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Tansley review

Agriculture and the new challenges for photosynthesis research

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Summary

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A rising human population and changing patterns of land use mean that world food production rates will need to be increased by at least 50% by 2050, a massive rise in harvestable yield per hectare of the major crops such as rice (Oryza sativa) and wheat (Triticum aestivum). Combinations of breeding for improved morphologyrelated traits such as harvest index and increased inputs of water and fertilizer, which have sustained yield increases since the 1960s, will be neither sufficient nor sustainable. An important limiting factor will be the capacity to produce sufficient biomass during favourable growing periods. Here we analyse this problem in the context of increasing the efficiency of conversion of solar energy into biomass, that is, leaf and canopy photosynthesis. Focussing on crops carrying out C₃ photosynthesis, we analyse the evidence for 'losses' in the process of conversion of solar energy into crop biomass and we explore novel mechanisms of improving biomass production rates, which have arisen from recent research into the fundamental primary processes of photosynthesis and carbohydrate metabolism. We show that there are several lines of evidence that these processes are not fully optimized for maximum yield. We put forward the hypothesis that the chloroplast itself should be given greater prominence as a sensor, processor and integrator of highly variable environmental signals to allow a more efficient transduction of energy supply into biomass production.

I. Introduction

The years 2007 and 2008 have seen an unprecedented rise in global food prices. According to the Food and Agriculture Organization (www.fao.org), record world prices for most staple foods have led to 18% food price inflation in China, 13% in Indonesia and Pakistan, and 10% in Russia, India and Latin America. The FAO also state that global food reserves are at their lowest in 25 yr and that prices will remain high for many years. The causes are multiple and they demonstrate emphatically that agricultural systems are increasingly sensitive to changes in land use, economy and climate. It is clear that rising human population sizes and predictable conflicts over land use in the near future mean that present production rates per hectare will need to be improved by c. 50% if disaster is to be avoided. Meeting such a challenge will require major investment in plant and crop science research, the mobilization of effort across disciplines and a vision akin to that which transformed agriculture over 50 yr ago (Hardin, 2008).

II. World demand and future food production

In the near future the demand for food will be enormous. Considering the increase in population and the increase in per capita food consumption, it is predicted that world demand for food will increase from 12 Teracalories d^{-1} at present to almost 25 Teracalories d^{-1} in 2030 (Fig. 1). Most of this extra demand will come from developing countries, with grain demand projected to increase substantially during the next two decades. Average world wheat production in recent years has been *c*. 590 million metric tons per year (www.faostat.fao.org). By the year 2025, the required amount will be approx. 840 million metric tons per year, and it is predicted that by this time almost 70% of world wheat (*Triticum aestivum*) consumption will occur in developing



Fig. 1 World food consumption calculated from Food and Agriculture Organization (FAO) world population predictions and per capita food consumption data. World consumption, grey bars; developing countries, black bars; industrial and transition countries, white bars.

countries. Considering that the current average yield of wheat is approx. 2.5 tons ha⁻¹, by 2020 the yield will need to be increased to 3.5 tons ha⁻¹ (Rosengrant *et al.*, 1995). This is translated into an annual increase of over 50 kg ha⁻¹ yr⁻¹, which is almost the same rate seen for wheat during the second half of the last century (Evans, 1993). In the case of rice (*Oryza sativa*), because of population growth in Asia and increasing urbanization, an estimated 50% yield increase will be needed over the next 40 yr. Currently 700 million people rely on rice for > 60% of their daily calorific intake. To prevent mass malnutrition by 2050 each hectare of riceproducing land will have to feed 43 people instead of the 27 fed at present. This equates to 400 million tonnes of carbon being fixed into rice grains in comparison with 250 million tonnes in 2008 (Sheehy *et al.*, 2007).

It is likely that rice yields are approaching the theoretical upper limit for a C₃ crop growing in Asia (Cassman, 1994). Furthermore, there is strong evidence of increasing pressure placed on crop production by a combination of water availability and climatic factors. The 'green revolution' which drove yields in the latter half of the 20th century relied upon maintaining favourable conditions for plant growth, for example high inputs of water and nutrients (Evans, 1993). A notable exception is sub-Saharan Africa, which could not benefit from these production methods (Dingkuhn et al., 2006). Competition for land and resources may mean that many regions now face the prospect of producing yields with lower water availability and a growing population. Many regions of the world are increasingly affected by drought. Recent assessments of climate impact upon crop production concluded that, whilst yields in some high latitudes may benefit from rising temperatures, the overall impact in latitudes closer to the equator, where many developing countries are located, may be negative (Parry et al., 2005; Easterling et al., 2007). Concerns over energy and oil availability also raise the problem of fertilizer cost in vulnerable systems.

Therefore, a critical question for crop scientists is whether current trends in the improvement of yield in crops will be sufficient to meet future human need. In the next section we address this question using fundamental principles of crop growth and yield component analysis.

III. Photosynthesis from an agricultural perspective

Where will the required increase in crop yield arise? There are theoretical limits to productivity, which are set by the thermodynamic properties of the crop and its environment. In this context (of theoretical maximum yield), the limitations are set by the efficiency of absorption (capture) of light energy and the efficiency of its transduction into biomass. The vital question is whether these limits have been reached already within crop systems or whether there is potential for improvements that have not yet been exploited.

Obviously, improvements in the capture and conversion of light energy have been a central part of crop improvement during the last century. For example, the increase in the erect nature of leaves has permitted a higher leaf area per unit ground area (leaf area index (LAI)), allowing crop canopies to be extremely efficient at absorbing radiation. The rate of conversion has also been improved by input management: the application of fertilizers increases leaf area and also the rate of photosynthesis per unit leaf area. Additionally, enhanced resistance to pests and diseases and a multitude of adaptations to local requirements (photoperiod, growing season duration, and temperature) have resulted in yield progress in a range of agroecological zones (Evans, 1993). However, many of these features of crop plants, which played such a prominent role in creating the ideotypes of the green revolutions (harvest index, nitrogen responsiveness, stature and canopy architecture) may already be optimized or close to optimization (Horton, 2000; Peng et al., 2000; Sheehy, 2000; Long et al., 2006).

Therefore, the question remains as to whether the crop biomass production rate is similarly optimized. It might be assumed that yield progress has been associated with an improvement in total biomass production, but some studies show a nonsignificant relationship between yield and biomass (Slafer et al., 1994; Calderini et al., 1995). Nonetheless, evidence suggests that a critical component of crop production is increasingly dependent upon the capacity to produce more biomass (Peng et al., 2000; Reynolds et al., 2000; Shearman et al., 2005; Hubbart et al., 2007). In the case of rice, the rate of biomass production only seems to have correlated with yield since the early 1980s (Peng et al., 2000). In the UK, wheat yield progress in recent decades has been shown to involve an improvement in biomass production (Shearman et al., 2005). Direct experimental evidence is found in the higher biomass and yield of crops grown in elevated CO₂ in field experiments (Ainsworth et al., 2004; Long et al., 2006).

Classical crop physiology tells us that total dry matter content at harvest is closely and linearly correlated with accumulated intercepted solar radiation. The slope of this relationship gives the radiation use efficiency (*E*); in other words, the amount of dry matter produced per unit radiation intercepted (measured in g dry matter (DM) MJ^{-1}). Total biomass production can be described by the following equation (Monteith, 1977):

$$\begin{array}{c} \text{harvest} \\ \text{Total biomass} = \Sigma Q \times I \times E \\ \text{sowing} \end{array}$$
 Eqn 1

(*Q*, the solar radiation over the duration of the crop period; *I*, the interception of the solar radiation by the crop canopy.) It follows that the ways to increase total biomass are:

• to increase the duration of crop photosynthesis;

• to increase the interception of the solar radiation by the crop canopy, and

• to increase the efficiency of the conversion of the light energy into plant dry matter.

The duration of crop photosynthesis is of critical importance. It is thought that both selection for higher yields and the increased input of nitrogen fertilizer have acted to increase leaf lifespan in modern crops (Hay & Porter, 2006). Temperature determines the rate of development and therefore the time available for radiation capture. In tropical regions, it is possible to obtain more than one harvest per year and one focus has been on shortening crop duration to allow rapid harvest (Peng et al, 2000). In temperate regions, high temperatures can reduce the grain-filling duration, reducing the biomass production rate during this period. There has been interest in manipulating the timing of senescence to obtain higher crop yields. However, senescence is an essential physiological process that remobilizes nutrients for grain production (Gan & Amasino, 1995) and its manipulation has to be integrated into the regulation of reproductive physiology and appropriate responses to environmental factors (Wingler et al., 2006; Yang & Zhang, 2006; Murchie & Horton, 2007).

The efficiency of solar radiation interception (defined as the proportion of incident irradiance absorbed corrected for reflection) by fully formed crop canopies is considered to be generally high. In the case of many cereals, this is a result of a high LAI combined with erect leaves, which increase light penetration into the canopy. The introduction of semi-dwarf growth habit with reduced height genes (Rht) had a massive impact on yield in cereals, greatly increasing the harvest index (dry weight of product : dry weight of plant; Austin et al., 1980). It is often assumed that this also improves radiation interception, but the semi-dwarf lines have similar radiation use efficiencies to tall lines (rht) (Miralles & Slafer, 1997). The genes responsible for dwarfing in other major crops have been identified (Spielmeyer et al., 2002) and there may be further potential for improvement. There may be scope for further improvements in canopy architecture and development so that the formation of a full canopy coincides with periods when radiation intensities are highest. For example, more rapid formation of a crop canopy may be important in colder temperate regions where developmental processes such as leaf emergence are temperature-limited (Hay & Porter, 2006).

The duration of crop photosynthesis and the interception of solar radiation are the two components of the Monteith equation that have contributed most to the increase in yield of most important crops. This review will focus on the third component, the efficiency of conversion of absorbed radiation to dry matter. We will argue that herein lies the best (perhaps only) way to promote yield increases on the scale required. Because biomass has on average 40% carbon by dry weight, any improvement in total biomass production means an improvement in photosynthetic carbon fixation. As described above, there is general agreement that an improvement in carbon fixation during the second half of last century was an essential ingredient of the increase in crop yield. Surprisingly, this enormous increase in carbon fixation was largely achieved not by increasing the CO2 assimilation per unit leaf area, but by increasing CO₂ assimilation per unit land area. For this, improved agronomic practices (in terms of plant density, nutrition, water supply, pesticides, herbicides, etc.) created favourable microenvironments for plant growth, effectively mitigating the negative impacts of external constraints (biotic and abiotic). Thus, there has been little or no increase in the intrinsic conversion efficiency of light energy into plant dry matter (photosynthetic efficiency) by individual leaves. In fact, studies across a range of crops show that increase in photosynthetic rate per unit leaf area rarely coincides with yield progress (Evans, 1993). In many cases, there may be a negative relationship. In wheat there seems to have been a decline in assimilation rate following domestication (Evans & Dunstone, 1970; Austin et al., 1982), although one example shows yield progress linked to an improvement in leaf assimilation rate (Fischer et al., 1998). In the case of rice, photosynthesis tended to be lower in the wild Oryza species than in O. sativa (Cook & Evans, 1983), and among varieties there is evidence for a trend towards higher rates of assimilation in more recent varieties (Sasaki & Ishii, 1992; Zhang & Kokubun, 2004). By contrast, other studies show either no trend or even a lower rate of assimilation in cultivated varieties (Yeo et al., 1994). However, it should be pointed out that yield improvement has targeted traits and practices that did not necessarily depend on increasing or even maintaining the rate of leaf photosynthesis, meaning that the increases in photosynthesis per unit ground area could have happened with no change (or paradoxically even a decline) in photosynthesis per unit leaf area. Attempts to improve yield by directly selecting/ breeding for crop plants with high rates of leaf photosynthesis have been rather limited and have had mixed success (Austin et al., 1989; Gutierrez-Rodriguez et al., 2000).

It has therefore been tacitly assumed that photosynthetic efficiency is a constant in crop systems, already optimized and therefore not a modifiable determinant factor for the increase of crop yield. This assumption was considered to be consistent with research into the mechanisms of the photosynthetic process itself and demonstrations that fundamental photosynthetic parameters such as quantum yield are highly conserved among higher plants (e.g. Björkman & Demmig, 1987). However, although the radiation use efficiency of crops (E) is claimed to be fairly consistent for a given crop species, much variation has also been reported (Long et al, 2006; Hay & Porter, 2006), and in the field E may fall well below the theoretical maximum (Mitchell et al., 1998; Zhu et al., 2008). To determine the impact of photosynthesis per unit leaf area on yield it is necessary to minimize the effect of other variables. Thus, experiments in which the background genetic variation is reduced have had greater success (Watanabe et al., 1994; Gutierrez-Rodriguez et al., 2000). Similarly, leaf photosynthesis exerts a greater control on biomass production and grain yield when variation in factors such as partitioning, nutrient

responsiveness and LAI is minimized (Long et al., 2006; Hubbart et al., 2007). Interestingly, an increase in yield observed in varieties of rice released after 1980 is more closely correlated with an increase in biomass than with an increase in harvest index (Peng et al., 2000; Hubbart et al., 2007). The fact that these varieties present higher light-saturated rates of photosynthesis (P_{\max}) than many older varieties released before 1980 suggests that an increase in leaf-level photosynthesis in rice is more likely to be observed in circumstances where an increase in biomass production dominates. This implies that selection, either directly or indirectly, for improved biomass production has effects on leaf photosynthetic physiology. For many authors (Kimball, 1983; Drake et al., 1997; Ainsworth & Long, 2005; Long et al., 2006), the positive response in yield for crops grown under elevated atmospheric CO₂ is strong evidence that an increased rate of leaf photosynthesis can induce more yield.

The arguments in this section reveal the potential for increasing crop biomass production through alteration of leaf photosynthesis. We now need to identify the specific targets that will directly improve leaf photosynthesis, so that further increases in yield will be realized. However, the mechanisms linking whole-plant events to leaf-level events are poorly understood. Photosynthesis in agriculture should be viewed holistically, as an integrated part of a much more complex process, which includes not only the primary events of light harvesting and carbon fixation, but also carbohydrate synthesis, partitioning of biomass (sink size and activity) and harvest of yield, together with the transport efficiencies of water, assimilates and nutrients. Two potential ways forward will be presented: firstly, the direct improvement of the mechanism of photosynthesis itself, resulting in increased photosynthetic capacity and/or efficiency; and secondly, by exploring and analysing the complexity of photosynthetic regulation in the field we can make more effective use of existing photosynthetic capacity by optimizing dynamic responses to the environment. In either case, the resulting improvements in crop yield should not depend upon increased nitrogen (N) fertilization or water supply, but instead should increase the N use and water use efficiencies.

IV. Routes to improving the mechanism of photosynthesis

1. Rubisco-related targets

Many of the suggested routes to improving the leaf CO_2 assimilation rates of crops have focussed on the enzyme ribulose bisphosphate carboxylase oxygenase (Rubisco). Rubisco catalyses the reaction that fixes CO_2 into a threecarbon compound (C_3 photosynthesis). However, O_2 competes successfully with CO_2 at ambient concentrations, leading to the formation of phosphoglycollate, which is broken down to release CO_2 in the process termed photorespiration, thereby reducing photosynthetic efficiency. Under current atmospheric CO₂ and O₂ concentrations and saturating light, the amount and in vivo activity of Rubisco are considered a rate-limiting factor for carbon fixation (Makino et al., 1985, 2000; Parry et al., 2003). To overcome this limitation, increasing the Rubisco content in leaves is one simple possibility. In principle, the rate of light-saturated photosynthesis per unit leaf area can be increased further by increasing the total amount of photosynthetic machinery per unit leaf area. In practice, there is an optimal concentration of leaf N, which is determined partly by leaf thickness limitations driven by intra-leaf shading. There is also a limit to the amount of protein that can be accumulated in the chloroplast, and the number of chloroplasts in the mesophyll cell (Pyke & Leech, 1987). Plants already accumulate large pools of Rubisco in leaves to compensate for its relative inefficiency and it can already account for 15–30% of the total leaf N in C₃ plants (Mae et al., 1983; Makino et al., 2000). Moreover, an increased investment in N for the plant, requiring an even higher rate of N fertilization, is not sustainable in future crops. High oil prices and the very low N use efficiency (NUE) of crop systems, c. 33% for cereal crops (Raun & Johnson, 1999), seem to make this option nonviable, which highlights the urgent need to improve the NUE of cereal crops. The question of whether N is optimally distributed among photosynthetic components has received attention (Medlyn, 1996; Poorter & Evans, 1998). However, an increased Rubisco content without an extra input of N could force the plant to redistribute its internal N, decreasing the amount of other essential enzymes and establishing new bottlenecks for CO₂ fixation. This may be one of the reasons why transformed plants with increased amounts of Rubisco do not present improved photosynthesis (Suzuki et al., 2007).

It has been questioned whether such a large concentration of Rubisco in leaves is necessary. Studies of plants with reduced contents of Rubisco suggest that there is an excess accumulation (Quick et al., 1992; Lauerer et al., 1993). Similarly, Rubisco accumulation in excess of that required to sustain measured photosynthetic rates has been found in some varieties of rice (Murchie et al., 2002). Light limitation is a common condition for a significant proportion of the canopy in most crops, particularly when the maximum LAI is reached, and for such plants, decreasing the Rubisco content could increase the NUE. Furthermore, it has been suggested that, as a result of the rising concentration of atmospheric CO_2 , a reduction in the amount of Rubisco may even be desirable (Parry et al., 2003), as the photosynthetic NUE is higher in plants grown at elevated CO₂ (e.g. Davey et al., 1999) even under current CO_2 concentrations. However, it is important to note that Rubisco also acts as a large store of N, which is mobilized for grain N content and growth of new tissues (Mae et al., 1983; Murchie et al., 2002; Hirel & Gallais, 2006). Both the absolute amount of Rubisco and the timing of its degradation are critical, but how the balance between the role of Rubisco as an N store and its photosynthetic function

is regulated is not known (Horton & Murchie, 2000). It may be possible to increase NUE by achieving the same assimilation rate with less protein by maximizing Rubisco activity. The activity of Rubisco is determined by a number of inhibitors, the enzyme Rubisco activase determining the proportion of Rubisco active sites that are free of inhibitors and thus capable of catalysis. It has recently been argued that the regulation of Rubisco activity is not optimized for maximum crop productivity and that Rubisco activase may be a fruitful target for manipulation (Parry *et al.*, 2008).

An alternative strategy for Rubisco improvement is to increase its specificity for CO₂ relative to O₂ by direct manipulation of the enzyme (Parry et al., 2003). There is evidence of biological variation in specificity. Forms of Rubisco present in plants of the genus Limonium acclimated to stress conditions have a higher specificity factor than those of many crop plants (Galmes et al., 2005). However, it seems that Rubisco forms with high specificity for CO₂ tend to have low maximum catalytic rates of carboxylation per active site and there is a well-cited inverse relationship between these two parameters (Zhu & Spreitzer, 1996). Therefore, if the specificity factor is increased while the rate of carboxylation is reduced, then no gain in carbon fixation will result. However, recent examination of the mechanism of the active site of Rubisco indicates that, far from its image as 'sluggish and inefficient', Rubisco shows a wide range of adaptation to substrate availability (Griffiths, 2006; Long et al., 2006; Tcherkez et al., 2006). This leads for the first time to the suggestion that different forms of Rubisco with different kinetic properties could be engineered, even within the same individual, each one tailored for particularly conditions of light, temperature and sub-stomatal CO₂ (C_i ; Griffiths, 2006).

There is evidence that the amounts of other enzymes, not just Rubisco, may not be optimized for maximum biomass production in plants (Raines, 2006). Thus, increasing the level of sedoheptulose-1,7-bisphosphatase in tobacco (*Nicotiana tabacum*) plants leads to significant improvements in photosynthetic rate and growth at an early phase of growth (Lefebvre *et al.*, 2005). This suggests that levels of this enzyme may be only just sufficient or even insufficient to sustain maximum photosynthetic rates. A theoretical analysis based on mathematical modelling of photosynthesis confirms this suggestion (Zhu *et al.*, 2007).

2. Decreasing photorespiration

Although photorespiration has been assigned metabolic and protective roles, the negative impact of photorespiration on crop yield has been demonstrated by the fact that doubling the CO_2 concentration dramatically increases the performance of several crops (Kimball, 1983). Theoretical models suggest that eliminating photorespiration will increase yield under favourable conditions. However, totally blocking photorespiration metabolism downstream of Rubisco has been shown to be ineffective (Medrano *et al.*, 1995; Somerville & Ogren, 1982) and it is not clear what would be the implications of this in plants grown under stress. It is thought that simply blocking photorespiratory flux without altering oxygenation leads to an unfavourable accumulation of intermediates. Recently, an alternative approach has been taken (Kebeish *et al.*, 2007): diversion of part of the chloroplast glycollate directly to glycerate produced a partial reduction in the flux of photorespiratory metabolites and increased biomass production. This approach maintains any putative protective role for photorespiration, and opens up the possibility of having plants with increased efficiency also performing well under less favourable conditions.

3. Transforming C_3 crops into C_4

Some of the most productive crops, such as maize (*Zea mays*) and sugar cane (*Saccharum officinarum*), have the ability to concentrate CO_2 , thereby eliminating oxygenase activity and increasing photosynthetic efficiency. CO_2 concentration is achieved via the C_4 pathway, which involves the initial fixation of CO_2 into C_4 acids using phosphoenolpyruvate carboxylase (PEPC). In the next stage of the pathway CO_2 is released from the C_4 acids for fixation by Rubisco. It has been questioned whether it is possible to introduce the C_4 pathway into C_3 crops such as rice. It has been argued that this is the only way to bring about an increase in biomass production sufficient to sustain the required yield enhancement. This is an ambitious undertaking but the underlying science is compelling and is attracting more attention (Mitchell & Sheehy, 2006).

Initial attempts involved simply transforming rice with genes encoding C₄ enzymes such as PEPC, pyruvate orthophospate dikinase (PPDK) and the NADP-malic enzyme (NADP-ME) (Ku et al., 2001; Matsuoka et al., 2001). Similar transformations have been carried out in potato (Solanum tuberosum) (Rademacher et al., 2002) and tobacco (Häusler et al., 2001; Häusler et al., 2002). Despite claims of increased assimilation rates and some C₄ properties, the underlying mechanisms of these effects have not been confirmed. Significantly, these approaches ignore the fact that, although C4 and C3 carboxylation in some species can operate in a single cell (Voznesenskaya et al., 2001, 2002), in the most productive species, the C₄ pathway depends upon Kranz anatomy (although see Edwards et al., 2007). This produces spatial separation of the fixation of atmospheric CO_2 in the mesophyll cells from the fixation of the CO2 released from C4 acids in the bundle sheath cells, avoiding CO₂ leakage from the mesophyll to the atmosphere and maintaining an adequate CO2:O2 ratio at the Rubisco site in the bundle sheath. At first sight, it seems overwhelmingly complex to alter cellular differentiation, partitioning of enzymes, chloroplast morphology and differential regulation of the metabolic pathways in each cell type. However, encouragement comes from observations that the two metabolic

strategies co-exist in both C_3 and C_4 plants (Hibberd *et al.*, 2008), that species exist that can switch between C_3 and C_4 depending on environmental conditions and that the evolution of C_4 has independently occurred at least 45 times in angiosperms. Much of the current focus is therefore on obtaining Kranz anatomy rather than developing a single-cell system (Hibberd *et al.*, 2008). All of this indicates that is there no intrinsic reason why the C_4 pathway could not be introduced into a crop such as rice. It has been argued that a combination of advanced molecular techniques, transformation of key genes and smart screening of germplasm could achieve results in a reasonable timescale (Sage & Sage, 2007).

Because the sizes of sinks have generally been tailored by C₃ crops over their evolution in a way proportional to the size of the photosynthetic source, more efficient carbon fixation in the potential C4 transformed crop would need a correspondingly adapted sink to efficiently accumulate the harvestable products. This may or may not require a higher harvest index. New increases in harvest index in main crops would have to come mainly from an increase in the size of the sink and not from a decrease in the dry matter allocated in the other structures of the plants (stems, roots, leaves etc.) as in the past. This still seems to be possible in the main grain crops (Long et al., 2006). However, recent work on fruit crops such as tomato (Solanum lycopersicum; Nunes-Nesi et al., 2005) shows that increases in the size of the sink are not only linked to an increase in CO₂ assimilation, but also to a reduction in dark respiration. This last finding may re-open the discussion on the importance of the respiratory pathways in photosynthetic metabolism. New evidence shows that chloroplasts and mitochondria are not as independent as once thought (Priault et al., 2006), and interactions between them can be beneficial particularly under stress conditions (Raghavendra & Padmasree, 2003). Related to this, the evaluation of discrepancies between theoretical and *in situ* measured values of respiratory coefficients, for example waste respiration (Amthor, 2000), suggests that targets for improvement may remain.

V. Photosynthesis in the field: potential and actual rates

Many studies clearly show that maximum photosynthetic potential is rarely realized, under field conditions. An analytical approach to describing such losses in potential photosynthesis was first presented by Cheeseman *et al.* (1991). When 'spot measurements' of photosynthetic rate were taken on a large number of leaves in a plant population, and the data points were plotted against irradiance, a high degree of scatter was found, with a theoretical irradiance curve represented as the ceiling below which all data were located. Measurements on a rice crop produced the same picture (Murchie & Horton, 2007). Confirmation of the underperformance of the majority of leaves was obtained by measurements of leaf photosynthesis during a diurnal cycle, which showed that peak photosynthetic



Fig. 2 Schematic depicting (a) the complexity of photosynthetic processes in the agricultural context with regulation needed at every step from chloroplast-level processes through to transport and storage of assimilate. (b) The losses that occur that reduce photosynthate production to below the potential rate.

rates were maintained for only a few hours each day (Black et al., 1995; Murchie et al., 1999). The reasons for this are many and varied (Horton, 2000), but there are two major influences - firstly, the direct limitation imposed by environmental stresses, even under apparently favourable conditions; and secondly, the presence in the plant's genotype of regulatory processes that reduce photosynthetic activity (Fig. 2b). There has predictably been a great deal of interest in the former, and increasing the stress tolerance of crops has become a major goal in agricultural improvement (Bohnert et al., 2006; Valliyodan & Nguyen, 2006). By contrast, little attention has been paid to the effect of regulatory mechanisms. These are particularly intriguing, and will be explored at length.

From an agricultural perspective, photosynthesis includes all the events from light interception to the export of photosynthate for biomass accumulation and grain production (Fig. 2a). As yield is an integration of this process over time, inevitably it has to include developmental aspects and most importantly the continual changes in environmental factors. The description of photosynthesis in these terms represents a challenge: not only does photosynthesis comprise a large number of integrated reactions and processes, but it is exceedingly complex, and hence difficult to describe in a way that is useful from an agricultural viewpoint. Equally, it is this complexity that provides so many unforeseen opportunities.

Photosynthetic complexity arises from several sources: heterogeneity - the leaf consists of a range of cell types in which photosynthetic capacities and even biochemical pathways are different; intracellular co-operation - photosynthesis depends upon the interaction of pathways in the chloroplast, cytosol, vacuole and mitochondria; metabolic regulation - many individual component parts of the process are regulated by metabolic signals generated in other parts, creating a network of feedback and feedforward regulatory networks which provide fine control over flux; acclimation - the capacities of component processes respond to changing environmental conditions, providing course control, and, together with regulatory mechanisms, establish balance in the face of differing environmental and development constraints. An important consideration is that one function of this complexity is to contain the potentially lethal cocktail in the plant cell-light, oxygen and photosensitizing pigments - which serves as a warning that intervention in this system has the possibility of increasing the likelihood of photo-oxidative damage (Horton et al., 2001).

Although the regulatory and acclimation processes were highlighted as potential targets for rice improvement, (Horton, 2000; Horton et al., 2001) in general these aspects have attracted very little attention. Indeed, their existence can be seen a negative factor - the plasticity that results from these processes means that genetic alteration of single enzymes or other components is much less likely to produce the desired changes in total photosynthesis because of compensatory adjustments. Feedback and feedforward regulation of photosynthesis occurs at many levels (Fig. 2a) and enables responses to changing external and internal conditions. In each case, the regulatory mechanism should ideally fulfil a number of criteria: it should react to enable the concentrations of key metabolites such as ATP to be maintained; it should prevent the build-up of potentially damaging species, such as triplet states, or conditions, such as extreme redox states; it should be sufficiently dynamic to produce prompt responses to the altered conditions; and it should have a dynamic range capable of responding to a wide range of changes in the signalling factor. However, fulfilling all of these criteria simultaneously may not be possible and we therefore need a way to quantitatively describe the imperfections in these processes. The application of systems approaches promises to provide a means of exploring these features in a way that produces practically useful outcomes. Only when the dynamic structure of the photosynthetic process has been analysed will it be possible to determine the robust targets for intervention.

It is not just plant metabolism that could be targeted in this way: recent data suggest that canopy photosynthesis may be amenable to further manipulation by smart alteration of 3D structure. In warm environments, air temperature and humidity are two factors thought to be critical for determining both stomatal-mediated and chloroplast-level reductions in photosynthetic capacity. In such environments, transpiration plays a key role in lowering leaf temperatures to temperatures that are optimal for C₃ photosynthesis. A recent paper (Helliker & Richter, 2008) found that leaf temperatures in trees are kept remarkably constant across a range of latitudes from subtropical to boreal regions. In cold regions they are even raised above ambient during the periods in which they accumulate most biomass. This homeostasis of leaf temperature is thought to occur by adaptation of canopy architecture and structure, notably the proximity of leaves to each other (Helliker & Richter, 2008). Were this to be applicable to crops it could be exploited in canopy design and in the manipulation of canopy temperature to beneficial manipulation. This may be especially effective in environments where temperature is the overriding limiting factor for photosynthetic rate. However, in a theme central to this review, one may ask: what are the consequences for other processes of such adaptation to temperature? Is light interception compromised and is dark respiration increased? What are the optimization criteria for canopy architecture?

VI. Optimization of photosynthesis as a highly dynamic responsive process

Understanding the mechanisms by which photosynthesis operates during environmental fluctuations is central to an understanding of photosynthesis itself. Models based upon the steady-state model of Von Caemmerer & Farquhar (1981) focus on the limitation by either Rubisco or the regeneration of ribulose 1,5-bisphosphate (RuBP), and have led to great improvements in our understanding of the processes limiting photosynthetic productivity. Many dynamic models of photosynthesis with varying levels of detail have since been constructed (e.g. Laisk & Walker, 1986; Woodrow & Mott, 1993) and used to explore the regulation of electron transport and carbon assimilation (Horton & Nicholson, 1987). For further understanding of photosynthetic responses during transients and to extend this understanding to growth patterns and into fields such as metabolomics, more extensive models are required, which include not only the reactions of the Calvin cycle, but also photorespiration and downstream carbohydrate metabolism. One recent model does this (Zhu et al., 2007). This model was used in an innovative manner: it consists of a series of linked differential equations each representing the concentration of one metabolite. Using an evolutionary algorithm, the partitioning of N associated with each enzyme was allowed to vary. The combination with the highest resulting light-saturated photosynthetic rate proceeded to the next generation. After 1500 generations it was found that photosynthesis was increased substantially. An overinvestment in enzymes of photorespiratory metabolism and an

underinvestment in Rubisco, sedoheptulose1,7-bisphosphatase and fructose 1,6-bisphosphate aldolase were implied. This experiment has startling implications for crop improvement because it provides evidence that C_3 photosynthesis is currently operating at suboptimal rates. There are two possible explanations for this: selection pressures for photosynthetic capacity during selection and breeding have been minimal, as discussed above; and crops have not had sufficient time for a process as complex as this to adapt to factors such as changing atmospheric CO_2 concentrations (Zhu *et al.*, 2007).

The distribution of different types of molecule among diverse functions, including storage, signalling, stress responses and defence, is highly regulated. Another way to approach the analysis of productivity in multi-process systems is to use metabolomics. This can provide global profiles of metabolite levels associated with particular productivity rates. By applying such methods within an appropriate genetic framework, metabolite signatures can be associated with rates of productivity, allowing an indication of which pathways dominate. Meyer et al. (2007) used recombinant inbred lines of Arabidopsis thaliana and observed a close correlation between biomass production rates and specific combinations of metabolites. Although it is the flux through particular pathways that is more important than metabolite concentrations, it is important that these methods now be applied to crop plants at appropriate stages of growth and development and linked to integrative models of the type described by Zhu et al. (2007).

VII. Principles governing dynamic responses of photosynthesis to the environment

1. Regulation, risk and compromise

The natural environment consists of predictable diurnal and seasonal rhythms in irradiance, photoperiod and temperature. These are punctuated by less predictable short-term fluctuations in irradiance, rainfall and temperature. It is claimed that short-term environmental shifts in temperature and rainfall (and by inference irradiance) will become less predictable in the near future as a result of anthropogenic climate change (IPCC, 2007). It is a self-evident property of plants that they 'match' their rate of growth (sink processes) to the availability of resources (light, water, N, etc.). This may appear a rather simple concept; however, it raises a number of fundamental questions regarding the mechanisms that determine the extent of resource 'capture' and the conversion efficiency into biomass during perturbations in the environment. If the use of photosynthate in growth is curtailed it is common to observe 'feedback' effects (down-regulation or inhibition) of photosynthesis (Paul & Foyer, 2001). Equally, there are examples of the opposite: increasing the photosynthetic capacity of a crop before flowering frequently leads to an increased sink capacity (e.g. Takai et al., 2005; also discussed in Evans, 1993). It is expected that these regulatory mechanisms would be optimally geared towards high productivity. However, this may not necessarily be the case, because of the 'conservative' nature of most plant species. Put simply, stability, survival and reproductive success in the natural environment are the driving forces of evolution, not necessarily high growth rate or high grain yield. The human demand for high agricultural yield may often be in conflict with key features of plant biology. A key feature of this conservative nature is that plants record, memorize and predict their environments, to ensure that they always have enough energy storage (from photosynthesis) to power their growth and development. For example, plants have to determine the size of their reproductive sinks in advance, predicting what the photosynthetic rate will be to give maximum grain filling. Overestimation of future photosynthesis results in poor grain filling and/or poor quality grain. Underestimation of future photosynthesis results in a decrease in the efficiency of solar energy use and losses of potential productivity. How plants record information about their environment, how this information is stored as memory and how it is used in predicting future environmental conditions are poorly understood. What is the level of 'risk' found in these processes? Intuitively, a strategy with minimized risk would result in less gain, whereas maximized gain would involve increased risk. Plants can be classified therefore in terms of the extent to which they are cautious, similar to the assignment of growth strategy used by Grime and co-workers (Grime et al., 1989). But what are the molecular bases of such terms, what type of strategy is found in crop plants, and does their particular strategy compromise yield? Thus, our first concern here is to investigate whether co-ordination and regulation of photosynthesis are optimized to growth rate and productivity during environmental perturbation. We will use examples from recent research and argue that this is not necessarily the case.

2. Optimization of carbon partitioning

There is not a simple linear pathway between photosynthesis and the production of biomass (either vegetative or reproductive). The plant is faced with a number of 'choices' in terms of how it partitions this fixed carbon. Does it invest in growth or storage? Firstly, it can synthesize sucrose and export this from the leaf towards sinks (broadly divided into root and shoot). Secondly, it can divert this carbon towards starch synthesis in the chloroplast, which is viewed as storage. It can also utilize a proportion of the fixed carbon in the synthesis of amino acids, nucleic acids and secondary plant compounds. The decisions made by the plant depend upon efficient signalling and quantification of the capacity for growth. A pertinent question is whether storage can ever occur at the expense of growth. If a high level of 'risk' is perceived by the plant, then a conservative response will see investment in storage. This can be to the detriment of the plant as storage will have associated maintenance respiration costs. An example of how plants balance supply of and demand for carbon is seen

in the patterns of inter-conversion of different forms of leaf storage carbohydrate that occur in response to environmental change (Smith & Stitt, 2007). Carbon is fixed during the daytime: however, a constant photosynthate supply is required for growth and maintenance processes, which occur throughout both the night and the day (Reddy et al., 2004). In order to cope with these demands, leaves convert a proportion of newly fixed carbon into chloroplastic starch, which is used for growth and metabolic processes during the night. The remainder is converted to sucrose to fulfil immediate requirements and for export to growing tissues. A striking feature of this is that the proportion of carbon that is fixed for nocturnal use is closely regulated: it declines in a linear manner during the night and is almost completely depleted by the following morning. This implies that leaves possess a mechanism that can quantify starch contents at the end of the day and match them to the rate of degradation (Gibon et al., 2004) Moreover, if the requirements for nocturnal starch use are altered by changing the daylength, the proportion of carbon allocated to starch is altered in proportion to the night-time requirements. This does not happen immediately: a short-term 'starvation response' in which growth ceases altogether is observed while leaves adjust the amount of carbon they allocate to different processes in order to balance requirements. This latter process is termed 'acclimation'.

Such acclimation processes probably occur continuously in response to resource availability and environmental change as the plant 'anticipates' how much carbon it will require for growth, depending on recent events. Carbohydrate starvation and the subsequent adjustment may occur frequently, depending on shifts in light intensity over spatio-temporal scales. Work with carbohydrate synthesis mutants supports these principles. For example, mutants that lack plastidial phosphoglucomutase, which converts Calvin cycle intermediates into starch, show lower rates of growth except under long days (Gibon et al., 2004; Smith & Stitt, 2007). A number of points in the starch and sucrose synthesis and degradation pathways have been identified as being key in regulating partitioning (Smith & Stitt, 2007). It comes as no surprise that sugars themselves have a prominent role as key signalling and sensing molecules, affecting expression of genes involved in photosynthesis, carbohydrate metabolism and growth (Smeekens, 2000; Rolland et al., 2006). It is likely that the ability of plants to sense carbohydrate status and respond accordingly involves the integration of a number of signalling pathways, such as those involving developmental events, circadian rhythms, light and nutrient status. A number of key metabolites have been identified that are involved in the signalling of leaf carbohydrate status; for example, trehalose 6-phosphate and fructose 2,6-bisphosphate. The enzyme hexokinase is recognized as an important sensor of leaf sugar status (Moore et al., 2003).

So, carbon supply is not directly connected to demand. As a generalization, carbohydrate is produced and stored 'on-site' simultaneously in proportions that are dictated by recent events and that anticipate nocturnal events. An important conclusion from this work is that allocation of carbon to storage can indeed occur at the expense of growth (Smith & Stitt, 2007), which is probably an evolutionary response to prevent 'feast and famine' events (Paul & Foyer, 2001). Moreover, the pattern of storage can be linked to the rate of overall growth of the plant: Cross *et al.* (2006) observed that *A. thaliana* accessions that allocated less carbon to starch storage had a higher growth rate. This is clear evidence that plant growth (including crops) is to various extents conservative in nature, and this is an emergent property of plants growing in variable conditions.

An important point to note here is that most of the research on carbohydrate flux has been carried out in plants that store starch preferentially. Major crop plants such as wheat and rice use alternative storage molecules and the regulation of their accumulation is less well known; wheat stores fructans in leaves and stems, whereas rice stores sucrose in leaves and starch in stems (Watanabe *et al.*, 1997; Yang *et al.*, 2002; Ishimaru, 2003; Murchie *et al.*, 2005). Although feedback inhibition of photosynthesis in rice has been demonstrated (Winder *et al.*, 1998), this difference may turn out to be very important: firstly, there is a negative correlation between starch formation and photosynthetic capacity (Paul & Foyer, 2001); and secondly, in nonstarch-formers such as rice and wheat, the removal of sinks does not seem to inhibit leaf photosynthesis (e.g. Nakano *et al.*, 1995).

The concept of a 'decision' on behalf of the plant for storage or growth also needs to consider the existence of all storage organs in the plant. In many cereals, the stem and leaf sheath lay down significant quantities of storage carbohydrate before flowering. In the case of rice, up to 40% of grain carbon can originate from pre-anthesis storage. Adequate carbon is needed for flower development so some storage would be deemed necessary, but the question arises of whether the amount of storage has adaptive value. Quantitative trait locus (QTL) analysis would indicate that it does: increased carbohydrate storage capacity was associated with higher yield under some conditions (Ishimaru, 2003). Other work suggests that the dynamics of remobilization, not just the amount of accumulation, are critical (Takai et al., 2005, 2006). Therefore, the storage vs growth issue occurs on many levels between source and sink as part of an overriding strategy to prevent carbon starvation during key periods. The work of Takai et al. (2005) suggests that the dynamics of such storage organs are crucial, as they 'set' the size of the sink in rice plants. Again, there must be mechanisms for 'measuring' the carbohydrate content in nonphotosynthetic as well as photosynthetic tissues.

This concept may be applicable to many analogous processes in plants. In many cases, it appears that precautionary measures induced in anticipation of further suboptimal conditions result in a decrease in growth. The underlying genetic basis for these responses is being uncovered. For example, the expression of *CBF* genes is involved in cold-hardening responses, but also results in a reduced growth rate regardless of temperature (Thomashow *et al.*, 2001; Gilmour *et al.*, 2004; Vogel *et al.*, 2005). DELLA proteins are negative growth regulators of central importance, which are now considered to integrate the effects of various growth-promoting hormones such as gibberellins (Achard *et al.*, 2006). *Arabidopsis thaliana* plants that lack DELLA proteins show higher rates of tissue growth and biomass production when exposed to abiotic stress such as salt stress (Achard *et al.*, 2008).

3. Optimization of light harvesting

Arguably, the most variable resource in space and time is light intensity. The sedentary nature of plants means that they are exposed to unpredictable extremes of high and low irradiance over the course of a day. Photosynthesis is highly responsive to irradiance. At low irradiance photosynthesis rises linearly, giving a highly conserved quantum yield (Björkman & Demmig, 1987; Ogren & Evans, 1993). At higher light intensities the light reactions cease to be limiting and photosynthesis saturates at a point that is co-determined by a number of processes, but frequently dominated by Rubisco activity and stomatal limitations. C3 photosynthesis in crop plants such as wheat and rice saturates at light intensities well below the maximum intensity of sunlight (Murchie et al., 1999). The consequence is that the light-harvesting pigment-protein complexes within the leaf will absorb more energy than is required for photosynthesis. This excess amount of excitation energy is potentially damaging and is dissipated through either photochemical or nonphotochemical processes to avoid photo-oxidative stress. The term 'nonphotochemical quenching' (NPQ) is applied to a number of processes that increase photoprotective thermal dissipation in light-harvesting complexes (Horton et al., 1996). NPQ includes the short-term protective process (qE), which relaxes on a timescale of minutes, and also long-term processes, which relax on scales of hours or even days (qI). The latter is sometimes termed 'photoinhibition' and can be accompanied by accumulated damage to photosystem II. A common feature of NPQ processes is that they cause a reduction in the quantum yield of photosynthesis, and hence the efficiencies of both photosystem II (ϕ PSII) and CO₂ assimilation (ϕ CO₂) of leaves (Long et al., 1994). Whilst NPQ does not reduce the assimilation rate at high irradiance, during fluctuating irradiance, the dissipation of energy will reduce assimilation, unless the dynamics of NPQ can track the dynamics of irradiance.

It has been hypothesized that this down-regulation of light-harvesting efficiency has the potential to limit not just leaf photosynthesis but also canopy photosynthesis in natural conditions where light intensities are variable (Long *et al.*, 1994; Raven, 1994; Murchie *et al.*, 1999; Horton, 2000). A model was recently presented which demonstrated the impact of slowly relaxing NPQ on canopy productivity. This model exploited a particular property of plant canopies (including those of crop species): that the movement of the sun and the movement of leaves give rise to a complex patchwork of light within leaves of the canopy in space and time. Zhu *et al.* (2004) used a ray-tracing algorithm to model the impact of these dynamics on the relaxation of ϕCO_2 within a 'typical' canopy. Direct sunlight will penetrate to lower leaves but these effects are transient, depending on solar movement and leaf movement. The conclusion was striking: up to 30% of canopy carbon gain is lost as a result of the slow relaxation of NPQ.

NPQ is regulated by a number of factors which determine the dynamics of the conformational changes in the photosystem II antenna that underlie the switch from an unquenched to a quenched state (Horton et al., 2008). These conformational changes are induced as the light-induced proton gradient builds up. The PsbS protein acts as a molecular sensor of the ΔpH and enables the rapid switching of the thylakoid membrane into a protective configuration (Kiss et al., 2008). PsbS appears to control the maximum capacity of NPQ, whilst the kinetics and capacity of NPQ also depend upon the Lhcb protein composition of the PSII antenna. The xanthophyll cycle plays a vital role in NPQ regulation, modulating the kinetics of formation and relaxation. Reversible conversion to zeaxanthin takes place in excess light, via the enzyme violaxanthin de-epoxidase. The re-conversion of zeaxanthin to violaxanthin is catalysed by zeaxanthin deepoxidase. De-epoxidation of violaxanthin to zeaxanthin causes activation of qE, lowering the ΔpH requirement and increasing the rate of formation and extent of qE, but decreasing the rate of relaxation. Accumulation of zeaxanthin kinetically correlates with the formation and relaxation of qI. Zeaxanthin also has crucial antioxidant properties that protect membrane lipids from peroxidation (Johnson et al., 2007). All of the factors that regulate NPQ are themselves variable according to irradiance conditions during growth and development, responses controlled principally by the light-dependent changes in the redox potential of the thyakoid membranes (see discussion of excitation pressure and photoacclimation below).

NPQ is therefore a process that incorporates 'memory' of previous light conditions and similarly anticipates a period of stress or potential resource limitation; the essential features are strikingly analogous to the starch storage strategies described in this section. Thus, a question that has been of great interest for some time now is whether NPQ is optimized (Horton et al., 2008; Johnson et al., 2008). It is important to consider whether, for a given crop under particular environmental scenarios, the extent and kinetics of NPQ are optimal for biomass production, or whether NPQ acts in a manner that is 'overprotective', as the work by Zhu, Long and colleagues suggests. For any given situation, NPQ should be induced at the appropriate irradiance, form at an optimal rate and decay at an optimal rate. Whilst such optimizations can be modelled, it is essential to investigate experimentally the effect of genetically manipulating the factors that regulate NPQ. The study of A. thaliana plants in which the xanthophyll cycle pool size is enlarged by overexpression of the gene encoding B-carotene hydroxylase provides some insights into the process of optimization. The increase in pool size and the resultant elevation in zeaxanthin concentration under stress conditions produce a significant increase in resistance to oxidative stress, via the antioxidant properties of this carotenoid (Davison et al., 2002; Johnson et al., 2007). However, although the increase in pool size does not affect the maximum capacity for NPQ, the rates of formation and relaxation of qE are altered, because of the 'inertia' inherent in having a large pool size (Johnson et al., 2008). This effect arises because NPQ formation is determined by the de-epoxidation state of the xanthophyll cycle pool, not the concentration of zeaxanthin. Similarly, the rate of NPQ relaxation in the dark is much slower in these plants because of the higher concentration of zeaxanthin. Therefore, the optimum size of the xanthophyll cycle pool is a trade-off between the beneficial antioxidant effect of a large pool and the negative effect on photosynthetic activity resulting from the sluggish response to environmental change. Thus, we find in this example a description of the key features mentioned above: recording information (increase in ΔpH), storing information (de-epoxidation state of the xanthophyll cycle) and its use in prediction (faster qE induction during a second illumination when zeaxanthin has accumulated). We see this operating also in a slower time domain - recording prolonged environmental change by means of redox potential, storing this information by altered gene expression (increasing the xanthophyll cycle pool size and content of PsbS, and altering the composition of antenna proteins), and predicting continued light stress by having a larger photoprotective capacity. Furthermore, in this simple example, we can see how risk assessment takes place, and how 'decisions' are made that set the optimum response in terms of having adequate photoprotection for a particular environmental scenario.

4. Growth strategies and photosynthetic productivity

There are many other examples that could be discussed, as nearly every aspect of a plant's development hinges upon its energy metabolism, which in turn is dependent upon photosynthetic activity. Alteration of optimization points in favour of higher yield may not be that complicated - a small number of proteins are involved in many of these regulatory mechanisms, as in the case of NPQ. Other alterations may be more difficult, in part because of the unexpected effects of various compensatory responses to genetic alterations (Labate et al., 2004) and, in many cases, there are significant gaps in our knowledge of the molecular mechanisms involved. Single genes appear to be able to confer traits that possess complex phenotypes but are extremely well co-ordinated. The ERECTA gene is a recent example (Masle et al., 2005). It appears to regulate water use efficiency in A. thaliana in combination with a series of morphological characteristics in different cell types including stomata, epidermal cells and mesophyll cells. Nevertheless, it is clear that optimization points of complex integrated responses

to the environment are also subject to genetic variation, suggesting that they are viable targets of crop improvement. This variation is observed when examining crop varietal differences. For example, a survey of 24 South American commercial varieties and accessions of common bean (*Phaseolus vulgaris*) revealed a negative correlation between productivity and stress tolerance. In general, those that are stress tolerant have a low growth rate under favourable conditions, whereas others have a high yield under favourable conditions but do not tolerate conditions of drought and temperature stress (Lizana *et al.*, 2006). This shows that the optimization points of these accessions are different and it also reinforces the importance of classifying the overall growth strategy of a crop before considering the ways in which can be genetically improved.

A persistent relationship emerges - that high yield potential and high stress tolerance are incompatible, showing that the development of new crop varieties must be matched to the specific range of conditions under which the crop is grown (local adaptation). More knowledge is needed about the molecular basis of this compromise between high yield potential and stress tolerance. What makes a high-yielding crop more sensitive to stress, and why does high stress tolerance limit yield? It can be hypothesized that this arises because of the intimate relationship between the rate of photosynthesis (the source) and the accumulation of material in grain (the sink). Examples of this could include tiller abortion and flower abscission. In common bean, the number of flowers, number of pods and size of pods are under the control of leaf energy status during the induction period of buds. Later on, seeds become the dominant sinks and extract photosynthates from the leaves. If flowers are induced under optimal growth conditions, many strong sink organs are initiated. Indeed, a highyielding bean crop should have a large number of pods filled with large seeds, which provides a large sink for photosynthate. In this respect, sinks may be regarded as dominant over 'the needs of leaf tissues'. If the photosynthetic activity becomes limited by external factors, such as drought or extreme temperatures, there is a high risk of producing a high number of small, underdeveloped seeds instead of maximal crop yield. Under such conditions, leaf cells may become depleted of sugars in the presence of a large sink. Therefore, the cell energy status of leaf cells may drop below a threshold value, oxidative stress will result and senescence will be initiated. This means that potentially high-yielding crops are under a higher risk of early flower and pod abscission because a high photosynthetic rate is more sensitive to inhibition by stress. In fact, abscission under stress is a physiological protective measure that limits the size of the sink and thus prevents early ripening and the eventual production of seeds that are too small and do not germinate competitively. These events are co-ordinated by complex signalling networks, in which the 'products' of photosynthesis are intimately involved (see later in this section).

These complex source and sink interactions require mechanisms that transmit information about energy status in

one part of the plant to another, in an analogous manner to the fluxes between chloroplast starch and cytosolic sucrose in plants such as *A. thaliana* and the fluxes between stem carbohydrate and flower development in rice. These fluxes will in turn be dependent on dominant signalling from systems such as the DELLA gene family. Therefore, it is necessary to understand not only how such dominant genes place limitations on growth, but also how these change under different conditions, where different responses are required, and how these interact with the information-rich signals operating between different plant parts.

5. How do plants 'decide' on a response that is appropriate for high productivity?

The environment consists of predictable rhythms overlaid by (unpredictable) high spatio-temporal complexity and we have discussed how important it is for plants to anticipate and acclimate to future conditions. However, the signalling mechanisms are complex and our understanding is still limited. It is clear that there is much overlap of different signalling transduction pathways. A good example is the regulation of stomatal aperture by guard cell turgor, which requires the action of several metabolic events. Each stimulus, such as light, CO2 or humidity, does not seem to possess its own distinct signal transduction pathway. Indeed, this may be inappropriate for plant responses in which acclimation is present and conditions preceding a stimulus can have a marked effect on the response; for example, growth in different environments influences stomatal responses to CO₂ (Frechilla et al., 2002) and drought (Wentworth et al., 2006). The processing of environmental information is made even more complex by the need of the plant to integrate stimuli over an appropriate period in order to accommodate natural fluctuations.

One way in which plants may be able to process complex signals in a precise and quantitative manner is via the structure of the signalling system itself. It has been suggested that plant cell signalling systems are 'scale-free' networks, systems that do not operate as linear pathways, but as a complex network of signalling components or nodes (Hetherington & Woodward, 2003). In a scale-free network, the signal that emerges is not a product of individual transduction pathways but is a property of the network itself, probably ideal for the functioning of a complex system, such the stomatal guard cells. Such networks possess a large number of interconnected 'nodes' and a small number of highly connected 'hubs'. Study of mutants reveals that the signalling network is both robust (it can tolerate the removal of single nodes) and fragile (it is sensitive to hub removal), consistent with the predicted properties of a scale-free network (Albert et al., 2000). However, currently it is impossible to establish whether a system is scale-free or not because detailed knowledge of at least 1000 nodes is required. If this is the correct description of plant signalling, there are important implications for improving plant responses to the environment, as they will have to involve engineering the network itself rather than any one part of it (Leymarie et al., 1998; Hetherington & Woodward, 2003). One may also ask whether the complexity of the networks themselves, and the consequent 'overprocessing' of signals, contribute to the 'conservative' behaviour of plants. Adaptations to stress involve a multitude of metabolic processes and include complex modulation of growth patterns according to suboptimal conditions or resource availability. The desired functional alteration may be facilitated if we understand the properties of the system operation, so that only the minimum number of key genes need to be manipulated. There is also insufficient evidence to determine whether species or varieties with high growth rates possess signalling systems that are structurally different from those of stress tolerators. Clearly, only an understanding of how networks operate on a systems level will enable intelligent 'engineering' of appropriate crop responses.

Can we also view the whole plant as a system that has the properties of a network? There is now considerable evidence for transmission of signals between different plant organs, including light (Karpinski et al., 1997, 1999; Yano & Terashima, 2001; Mullineaux et al., 2006), CO₂ concentration (Lake et al., 2002; Thomas et al., 2004) and biotic stress (Bowles, 1998). Thus, roots, leaves (sheaths and blades in the case of cereals), stems, flowers and grains are systems that each sense and process signals but that are also connected to and have strong influences on each other; they may be considered to be hubs in a whole-plant 'scale-free network'. Clearly, signalling within the whole plant is an important determinant of the agronomic properties of the crop, and yield improvement will again have to take into account the properties of the signalling network. Circadian rhythms exert overriding modulating effects on signalling networks and have a major effect on many key plant processes, including photosynthesis, essentially through regulation of stomatal aperture. Work has been carried out on mutants disrupted in the circadian clock such that the internal rhythms were not matched to the external environment (Dodd et al., 2005; Hubbard et al., 2006). These mutants showed reduced growth rate and reduced whole-plant photosynthesis, suggesting that circadian rhythms are critical for maximizing biomass production. Further understanding of how circadian rhythms regulate metabolism may reveal new targets for improvement of biomass production.

VIII. The chloroplast as sensor and integrator – photoacclimation of photosynthesis

Classically, the chloroplast has been described as the site of photosynthesis, which provides the carbohydrate that fuels plant growth and development. This restricted view of chloroplast function ignores not only the fact that chloroplast metabolism is tightly integrated with the rest of the cell, so that photosynthesis is the result of all of the activity of the cell, but also the fact that the chloroplast is involved in the recording, storage and transmission of *information*. As discussed in the previous section, these processes are of vital importance in determining the growth strategy of the plant and, we will argue, crop yield. Here we will discuss how the chloroplast is both a sensor and integrator of environmental information, playing a crucial role in the process of photoacclimation. We show how this role may be central to understanding the optimization of photosynthesis and suggest how manipulation of these chloroplastic processes could be the key to increasing crop photosynthesis.

1. What is photoacclimation?

Photoacclimation refers to the processes by which photosynthesis is adjusted to different light conditions by alteration of the composition of the leaf (Murchie et al., 2002, 2005; Walters, 2005). Photosynthetic capacity is not fixed, but is determined by the irradiance a plant receives during growth, or any sustained period during growth. Factors such as season, solar angle, shading and aspect determine the temporal and spatial alterations in the spectral quality and quantity of light available for absorption by photosynthetic pigments. Mechanisms exist within plants that respond to such changes, altering the composition and morphology of the leaf to balance incident irradiance with the capacity for utilization of photosynthetic product, and so maintain the efficiency of radiation conversion, whilst at the same time providing protection from photoinhibition by the excess light. Studies of large numbers of species show that there are two interlinked parts to photoacclimation - leaf-level acclimation and chloroplast-level acclimation (Murchie & Horton, 1997). Chloroplast-level acclimation refers to the differences in the contents of thylakoid proteins, pigments, Calvin cycle enzymes, etc., on a per chloroplast basis. Parameters such as chlorophyll (Chl) a:b ratio, PSII:PSI ratio, or P_{\max} per unit chlorophyll are indicative of chloroplast-level acclimation (Murchie & Horton, 1998). Leaf-level acclimation refers to the markedly different anatomies of high- and low-light leaves: a generalized picture of 'sun-type' morphology would show thicker leaves with more columnar mesophyll cells, although in rice, thicker leaves with larger cells are observed, with no change in cell number (Weston et al., 2000; Yano & Terashima, 2001; Murchie et al., 2005). Parameters such as total numbers of chloroplasts and total chlorophyll, protein and Rubisco contents per unit leaf area are strongly influenced by leaf-level acclimation. These two levels of acclimation appear to be differently regulated. Chloroplast-level acclimation is controlled by signals generated within the chloroplast itself (carbohydrates and redox control).

Leaf-level acclimation is determined at an unknown point early in leaf expansion, is not reversible, and generally cannot be induced in leaves grown under low light when they are transferred to high light (Mullet, 1988; Oguchi *et al.*, 2003; Murchie *et al.*, 2005). The origin of the signals that control leaf-level acclimation are unclear, but in dicotyledonous species there is evidence for a role of mature leaves in the cellular differentiation of expanding leaves (Yano & Terashima, 2001; Oguchi *et al.*, 2003). When mature leaves of *Chenopodium album* were shaded, a leaf expanding into a high-light environment had a shade anatomy, and vice versa. The signals involved are unknown but may be hormonal or be related to photosynthate supply. It has been proposed that the chloroplast redox state also has a role in long-distance signalling in relation to leaf-level acclimation, and indeed to other aspects of plant growth and development (Wilson *et al.*, 2006).

2. Why is photoacclimation important?

Photoacclimation is significant in relation to crop photosynthesis because, in principle, it is a determinant of the photosynthetic capacity of each leaf in the canopy. Extensive work on several genotypes of rice, both in the field and in the laboratory, shows that leaf composition and $P_{\rm max}$ respond to growth irradiance (Murchie *et al.*, 2002, 2005; Hubbart *et al.*, 2007). Moreover, the increase in $P_{\rm max}$ with increasing growth irradiance saturates well below full sunlight, explaining why photosynthesis of upper leaves is light saturated. Therefore, it is concluded that photoacclimation in C₃ crops is not optimized for high productivity under high-irradiance conditions, as in the tropics or in a warm temperate summer.

Photoacclimation is a part of the developmental processes involved in canopy dynamics. Cereal leaves are formed from the base of the plant from two intercalary meristems that give rise to an 'elongation zone', which is positioned within the sheaths of older leaves where leaf exposure to light is limited (Mullet, 1988; Murayama, 1995). Thus, as new cells are produced from the base and move towards the point of emergence (insertion) they are within, and shaded by, the leaf sheath and probably compromised in their ability to sense light in a quantitative manner (Murchie et al., 2005). Thus, photoacclimation in cereals must inherently have a strongly systemic component - the acclimation status of a leaf is 'predetermined' by long-distance signalling from older leaves. Therefore, photosynthetic productivity will inevitably be compromised when light intensities change because, as discussed earlier in this section, prediction (which is inherently conservative) of future light conditions will probably be inaccurate, giving rise to a decreased efficiency of photosynthesis. In particular, each leaf will be subsequently shaded as the canopy expands and will need to acclimate to a lower irradiance. The key question is whether this is a contributory factor in the photoacclimation ceiling, which sets photosynthetic capacity at apparently submaximum levels. The characteristics of systemic acclimation in the world's major food crops such as rice, wheat and maize need more detailed investigation (Murchie et al., 2005) to complement the work being carried out on model dicotyledons (Yano & Terashima, 2001; Lake et al., 2002; Thomas et al., 2004).

A second factor is also developmental – as new leaves develop, older leaves become shaded. Photosynthetic capacity falls not only because the leaves acclimate to shade, but also because nutrients are recycled from older leaves to the newly emerging ones. Because leaf-level acclimation is irreversible, the lower leaves inevitably cannot be optimally acclimated to the low-light conditions found within the canopy. Hence, could the lack of maximum acclimation to high irradiance of new leaves be part of a compromise, ensuring that leaves are subsequently not too far removed from acclimation to their new position in the shaded canopy? Prediction involves not only future climatic conditions but also future developmental states of the plant (and its neighbours).

3. Photoacclimation and the sensing of irradiance by chloroplasts

Photons absorbed by plants are either used in metabolic processes for storage and growth or dissipated harmlessly. The level of excitation of the chloroplast would therefore seem to be the ideal indicator of the potential for radiation use. If growth is curtailed, excitation should rise, and if conditions for growth are favourable, excitation should fall. This principle has been used in a number of studies that investigate the interactions among temperature, growth and chloroplast excitation. The redox state of photosystem II can be estimated from measurement of the chlorophyll fluorescence parameter qP, the term 'excitation pressure' (1 - qP) being introduced by Huner and co-workers (Huner et al., 1996) to gauge the 'pressure' forcing acclimation of the system. High irradiance and low temperature have similar effects on development and growth of plants and both cause an increase in (1 - qP). Acclimation then proceeds to reduce the excitation pressure either by increasing photosynthesis or by reducing excitation transfer to PSII; that is, the plant strives towards photostasis (Wilson et al., 2006). The balance of energy input and utilization can be manipulated by using different combinations of temperature and irradiance during growth: in each case the excitation pressure has been found to correspond to the growth habit, leading to the suggestion that the chloroplast can act as a quantitative sensor of the energy state of the whole plant (Huner et al., 1996, 1998; Wilson et al., 2006). Moreover excitation pressure changes can be associated with specific alterations in gene expression (Ndong et al., 2001). The chloroplast redox state operates in a quantitative manner and will integrate and balance the incoming light energy with the capacity for utilization in biochemical processes not just in the leaf cell but, through the mechanisms discussed above, throughout the whole plant. By definition, this will also include the regulation of energy status defined by carbohydrate content (Smith & Stitt, 2007) and is likely to involve considerable interaction with the complex sugar signalling networks already described.

The mechanisms of interaction between chloroplast energy status sensing and other networks such as sugar signalling have yet to be determined. However, progress may be swift: recent work suggests that certain genes may have pivotal roles in directing convergent signals, in particular sugar and energy (e.g. KIN10) (Baena-Gonzalez *et al.*, 2007). These genes seem to confer enhanced starvation tolerance, lifespan and architectural and developmental transitions. It is suggested that they act by linking stress, sugar and developmental signals. Recent work has identified a chloroplast-localized protein that is crucial for cytosolic responses to calcium (Ca²⁺) fluctuations (Webb, 2008; Weinl *et al.*, 2008). This may provide some of the first direct evidence for involvement of the chloroplast in signalling cytosolic events.

Chloroplast specialization deserves a mention in this context. There are of course examples of structural and functional differentiation: for example, the differences between mesophyll and bundle sheath chloroplasts in C4 plants are striking and are a reflection of the differing ATP:NADPH requirements of each cell type. However, C_4 photosynthesis has been identified in the stems of C₃ flowering plants (Hibberd & Quick, 2002), which is considered to be an adaptation to low gaseous diffusion rates in these tissues. More recently, it has been suggested that bundle sheath chloroplasts may have a specialized role in the systemic signalling processes operating in high light and/or high light stress (Fryer et al., 2003; Mullineaux et al., 2006). The chloroplasts exhibit photosynthetic electron transport but have a limited capacity for CO2 fixation; instead, following specific expression of the ascorbate peroxidase gene APX2, they generate large amounts of H_2O_2 , which is exported into the transpiration stream (Chang et al., 2004).

This level of specialization of chloroplasts in signalling roles supports the concept of the chloroplast as a sensor and processor of environmental signals (Fig. 3). Three types of signal may be initiated: firstly, the redox state of the thylakoid membrane in mesophyll chloroplasts (Huner et al., 1998; Walters, 2005; Wilson et al., 2006), which may act as a local or long-distance signal; secondly, the production and accumulation of specific metabolites in sucrose and starch synthesis, which act as an indicator of the 'energy status' of the plant cell and are sensitive to sink strength; thirdly, specific long-distance signals which are produced by chloroplasts and do not have localized effects, such as H2O2. In this way the chloroplast receives, stores and integrates environmental information, and then orchestrates the development of the plant, defining its biochemistry, physiology and morphology (and, in the case of a crop plant, its yield/biomass) by interfacing with the central signalling networks. The roles of these signals and how they integrate with each other should be a focus for future research.

IX. Concluding remarks: crops for future climates

In the future, both food and energy crops will have to become much more efficient, giving higher productivity on less land



Fig. 3 Schematic depicting the role of the chloroplast as a supplier of quantitative information that enables the plant to rapidly and accurately match supply of photosynthate with potential growth or storage capacity. This schematic differs from models that largely depict information flowing in the opposite direction only, that is, feedback from sink and feedback from metabolism acting to down-regulate or 'release' energy from the chloroplast. Recent data provide evidence for integration of the chloroplast with Ca^{2+} signalling in the cytosol (Weinl *et al.*, 2008). PAR, photosynthetically active radiation; ROS, reactive oxygen species.

area, with fewer inputs and in the face of increasingly frequent climate extremes. We have discussed how previous strides forward in crop improvement have come from manipulation of plant morphology to improve parameters such as harvest index and LAI and increased crop management. Many studies indicate that the former are at saturation for many crops, whereas crop management techniques are already having to adapt to the new scenario, as reflected in the expansion of some 'precision agriculture' techniques. However, whilst important, these methods maintain the 20th century condition that agricultural progress necessitates a high degree of human control to manipulate the microenvironment of plants. This review summarizes the evidence suggesting that future advances should arise from an enhancement of the precision of resource capture and conversion by the crops themselves. The basic recommendation in this review (summarized in Table 1) is that more consideration needs to be given to the biology of crop plant species - what are the inappropriate aspects of plant performance that are not

Table 1Breakdown of the processes described in this review to improve leaf and/or canopy C_3 photosynthetic rate

Proposed action	Target process	Mechanism of improvement	Estimated 'complexity' (number of gene targets)	Predicted impact level	Comment	Section
Rubisco improvement	O_2/CO_2 specificity	Protein engineering	Low	High	Nonplant Rubisco properties may be required.	IV.1
	Maximum catalytic activity per active site, activation state	Protein engineering, Rubisco activase, inhibitor response	Low?	Low/high	Nonplant Rubisco properties may be required. Inverse relationship between specificity and maximum catalytic activity. Improvement of activation state should have greater impact at high temperatures.	IV.1
	Amount of Rubisco enzyme per unit leaf area	Altered expression/ translation levels	Low	Low	Implications for N nutrition, e.g. Rubisco : N. Less impact at low irradiance.	IV.1
Introduce C4 pathway	Carbon-concentrating mechanisms	Introduction of C4 pathway	High	High	If successful, impact very high as shown by existing C4 plants. Much greater impact predicted for warm environments.	IV.3
Reduce photorespiration (nonRubisco target)	Photorespiration	Reduce/shortcircuit photorespiratory flux	Low?	High	Success achieved through the introduction of a bacterial gene.	IV.2
Optimal distribution of activity/capacity among primary processes	Relative activities of photorespiration/Calvin cycle/ sucrose synthesis/respiration	Manipulate pathway flux	High	High	Currently theoretical. Expected to be large number of genes involved and interaction among organelle types (chloroplast, mitochondria and vacuole)	IV,VI
Improve RuBP regeneration	Electron transport, Calvin cycle enzymes (not Rubisco)	Alter capacity of RuBP regeneration	Low?	High	Effect already shown for some (nonRubisco) enzymes of the Calvin cycle.	IV
Optimize carbon allocation	Short-term storage/growth allocation (changes in response to shifts in environment)	Alter signalling pathways and metabolic regulation	High	High where suboptimal response known	Patterns in carbon allocation can correlate with growth rate.	VII.1,2
Optimize photoprotective processes: 'down- regulation of photosynthesis'	Kinetics and magnitude of photoprotective processes	Alter levels of proteins and molecules known to regulate NPQ (e.g. PsbS, xanthophyll cycle)	High	High	Theoretical but modelling predicts high impact (30% or more in C3 species).	VII.3
Optimize photoacclimation	P_{\max} and the range of P_{\max} alteration	Alter signalling pathways which determine P _{max}	Probably high	High where suboptimal response known	Likely to involve manipulation of signalling and diverse processes.	VIII

Proposed action	Target process	Mechanism of improvement	Estimated 'complexity' (number of gene targets)	Predicted impact level	Comment	Section
Match fast/slow growth rate to resource availability	Long-term storage/growth allocation (no changes in response to shifts in environment)	Multiple: growth regulators?	Possibly high	High where suboptimal response known	Signalling responses may be straightforward if target is a 'master' regulator.	VII.2,5
Optimize canopy architecture light interception	Radiation interception and distribution of photosynthetic activity in canopy	Optimization of leaf and stem development. Genetically manipulate canopy structure, leaf shape/angle/distribution	Possibly high	High where suboptimal response known, e.g. canopy temperature	Difficult to quantify. May have global impact on resource use and N distribution.	V
Adjust circadian rhythms	For example, stomatal aperture, nocturnal allocation of C and N	Genes regulating circadian rhythm responses	Possibly high	High where suboptimal response known	Effect known for stomatal aperture	VII.5

This is intended as a summary only; details of the mechanisms and associated references are presented in the text. The estimated level of complexity is based on the likely number of genes involved in each process requiring alteration. The predicted impact level wherever possible uses data from the literature where attempts have been made to quantify the impact of this process by either experimentation or modelling.

C, carbon; N, nitrogen; NPQ, nonphotochemical quenching; P_{max} , light-saturated rate of photosynthesis; RuBP, ribulose 1,5-bisphosphate.

crops' and 'bioenergy' such as to any crop where energy conversion efficiency is paramount, opportunities for such crop improvement. We have shown arising from suboptimal performance therefore offers major possible. We suggest that reduced photosynthetic efficiency occur and what can optimized for the new agricultural environment, why do these in discussions not just of food production but also of 'energy improvement of photosynthesis to feature more prominently waste products are converted to fuel. It is timely for the be made. Such improvements would have generic application knowledge gaps that need to be filled before real progress can where the possible targets biomass will agricultural improvement on the scale required be increasing the efficiency of conversion of solar energy into manipulations should tailor each new variety to suit particular locations and seasons. Our analysis shows 'energy crops' and dual-purpose food crops where be done to manipulate them? Such are and identified some of the that only by

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