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Future food requirements: are improvements in photosynthesis required?

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Introduction

The total amount of carbon captured in photosynthesis each year by terrestrial ecosystems is approximately $120 \ 10^9$ t, of which half is lost in respiration (Steffen et al., 1998). Approximately $1.6 \ 10^9$ t C are fixed by the major cereals each year and about 43% of that is in the grain. Although cereals only account for approximately 3% of total net carbon fixed, they are of enormous importance in terms of food for humans.

Solar energy captured in photosynthesis gives plants the capacity to synthesize, organize and maintain a range of structural units housing a myriad of metabolic processes. The two aspects of energy capture that are of principal interest to crop physiologists set the limits for crop growth rate. The first is the quantity of energy captured in unit time and that depends on the available irradiance and the fraction absorbed by the crop canopy. The second is the efficiency with which the absorbed energy is used for the chain of synthetic processes that culminate in harvestable yield.

While it is true that we cannot rely on demographic predictions as we rely on astronomical ones (Medawar, 1987), their importance means we cannot ignore them. Over the next 50 years it is predicted that the population of Asia will rise from 3.7 billion to 5.3 billion (UNFPA, 1999). Increases in rice production will have to be produced with less water, less fertilizer and less land (Hossain and Pingali, 1998; Tilman et al., 2001; Evans, 1998). Currently, half of the people in Southeast Asia have a calorie intake inadequate for an active life. Yields in many Asian countries have reached a plateau (Cassman, 1999) and yields in breeders trials at IRRI have not increased for 30 years (Sheehy, 2001a); indeed it has been suggested that a yield barrier has been reached (Kropff et al., 1994). How can the projected rice demands for Asia be met? Clearly, water and nitrogen use efficiencies have to increase, as does yield by more than 44%.

The phenotype of a given genotype can vary markedly according to its interaction with the environment (Miflin, 2000). Given the genetic complexity that underlies that plasticity and that the 'same' crop is grown in geographically different regions with different climates, weather conditions and on different soil types with different histories of management, it is not surprising that in field experimentation precise repeatability, in the usual scientific sense, is the exception rather than the rule. As a result of this imprecision and the absence of universally acceptable theoretical models of crop growth, disagreements about what precisely determines both biomass and grain yield are commonplace. Why the yield potential of new rice cultivars at IRRI has remained approximately constant for more than 30 years (Sheehy, 2001a; Kropff et al., 1994) is also a matter for speculation. Nevertheless, it is simply not good enough to be optimistic that 'business as usual' will solve the problem of increasing rice yield. New and possibly radical approaches need to be explored urgently. What relevance has photosynthesis research in this context?

Link between photosynthesis, yield and radiation use efficiency

For crops, the law of mass conservation can be used to link growth rate, crop photosynthesis, respiration and the loss of biomass by detachment. The product of the integral of crop growth rate and harvest index gives grain yield; it should be noted that grain yields for rice are quoted at 14% moisture content. To make progress and to derive a simple equation linking yield and canopy gross photosynthesis, Sheehy (2000) assumed a constant root weight ratio and units of CH_2O, so that the equation is

$$Y = H \left\{ (1-\beta) \int_{t_i}^{t_f} [P_g(t) - R(t) - D(t)] \, dt \right\} \qquad (1)$$

where Y is grain yield, H is harvest index (unless otherwise stated calculated as the fraction of aboveground dry weight that is grain weight), β is the root weight ratio, P_g is the rate of canopy gross photosynthesis, R is the rate of shoot and root respiration, D is the loss of dry matter through detachment, t is time (usually a time step of a day is used), t_i could be the day of germination or some other suitable starting time and t_f is the day of harvest.

Equation (1) shows the link between photosynthesis and yield is mediated by several factors that could confound simple attempts to correlate photosynthesis with yield. The most obvious are differences in crop duration (t_f-t_i), or a difference in the partitioning of assimilates to roots, β. Harvest index, H, can be affected by many factors, e.g. differences in susceptibility to thermally induced sterility (Satake and Yoshida, 1978; Horie, 1993) or differences in the ability to partition nitrogen to the grain (Sinclair, 1998; Sinclair and Sheehy, 1999). Nevertheless, it would be most surprising if yield improvements in modern cultivars were unaccompanied by improvements in canopy photosynthesis (Robson, 1982; Long, 1999a,b). Surrogates of photosynthesis, such as canopy air temperature depression, are proving useful in screening wheat for yield (Reynolds et al., 2000; Evans and Fischer, 1999). It is interesting to note that measurements I made in high irradiance show erect leaves in rice canopies can have temperatures 2.5°C cooler than prostrate leaves (~31°C v 33.5°C) suggesting there may be a link between canopy architecture and canopy temperature. The relationship between leaf and canopy photosynthesis is presented later.

It is convenient to give a definition of radiation use efficiency here. It is assumed that radiation use efficiency (ε) is the slope of the linear relationship between shoot dry weight and accumulated intercepted radiation (Monteith, 1977). The value for any day (Sheehy, 2000) can be calculated as

$$\varepsilon = (dW_s/dt)/I_{int}, \qquad (2)$$

where dW_s/dt is the daily growth rate of the shoots, I_{int} is the total amount of photosynthetically active radiation (PAR) intercepted by the crop for the same day. By substituting for crop growth rate in equation (2), ε can be written

$$\varepsilon = [(1-\beta)(P_g(t) - R(t) - D(t))]/I_{int}. \qquad (3)$$

The average value of ε for rice is 2.2 g DW MJ^{-1} PAR and for maize is 3.3 g DW MJ^{-1} PAR (Kiniry et al., 1989, Mitchell et al., 1998). Using a simple model, Mitchell et al. (1998) concluded that the value of ε for rice would have to rise to that of maize to increase yields by 50% given a constant crop duration. The simplest of calculations using equation (3) shows that photosynthesis would account for the difference between maize and rice assuming the same dry weight, optimum nitrogen contents (Greenwood et al., 1990) and temperatures of approximately 30°C (Sage, 2000).

Based on the model of McCree (1970) respiration is often divided between synthetic and maintenance respiration. Differences in synthetic respiration can exist between species depending on the nature of the plant products synthesized (Penning De Vries et al., 1974). Processes such as biological nitrogen fixation require approximately 25% of daily photosynthate (Witty et al., 1983), but field-grown legumes can compensate and show no yield or quality loss when compared with nitrate-grown crops (Sheehy and McNeill, 1988). Large differences in the ratio of synthetic respiration to photosynthesis between varieties within a species are unlikely. Loomis and Amthor (1999) discussed maintenance respiration in some detail and only a brief synopsis will be given here. Variation can exist in the maintenance coefficient (Wilson, 1975; Robson, 1982), but the values obtained by McCree (1970) and Ryle et al. (1976) were broadly similar and the assumption that the maintenance coefficient is approximately constant, but strongly affected by temperature, is often made. Interestingly, Cock and Yoshida (1973) concluded that the maintenance coefficient for respiration during late grain filling was negligible. Cannell and Thornley (2000) suggested that current understanding of many plant processes was now sufficient to enable a more sophisticated approach to the modelling of respiration than that taken by McCree (1970). However, Mitchell et al. (1991) found the McCree (1970) approach useful for interpreting their field measurements of respiration.

In grain crops, senescence and detachment are largely associated with nutrient remobilization during grain filling. Sinclair and Sheehy (1999) used a simple model to show that differences between cultivars in the ability to transfer nitrogen to the grain from scenescent leaves was related to canopy erectness. The more or less continuous 'throw away lifestyle' with respect to leaves of plants (Thomas, 1994a) is more likely to deliver advantages to forage crops experiencing grazing than grain crops where plant breeders have selected for high harvest index and leaf senescence during grain filling.

This leads onto the link between canopy and leaf photosynthesis. There are many models of canopy gross photosynthesis and irradiance, and the relationship is approximately hyperbolic (Cock and Yoshida, 1973; Sheehy and Peacock, 1975; Thornley and Johnson, 1990; Luo et al., 2000); the operative part of the curve is usually far from the plateau. What is common to most models is a combination of parameters describing individual leaf photosynthesis, leaf area index and light distribution. The initial slope of the relationship is a function of the quantum yield of an individual leaf at vanishing levels of PAR irradiance, light interception and the leaf transmission coefficient (Sheehy and Johnson, 1988). The asymptotic value is a function of the product of leaf area index and the maximum rate of leaf photosynthesis.

Farquhar et al. (1980) and Von Caemmerer (2000) have modelled leaf photosynthesis mechanistically in terms of the kinetic properties of rubisco. Those models have enabled both the quantum yield of leaf photosynthesis and its maximum rate to be described at a process level. The rate of carboxylation is the minimum of the rubisco limited rate, the rate of photosynthetic electron transport rate and the rate of triose phosphate conversion to photosynthetic end products (Farquhar and Sharkey, 1994). These equations have appealed sufficiently to ecologists to use them in modelling vegetation at a global scale in relation to climate change (Osborne et al., 2000; Woodward, 1999). Finally, in moving from measurements of leaf photosynthesis on spaced plants to crop plants, changes in leaf area (Bhagsari and Brown, 1986; Pearce et al., 1969) and leaf nitrogen content in response to competition for light can confound the unwary (Evans, 1993; Peng et al., 1995).

Upper limits to canopy photosynthesis

Sheehy (2000) used the conveniently simple model of Monteith (1965) to show that the maximum photosynthetic leaf area index of an erect canopy is approximately 6.6. The sunlit leaf area index (L_0) reached a maximum of 3.3 and photosynthetically active shaded leaf area

index (L_s) reached its maximum at approximately 3.0. Cock and Yoshida (1973) observed little increase in canopy photosynthesis above an LAI of 5.0 in both tall and short rice varieties; a similar result was obtained for grasses (Parsons, 1988). Sinclair and Sheehy (1999) proposed that the third class of leaves in the canopy (L_N) were those that were close to the light compensation point and largely useful for the N they contributed to the grain ($L_N = L - L_0 - L_s$; where L is the total LAI). Sheehy (2000) went on to show that the loss through senescence of L_s and L_N would reduce canopy photosynthesis by about 22-27%. In rice canopies, the distal parts of some leaves are exposed to full sunlight while the proximal parts are at the compensation point.

The maximum rate of canopy photosynthesis (P_{gmax}) has an asymptotic value given by

$$P_{gmax} = L_o\,A_{mo} + L_s\,A_{ms} \qquad \text{as } I \rightarrow \infty , \qquad (4)$$

where A_{mo} is the maximum rate of sunlit leaf photosynthesis and A_{ms} is the maximum rate of shaded leaf photsynthesis. The maximum quantum yield of the canopy at full light interception is

$$dP_g/dI_o = \alpha(1 + \tau) \qquad \text{as } I \rightarrow 0 , \qquad (5)$$

where α is the leaf quantum yield in low irradiance and τ is leaf transmittance. It can be seen that the limits for canopy photosynthesis are set by the properties of the individual leaves. At LAIs greater than approximately 6.0, improvements in canopy photosynthesis can only result from improvements in leaf quantum yield and/or leaf photosynthesis.

Leaf quantum yield is almost constant for all C_3 plants and within subtypes of C_4 plants (Ehleringer and Pearcy, 1983; Long et al., 1993); it is influenced by the relative concentrations of O_2 and CO_2 around rubisco and the costs of the biochemical transactions involved in carboxylation. The maximum rate of leaf photosynthesis for both C_3 and C_4 plants appears to vary linearly with nitrogen content per unit leaf area over a wide range of nitrogen concentrations (Evans and von Caemmerer, 2000; Peng et al., 1995). Assuming the data shown by Evans could be described by linear relationships, then maize had a gradient of approximately 0.74 μmol CO_2 s^{-1} mmol^{-1} N compared with that for C_3 plants (rice and wheat) of 0.26 μmol CO_2 s^{-1} mmol^{-1} N; a threefold difference in leaf photosynthetic nitrogen use efficiency. Sinclair and Horie (1989) showed saturation values for the photosynthesis-nitrogen relationship and that would be expected at 'luxury' N levels. Indeed, the Greenwood et al. (1990) critical nitrogen model relating nitrogen content to shoot biomass states that there is an optimum relationship for both C_3 and C_4 crops. It is clear that very high rates of leaf photosynthesis are possible in C_3 leaves, but past some critical nitrogen content, the Greenwood relationship means such high rates are probably purchased at the cost of lower leaf area indices in crops and resulting in no overall gain in biomass (Lawlor, 1995). The issue of what sets the maximum rate of nitrogen acquisition and utilization by a crop is not a simple question to answer, but it is likely that the availability of energy will be a major part of the answer. High nitrogen fertilizer applications are a source of nitrogen pollution because of the low recovery ($< 40\%$) in rice systems (Dobermann, 2000). An improvement in the both the rate of leaf photosynthesis and the rate per unit of leaf nitrogen is desirable if improvements in canopy photosynthesis are needed.

A yield decline across 30 years and possible threats from climate change

From seasonal observations showing positive effects of elevated CO_2 on yield (Baker et al., 1992; Ziska et al., 1997), it is often concluded that projected increases in the partial pressure of atmospheric CO_2 (pCO_2) will result in yield increases. However, the yield of the best entry in breeders' trials at IRRI for the past thirty years has not increased (Sheehy, 2001a).

Furthermore, the data of Peng et al. (1999) shows that the yields for the same cultivar (IR8) grown on the IRRI farm in 1998 were about 2.6 t ha^{-1} lower than in 1966 at nitrogen inputs of approximately 150 kg N ha^{-1}. Those authors attributed the yield differences to differences in grain filling, but what caused grain filling to be lower in 1998 is obscure. Weather data collected from nearby meteorological stations for the two growing seasons are very similar and offer no explanation. Average atmospheric pCO$_2$ increased by approximately 4.6 Pa between 1966 and 1998 (Keeling and Whorf, 1999). Peng et al. (1999) also showed that the modern cultivar IR72 outyielded IR8 in 1998, suggesting that plant breeders may have been selecting unwittingly, but successfully, for tolerance of some adverse environmental factor or factors. The adverse factors could be additional quantities of atmospheric pollutants such as SO$_2$ or O$_3$ (Mansfield, 1999; Unsworth and Colls, 1994; Maggs and Ashmore, 1998; Ewert and Porter, 2000) and/or toxic phenolic acids formed in soil reduction (Kirk, pers. com.). In that context, it is interesting to note that vehicle numbers increased from approximately 3 10^5 to 3 10^6 between 1966 and 1998 in the Philippines. The added complication of rises in temperature that will accompany rises in CO$_2$ have been considered by Mathews et al. (1995), Horie et al. (1995), Ziska et al. (1997) and Baker et al. (1992) and they showed that temperature effects on sterility could offset such gains. The risk of exceptional high temperature events on photosynthesis itself has not been calculated.

Do crop physiologists really understand enough about the processes shaping yield to clearly identify the yield-limiting problems requiring solutions?

In high yielding rice grown at IRRI, two distinct phases of shoot growth appear to be separated by the onset of flowering. Shoot growth does not follow a simple law of diminishing returns and this unusual aspect of crop ontogeny was not described by Horie (1994) or Thomas (1994b). Why growth slows down at the start of flowering and then speeds up towards maturity is again, a matter of speculation. The first phase of shoot growth is relatively simple, being concerned largely with the production of tillers, leaves and roots. That phase is characterized by increasing leaf area index and light interception, it ends with the simultaneous growth of the flag leaf, culm and the panicle within the leaf sheaths. The second phase is more complex, characterized by the emergence and growth of the panicle, flowering and grain filling. Developing spikelets act as a powerful sinks for both current and stored assimilates accumulating nearly 50% of the total biomass by maturity. Roots, for whatever reason, do not supply sufficient nitrogen to support the demand from the developing grains and the leaf area index declines as leaves die and transfer much of their nitrogen to the grains (Sinclair and Sheehy, 1999; Sheehy, 2001a). Short-term estimates of radiation use efficiency (Sheehy et al., 1998) show it to be relatively constant prior to flowering and very variable afterwards, perhaps reflecting short-term changes in the balance between photosynthesis and respiration (Equation 3). Cock and Yoshida (1971) observed that respiration decreased between flowering and maturity in rice, and in a later paper concluded that maintenance respiration in rice decreased to approximately zero towards the end of grain filling (Cock and Yoshida, 1973). Such changes in respiration could go some way to explaining the variation in ε observed by Sheehy et al. (1998) between flowering and maturity.

   Ten days before flowering, potential sink size in the form of juvenile spikelet number per square meter in IR72 was very large, 106,131 spikelets m^{-2}, but the number decreased by 46% between panicle emergence and flowering, resulting in 56,979 spikelets m^{-2} of which 77% were eventually filled. The failure to convert juvenile spikelets into mature spikelets and to fill them suggests resource availability was the limiting factor not sink size (Sheehy et al., 2001b). That conclusion is partly supported by the increases in spikelet number, filled grains and grain weight resulting from short-term manipulation of CO$_2$ at different stages of panicle development (Yoshida, 1973). Because crop growth rate increases towards maturity, failure to

fill mature spikelets could mean that they were sterile by the time resources became sufficiently available to fill them, or that developing tillers became relatively stronger sinks. It is possible that during the period between the formation of the maximum number of juvenile spikelets and the emergence of the panicle bearing mature spikelets, thermally driven demands for assimilates exceeded the ability of the photosynthetic system to supply them (Baker et al., 1992).

Conclusions

In this paper, I have described the link between yield and crop photosynthesis. In Asia, we cannot be laissez faire with respect to yield improvements resulting simply from increasing pCO_2. Other factors might offset such gains; Mitchell and Sheehy (2000) felt that such gains might be too small during the next 50 years. My conclusion is that to improve yields to meet the future demands of Asia for rice, using less nitrogen, water and land, large improvements in photosynthesis will have to be made soon. As a non-expert on photosynthesis, I can only make tentative suggestions on what improvements would be useful based on my reading of the literature. I am aware that Sharkey et al. (2000) suggested that sucrose-phosphate synthetase activity might also have to be enhanced in order to capture the benefits of high photosynthesis, but that is an interface problem I leave to others.

Without access to light energy plants die, so the ability to compete for light must be one measure of fitness in an evolutionary context. For spaced plants, two extreme scenarios can be imagined for the way a unit of nitrogen, captured in unit time, is utilized in different ways to gain the same quantity of photosynthate in the next unit of time. The first is building more photosynthetic apparatus by thickening the existing growing leaf, the second is expanding the area of the growing leaf and distributing the same amount of apparatus in thinner leaves. In communities of plants, the second strategy would disadvantage neighbors adopting the first strategy and it is not surprising that crop plants tend to maximize leaf area rather than the amount of photosynthesis per unit area. Given the evolutionary strategy outlined above, would it be possible to improve crop photosynthesis by suppressing the tendency of crop plants to dilute 'photosynthetic' nitrogen in leaves of high specific leaf area? The detection of neighbors and the adjustment of specific leaf area through the phytochrome system is well understood physiologically, and the molecular biology is becoming known (Smith, 2000). This topic appears ripe for functional genomics to reveal the mechanism, followed by genetic engineering to create the plant with a desired trait that could not be favored by natural selection during evolution, but could be useful in agriculture.

Hauska and Arnold (2000) suggest that the major heat loss in photosynthesis occurs in the very early steps within nanoseconds following quantum absorption. Those authors also asked why there are two light reactions when half the energy, i.e. 4 photons of red light, would suffice. I am left wondering if the quantum yield of photosynthesis in low irradiance could be doubled, thus enabling shaded leaves to photosynthsize at greater rates. Would such an improvement overload the mechanisms of photoprotection and photoinactivation (Osmond et al., 1999) at high irradiance? Horton and Murchie (2000) even suggested that rice was poorly adapted to high light conditions in the tropics.

Mitchell and Sheehy (2000) suggested that transferring the C_4 syndrome to rice would provide a complete solution to how to increase yield, water and nitrogen efficiency simultaneously. Our optimism was based on the pace with which sequencing plant genomes was being made, indications of synteny (Gale and Devos, 1998) between the cereals, and the hope that comparisons made between C_4 and C_3 genomes would enable nature to be imitated even if we could not fully understand the processes. Data of Pamplona et al. (1990) was used to compare water use efficiencies and photosynthetic characteristics of the leaves of the C_4 rice-weed *Echinochloa crus-galli* and rice cv. IR64. The ratio of C_4 to C_3 values show water

use efficiency was three times greater, the quantum yield at low irradiance was 50% greater and the maximum rate of leaf photosynthesis was 30% greater. Björkman (1976) suggested that relatively few genes, inherited independently, were responsible for the C_4 syndrome. However, Edwards and Ku (1987) pointed out that organization was perhaps most important for full expression of C_4, that without proper compartmentation and interconnection of all the components the C_4 cycle was likely to be futile. Nevertheless, the high level of expression of C_4 genes observed in rice by Ku et al. (1999) is indicative of progress using biotechnological tools.

Evans and von Caemmerer (2000) properly felt that improvements in the properties of rubisco offered greater advantages and a rubisco from red algae with a high specificty for CO_2 has been reported (Uemura et al., 1997). However, Andrews and Lorimer (1987) pointed out that rubisco has been under intense selection for more than 3 billion years suggesting that simple structural improvements are unlikely. Edwards et al. (2001) analyzed what it takes to be C_4 and concluded that $p$$CO_2$ late in the 21st century might only have a competitive advantage in habitats characterized by high temperatures and drought. The rice yield problem is one of the first half of the century and needs a solution on an appropriate time scale: a decade.

It is clear that improvements leading to yield increases must be the result of placing an emphasis on traits that retain their importance in the phenotypes (Miflin, 2000) and the C_4 syndrome, an improved rubisco, higher rates of C_3 canopy photosynthesis or higher efficiency of energy use in photosynthesis would satisfy that requirement. All of the aforementioned could increase yields, the first two would increase water and nitrogen use efficiency to a greater extent than the third or fourth options in a future world of increased temperatures and atmospheric $p$$CO_2$. The need to improve photosynthesis is urgent. Failure to meet the rising rice demands of Asia would result in misery for hundreds of millions; the consequences of that are a matter for speculation, but are unlikely to contribute to a better world.

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