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REVIEW

CO_2 sequestration in plants: lesson from divergent strategies

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Abstract

Most organisms inhabiting earth feed directly or indirectly on the products synthesized by the reaction of photosynthesis, which at the current atmospheric CO_2 levels operates only at two thirds of its peak efficiency. Restricting the photorespiratory loss of carbon and thereby improving the efficiency of photosynthesis is seen by many as a good option to enhance productivity of food crops. Research during last half a century has shown that several plant species developed CO_2-concentrating mechanism (CCM) to restrict photorespiration under lower concentration of available CO_2. CCMs are now known to be operative in several terrestrial and aquatic plants, ranging from most advanced higher plants to algae, cyanobacteria and diatoms. Plants with C_4 pathway of photosynthesis (where four-carbon compound is the first product of photosynthesis) or crassulacean acid metabolism (CAM) may consistently operate CCM. Some plants however can undergo a shift in photosynthetic metabolism only with change in environmental variables. More recently, a shift in plant photosynthetic metabolism is reported at high altitude where improved efficiency of CO_2 uptake is related to the recapture of photorespiratory loss of carbon. Of the divergent CO_2 assimilation strategies operative in different oraganisms, the capacity to recapture photorespiratory CO_2 could be an important approach to develop plants with efficient photosynthetic capacity.

Additional key words: aquatic, carbon-concentrating mechanisms, crassulacean acid metabolism, C_4 photosynthesis, Rubisco.

Introduction

Estimates suggest a stupendous increase in the global food demand, requiring nearly 40% increases in yield of wheat and rice alone by the year 2020 (Datta 2004, Swaminathan 2006). Yield potentials of major cereal crops, achieved by genetic improvement and improved management practices, cannot further be increased by addition of nitrogen. It is therefore argued that photosynthesis could likely be the major trait available to increase yield on the scale of last 50 years (Surridge 2002, Long *et al.* 2006, Reynolds *et al.* 2009, Zhu 2010). A number of studies have discussed the prospects of enhancing photosynthetic capacity in agricultural crops by genetic manipulation (Matsuoka *et al.* 2001, Häusler *et al.* 2002, Leegood 2002, Surridge 2002, Miyao 2003, von Caemmerer 2003, Reynolds *et al.* 2009). The basic theme of these approaches is to improve the inefficiency of C_3 photosynthesis, owed largely to the bifunctional character of the main carboxylating enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), and its low catalytic rates.

The atmosphere in which Rubisco evolved around 3.5 milliard years had concentration of CO_2 nearly ten times higher than that of today (Ehleringer *et al.* 1991, Blankenship 1992). This high CO_2 atmosphere would provide optimal condition for Rubisco to catalyse combination of CO_2 with the phosphorylated 5-carbon RuBP for the synthesis of sugars. However, as discovered about half a century ago, Rubisco also acts as an oxygenase under conditions of low concentrations of CO_2 or high-oxygen environment or high temperature (Bowes

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Abbreviations: CA – carbonic anhydrase; CAM – crassulacean acid metabolism; CCM – CO_2-concentrating mechanism; HCO_3^- – bicarbonate; PEPCase – phospho*enol*pyruvate carboxylase; PEPCK – phosphoenolpyruvate carboxykinase; PPDK – pyruvate orthophosphate dikinase; RA – Rubisco activase; Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase.
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et al. 1971). At the current atmospheric levels O_2 accounts for about 30% of the reaction catalyzed by Rubisco (Moroney and Somanchi 1999), which may increase as much as up to 50% at higher temperature (Nelson and Langdale 1992). This competitive inhibition of carboxylase activity of Rubisco leads to loss of carbon by way of photorespiration (Ogren and Bowes 1971). Therefore it is the concentrations of CO_2 and O_2 around Rubisco that determine the ratio of rates of carboxylation to oxygenation and the efficiency of CO_2 fixation. Studies have shown that photorespiration can be reduced by growing plants under higher concentration of CO_2, such as in greenhouses, for better growth and yields (Long *et al.* 2006). It means that the rising levels of atmospheric CO_2 would promote photosynthetic efficiency, though this capacity could subsequently be impeded by other associated problems like increased temperature, decreased soil moisture, and increase in phytotoxic ozone (Long *et al.* 2005).

Another limitation of photosynthesis lies in the low catalytic property of Rubisco, meaning that large quantity of this protein is required to accomplish the reaction (Long *et al.* 2006). The already high abundance of Rubisco in leaves, which accounts for 30–50% of total soluble protein in chloroplasts (Ellis 1979, Dhingra *et al*. 2004), generally precludes the possibility of adding more Rubisco (Pyke and Leech 1987). Alternately, the possibility of finding an efficient Rubisco that selectively discriminates for its two reactions could be a good option. Rubisco extracted from some Mediterranean plant species of hot, arid, and saline environments have shown higher specificity for CO_2 relative to O_2 (Uemura *et al.* 1996, 1997; Galmes *et al.* 2005). However, available information from a limited number of species showed that Rubisco specificity has an inverse relationship with its catalytic rates (Bainbridge *et al.* 1995). Therefore, the benefit of increased specificity is likely to be outweighed by the lowered catalytic rates (Zhu *et al.* 2005). Further on, CO_2/O_2 specificity values of Rubisco in some dinoflagellates are so low that photosynthesis in air-equilibrated solutions appears impossible on the basis of diffusive CO_2 entry, except aided by some mechanisms to concentrate carbon (Raven 2003). Carbon-concentrating abilities have now been known in diverse life-forms, ranging from cyanobacteria, micro- and macroalgae, bryophytes to higher plants in terrestrial and aquatic systems (Kaplan and Reinhold 1999, Moroney and Somanchi 1999, Reinfelder *et al.* 2000, Badger *et al.* 2002, Beardall and Giordano 2002, Bowes *et al.* 2002, Hanson *et al.* 2002, Mercado *et al.* 2006).

CO_2-concentrating mechanism (CCM)

Photosynthesis in C_3 (Fig. 1*A*) and C_4 plants (Fig. 1*B*) differs due to the ability of the later to operate CCM. Now reported in several organisms, CCM is believed to provide adaptation to low carbon dioxide concentrations (Moroney and Ynalvez 2007), by developing micro-environment of high CO_2 concentration around Rubisco that helps to suppress the oxygenase activity of Rubisco and the process of photorespiration. Plants whose follow C_4 pathway of photosynthesis or CAM were the earliest known examples of CCM in higher plants from terrestrial ecosystem. Later, CCM was reported in lower plants and more importantly from aquatic environment. The poor availability of CO_2 in aquatic system called for different strategies in different life forms. More lately, it was shown that some plant species can shift their photosynthetic metabolism with change in set of environmental conditions. This inherent potential of some plant species to develop CCM offers additional possibilities to improve photosynthetic performance and consequently the yield in crop plants.

CCMs in terrestrial plants

The CO_2-concentrating pump of C_4 plants

C_4 photosynthesis is a metabolic cooperation between two spatially separated cell types, generally the mesophyll cells (photosynthetic carbon assimilation or PCA tissue) containing enzyme phospho*enol*pyruvate carboxylase (PEPCase), and the chlorenchymatous bundle sheath (photosynthetic carbon reduction or PCR tissue) that contain Rubisco. PEPCase being insensitive to the surrounding concentration of O_2 has high affinity for HCO_3^- and acts as the primary carboxylase in C_4 plants on a substrate which is bicarbonate (HCO_3^-) and not CO_2. The $K_m(HCO_3^-)$ of PEPCase is about 8 μM, whereas HCO_3^- concentration in the cytoplasm of mesophyll cells is about 50 μM (Moroney and Somanchi 1999). The atmospheric CO_2 entering through leaf stomata is converted to HCO_3^- by the action of enzyme carbonic anhydrase (CA) located in the mesophyll cells (Hatch and Burnell 1990).

PEPCase catalyses the carboxylation of phospho*enol*-pyruvate (PEP) to synthesize C_4 compounds like aspartic, citric or malic acids, as the case may be in different C_4 subtype species, which are then transported to bundle sheath where decarboxylation by one of the three decarboxylating enzymes, *viz.* chloroplastic NADP-malic enzyme (NADP-ME), mitochondrial NAD-malic enzyme (NAD-ME), or cytosolic phospho*enol*pyruvate carboxykinase (PEPCK) takes place to liberate CO_2 that finally get fixed in the Calvin cycle.

The three-carbon residue diffuses back to mesophyll and is converted to PEP. Regeneration of PEP is the third key step of C_4 pathway (after the initial fixation of CO_2 and its subsequent decarboxylation) catalysed by pyruvate orthophosphate dikinase (PPDK) located in mesophyll chloroplast in all C_4 subtypes (Miyao 2003). While Kranz anatomy provides the critical structural

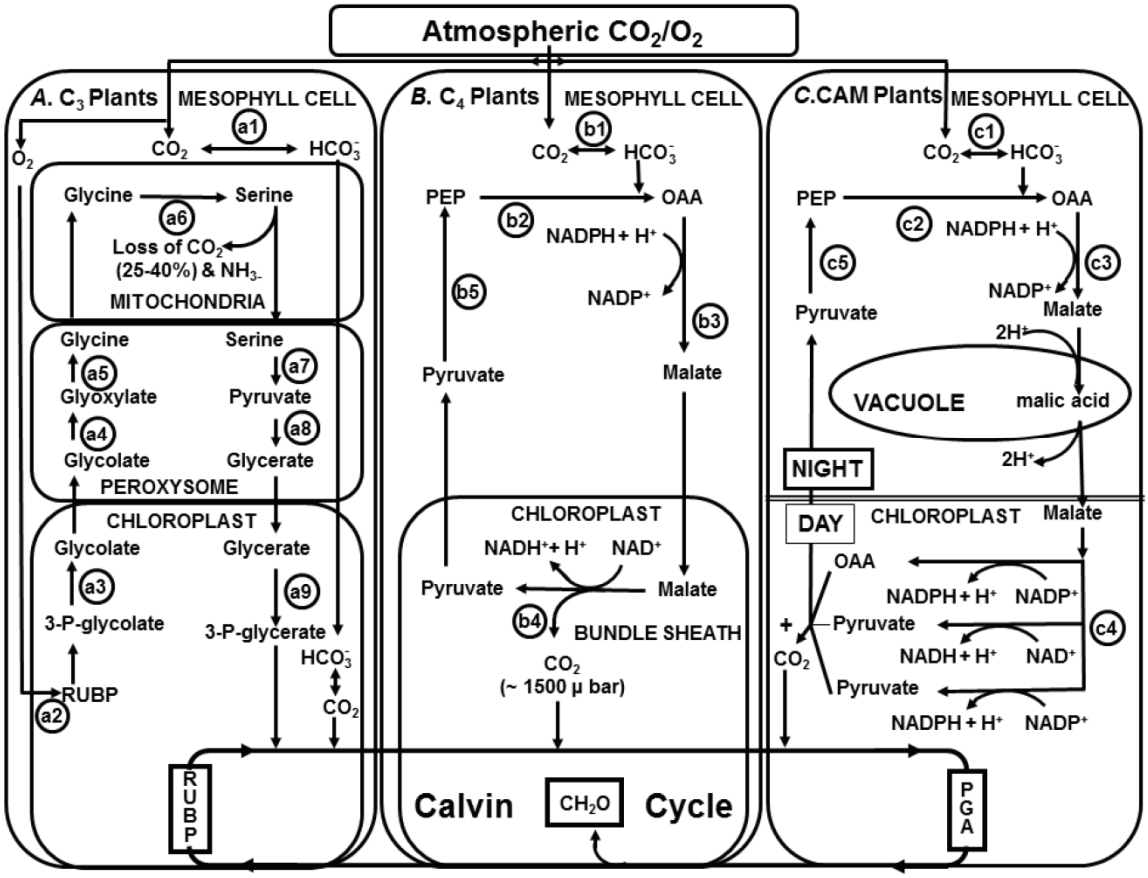

Fig. 1. Photosynthetic assimilation of atmospheric CO_2, mediated by different enzymes in *A*: C_3 plants, *B*: C_4 plants, and *C*: CAM plants. In each of these three categories, enzymes are numbered, prefixed with small respective alphabets and encircled. C_3 plants: a1 – carbonic anhydrase, a2 – RUBP oxygenase, a3 – phosphoglycolate phosphatase, a4 – glycolate oxidase, a5 – glutamate:glyoxylate aminotransferase, a6 – glycine decarboxylase complex, a7 – Serine-glyoylate aminotransferase, a8 – pyruvate reductase, a9 – glycerate kinase; C_4 plants: b1 – carbonic anhydrase, b2 – PEP carboxylase, b3 – malic dehydrogenase, b4 – NAD-malic enzyme, b5 – pyruvate orthophosphate dikinase, CAM plants: c1 – carbonic anhydrase, c2 – PEP carboxylase, c3 – malic dehydrogenase, c4 – NAD-malic enzyme, c5 – pyruvate orthophosphate dikinase, CH_2O – sugars, RUBP – ribulose-1,5-bisphosphate, PGA – phosphoglyceric acid. (based on Salisbury and Ross 1886, Häusler *et al.* 2002)

support for PCA and PCR cycles to operate, the merit of C_4 photosynthesis lies in building high CO_2 concentration around Rubisco in bundle sheath cells and recapturing the photorespiratory CO_2.

CAM - temporal regulation of CCM

Similarly to C_4 plants, PEPCase catalyses the first step in the photosynthetic assimilation of CO_2 in CAM plants where the two carboxylases (other being Rubisco) are temporally, rather than spatially, separated. Other important features of CAM are circadian expression of key genes related to the photosynthetic pathway and their control by metabolites (Dodd *et al.* 2002). The day-night cycle operates with opening of stomata during night to allow atmospheric CO_2 to move in. During day, when sufficient light is available but the stomata are closed as a measure to conserve water, decarboxylation of the four carbon compound takes place to release CO_2 for fixation through Calvin cycle (Fig. 1*C*). In CAM plant *Littorella uniflora*, intensive decarboxylation rates can concentrate CO_2 to levels as high as 30,000 ppm and imparts stimulating effect on photosynthesis (Madsen 1987).

Expression of CAM activity, however, can vary and may range from no net CO_2 uptake (CAM-idling) to fixation of atmospheric CO_2 round the clock (Dodd *et al.* 2002). Under the nonlimiting conditions of light and water, certain species like those of *Clusia* operate CAM (CAM cycling) for the modest benefit of reducing respiratory CO_2 losses (Wanek *et al.* 2002). CAM plants have an exclusive advantage under conditions of acute water scarcity such as in arid habitats (Winter and Smith 1996, Moore 1999, Grams and Thiel 2002), but its representation in aquatic system (Keeley 1981) is unusual, highlighting the role of PEPCase to capture CO_2 in dissolved state, especially during night when concentrations of CO_2 are relatively much higher than normal (Moore 1999).

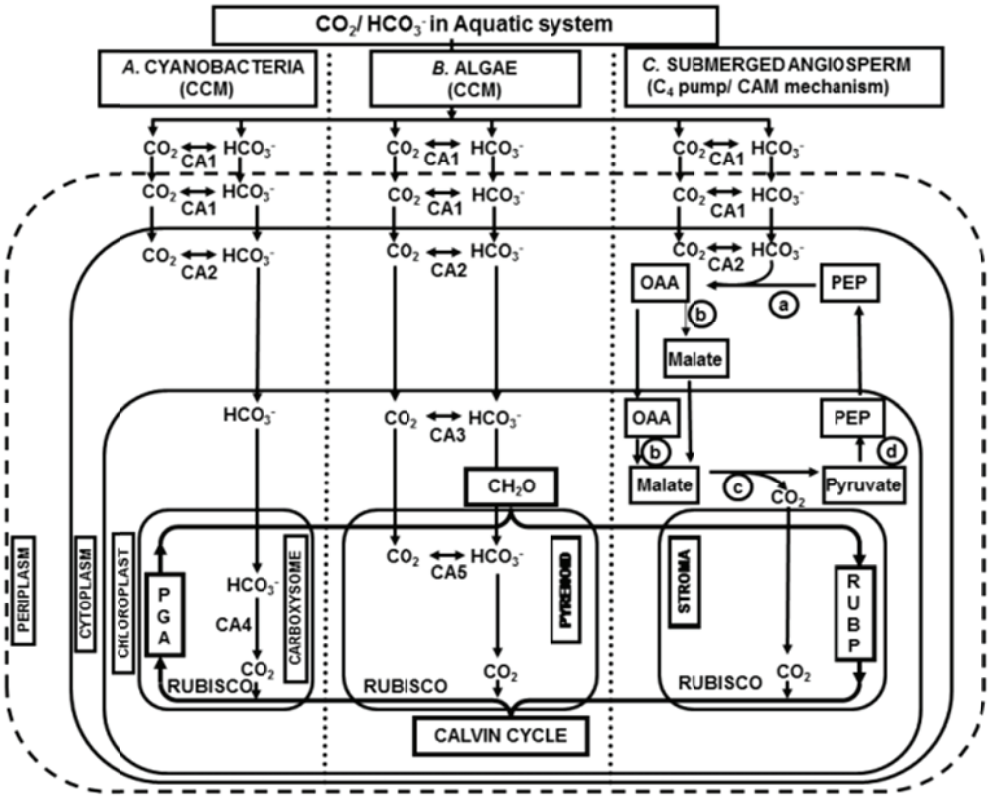

Fig. 2. A schematic depiction of path of carbon (CO_2/HCO_3^-) in cyanobacteria, algae and submerged angiosperms and its subsequent fixation in Calvin cycle. Carbonic anhydrase (CA1 – periplasmic carbonic anhydrase; CA2 – cytosolic carbonic anhydrase; CA3 – chloroplastic carbonic anhydrase; CA4 – carboxysomal carbonic anhydrase; CA5 – luminal carbonic anhydrase) plays a critical role in its transportation across different membrane surfaces in cyanobacteria, algae and higher plants. In submerged C_4 plants, C_4 cycle and Calvin cycle operate in the same cell. The enzymes (a – phosphoenolpyruvate carboxylase; b – NAD-malic dehydrogenase; c – NADP malic dehydrogenase; d – PPDK – pyruvate phosphate dikinase) are shown by encircled alphabets. Calvin cycle metabolites are CH_2O – sugars; RUBP – ribulose-1,5 – bisphosphate; PGA – phosphoglyceric acid. (based on Moroney *et al.* 2001, Badger 2003, Tiwari *et al.* 2005, Raven *et al.* 2007).

CCM in aquatic system

The most critical constraint to photosynthesis in aquatic environment is the slow rate of CO_2 diffusion in water, which could be ten thousand times lower than in air (Price and Badger 2002, Maberly and Madsen 2002). CO_2 solubility could be lowered further in saline water and at high pH that favours higher bicarbonate HCO_3^-: CO_2 ratio (Beardall and Giordano 2002, Price and Badger 2002). It is reported that about 90% of the inorganic carbon in sea is in form of HCO_3^- – a form not required by Rubisco for photosynthetic carbon fixation (Riebesell 2000). Moreover, the concentration of CO_2, which is relatively constant in air at a given point of time, may vary considerably in aquatic system - at different layers and with the varying abundance of life it supports (Keeley 1999, Moore 1999). In lakes that support productive vegetation, photosynthesis can nearly deplete surface concentration of CO_2 (Maberly 1996). Rubisco efficiency in water is further undermined by the concentrations of ambient O_2 which may rise to twice those in air-saturated water (Leegood 2002). Since Rubisco is the only enzyme capable of carbon fixation in Calvin cycle, adequate level of CO_2 would be required to avoid competitive inhibition by O_2. To effectively tackle this, most aquatic autotrophs have developed the ability to use HCO_3^- (Fig. 2) and additional biochemical carboxylation pathways like CAM or C_4 photosynthesis (Raven 1970, Casati *et al.* 2000, Maberly and Madsen 2002).

CCM in aquatic life forms – cyanobacteria and algae

Photosynthetic microorganisms display enormous ability to acclimate to a wide range of CO_2 concentrations (Kaplan *et al.* 2001). Some microalgae can accumulate intercellular inorganic carbon to overcome its natural limitation in aquatic system (Beardall and Giordano 2002). The mode of carbon uptake in eukaryotic microalgae ranges from diffusive CO_2 uptake to active transport of CO_2 and HCO_3^- (Colman *et al.* 2002). Most of these species can also take up both CO_2 and HCO_3^-, while species selectively utilizing either of the two carbon species are also known (Rotatore *et al.* 1992, Colman *et al.* 2002, Huertas *et al.* 2002). Endowed with the capacity to accumulate HCO_3^-, microalgae have means to package Rubisco in specific locations (Moroney

and Somanchi 1999). Cyanobacteria can concentrate HCO_3^- more than 100-fold within the cell (Miller *et al.* 1990) using active transporters (Badger *et al.* 2002).

The role of CA is very critical in these organisms in converting HCO_3^- to CO_2 (Riebesell 2000) before it can be fixed by Rubisco (Fig. 2*A,B*), and both CA and Rubisco are in close vicinity, usually packaged in specific organelles like pyrenoid in algae, carboxysome in cyanobacteria, or periplasmic space in case of eukaryotic algae (Moroney and Somanchi 1999). This close association of CA with Rubisco is helpful to build high concentration of CO_2 under aquatic condition (Badger 2003, Mercado *et al.* 2006). Some of the green unicellular algal diatoms which lack CCM and take CO_2 by diffusion have Rubisco with high specificity for CO_2 uptake (Palmqvist *et al.* 1995, Colman *et al.* 2002).

CCM in aquatic angiosperms

Maberly and Madsen (2002) have reviewed different carbon acquisition strategies in freshwater angiosperms which utilize HCO_3^- or CO_2 from atmosphere or sediments, through C_4 or CAM photosynthesis (Fig. 2*C*). Interestingly, about 50% of the submerged plants use HCO_3^- for photosynthesis (Madsen and San-Jenson 1991). Some aquatic plants can secrete H^+ into leaf boundary layer to enhance the conversion of HCO_3^- to CO_2 for subsequent assimilation (Prins *et al.* 1982). Submerged grass species of *Neostapfia*, *Orcuttia*, and *Tuctoria* can take up CO_2 and maintain C_4 photosynthesis underwater (Keeley 1998). *Hydrilla verticillata* is a freshwater submerged angiosperm that has the capacity to use both CO_2 and HCO_3^-. The basic difference in C_4 cycle that operates in aquatic angiosperms compared to that in terrestrial C_4 plants lies in operation of β-carboxylation in cytosol and the process of decarboxylation and Rubisco carboxylation taking place in chloroplast (Bowes *et al.* 2002). As an important distinction, CCM operates within a single cell in most of the aquatic plants as well as terrestrial CAM species. Despite being energetically more costly CCM is a way to overcome the limiting environmental constraint on carbon fixation, and probably suggests a route to enhance photosynthetic efficiency.

Maintaining the high levels of CO_2

Subsequent to acquisition of carbon, the major issue in operating an effective CCM is to prevent diffusion of CO_2. In aquatic system, leakage is less of a concern because of the surrounding aqueous matrix that restricts diffusion of CO_2 out of the cell (Sage 2002a). Microalgae that accumulate HCO_3^- rather than CO_2, has an advantage of its slower diffusion through membranes and are thus able to maintain higher concentrations of the carbon at the site of fixation. In C_4 plants, bundle sheath cells have thickened cell walls that prevent CO_2 generated by decarboxylation reactions from diffusing out. The ability to efficiently curve diffusive loss of CO_2 from bundle sheath determines the efficiency of C_4 photosynthesis (Furbank *et al.* 1989).

Shift in photosynthetic metabolism with change in environmental variables

Higher plant species are nearly always consistent in following either, C_3, C_4 or CAM mode of photosynthesis. However, variation in growth conditions can induce certain plants to switch from one mode to another. It was observed quite earlier in *H. verticillata* and *Egeria densa* that malate content in leaves increased at the expense of carbon cycle intermediates when plants were grown at low CO_2 levels (Bowes *et al.* 1971, Browse *et al.* 1977, Salvucci and Bowes 1983). Submergence in these two species was shown to decrease CO_2 compensation point but increase the activities of enzymes PEPCase and NADP-ME, which in turn were related to reduced photorespiration (Salvucci and Bowes 1981). Now several plant species are known to shift their photosynthetic metabolism between C_3, C_4, and CAM modes with changes in environmental variables (Fig. 3).

Meanwhile, some individuals can display more than one photosynthetic pathway at the same time. In aquatic grass *Orcuttia californica*, which has floating and submerged leaves, the submerged leaves showed CAM characteristics while aerial leaves followed C_4 photosynthesis (Keeley 1999). The marine diatom *Thalassiosira weissflogii* simultaneously operates both CCM and C_4 photosynthesis within the single cell. The C_4 cycle is confined to cytoplasm and is spatially separated from the Rubisco process located in the chloroplasts (Reinfelder *et al.* 2000). The diatom has a deep vertical movement in sea water and needs to adapt to the fluctuating light conditions. While operation of CCM ensured a steady carbon sequestration at low CO_2 concentrations in this organism, C_4 photosynthesis is advantageous under burst of high light in surface water (Riebesell 2000).

Shift between C_3-C_4 modes of photosynthesis

C_3 plants can also switch over to C_4 or C_4-like metabolism with change in environmental conditions like drought, high light, low CO_2 levels, high temperature, and submergence. A freshwater amphibious sedge *Eleocharis vivipara*, which lacks Kranz cells and follows C_3 photosynthesis in submerged leaves, could induct Kranz anatomy and C_4 photosynthesis in terrestrial leaves (Ueno *et al.* 1988). Similarly, C_3 plants *E. baldwinii* and *E. densa* can shift to C_4 and C_4-like photosynthesis under submerged conditions (Uchino *et al.* 1995, Casati *et al.* 2000). However, C_4 grasses like *Neostapfia colusana* and *Tuctoria greenei* exhibit Kranz anatomy and C_4 photosynthesis in both aquatic and terrestrial leaves forms (Keeley 1998). In *Hydrilla*, under depleting CO_2 conditions, coupled with high O_2 fluxes during its dense growth at high summer temperature, C_4-like biochemistry

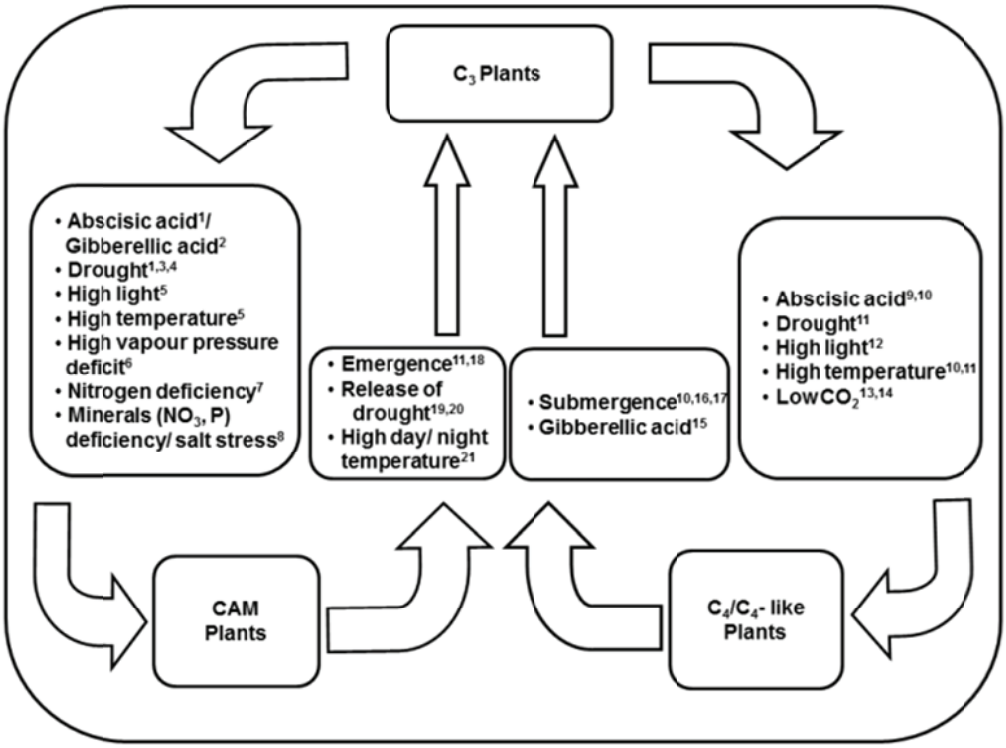

Fig. 3. Environmental and nonenvironmental factors reported to induce shift in C_3, C_4 and CAM modes of photosynthesis in some higher plants. Studies indicated by different numerals and species name given in parenthesis: 1. Chu *et al.* 1990 (*Mesembryanthemum crystallinum*); 2. Guralnick 2001 (*M. crystallinum*); 3. Nobel and Hartsock 1987 (*Opuntia ficus-indica*); 4. Winter *et al.* 2008 (*Clusia pretensis*); 5. Haag-Kerwer *et al.* 1992 (*Clusia minor*); 6. Borland *et al.* 1992 (*C. minor*); 7. Franco *et al.* 1991 (*C. minor*); 8. Paul and Cockburn 1990 (*M. crystallinum*); 9. Ueno *et al.* 1998 (*Eleocharis vivipara*); 10. Casati *et al.* 2000 (*Egeria densa*); 11. Keeley 1999 (*E. acicularis*, *I. orcuttia*); 12. Cheng *et al.* 1989 (*Flaveria brownii*); 13. Bowes and Salvucci 1989 (*Hydrilla verticillata*); 14. Holaday and Bowes 1980 (*H. verticillata*); 15. Ueno 2001 (*E. vivipara*); 16. Uchino *et al.* 1995 (*E. baldwinii*); 17. Ueno *et al.* 1988 (*E. vivipara*); 18. Keeley 1996 (*Isoetes howelli*); 19. Reddy *et al.* 2003 (*Pedilanthus tithymaloides*); 20. de Mattos and Lüttge 2001 (*C. minor*); 21. Nievola *et al.* 2005 (*Ananas comosus*).

is induced (Spencer *et al.* 1996, Reiskind *et al.* 1997). High light can trigger C_4 metabolism in *Flaveria brownii* (Cheng *et al.* 1988). In addition to effect of environmental variables, exogenous ABA could induce Kranz anatomy and C_4-like biochemistry in the submerged leaves of C_3 plant *E. vivipara* (Ueno *et al.* 1998), and C_4-like traits in *E. densa* (Casati *et al.* 2000).

Shift between C_3-CAM modes of photosynthesis

Environmental stimuli like low CO_2, high irradiance, drought, reduced day/night temperature difference, and nitrogen or phosphate deficiency may induce some C_3 plants to shift to CAM mode (Nobel and Hartsock 1987, Paul and Cockburn 1990, Haag-Kerwer *et al.* 1992, Grams and Thiel 2002). Species that respond to change in environmental stimulus (*Clusia minor*) are termed as facultative CAM compared to those (*C. rosea*) where development of CAM photosynthesis is constitutive or an obligate process, though both these cases represent rather extreme stages along a continuum depicting C_3 and CAM photosynthesis (Winter *et al.* 2008). CAM expression could be experimentally modified by altering natural temperature regime, *i.e.* removing day-night temperature fluctuations, increasing night or lowering day temperatures (Winter *et al.* 2008). *C. minor* can switch over to CAM within few days of exposure to high light or drought (Borland *et al.* 1992, Grams and Thiel 2002, Wanek *et al.* 2002). In some species like *C. uvitana*, a shift from C_3 and CAM photosynthesis could be associated with the developmental stage, such that the young and old leaves show C_3 and CAM modes, respectively (Zotz and Winter 1996). However, drought can induce CAM mode in both young shoots and mature plants in *C. pretensis* (Winter *et al.* 2008). CAM can also be induced experimentally by high soil salinity (Winter and Gademann 1991) and by ABA in *Mesembryanthemum crystallinum* (Chu *et al.* 1993).

On the contrary, plantlets of CAM plant *Ananas comosus*, when grown under constant temperature (28°C light/dark) developed C_3 mode of photosynthesis (Nievola *et al.* 2005). *C. minor* can shift from CAM to C_3 photosynthesis with release of drought or under well

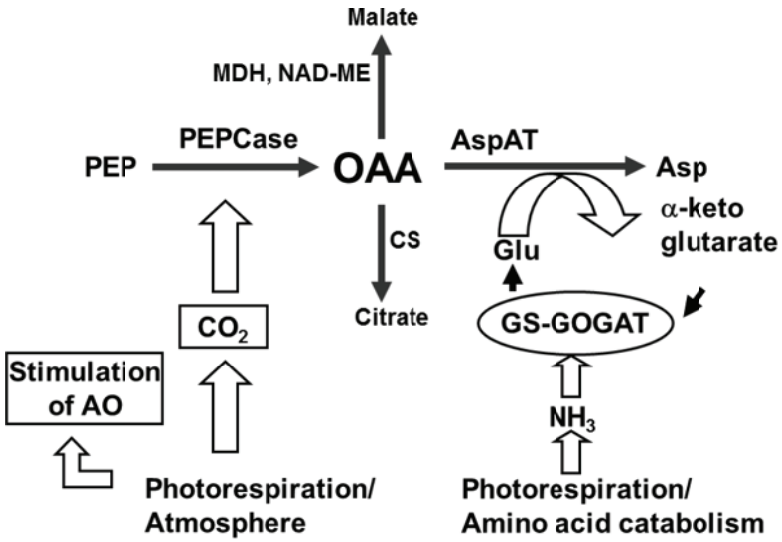

Fig. 4. Diagrammatic representation of the possible fate of oxalacetate (OAA) produced through a phospho*enol*pyruvate carboxylase (PEPCase) catalysed reaction at high altitude (HA) in some C_3 plants (Kumar *et al.* 2006, 2008) which showed enhanced activity of enzymes PEPCase, aspartate aminotransferase (AspAT) and glutamine synthetase (GS). Higher PEPCase activity is likely to result in enhanced OAA production that could get channelised to malate, citrate and aspartate (Asp). Enhanced AspAT activity in plants at HA suggested additional routing of carbon towards Asp synthesis. The requirement of amino group for Asp synthesis could be met via glutamine synthetase:glutamine:2-oxoglutarate aminotransferase (GS-GOGAT) pathway that supplies glutamate (Glu) as a source of amino group. The increased GS activity is likely to support the enhanced AspAT catalysed reaction by way of supplying Glu as a donor of amino group. A possible source of ammonia for GS catalysed reaction could be through photorespiratory reactions.

watered conditions (de Mattos and Lüttge 2001). Similarly, a drought-induced CAM activity could get reversed to C_3 mode in *Pedilanthus tithymaloides* (Reddy *et al.* 2003). The ecological advantage associated with CAM cycling is to improve carbon economy by reducing respiratory CO_2 losses (Wanek *et al*. 2002). While such a photosynthetic plasticity is seen mostly between C_3 and CAM species (Holtum 2002), a few species are known to show a relationship of CAM with C_4 photosynthesis.

Shift between C_4-CAM mode of photosynthesis

C_4 and CAM pathways have a common set of enzymes to facilitate CO_2 capture and concentrate it around Rubisco, but are considered rather incompatible due to the basic difference in their requirement of spatial and temporal differentiation of the PCA and PCR processes (Sage 2002b). In some species of *Portulaca*, a weak CAM and C_4 photosynthesis operate within the same leaf – CAM activity restricted to succulent cells in the interior of the leaf cells, while C_4 photosynthesis active in the periphery cells (Koch and Kennedy 1980, Guralnick 2001, Sage 2002b). In *Peperomia camptotricha*, which is a CAM plant, evidence of C_4 metabolism has been reported, thus suggesting that there are some C_4/CAM intermediate species (Nishio and Ting 1993, Lüttge 2004).

Shift in photosynthetic metabolism with altitude

Plants distributed along a wide altitudinal gradient are exposed to different partial pressure of CO_2 which drops with elevation. This is in contrast to all other terrestrial plants which experience relatively constant atmospheric CO_2 levels. Low CO_2 levels can substantially reduce photosynthetic productivity in C_3 plants, particularly at higher temperatures and during stress (Sage and Coleman 2001). The possibility that these low levels of CO_2 could suppress the net rate of photosynthesis at high altitude has been expressed by several researchers over a period of time (Decker 1959, Billings *et al.* 1961, Mooney *et al.* 1966, Friend and Woodward 1990). Acclimation of photosynthesis at reduced CO_2 levels is likely to help plants to optimize their performance. Some clues in this regard can be seen in the altitude-related increase in activity of enzyme Rubisco (Pandey *et al.* 1984) and the enhanced efficiency of carbon uptake (Körner and Diemer 1987, 1994;, Kumar *et al.* 2005, Vats and Kumar 2006). However, a definite shift in photosynthetic metabolism triggered by altitude has recently been reported in some crop (Kumar *et al.* 2006) and wild (Kumar *et al.* 2008) plants (Fig. 4).

Engineering plants to improve photosynthesis

C_4 photosynthesis - a model for C_3 crops

Approaches targeting to engineer plants with improved photosynthesis have largely focused on improving the inefficiency of C_3 photosynthesis. This could be achieved

by inducting traits of C_4 photosynthesis like over-expression of C_4 enzymes, improving CO_2/O_2 specificity of Rubisco, introduction of pyrenoid or carboxysomes into the chloroplast of C_3 crops to concentrate CO_2 on the pattern of algae and cyanobacteria for suppression of photorespiration (Häusler *et al.* 2002, Leegood 2002, Miyao and Fukayama 2003, Galmes *et al.* 2005), *etc*. The possibility of improving efficiency of photosynthesis also depends a great deal on overcoming its limitation under different sets of environmental conditions. At elevated levels of atmospheric CO_2, the efficiency of photosynthesis depends on the capacity of plants to regenerate RuBP (Miyagawa *et al.* 2001). It is speculated that the anticipated increase in CO_2 levels by the middle of this century would require about 30% increase in RuBP regeneration capacity to reap the maximum advantage (Long *et al.* 2004). Transgenic plants with higher RuBP regeneration capacity have shown substantial gain in photosynthesis and dry matter production (Miyagawa *et al.* 2001). Photosynthetic capacity can also greatly benefit if photooxidative damage in leaf can be avoided by inducing increase in thermal dissipation of energy *via* the formation of epoxidated xanthophylls (Baroli and Niyogi 2000, Havaux and Niyogy 1999), or altering plant canopy architecture to optimize light harvest at different leaf-layers that could nearly double the efficiency of light energy use in full sunlight (Havaux and Niyogy 1999, Ort and Long 2003, Long *et al.* 2006, Zhu *et al.* 2010). Improved light-use efficiency leading to increase in total assimilates available along with improved spike fertility could considerably raise yield potential in crops like wheat (Reynolds *et al.* 2009).

What does it take to make a C_4 plant?

The repeated evolution of C_4 syndrome in plants, despite its structural and enzymatic complexity, shows it to be a much potent route to counter the limitation of CO_2 (Long *et al.* 2006). C_4 cycle can bestow additional advantage of water and nitrogen use efficiencies. The capacity of C_4 plants to efficiently deliver CO_2 to Rubisco restrict photorespiration to a great extent and therefore inducting traits of C_4 photosynthesis in C_3 crops have most repeatedly been suggested to improve yield potential in agricultural crops (Matsuoka *et al.* 2001, Häusler *et al.* 2002, Leegood 2002, Surridge 2002, Miyao 2003, von Caemmerer 2003). C_4 cycle is actually accomplished by more than a dozen biochemical and anatomical combinations (Sage 2002b).

Kranz anatomy

For a very long time Kranz anatomy had been considered critical for the functioning of C_4 photosynthesis, and detection of any one aspect of the Kranz syndrome was accepted as a convenient measure to identify the presence of whole syndrome (Tregunna *et al.* 1970). Later, it was shown that a chlorenchymatous bundle sheath may not help a plant to be C_4 if not surrounded by mesophyll cells (Edwards *et al.* 1990), and the arrangement of mesophyll cells surrounding the chlorenchymatous bundle sheath must be such so as to resist CO_2 diffusion, and help build its concentration high enough to suppress photorespiration (Furbank *et al.* 1990). Leakage of CO_2 from the bundle sheath could impair the efficiency of C_4 photosynthesis (Furbank *et al.* 1989). For all these reasons, development of adequate structural components becomes critical for the effective functioning of C_4 photosynthesis. Our understanding regarding the genes controlling the development of different cell types in C_4 plants, however, continues to be scant (Leegood 2002).

How critical is Kranz anatomy for C_4 photosynthesis?

In terrestrial plants *Borszczowia aralocaspica* and *Bienertia cycloptera*, the PCA and PCR cycles of C_4 photosynthesis are reported to function without Kranz anatomy. C_4 photosynthesis operates within a single photosynthetic cell through spatial compartmentation of photosynthetic enzymes, and by separation of two types of chloroplast and photosynthetic enzymes within chlorenchyma cell cytoplasm (Voznesenskaya *et al.* 2001, 2002). In *B. aralocaspica*, PCR metabolism occurs at the end, which lies in proximity to vascular bundles, whereas PCR activity takes place at the distal end. In *B. cycloptera*, PCR and PCA were reported to function at the central and peripheral regions of the cytoplasm, respectively. These studies have shown that the critical feature regarding structural characteristics is to separate the PCR and PCA events in two different tissues or parts of the cell. The operation of C_4 cycle in a single cell has given new dimension for induction of C_4 traits into C_3 crops (Sage 2002a).

Overexpression of C_4 enzymes

In C_3 plants, the ratio of Rubisco to PEPCase is 15:1, and enzyme PEPCase may play a minor role in recapturing respiratory CO_2 in tissues from developing fruits and seeds (Latzko and Kelly 1983, Häusler *et al.* 2002). Whereas in C_4 plants, the Rubisco to PEPCase ratio is 1:1 (Latzko and Kelly 1983, Melzer and O'Leary 1987), which highlights the role and significance of PEPCase in C_4 species. Also, the properties of PEPCase in C_4 plants are modified compared to the C_3 form, such that the mutants lacking it, are unable to assimilate atmospheric CO_2 (Dever *et al* 1995, Cholett *et al.* 1996). Since PEPCase has a high affinity for CO_2, overexpression of the enzyme is considered to be a promising approach to enhance the efficiency of carbon fixation (Miyao and Fukayama 2003, Jiao *et al.* 2005, El-Sharkawy 2009).

Overexpression of single gene like *PEPCase* or double genes of C_4 cycle has been tried in crop and other plants with mixed results (Hudspeth *et al.* 1992, Gehlen *et al.* 1996, Ishimaru *et al.* 1997, Ku *et al.* 1999, Suzuki *et al.* 2000, Takeuchi *et al.* 2000, Häusler *et al.* 2002). Introduction of maize *PEPCase* in tobacco plant while

resulted in two-fold increase in its activity did not result in any significant increase in the rate of CO_2 assimilation (Hudspeth *et al.* 1992). Overexpression of enzymes like PEPCase in transgenic plants resulted in perturbation in metabolic fluxes, and in the absence of any photosynthetic gain, the changes in primary metabolism could be quite a waste of photosynthetic assimilates (Häusler *et al.* 2002, Miyao 2003). Suggestions were also made that introduction of *PEPCase* for C_4-like advantage, as in case of *Hydrilla* that has rapid induction kinetics, would shape up only after all the C_4 enzymes are fully induced (Magnin *et al.* 1997). However, overexpression of *PEPCase* in indica rice lead to enhancement in photosynthetic rate under conditions of high temperature (Bandyopadhyay *et al.* 2007). Similarly, overexpression of *PEPCase* and *PPDK* in rice improved its photosynthetic capacity with enhanced tolerance to photo-oxidation and produced 22–24% more grains (Jiao *et al.* 2002). Transgenic rice overexpressing *PEPCase* was shown to be more tolerant to photoinhibition that could improve protection from photooxidation (Jiao *et al.* 2005, Zhang *et al.* 2009).

To improve photosynthesis of crop plants on the pattern that of C_4 photosynthesis, Ku *et al.* (1999) introduced into rice maize genes encoding for enzymes PEPCase, PPDK, and NAD-ME, which are responsible for CO_2 capture, regeneration of PEP, and decarboxylation to liberate CO_2 around Rubisco, respectively. The transgenic rice thus produced showed gain in the photosynthetic rates and grain yield by about 30% and 35%, respectively. In the absence of any evidence of a functional C_4 cycle, these gains are presumably due to improvement in plant's ability to tolerate stress and increase in stomatal conductance (Surridge 2002). Nonetheless, the study lends support to the efforts to reengineer crops to improve its photosynthetic efficiency under specific set of conditions in which CO_2 availability is limited. While overproducing multiple enzymes for enhanced photosynthetic efficiency appear to be more promising (Häusler *et al.* 2001, Miyagawa *et al.* 2001, Häusler *et al.* 2002, Wu *et al.* 2002, Miyao 2003), there are no published results to show that plants co-express all the enzymatic steps required for a C_4 cycle, including overexpression of CA (Leegood 2002, Raines 2006).

Manipulating Rubisco, Rubisco activase and carbonic anhydrase

Rubisco

Rubisco, being the key enzyme of Calvin cycle, is the most obvious target for attempts to improve photosynthetic rate. The enzyme has eight large, chloroplast-encoded and eight small, nuclear-encoded protein subunits. The large subunits contain structural information necessary for catalyses, and have been the center of focus for genetic screening and site directed mutagenesis. Efforts like amino acid substitution of large subunits with an objective to improve the catalytic properties of Rubisco have though not been fruitful (Spreitzer and Salvucci 2002, Parry *et al.* 2003). Much is not known regarding the nuclear encoded small subunits, but there are suggestions that the observed differences in these units (Andersson and Taylor 2003) might contribute to catalytic efficiency of Rubisco (Spreitzer 2003), and remains an area to be further explored (Raines 2006).

Natural variation in the catalytic properties of Rubisco in different photosynthetic organisms could be exploited to engineer Rubisco with higher CO_2 specificity, with a specific advantage under high temperature (Kostov *et al.* 1997, Tabita 1999). It has been calculated that introduction of such a Rubisco would increase catalytic value two times in crop plants and could increase photosynthesis by 20% (Reynolds *et al.* 2000, Raines 2006). However, introducing Rubisco with high specific factor in transgenic plants would only be advantageous if not accompanied by any loss in the rate of carboxylation (Andrews and Witney 2003, Parry *et al.* 2003, Raines 2006). Attempts to engineer a better Rubisco could be further complicated owing to different complexities like species specificity of Rubisco activase, need for different activase inhibitors, proteins, *etc*. (Spreitzer 2003). Some tight binding inhibitors of Rubisco like CA1P (2-carboxyarabinitol-1-phosphate) accumulate under stress conditions and are responsible for low Rubisco activity, release of which can be affected by another enzyme Rubisco activase (Keys *et al.* 1995, Medrano *et al.* 1997). In addition to decreasing the activity of Rubisco such inhibitors also confer protection from oxidative or proteolytic damage (Khan *et al.* 1999). Elucidating biosynthetic and degradative pathways for the synthesis or degradation of these inhibitors can help modulate Rubisco activity and stability (Parry *et al.* 2008).

Rubisco activase (RA)

There is evidence to show that Rubisco activation in C_3 plants markedly decreases above 30–35^{o}C (Robinson and Portis 1988). It is also well known that limitation of photosynthesis at high temperature owes much to susceptibility of enzyme RA rather than Rubisco itself (Feller *et al.* 1998, Rokka *et al.* 2001). RA therefore is an important component to be addressed in order to improve photosynthetic performance under high temperatures – a likely condition under changing climate scenario. Overexpression of RA or changing it to a more stable form is expected to impart advantage under moderate heat stress (Parry *et al.* 2003). Since certain C_4 plants are known to be photosynthetically active even at critically high temperature up to 48^{o}C, it is suggested that these could be a source of RA for plants under hot environment (Raines 2006). RA with increased thermostability produced by DNA shuffling resulted in increase in photosynthetic rates and leaf area (Zhu *et al.* 2005).

Carbonic anhydrase (CA)

CA has a role in catalyzing reversible conversion of CO_2 and HCO_3^- in the leaf tissues of both C_3 and C_4 plants. In C_3 plants, it is believed to facilitate diffusion of CO_2 across the chloroplast membrane (Price *et al.* 1994, Williams *et al.* 1996). In C_4 plants, PEPCase uses HCO_3^- as its primary substrate for fixation of CO_2 into oxal-acetate, a conversion accomplished by CA in the meso-phyll cell cytosol (von Caemmerer *et al.* 2004). In the absence of cytoplasmic CA, photosynthesis in C_4 plants was reported to slow down by a factor of 10^4 (Badger and Price 1994).

Three evolutionarily unrelated families of CAs, *viz.* α-, β - and γ-CA are reported from higher plants, algae and cyanobacteria (Moroney *et al.* 2001). While all of the three types are present in higher plants, only α-CA and β-CA have been reported from cyanobacteria and α-CA from animals. *Arabidopsis* database shows nearly 14 genes potentially encoding CA (Moroney *et al.* 2001). CA represents 1–20% of the total soluble protein which put it next only to Rubisco protein (Tiwari *et al.* 2005). In aquatic angiosperms and algae, CA located external to cell membrane plays a key role in facilitating CO_2 to enter the cell surface. Since HCO_3^- is the predominant species at alkaline pHs, the periplasmic CA are critical for both active and passive entry of CO_2 into the cell (Badger 2003). In cyanobacteria, carboxysomal CA supplies CO_2 to Rubisco. Absence of CA in certain regions helps HCO_3^- to accumulate in high concentrations, thereby minimizing leakage of CO_2 (Badger 2003). Much needs to be understood regarding the number, location and physiological roles of the CAs in different organisms. In most of the discussions on biotechnological approaches aiming to transfer C_4-like features into C_3 plants, CA has received much less attention (Häusler *et al.* 2002).

Can we do away with photorespiration?

If oxygenase reaction of Rubisco is merely a waste of carbon resource, eliminating it by impairing one of the associated enzymes or reaction of the pathway could perhaps be a simpler option to inhibit photorespiration. However, work carried out in this direction revealed that mutants lacking any one of the associated enzyme of photorespiratory metabolism do not survive, except under conditions of high CO_2 or low oxygen – both conditions decrease oxygenation (Somerville 2001). Attempt to reduce the activity of glycine decarboxylase, which is one of the associated enzymes of photorespiration, has resulted in reduction in photosynthesis and growth rates (Henkes *et al.* 2001). Leaves of some high altitude plants are shown to operate photorespiratory cycle as one of several other strategies to provide strong electron sink for photoprotection (Streb *et al.* 1998). Photorespiratory cycle may also provide metabolites for other metabolic processes, such as glycine for the synthesis of glutathione which has a role in stress protection (Wingler *et al.* 2000). Therefore, important thing is not to do away with photorespiration but to recapture carbon of the photorespiratory cycle.

Exploiting the underutilized photosynthetic capacity in plants

History of intensive selection to increase crop yield over the past century has not shown any increase in the rate of photosynthesis per unit leaf area. Increase in yield capa-city instead relates better to increase in photosynthesis per unit ground area as a result of increases in leaf area and nitrogen content (Reynolds *et al.* 2000) due to application of nitrogen fertilizer. Total photosynthesis and its underutilized capacity in plants therefore remains a great potential to be tapped.

Decades of research has shown that older wheat cultivars were severely sink-limited, a situation that has not improved appreciably in modern cultivars. Sink potential in crop plants can however be enhanced by genetic improvement in radiation-use efficiency under different stages of growth and fluctuating environmental conditions (Reynolds *et al.* 2000). It has been suggested that improved radiation use efficiency may not only increase the total assimilates available for spike growth as in case of wheat but could minimise floret abortion affected by underutilized photosynthetic capacity during grain filling (Reynolds *et al.* 2009). Sink strength of crop plants could also be improved by manipulating the spike morphology (number of spikelets/spike, increased grain number and size) (Dencic 1994, Reynolds *et al.* 2000). Optimizing composition of the photosynthetic apparatus, as well as leaf nitrogen distribution, throughout the canopy could make photosynthesis equally efficient at different light intensities (Evans 1993, Zhu *et al.* 2010). Improved yield potential in modern maize owes largely to tolerance of photosynthesis to low temperatures during the early part of the day and soil moisture deficits during grain filling (Tollenaar and Wu 1999). Studies conducted on cotton and bread wheat showed stomatal conductance related positively to crop yield during period of heat stress (Lu *et al.* 1998), and the trait can serve to screen better cultivars for higher temperature regimes.

Photosynthetic rate of the whole canopy can be enhanced by manipulation of leaf angle, which is under relatively simple genetic control, regulated by only two to three genes (Reynolds *et al.* 2000). In wheat again, erect leaf lines showed improvement in both biomass and grain yield compared to control (Innes and Blackwell 1983).

Some other traits that could be targeted for crop improvement may include delaying leaf senescence or extending crop duration and the timing of crop development to suit the type of environment in which crop is grown (Richards 2000). By delaying leaf senescence in genetic variants in *Sorghum*, deconstruction of the photosynthetic apparatus during leaf senescence could be partially or completely prevented (Thomas and Howarth 2000). Suppression of drought-induced leaf senescence in transgenic plants (*Nicotiana tabaccum*), by expressing an isopentenyltransferase gene, resulted in outstanding drought tolerance, accompanied by vigorous growth after a long drought period that killed the control plants. Such drought-tolerant crops can grow under restricted water regimes without diminution of yield (Rivero *et al.* 2007).

Finally, global climate change is expected to increase the frequency and severity of abiotic constraints, leading to greater prevalence or incidences of drought and or temperature stresses, water logging, and salinity. The renewed agricultural goals call for engineering more versatile and resilient crops, tolerant to environmental stresses like drought, submergence, salt or metal toxicity, in addition to improving yield potential from both irrigated and nonirrigated lands (Herring 2008, Takeda and Matsuoka 2008).

Conclusion

Meeting future world food demand banks heavily on biotechnological approaches important among which is to improve photosynthesis or exploit its underutilized capacity in plants. The inefficiency of C_3 photosynthesis, which owes largely to the bifunctional character of Rubisco and its low catalytic rates, could greatly be improved taking examples from photosynthetic organisms where such limitations have successfully been overcome. Apart from improving CO_2 sequestration, optimizing photosynthetic performance in relation to different stresses like temperature and drought could also appreciably enhance yield potential of crops under field conditions. The enormous plasticity found within photosynthetic organism offers some clues in this regard.

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