with limited water is determined by multiple genes. Improvement of water productivity, as noted above for C or nutrient resources, also requires a multifaceted and integrated approach that considers both agronomic practices and germplasm and the effective transfer of 'best practice' to individual farmers. This must include, for example, the management of soils to conserve water and the management of nutrition to control the development of the crop canopy in addition to the development of improved genotypes with high water productivity. Existing natural variation or induced variation (mutagenesis and transgenesis) can be used in multi-site, multi-environment field studies to identify key traits associated with water productivity in different environments (e.g. phenology, architecture and metabolism); often these traits may themselves be determined by a number of component traits<sup>(5)</sup>. Furthermore, there are strong genotype–environment interactions; component traits relevant to an environment in which water was limited at germination will be very different from those where water is limited during grain filling. Some important traits may not themselves be directly linked to water use efficiency, but to avoidance by allowing a crop to escape periods of limited water availability by having a shorter life cycle. For annual crops like wheat, these traits must enable the crop to thrive and produce grain with a limited water supply, rather than to merely survive<sup>(60)</sup>. Survival traits are, however, important for perennial crops<sup>(55)</sup>.

An example of a success story is the Australian wheat variety 'Drysdale' which was selected by C isotope discrimination, because it uses water more efficiently; this is achieved by slightly restricting stomatal aperture and thereby the loss of water from the leaves<sup>(61)</sup>. While this reduces photosynthetic performance slightly under ideal conditions, the plants have access to water later in the growing season thereby increasing total photosynthesis over the life of the crop.

Association genetics and mapping populations can be used to identify genetic loci (QTL) in the genomic regions underlying individual component traits<sup>(59)</sup>. Although QTL have been identified, the available genetic maps are at too low resolution, and it is difficult, even when exploiting the synteny between species, to identify the genes for the underlying traits; very few of the genes responsible for QTL have been identified<sup>(62)</sup>. However, in the near future, the availability of a complete wheat genome sequence and of high-resolution maps saturated with markers should enable the genes for the underlying traits to be more easily de-convoluted. In contrast, there are numerous examples where the genes underlying QTL in model species have already been identified. Such candidate genes can be validated in crop plants by functional genomics approaches such as transformation and TILLING (targeting induced local lesions in genomes)<sup>(63–65)</sup>.

Much research effort has focused on the identification and manipulation of drought responsive genes that relate to

a wide range of biological processes. This includes genes involved in the biosynthesis of osmolytes, scavenging active oxygen, molecular chaperones, signalling molecules, transporters and transcription factors (see review<sup>(66)</sup>). While the results are interesting and have provided detailed understanding of the mechanisms involved in response to drought stress, many of the reports of increased drought tolerance relate to survival rather than sustained growth under limited water. Since performance under all but the most severe drought is closely related to yield potential, a shift in emphasis to those constitutive traits related to yield potential in any environment is most likely to be beneficial; for example, traits related to architecture<sup>(67)</sup> or, as described above, photosynthetic performance. Similarly, the potential benefit of indirect effects such as the introduction of herbicide tolerant transgenics that permit the introduction of water conserving minimum tillage systems should not be ignored.

### Conclusions and prospects

Food security will be a major issue for the increasing world population. The problem will be almost certainly increased by climate change. The green revolution of the last century was achieved through the adoption of both new germplasm and agricultural practice and led to a several-fold increase in yields. In recent times, yield increases for most crops have been more modest and incremental. The immediate future will see further such incremental increases for most crops, with longer-term possibilities of greater improvements. Major yield increases may come about as varieties are developed which are able to exploit inhospitable environments, thus increasing agricultural land use. In the best agricultural land, economic demand will always favour high yields and production; however, in addition, efficient use of resources in agricultural and consumer systems will be a priority.

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### References

1. Lele U (2010) Food security for a billion poor. *Science* **327**, 1554.
2. <http://www.fao.org/newsroom/en/news/2007/1000674/index.html> (validated 27 April 2010).
3. Sage TL & Sage RF (2009) The functional anatomy of rice leaves: implications for refixation of photorespiratory CO<sub>2</sub> and efforts to engineer C<sub>4</sub> photosynthesis into rice. *Plant Cell Physiol* **50**, 756–772.
4. Ainsworth EA & Long SP (2005) What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytol* **165**, 351–372.
5. Richards RA (2000) Selectable traits to increase crop photosynthesis and yield of grain crops. *J Exp Bot* **51**, 447–458.
6. Dunwell JM (2000) Transgenic approaches to crop improvement. *J Exp Bot* **51**, 487–496.
7. Horton P (2000) Prospects for crop improvement through the genetic manipulation of photosynthesis: morphological and biochemical aspects of light capture. *J Exp Bot* **51**, 475–485.
8. Fischer RA, Rees D, Sayre KD *et al.* (1998) Wheat yield progress associated with higher stomatal conductance and photosynthetic rate and cooler canopies. *Crop Sci* **38**, 1467–1475.
9. Reynolds MP, Maarten van Ginkel M & Ribaut J-M (2000) Avenues for genetic modification of radiation use efficiency in wheat. *J Exp Bot* **51**, 459–473.
10. Long SP, Zhu XG, Naidu SL *et al.* (2006) Can improvement in photosynthesis increase crop yields? *Plant Cell Environ* **29**, 315–330.
11. Furbank RT, von Caemmerer S, Sheehy J *et al.* (2009) C<sub>4</sub> rice: a challenge for plant phenomics. *Funct Plant Biol* **36**, 845–856.
12. Carmo-Silva AE, Powers SJ, Keys AJ *et al.* (2008) Photorespiration in C-4 grasses remains slow under drought conditions. *Plant Cell Environ* **31**, 925–940.
13. Sheehy JE, Mitchell PL & Hardy B (editors) (2007) *Charting New Pathways to C<sub>4</sub> Rice*. Los Banos, Philippines: International Rice Research Institute.
14. Hibberd JM, Sheehy JE & Langdale JA (2008) Using C-4 photosynthesis to increase the yield of rice – rationale and feasibility. *Curr Opin Plant Biol* **11**, 228–231.
15. <http://beta.irri.org/projects15/c4rice> (validated 27 April 2010)
16. Edwards GE, Franceschi VR & Voznesenskaya EV (2004) Single-cell C<sub>4</sub> photosynthesis versus the dual-cell (Kranz) paradigm. *Annu Rev Plant Biol* **55**, 173–196.
17. Taniguchi Y, Ohkawa H, Masumoto C *et al.* (2008) Overproduction of C<sub>4</sub> photosynthetic enzymes in transgenic rice plants: an approach to introduce the C-4-like photosynthetic pathway into rice. *J Exp Bot* **59**, 1799–1809.
18. Price GD, Badger MR, Woodger FJ *et al.* (2008) Advances in understanding the cyanobacterial CO<sub>2</sub>-concentrating-mechanism (CCM): functional components, Ci transporters, diversity, genetic regulation and prospects for engineering into plants. *J Exp Bot* **59**, 1441–1461.
19. Parry MAJ, Madgwick PJ, Carvahlo JFC *et al.* (2007) Prospects for increasing photosynthesis by overcoming the limitations of Rubisco. *J Agric Sci* **145**, 31–43.
20. Kebeish R, Niessen M, Thiruveedhi K *et al.* (2007) Chloroplastic photorespiratory bypass increases photosynthesis and biomass production in *Arabidopsis thaliana*. *Nat Biotechnol* **25**, 593–599.
21. Parry MAJ, Andralojc PJ, Mitchell RAC *et al.* (2003) Manipulation of Rubisco: its amount, activity, function and regulation. *J Exp Bot* **54**, 1321–1333.
22. Reynolds M, Foulkes MJ, Slafer G *et al.* (2009) Raising yield potential in wheat. *J Exp Bot* **60**, 1899–1918.
23. von Caemmerer S (2000) *Biochemical Models of Leaf Photosynthesis*, vol. 2. Collingwood, Australia: CSIRO Publishing.

24. Galmes J, Flexas J, Keys AJ *et al.* (2005) Rubisco specificity factor tends to be larger in plant species from drier habitats and with persistent leaves. *Plant Cell Environ* **28**, 571–579.
25. Mitchell RAC, Theobald JC, Parry MAJ *et al.* (2000) Is there scope for improving balance between RuBP-regeneration and carboxylation capacities in wheat at elevated CO<sub>2</sub>? *J Exp Bot* **51**, 391–397.
26. Zhu X-G, Sturler E & Long SP (2007) Optimizing the distribution of resources between enzymes of carbon metabolism can dramatically increase photosynthetic rate: a numerical simulation using an evolutionary algorithm. *Plant Physiol* **145**, 513–526.
27. Harrison EP, Willingham NM, Lloyd JC *et al.* (1998) Reduced sedoheptulose-1,7-bisphosphatase levels in transgenic tobacco lead to decreased photosynthetic capacity and altered carbohydrate accumulation. *Planta* **204**, 27–36.
28. Lefebvre S, Lawson T, Zakhleniuk OV *et al.* (2005) Increased sedoheptulose-1,7-bisphosphatase activity in transgenic tobacco plants stimulates photosynthesis and growth from an early stage in development. *Plant Physiol* **138**, 451–460.
29. Tamoi M, Nagaoka M, Miyagawa Y *et al.* (2006) Contribution of fructose-1,6-bisphosphatase and sedoheptulose-1,7-bisphosphatase to the photosynthetic rate and carbon flow in the Calvin cycle in transgenic plants. *Plant Cell Physiol* **47**, 380–390.
30. Feng L, Wang K, Li Y *et al.* (2007) Overexpression of SBPase enhances photosynthesis against high temperature stress in transgenic rice plants. *Plant Cell Rep* **26**, 1635–1646.
31. Miyagawa Y, Tamoi M & Shigeoka S (2001) Overexpression of a cyanobacterial fructose-1,6-/sedoheptulose-1,7-bisphosphatase in tobacco enhances photosynthesis and growth. *Nat Biotechnol* **19**, 965–969.
32. Salvucci ME & Crafts-Brandner SJ (2004a) Inhibition of photosynthesis by heat stress: the activation state of Rubisco as a limiting factor in photosynthesis. *Physiol Plant* **120**, 179–186.
33. Salvucci ME & Crafts-Brandner SJ (2004b) Relationship between the heat tolerance of photosynthesis and the thermal stability of Rubisco activase in plants from contrasting thermal environments. *Plant Physiol* **134**, 1460–1470.
34. Kurek I, Kai Chang T, Bertain SM *et al.* (2007) Enhanced thermostability of *Arabidopsis* Rubisco activase improves photosynthesis and growth rates under moderate heat stress. *Plant Cell* **19**, 320–3241.
35. Parry MAJ & Hawkesford MJ (2010) Genetic approaches to reduce greenhouse gas emissions: increasing carbon capture and decreasing environmental impact. In *Climate Change and Crop Production*, pp. 139–150 [MP Reynolds, editor]. Wallingford, UK: CAB International.
36. Raun WR & Johnson GV (1999) Improving nitrogen use efficiency for cereal production. *Agron J* **91**, 357–363.
37. Barraclough PB, Howarth JR, Jones J *et al.* (2010) Nitrogen efficiency of wheat: genotypic and environmental variation and prospects for improvement. *Eur J Agron* **33**, 1–11.
38. Monaghan JM, Snape JW, Chojek AJ *et al.* (2001) The use of grain protein deviation for identifying wheat cultivars with high grain protein concentration and yield. *Euphytica* **122**, 309–317.
39. Hawkesford MJ & Zhao FJ (2007) Strategies for increasing the selenium content of wheat. *J Cereal Sci* **46**, 282–292.
40. Uauy C, Distelfeld A, Fahima T *et al.* (2006) A NAC gene regulating senescence improves grain protein, zinc, and iron content in wheat. *Science* **314**, 1298–1301.
41. Dawson JC, Huggins DR & Jones SS (2008) Characterizing nitrogen use efficiency in natural and agricultural ecosystems to improve the performance of cereal crops in low-input and organic agricultural systems. *Field Crops Res* **107**, 89–101.
42. Godfrey D, Hawkesford MJ, Powers SJ *et al.* (2010) Effects of crop nutrition on wheat grain composition and end use quality. *J Agric Food Chem* **58**, 3012–3021.
43. Guo JH, Liu XJ, Zhang Y *et al.* (2010) Significant acidification in major Chinese croplands. *Science* **327**, 1008–1010.
44. Subbarao GV, Tomohiro B, Masahiro K *et al.* (2007) Can biological nitrification inhibition (BNI) genes from perennial *Leymus racemosus* (Triticeae) combat nitrification in wheat farming? *Plant Soil* **299**, 55–64.
45. Ma JF & Ryan PR (2010) Understanding how plants cope with acid soils. *Funct Plant Biol* **37**, iii–vi.
46. Kochian LV, Hoekenga OA & Pineros MA (2004) How do crop plants tolerate acid soils? - Mechanisms of aluminum tolerance and phosphorous efficiency. *Annu Rev Plant Biol* **55**, 459–493.
47. Habash DZ, Bernard S, Schondelmaier J *et al.* (2007) The genetics of nitrogen use in hexaploid wheat: N utilisation, development and yield. *Theoret Appl Genet* **114**, 403–419.
48. Good AG, Johnson SJ, De Pauw M *et al.* (2007) Engineering nitrogen use efficiency with alanine aminotransferase. *Can J Bot* **85**, 252–262.
49. Shrawat AK, Carroll RT, DePauw M *et al.* (2008) Genetic engineering of improved nitrogen use efficiency in rice by the tissue-specific expression of alanine aminotransferase. *Plant Biotech J* **6**, 722–732.
50. Vitousek PM, Naylor R, Crews T *et al.* (2009) Nutrient imbalances in agricultural development. *Science* **324**, 1519–1520.
51. Foulkes MJ, Hawkesford MJ, Barraclough PB *et al.* (2009) Identifying traits to improve the nitrogen economy of wheat: recent advances and future prospects. *Field Crops Res* **114**, 329–342.
52. Baldocchi D & Valentini R (2004) Geographic and temporal variation of carbon exchange by ecosystems and their sensitivity to environmental perturbations in SCOPE 62. In *The Global Carbon Cycle: Integrating Humans, Climate, and the Natural World*, pp. 295–315 [CB Field and MR Raupach, editors]. Washington DC, USA: Island Press.
53. Wallace JS (2000) Increasing agricultural water use efficiency to meet future food production. *Agric Ecosyst Environ* **82**, 105–119.
54. Morison JIL, Baker NR, Mullineaux PM *et al.* (2008) Improving water use in crop production. *Phil Trans R Soc B* **363**, 639–658.
55. Parry MAJ, Flexas J & Medrano H (2005) Prospects for crop production under drought. *Ann Appl Biol* **147**, 211–278.
56. Marris E (2008) Water: more crop per drop. *Nature* **452**, 273–277.
57. <http://www.waterfootprint.org/?page=files/Productwaterfootprint-statistics> (validated 27 April 2010).
58. Gleick PH (2000) Water for food: how much will be needed? In *The World's Water 2000–2001*, pp. 63–91 [PH Gleick, editor]. Washington DC: Island Press.
59. Wang J, Chapman SC, Bonnett DG *et al.* (2009) Simultaneous selection of major genes and QTL in plant breeding: a case study using coleoptile length in wheat (*Triticum aestivum* L.). *Theoret Appl Genet* **119**, 65–74.
60. Sinclair TR & Purcell LC (2005) Is a physiological perspective relevant in a 'genocentric' age? *J Exp Bot* **56**, 2777–2782.



61. Condon AG, Richards RA, Rebetzke GJ *et al.* (2004) Breeding for high water use efficiency. *J Exp Bot* **55**, 2447–2460.
62. Salvi S & Tuberosa R (2005) To clone or not to clone plant QTLs: present and future challenges. *Trends Plant Sci* **10**, 297–304.
63. Pastori GM, Wilkinson MD, Steele SH *et al.* (2001) Age-dependent transformation frequency in elite wheat varieties. *J Exp Bot* **52**, 857–863.
64. Parry MAJ, Madgwick PJ, Bayon C *et al.* (2009) Mutation discovery for crop improvement. *J Exp Bot* **60**, 2817–2825.
65. He Y, Jones HD, Chen S *et al.* (2010) Agrobacterium-mediated transformation of durum wheat (*Triticum turgidum* L. var. *durum* cv Stewart) with improved efficiency. *J Exp Bot* **61**, 1567–1581.
66. Shinozaki K & Yamaguchi-Shinoza K (2007) Gene networks involved in drought stress response and tolerance. *J Exp Bot* **58**, 221–227.
67. Zhang S-W, Li C-H, Cao J *et al.* (2009) Altered architecture and enhanced drought tolerance in rice via the down-regulation of indole-3-acetic acid by TLD1/OsGH3.13 activation. *Plant Physiol* **151**, 1889–1901.