Potential targets for improving photosynthesis and crop yield

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There has been considerable improvement in yield of many crops during the past fifty years. This has mainly been the result of empirical selection for yield per se. However, there is now some concern that both potential and actual yields are levelling-off at least in some important crops. This is because genetic gains in yield are becoming harder to achieve. A physiological approach to yield improvement would help target the key constraints currently limiting yield. Since yield of a crop is a function of biomass × harvest index (HI), yield can be improved by increasing biomass or HI or both. In those crops where HI is low, selection for higher HI continues to be important. However, HI in many crops is approaching a ceiling value, therefore, in order to increase potential yield, crop biomass has to be increased, i.e. there will have to be more photosynthesis. Theoretically, there is considerable scope for improvement of solar energy utilization in photosynthesis. The means of achieving this through enhancing solar radiation interception, photosynthetic metabolism and source–sink balance have been discussed.

Crop plants grow almost entirely by photosynthesis. Thus, plant productivity in terms of primary production of biomass is simply a measure of the total photosynthesis of the plants less respiration, which has occurred during its growth. Agriculturists are, however, concerned more with economic yield than with total biomass. The proportion of total biomass production, which is invested into harvested parts of the plant is termed the harvest index (HI). In many crop plants, genetic improvement of yield has been achieved by selection of genotypes with higher HI and not necessarily by selection of plants with a higher total productivity. In maize, on the other hand, increase in biomass accounted for most of the increase in grain yield. In mungbean, increase in yield by foliar application of urea during post-flowering period or by growing under elevated CO₂ was found to be associated with increase in biomass without much effect on HI. For important crops, including wheat, rice, maize, barley and oat, HI averaging near 50% has been reached. The theoretical limit to HI for wheat is estimated at approximately 60%. Further increase in HI may come from reduction in the investment in leaves and other vegetative structures. This in itself may only be counterproductive, as it may also reduce biomass. Selection for greater HI therefore, is of limited value in crops where HI is approaching a ceiling value and those where the bulk of plants forms harvestable component, e.g. forage and biomass crops.

Selection for higher HI, however, continues to be important for increasing yield in those crops where it is still low, provided higher HI is achievable. In many grain legumes, HI is very low. In order to improve HI, the plant architecture has to be changed to make it short, upright, determinate with synchronous flowering. Such characteristics are beneficial under assured input conditions. For instance, Vigna radiata (L.) Wilczek (mungbean) and Vigna mungo L. Hepper (black gram) are similar in many respects. Black gram, however, is relatively more indeterminate than mungbean. The yield of these crops is more or less similar under unfavourable conditions. However, black gram yields more than mungbean under favourable environment, as the number of nodes produced is greater in black gram because of its greater indeterminate nature. Since most grain legumes are grown in relatively dry land of low fertility with extremely low level of agronomic management, such an improved plant type may not prove advantageous. In this context, it has been suggested that some management support is necessary if we wish to increase the productivity of grain legumes.

Yield of a crop is a function of biomass × HI. Hence yield can be improved by increasing biomass or HI or both. Since HI of many crops is approaching a ceiling value, so to increase yield potential we have to increase crop biomass, i.e. there will have to be more photosynthesis. The theoretical limits of solar energy utilization efficiency in photosynthesis and the efficiency attained by crop plants provide possibilities and scope for improvement of photosynthetic productivity. Assuming theoretically, that minimum quantum requirement is 8 mol photon mol⁻¹ CO₂ fixed as CH₂O and average photon in PAR region (400 to 700 nm) has a wavelength of 550 nm, the energy conversion efficiency would be 27% of the absorbed short-wavelength light. It is generally accepted that on an average only about 45% of the energy of sunlight falling on the field consists of photosynthetically useful wavelength, of which some is reflected and transmitted. Consequently, only 40% of the total light falling on a field can be used for photosynthesis, even when the field is fully covered with vegetation. The theoretical maximum utilization of energy of sunlight in gross photosynthesis is thus only about 11% (40 of 27%). It is important to realize that nothing whatsoever can be

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done about this upper limit to efficiency until evolution develops an entirely new mechanism of photosynthesis. It may, however, be mentioned that mutants of a single-celled alga, *Chlamydomonas reinhardii* have been shown to contain PS II but lack PS I, and can grow photoautotrophically with O₂ evolution using atmospheric CO₂ as the sole carbon source. The minimum quantum requirement is 4 hv/O₂ for these mutants. The theoretical maximum efficiency would, therefore, be doubled. Many researchers have expressed concern that these mutant cells might have retained undetected PS I activity.

The above theoretical maximum efficiency is attained at low light intensities. At full sunlight, plants may suffer the effect of absorbing excess light energy resulting in a decline in radiation conversion efficiency and a potential for photoinhibition. Furthermore, there is a fixed energy cost for maintenance respiration using approximately 20% of gross assimilates plus the cost of growth respiration using approximately 30% of the remaining assimilates. In view of the above, it appears that actual field efficiency may be approaching the upper limit when it reaches 5%. Such an efficiency is attainable and has been shown for field-grown maize during the period of rapid growth and during maximum growth phase of wheat grown under controlled environment conditions. Plants under most field conditions, however, conserve less than 1% of the energy of sunlight falling on a field during the growing season. From such observations, it has been inferred that there is remarkable scope for improvement of photosynthetic productivity and consequently, agriculture.

An increase in photosynthetic productivity, i.e. biomass production may be achieved by increasing the amount of photosynthetically active radiation intercepted and/or the efficiency of the photosynthetic tissues to use the intercepted radiation.

**Interception of solar radiation**

The amount of radiation intercepted by the crop during the growing season depends on the amount of incident radiation and the ability of the crop to intercept it. The total amount of incident radiation to which the crop is exposed may be increased by changing the developmental response of the crop, so that the duration of the growing season may be longer. This has to take into account that anthesis should occur at the optimum time for a particular location. Such a trait has, however, already been optimized for most regions and crops. Optimizing the interception of solar radiation by the canopy is an important component of biomass production. This is influenced by rate of development of leaf area, so as to achieve full light interception more quickly. After attaining full light interception by canopy, leaf area duration is important. Conventional breeding and agronomic practices together have contributed considerably in increasing the interception of solar radiation. Light interception is close to 100% when the canopy is closed. Losses occur before canopy closure and towards physiological maturity due to senescence. A number of traits have been identified that may increase light interception during the early development period of the crop. The most important factors contributing to the differences in leaf area development are size of the embryo, specific leaf area (SLA), speed of germination, faster rate of leaf expansion, shallow crown depth, coleoptile tiller and absence of GA-insensitive major dwarfing genes. Semi-dwarf GA-sensitive dwarfing genes are available, which result in better emergence and early leaf area growth. A high SLA is one way that barley achieves its early growth advantage over wheat. But a higher SLA also results in lower assimilation rate, because of a likely reduction in the amount of photosynthetic machinery per unit leaf area associated with a higher SLA. The increase in leaf area, however, more than compensates for this reduction in photosynthesis through greater light interception early in crop development. Thus, for early growth stages of cereals, a high SLA results in higher net assimilation rate (NAR). After canopy closure a high SLA becomes a hindrance to photosynthesis.

Canopy architecture becomes important once the leaf area index (LAI) exceeds 3. An erectophile leaf canopy could theoretically increase crop assimilation rate especially in high-radiation environment. Most of the highest yielding cultivars of maize, rice and wheat already have erect leaf canopies. Data are not available to determine whether current high-yielding agronomic types with partially erect leaf canopy represent a leaf angle ideotype or if further improvement is possible. Simulation work in rice suggests that the benefits of very erect leaf angle in high-radiation environment could only be realized at leaf area indices over 7. In many grain legumes, there is enough scope for improvement of leaf orientation and canopy architecture. It may, however, be mentioned that LAI beyond the critical value (LAI at which the canopy first reached maximum crop growth rate (CGR)) would be detrimental for a grain crop, because it means that sugars that could have been used to make grain are instead being used to keep useless leaves alive. The terms used are explained in Table 1.

The capacity of photosynthesis is dependent on light intensity. It has been shown that leaf metabolism can adapt to different light intensities according to the position in the

### Table 1. Explanation of terms used in text

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
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<tr>
<td>Leaf area index</td>
<td>Ratio of leaf area (one side only) of the crop to the ground area.</td>
</tr>
<tr>
<td>Specific leaf area</td>
<td>Leaf area per unit leaf dry weight.</td>
</tr>
<tr>
<td>Net assimilation rate</td>
<td>Dry matter accumulation rate per unit of leaf area per unit of time (g m⁻² (leaf area) day⁻¹).</td>
</tr>
<tr>
<td>Crop growth rate</td>
<td>Dry matter accumulation per unit of land area per unit of time (g m⁻² (land area) day⁻¹).</td>
</tr>
<tr>
<td>Harvest index</td>
<td>Proportion of biological yield represented by economic yield.</td>
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canopy\textsuperscript{29}. The upper leaves in a canopy may show elevated photo-protective responses. On the other hand, the partially shaded lower leaves may have different contents of photosynthetic components from the upper leaves. Consequently, lower leaves have a reduced overall photosynthetic capacity in normal light but equally efficient radiation use efficiency per unit of N at low light intensities. Such canopies would be more efficient. It has been argued that the majority of photosynthesis in field occurs at non-saturating light; therefore, it would be more profitable to improve genetically photosynthetic efficiency at low light intensities\textsuperscript{30}.

Maintaining green leaf area longer, particularly after anthesis when there is usually a rapid decline in leaf area index, is another important means of increasing total crop photosynthesis and hence biomass production through increased and extended light interception. Indeed, a longer duration of leaf photosynthetic activity has contributed to increased yield in most major crops\textsuperscript{23}. In maize, there has been an increase in the duration of photosynthetic activity by the leaves, manifested in their greater 'stay green'\textsuperscript{31}. A slower decline in the photosynthetic activity of canopies has been reported in soybean (\textit{Glycine max} (L.) Merr.)\textsuperscript{32} and rice\textsuperscript{33}. Improved agronomy and crop protection have made such changes possible\textsuperscript{34}. Moreover, higher N availability also led to selection for increased chlorophyll and rubisco content in wheat. Genetic manipulation of the synthesis of cytokinins has resulted in a delay of leaf senescence and an increase in growth rate of tobacco\textsuperscript{35}. In pulses, there is faster senescence of leaves after flowering due to the mobilization of leaf N and rubisco for development of protein-rich seeds\textsuperscript{36-39}. Mobilization of leaf nitrogen decreases leaf photosynthesis, induces senescence and restricts the duration of seed-fill period\textsuperscript{40-42}. In chickpea, however, leaf N mobilization was decreased by irrigation after flowering under north Indian conditions. This resulted in decreased HI, thus indicating the significance of such mobilization for seed yield in chickpea\textsuperscript{\textsuperscript{43}}.

Net photosynthesis

The crop plants need to perform at optimal level not only with respect to capturing light in crop canopy, but to efficiently utilize it for greater dry matter yield. The higher rate of photosynthesis (Pn) per unit leaf area, therefore becomes important. In most crop species, however, there has been little change in the rate of leaf photosynthesis per unit area to accompany the substantial genetic increase in grain yield. Most often, photosynthesis yield relationships are considered in terms of single leaf photosynthesis. Photosynthesis measurements of a few minutes duration using defined leaf position at radiation saturation may not be assumed to represent the productive potential of the crop. Leaf photosynthesis rate varies with leaf age, position, time of the day and sink strength\textsuperscript{44-47}. An inverse relationship between leaf size and photosynthesis rate has been observed\textsuperscript{48-50}. It was suggested that the smaller leaf tending to compensate its size by enhanced activity per unit leaf area and causing less mutual shading in a canopy, is a desirable trait\textsuperscript{48}. This would imply that selection for increased Pn would result in concomitant decrease in leaf area\textsuperscript{51}. It is, therefore, argued that selection for increased maximum leaf photosynthesis has not resulted in increased yield\textsuperscript{52}. Some genotypes of wheat, however, combine both high photosynthesis rates and large leaves\textsuperscript{53,54}. Such genotypes might prove useful sources of germplasm for increasing photosynthesis rate in commercial breeding programmes.

Attempts were made to relate variation in Pn with ploidy level in different plant species. In wheat, Pn decreased in hexaploids compared to tetraploids and diploids\textsuperscript{55,56}. An increase in Pn was observed in polysomple \textit{Festuca arundinacea} and polyploid \textit{Panice virgatum}. In \textit{Medicago sativa}, Pn did not change with increase in ploidy\textsuperscript{57}. In \textit{Brassica}, Pn was not associated with ploidy differences among species\textsuperscript{58}. In general, when expressed on per cell Pn, rubisco content, chloroplast number and DNA content increase with increase in ploidy. Cell size generally increases with increase in ploidy\textsuperscript{57}. The degree of increase in Pn per cell combined with the extent of change in cell number per unit leaf area might result in the above mentioned differential effects of ploidy on photosynthesis per unit leaf area.

Cytoplasmic influence on several agronomic traits has been reported for various crop species\textsuperscript{59}. Maternal influence on inheritance of these traits could be because of extra nuclear genes located in chloroplast and mitochondria. It has been proposed that \textit{Triticum monococcum} (male) genome A combined with \textit{Aegilops speltoides} (female) B genome to form \textit{T. dicoccum} and that \textit{T. dicoccum} AB (female) then combined with \textit{A. squarrosa} (male) genome D, to form \textit{T. aestivum} ABD\textsuperscript{60}. The higher specific activity of RuBP was shown to be associated with the possession of a large subunit derived from the B genome of \textit{A. speltoides} (female)\textsuperscript{61,62}. In fact substitution of the same nuclear genome into different cytoplasts of wheat (\textit{T. aestivum} L.) showed that ribulose bisphosphate carboxylase/oxygenase (rubisco) specific activity was consistent with the type of cytoplasm\textsuperscript{61-63}. Cytoplasmic (maternal) influence on the inheritance of photosynthesis and rubisco activity was also observed in \textit{Brassica} species\textsuperscript{58}.

\textbf{Rubisco}

Rubisco catalyses carboxylation and oxygenation of RuBP to initiate photosynthesis and photorespiration respectively\textsuperscript{64}. Its slow catalytic rate, low affinity for atmospheric CO\textsubscript{2} and use of O\textsubscript{2} as an alternative substrate for the competing process of photorespiration together makes rubisco inefficient. As the rate-limiting step of photosynthesis, Rubisco is often viewed as a potential target for genetic manipulation to improve photosynthesis and yield\textsuperscript{65}. A substantial
increase in photosynthesis rate can, therefore, be achieved by decreasing or eliminating photorespiration. This could be done by increasing the affinity of rubisco for CO$_2$, thereby decreasing its oxygenase activity. The substrate specificity factor determines the relative rates of two reactions at any given CO$_2$ and O$_2$ concentration. A high specificity value indicates greater specificity for CO$_2$. Rubisco enzyme from diverse species showed substantial differences in CO$_2$/O$_2$ specificity and that carboxylase/oxygenase ratio increased during the natural evolution of photosynthesis. Furthermore, higher temperature increasingly favours oxygenation. Among chemicals tested, Mn$^{2+}$ and urea in vitro have been shown to alter the ratio of two activities for greater oxygenation. These studies indicate that balance between RuBP carboxylation and oxygenation is not immutable and alteration in ratio is possible. However, successful manipulation of rubisco is yet to be achieved.

Hope for a better rubisco reawakened when it was discovered that some marine algae have more specific rubisco than higher plants. Uemura et al. found that rubisco of red algae is about 2 to 3 times more efficient. The relative specificity, $V_{c}/V_{o}$ of Galdieria partita and Cyanidium caldarium rubisco was 238 and 222 respectively, which is 2.4 to 2.5-fold higher than plant rubiscos (Table 2). The apparent $K_{m}$ of rubisco from the thermophilic red algae for CO$_2$ was 6 to 7 μM, and is the smallest of the values reported so far for other rubiscos. Attempts are being made to insert rubisco genes from red algae chloroplast into chloroplasts of higher plants in trying to improve rubisco in food crops. If this is achieved, substantial increase in photosynthesis rates is predicted.

Rubisco must be activated to function fully in CO$_2$ fixation. Rubisco active is the enzyme specifically involved in the activation of rubisco at physiological concentration of CO$_2$ and Mg$^{2+}$. Rubisco active is, therefore, essential for activation of rubisco and consequently for efficient photosynthesis. Any strategy for improving rubisco, however, should be mindful of the possible need to co-design activate, because it would be ineffective in vivo if activase is unable to recognize rubisco. It has also been observed that rubisco activase becomes impaired by certain environmental conditions, namely high temperature and high carbon dioxide. Rubisco activase, not rubisco, is more vulnerable when temperature and carbon dioxide levels increase. Crafts-Brandner and Salucci reported that heat denatures rubisco activase, rendering it unable to fit correctly onto rubisco. Consequently, inactive rubisco is not efficiently converted to the active form. Denaturing of rubisco activase can occur at temperatures as low as 32°C, whereas rubisco continues to function until the temperature reaches 55°C. High carbon dioxide impedes rubisco activase by decreasing the ATP/ADP ratio.

Brisson et al. reported that by increasing the amount of catalase, photorespiration can be reduced in transgenic tobacco plants. It has been estimated that 25% of the glycolate metabolized during photorespiration is released as CO$_2$ at 25°C. There is evidence that stoichiometry of the CO$_2$ produced per mol of glycolate oxidized, increases under conditions favouring rapid photorespiration, such as increase in O$_2$ and temperature. During photosynthetic carbon flow, huge amounts of H$_2$O$_2$ are generated in the peroxisomes as a result of oxidation of glycolate. The excess of H$_2$O$_2$ rapidly decarboxylates keto acids such as hydroxypyruvate and glyoxylate to generate additional CO$_2$. This additional loss of assimilated CO$_2$ might be avoided with higher catalase activity, thereby reestablishing the stoichiometry close to 25% and increasing net photosynthesis. Another strategy that is being tried out concerns the introduction of gene(s) involved in C$_4$ type of photosynthesis into C$_3$ plants. The justification for this approach is based on the fact that C$_3$ photosynthesis suffers from O$_2$ inhibition due to the oxygenase reaction of rubisco and the subsequent loss of CO$_2$ through photorespiration. In contrast, in C$_4$ plants such as maize and many weedy species, C$_4$ cycle acts as a CO$_2$ concentration mechanism to provide high CO$_2$ concentration in the vicinity of rubisco in bundle sheath cells, which offsets the competitive effect of O$_2$ on rubisco. Matsuoka et al. have been attempting to reproduce the C$_4$ cycle in rice. For the transformation to succeed, a host of altered enzymes would have to work together properly and the plant structure may have to be changed to create the equivalent of mesophyll cells. His team is trying to identify non-functioning equivalents of C$_4$ type genes in rice and selectively replace them with their active counterparts from maize.

Table 2. Specificity factor for RuBP carboxylase/oxygenase purified from several species

<table>
<thead>
<tr>
<th>Species</th>
<th>Specificity factor ($V_{c}/V_{o}$)</th>
</tr>
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<tbody>
<tr>
<td>C$_3$ plants</td>
<td></td>
</tr>
<tr>
<td>Glycine max</td>
<td>82 ± 5</td>
</tr>
<tr>
<td>Triticum spp.</td>
<td>90</td>
</tr>
<tr>
<td>Hordeum vulgare</td>
<td>87</td>
</tr>
<tr>
<td>Oryza sativa</td>
<td>85</td>
</tr>
<tr>
<td>Nicotiana tabacum</td>
<td>77 ± 1</td>
</tr>
<tr>
<td>C$_4$ plants</td>
<td></td>
</tr>
<tr>
<td>Amaranthus hybridus</td>
<td>82 ± 4</td>
</tr>
<tr>
<td>Zea mays</td>
<td>78 ± 3</td>
</tr>
<tr>
<td>Green algae</td>
<td></td>
</tr>
<tr>
<td>Scenedesmus obliquus</td>
<td>63 ± 2</td>
</tr>
<tr>
<td>Chlamydomonas reinhardii</td>
<td>61 ± 5</td>
</tr>
<tr>
<td>Cyanobacteria</td>
<td></td>
</tr>
<tr>
<td>Aphanothece flos-aquae</td>
<td>48 ± 2</td>
</tr>
<tr>
<td>Coccolithus penicystis</td>
<td>47 ± 2</td>
</tr>
<tr>
<td>Photosynthetic bacteria</td>
<td></td>
</tr>
<tr>
<td>Rhodospermum rubrum</td>
<td>15 ± 1</td>
</tr>
<tr>
<td>Rhodospirillum sphaeroides II</td>
<td>9 ± 1</td>
</tr>
<tr>
<td>Red algae</td>
<td></td>
</tr>
<tr>
<td>Galdieria partita</td>
<td>238</td>
</tr>
<tr>
<td>Cyanidium caldarium</td>
<td>222</td>
</tr>
<tr>
<td>Porphyridium purpureum</td>
<td>144</td>
</tr>
</tbody>
</table>
An intact maize gene for phosphoenolpyruvate carboxylase (PEPC) has been introduced in C₃ rice. The transgenic rice plant showed high level of expression of maize gene. PEPC was 2–3 times more active in the leaves of some transgenic plants than in maize leaves. In transformants, the sensitivity of photosynthesis to O₂ inhibition was reduced with increased activity of maize C₄ PEPC. O₂-insensitive photosynthesis in the PEPC transformants was found to be caused by a Pi limitation of photosynthesis. There is, however, skepticism about importing the C₄ cycle into crops like wheat and rice, because the cycle imposes high energy cost on plant metabolism and only pays-off at high temperature. It is also considered that photorespiration confers adaptation to high-radiation intensity. Therefore, while eliminating photorespiration, its protective role may have to be compensated for.

Stomatal conductance

Photosynthesis can be enhanced through bioengineering the stomata, so that in water-rich areas they might be modified to stay open even longer. This could give better ventilation in the leaf, decreasing the canopy temperature, and giving better transport of CO₂ which could boost the rate of photosynthesis. Researchers are targetting two molecules that play a role in regulating the stomata, the plant hormone abscisic acid (ABA), which triggers closing and an enzymatic process called farnesylation, which seems to impede ABA. By altering farnesylation, researchers may, in theory, be able to adjust the sensitivity of the plant to ABA and thus the tendency of stomata to close. Indeed, an analysis of wheat bred at CIMMYT, Mexico revealed that stomatal conductance, canopy temperature depression, maximum photosynthesis rate, and carbon isotope discrimination (δ¹³C/δ¹²C) were all associated with yield progress. It has, however, been suggested that increased stomatal conductance and corresponding increase in Pn may be a direct response to the increased demand for assimilates driven by greater grain number, i.e. greater sink strength.

A decrease in stomatal number with increase in atmospheric CO₂ concentration has been observed. Gray et al. have reported identification of the Arabidopsis gene HIC (for high carbon dioxide), which encodes a negative regulator of stomatal development that responds to CO₂ concentration. Mutant hic plants exhibited up to 42% increase in stomatal density in response to a doubling of CO₂. It may thus be possible to have higher stomatal conductance at high CO₂ concentration and this is of particular significance in the context of rising level of CO₂ in the atmosphere.

Respiration

An alternative approach for increasing net leaf photosynthesis would be to reduce respiration rate. There is substantial loss of carbon by respiration, yet few serious attempts have been made to reduce this loss. Respiration in plants has been examined in terms of two conceptual components—growth and maintenance. Growth respiration is considered as the energy source for the synthesis of new phytomass. Maintenance respiration supplies energy to maintain current phytomass, is independent of substrate concentration and includes processes such as protein turnover, ion balance and tissue acclimation to environmental change. There is higher maintenance cost for plant products rich in N and with high caloric value. The turnover of organic N compounds represents a major expenditure of energy. Pening de Vries calculated that 50–60% of the maintenance cost was associated with protein turnover. Barneix et al. observed a smaller, and yet a significant proportion (27–36%) of mature leaf respiration in perennial ryegrass, due to protein turnover. Evidence that a substantial proportion of the total carbon assimilated by wheat crop is used in maintenance respiration indicates that respiration efficiency may also be improved by decreasing maintenance in favour of growth respiration. This has been shown to be a real possibility for forages. Another approach could be through decreasing or eliminating energetically less-efficient cyanide-resistant respiration. Cyanide-resistant respiration evolves heat and is considered as an adaptation to suboptimal temperatures. This should be considered while selecting against this trait.

Source–sink balance

In order to sustain photosynthesis at the maximum rate, sink capacity of the system must be able to utilize the assimilates. Otherwise, there would be accumulation of assimilates in the leaves, resulting in end-product inhibition of photosynthesis. A metabolic or storage sink capacity would, therefore, be required to sustain high photosynthesis rate. It may, however, be mentioned that accumulation of carbohydrates in the leaves during the day is also important, as it is mobilized during the night to maintain timely supply of carbon for growth and metabolism in plants. There are large interspecific variations in the relative amounts of sucrose and starch accumulated in the leaves. Some species make sugar alcohols rather than starch and sucrose; others, particularly monocotyledons, accumulate fructans instead of starch.

In wheat, end-product inhibition of Pn has been clearly shown. Ghildiyal and Sirohi observed that faster decrease in Pn of diploid wheat after anthesis was due to its lower sink demand in terms of lesser starch-synthesizing capacity of their grains compared to tetraploid and hexaploid wheat. The diurnal decrease in photosynthesis and down-regulation of photosynthesis under elevated CO₂ has been shown to be due to saccharides accumulation, leading to decrease in activation state and amount of rubisco.

Sugar accumulation in leaves decreases Pn by tying up inorganic phosphate (Pi) (Figure 1), resulting in Pi limita-
tion of RuBP regeneration capacity\textsuperscript{109,110}. To become catalytically competent, rubisco is activated by rubisco activase\textsuperscript{22,111} at physiological concentration of CO\textsubscript{2} and Mg\textsuperscript{2+}. This energy-driven activation, however, requires ATP. A decrease in ATP/ADP ratio when Pi is depleted decreases rubisco activation\textsuperscript{109}. This explains how decrease in activation state of rubisco is associated with sugar accumulation in wheat leaves\textsuperscript{103,105,112}. The decrease in rubisco content associated with sugar accumulation appears to be through repression of the expression of photosynthetic genes (Figure 1), including those encoding small and large subunits of rubisco by sugars\textsuperscript{109,113-117}. The decreased expression of such genes seems to be associated with the metabolism of hexoses derived from sucrose hydrolysis by acid invertase\textsuperscript{118}. Hexokinase has been proposed to function as a sugar sensor in the cytosol of plant mesophyll cells\textsuperscript{118,120}. During phosphorylation of hexoses, hexokinase is hypothesized to initiate a signal cascade that results in the repressed expression of a number of photosynthetic genes\textsuperscript{113,121}. There are however, still many aspects of this process that are not known.

Sunflower, mungbean and soybean accumulate excess carbohydrates as starch in the leaves. However, associated with starch accumulation, there was little or no down-regulation of photosynthesis\textsuperscript{9,106,122-125}. This could be because the starch accumulator continued to recycle Pi for photosynthesis and consequently sustained Pn (Figure 1). Shading and disruption of chloroplast by starch granules probably occur at extreme levels of accumulation\textsuperscript{123}. Therefore, starch accumulation in leaf does not represent a significant feedback inhibition mechanism on photosynthesis activity\textsuperscript{122,124,126-128}. Rubisco activity, activation state and amount were, therefore, not significantly affected in these plants under high CO\textsubscript{2} concentration\textsuperscript{25,129}. Less sensitivity of Pn to starch accumulation has been reported in mungbean\textsuperscript{122,124} and soybean\textsuperscript{130}. Plant species showing little or no down-regulation of Pn in high CO\textsubscript{2} grown plants such as soybean\textsuperscript{131}, mungbean\textsuperscript{106}, sunflower\textsuperscript{123}, potato\textsuperscript{132} and radish\textsuperscript{133}, all happen to be starch accumulators. Using transgenic potato which is unable to accumulate transitory starch due to leaf mesophyll-specific antisense expression of AGPaseB, Ludwig\textsuperscript{127} also demonstrated that down-regulation of photosynthesis to elevated CO\textsubscript{2} is not caused by accumulation of starch.

Trehalose-6-phosphate (T6P) content has been shown to be correlated with photosynthesis activity (Figure 2). Transgenic tobacco expressing the Escherichia coli otsA gene encoding trehalose phosphate synthase (TPS) showed significantly higher photosynthetic activity per unit leaf area than wild type. The precise mechanism, however, is not clear\textsuperscript{134,135}. Schluempmann et al.\textsuperscript{136} expressed E. coli genes for trehalose metabolism in Arabidopsis thaliana, which altered T6P contents in transgenic plants. The marked phenotype of plants accumulating T6P (expressing TPS) was
opposite that of plants with low T6P level, obtained by expressing either trehalose phosphate phosphatase or trehalose phosphate hydrolyase and consistent with a critical role for T6P in growth and development. Data indicate that T6P controls carbohydrate utilization and hence growth via control of glycolysis.

Enhancing Pn either through efficient rubisco or incorporation of C4 pathway or otherwise, may thus lead to accumulation of assimilates in the leaves resulting in down-regulation of photosynthesis, unless plants accumulate excess assimilates in a form that is less inhibitory or have efficient sink capacity that would prevent accumulation of sugars in the leaves.

Another approach through which end-product inhibition of Pn could be minimized is by enhancing the sink capacity. For instance, increase in yield in wheat has so far been achieved through increasing HI by increasing storage sink capacity. A further increase in sink capacity in terms of grain number per ear, however, results in a decrease in individual grain weight. A negative correlation between grains per ear and individual grain weight has been frequently observed. Studies showed that wheat spike structure does not allow sufficient flow of assimilates to distally located grains in spikelets85,157,158. A change in ear structure, whereby grain number is increased by increasing spikelet number per ear instead of increasing grain number per spikelet was suggested. A new plant type of wheat based on the above ear characteristics has been developed by wheat breeders of IARL, where the reverse relationship of grain number and grain weight has been minimized and has led to increase in biomass and yield.

There is, however, a need to enhance the growth potential of grains. In cereals, starch constitutes more than 70% of the grain dry matter. ADPG pyrophosphorylase (AGPase) is the key regulatory enzyme in the pathway leading to starch synthesis and is regulated by PGA/Pi ratio. It has been shown that expression of E. coli AGPase, which is insensitive to regulation by PGA and Pi, resulted in an increase in starch content as well as yield in potatoes130. In wheat, high temperature-sensitive soluble starch synthase appears to be more important in determining starch synthesis in grains140. In many grain legumes there is large unrealized sink capacity, as evident from shedding of flowers and immature fruits, hence they are considered to be source-limited8,28,37,40. The sink, however, is instrumental in hastening the decrease in photosynthesis directly by mobilization of leaf nitrogen, including rubisco for seed development and indirectly by effecting nodulation3,38,39,41.

Summary

It appears from the above analysis that improvement in yield of many cereal crops has been achieved by increasing HI. In pulses and oilseed crops, HI is low, hence, selection for higher HI continues to be important. This would require determinate type with synchronous flowering. Such a plant type is benefitted only under assured input condition, which is a limitation in improvement of these crop plants. In many cereals, HI is approaching a ceiling value. Therefore, in order to increase potential yield, crop biomass has to be increased, i.e. there will have to be more photosynthesis. Theoreti-
cally, there is considerable scope for improvement of solar energy utilization in photosynthesis. Much efforts, however, have been directed in improving crop architecture for greater light interception. Efforts are now being made to improve biochemical efficiency of photosynthesis through improvement in specificity of rubisco, incorporation of C4 type of photosynthesis in C3 plants and elimination of wasteful respiration. Accumulation of sugars in leaves and stem causing feedback inhibition of photosynthesis appears to be the key factor limiting photosynthetic efficiency. Enhancement in potential photosynthesis under such conditions, therefore, would be of little consequence unless end-product inhibition of photosynthesis is overcome. Accumulation of excess assimilates in a form that is less inhibitory and improvement in physiological and biochemical efficiency of storage sink organs appeared important in this context.


Reviewer Article


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