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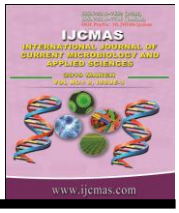

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# Enhancement of Photosynthetic Efficiency of C3 Plants

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**A B S T R A C T**

A new "Green revolution" is needed in world agriculture to increase crop yields for food and bioenergy, because gains from conventional breeding method are less than world population growth. Efforts to increase crop productivity must also consider global change. Carbon-dioxide, methane and other greenhouse gases in atmosphere leads to global warming. Photosynthesis is the single most effective natural regulator of carbon dioxide in the Earth's atmosphere. It is timely to consider what new opportunities exist in the current "omics" era to engineer increases in photosynthesis. Significant enhancement of photosynthesis in several C3 plants like rice, wheat and potato occurs due to insertion of C4 genes into C3 plants. It has been suggested that the C4 pathway evolved from C3 ancestors as an adaptation to high light intensities, high temperatures, and dryness. The C4 plants have several important characteristics such as high photosynthetic rates, high growth rates, low rates of water loss and a specialized leaf structure, high yields and water & nitrogen-use efficiencies, by concentrating $CO_2$ around Rubisco, C4 plants drastically reduce photorespiration and concentration Of CO2 to the vicinity of Rubisco in C4 plants favours the carboxylation of RuBP over its oxygenation. There are three major strategies to improve the photosynthetic efficiency of C3 plants, such as Improving the quality and quantity of rubisco, Increasing thermotolerance of Rubisco Activase, Increasing $Co_2$ concentration around Rubisco to enhance catalytic rate of Rubisco and to minimize the photorespiration and Over expression of C4 genes.

## Introduction

All people, at all times, have physical and economic access to sufficient, safe and nutritious food to meet their dietary needs and food preferences for an active and healthy life'. However, with a burgeoning population, decreasing arable land, stagnation in agricultural production, the erratic and extreme environmental changes due to global warming along with various biotic and abiotic stresses, it becomes an overwhelming task to ensure complete food and nutrient security. Recent statistics reveal that over 870 million people are chronically undernourished in terms of dietary energy supply (FAO, 2012). It is estimated that global food production must increase 50% by 2030 and 70%–100% by the year 2050, to feed adequately a global population of around nine billion people

(Covshoff and Hibberd, 2012; Long, 2012; Zhu *et al.*, 2010a). A new "green revolution" is needed in world agriculture to increase crop yields for food and bioenergy, because gains from conventional breeding method are less than world population growth. Efforts to increase crop productivity must also consider global change. Owing to increases in climate uncertainty, it would be most beneficial if genetic improvements increased yields across a range of environments. Increasing the maximum attainable yield of existing food crops could be part of the solution. It is theoretically possible to increase yield potential by 50% in some species by raising their photosynthetic capacity [Mitchell *et al.*, 2006, Parry *et al.*, 2011, Hibberd *et al.*, 2008]. If this proved possible in practice, then it would greatly contribute to food security. Increasing photosynthetic capacity raises yield potential. Dramatically increasing yield potential is not trivial because the outcome results from complex interactions between contributing components.

During the Green Revolution, light interception and harvest index were maximised. Extending the growing season is undesirable because management practices are tied to cyclical weather patterns that allow production within specific time frames, and canopy production and architecture are thought to be optimized. Yield potential of C3 crops would be improved by approximately 50% by increasing the photosynthetic efficiency of C3 by converting C3 plants to C4. This led to the suggestion that converting crops from C3 to C4 could mitigate the global food crisis [Reynolds *et al.*, 2011].

## Photosynthesis

Photosynthesis is the most important metabolic process relative to crop productivity because carbohydrates account for more than 85% of the dry weight in plants. It is the process by which green plants and certain other organisms transform light energy into chemical energy. During photosynthesis in green plants, light energy is captured and used to convert water, carbon dioxide, and minerals into oxygen and energy-rich organic compounds.

## Modes of photosynthesis

C3 pathway
C4 pathway
Crassulacean Acid Metabolism

The C3 pathway of photosynthesis evolved first in autotrophic organisms. However, over geologic time plants evolved several CCMs ($Co_2$ concentrating mechanisms) in response to decreases in atmospheric $CO_2$ level. Bicarbonate transport system in cyanobacteria, algae and aquatic plants and the C4 pathway and CAM in higher plants. The most productive crops, such as corn, sorghum and sugarcane, use the C4 pathway while most of the important agronomic crops, such as rice, wheat and potato, use the C3 pathway.

## C3 pathway

Plants that survive solely on $C_3$ fixation ($C_3$ plants) tend to thrive in areas where sunlight intensity is moderate, temperatures are moderate, carbon dioxide concentrations are around 200 ppm or higher, and groundwater is plentiful. The $C_3$ plants, originating during Mesozoic and Paleozoic eras, predate the $C_4$ plants and still represent approximately 95% of Earth's plant biomass. $C_3$ plants lose 97% of the water taken up through their roots to transpiration.[2] Examples include rice and barley.

$C_3$ plants cannot grow in very hot areas because RuBisCO incorporates more oxygen into RuBP as temperatures increase. This leads to photorespiration (also known as the

oxidative photosynthetic carbon cycle, or C2 photosynthesis), which leads to a net loss of carbon and nitrogen from the plant and can therefore limit growth. In dry areas, $C_3$ plants shut their stomata to reduce water loss, but this stops $CO_2$ from entering the leaves and therefore reduces the concentration of $CO_2$ in the leaves. This lowers the $CO_2$:$O_2$ ratio and therefore also increases photorespiration. $C_4$ and CAM plants have adaptations that allow them to survive in hot and dry areas, and they can therefore out-compete $C_3$ plants in these areas. The isotopic signature of $C_3$ plants shows higher degree of $^{13}C$ depletion than the $C_4$ plants, due to variation in fractionation of carbon isotopes in oxygenic photosynthesis across plant types.

## C4 photosynthesis

$C_4$ fixation is an elaboration of the more common $C_3$ carbon fixation and is believed to have evolved more recently. $C_4$ overcomes the tendency of the enzyme RuBisCO to wastefully fix oxygen rather than carbon dioxide in the process of photorespiration. This is achieved by ensuring that RuBisCO works in an environment where there is a lot of carbon dioxide and very little oxygen. $CO_2$ is shuttled via malate or aspartate from mesophyll cells to bundle-sheath cells. In these bundle-sheath cells $CO_2$ is released by decarboxylation of the malate. C4 plants use PEP carboxylase to capture more $CO_2$ in the mesophyll cells. PEP Carboxylase (3 carbons) binds to $CO_2$ to make oxaloacetic acid (OAA). The OAA then makes malate (4 carbons). Malate enters bundle sheath cells and releases the $CO_2$. These additional steps, however, require more energy in the form of ATP. Using this extra energy, $C_4$ plants are able to more efficiently fix carbon in drought, high temperatures, and limitations of nitrogen or $CO_2$. Since the more common $C_3$ pathway does not require this extra energy, it is more efficient in the other conditions.

The $C_4$ plants often possess a characteristic leaf anatomy called *kranz anatomy*, from the German word for wreath. Their vascular bundles are surrounded by two rings of cells; the inner ring, called bundle sheath cells, contains starch-rich chloroplasts lacking grana, which differ from those in mesophyll cells present as the outer ring. Hence, the chloroplasts are called dimorphic. The primary function of kranz anatomy is to provide a site in which $CO_2$ can be concentrated around RuBisCO, thereby avoiding photorespiration. In order to maintain a significantly higher $CO_2$ concentration in the bundle sheath compared to the mesophyll, the boundary layer of the kranz has a low conductance to $CO_2$, a property that may be enhanced by the presence of suberin. The carbon concentration mechanism in $C_4$ plants distinguishes their isotopic signature from other photosynthetic organisms.

## Crassulacean acid metabolism (CAM)

Crassulacean acid metabolism is a carbon fixation pathway that evolved in some plants as an adaptation to arid conditions. In a plant using full CAM, the stomata in the leaves remain shut during the day to reduce evapotranspiration, but open at night to collect carbon dioxide ($CO_2$). The $CO_2$ is stored as the four-carbon acid malate in vacuoles at night, and then in the daytime, the malate is transported to chloroplasts where it is converted back to $CO_2$, which is then used during photosynthesis. The pre-collected $CO_2$ is concentrated around the enzyme RuBisCO, increasing photosynthetic efficiency. CAM is an adaptation for increased efficiency in the use of water, and so is typically found in plants growing in arid conditions.

Minimum energy losses showing the percentage remaining (inside arrows) and percentage losses (at right) from an original 100% calculated for stage of photosynthetic

energy transduction from sunlight incident on a leaf to plant biomass. Both $C_3$ and $C_4$ (NADP–malic enzyme type) photosynthesis are presented. Calculations assume a leaf temperature of 30 ◦C and an atmospheric [$CO_2$] of 387 ppm. The theoretical maximal photosynthetic energy conversion efficiency (εc) is 4.6% for $C_3$ and 6% for $C_4$ plants. These values are for total full-spectrum solar radiation. If the analysis is limited to photosynthetically active radiation (400–700 nm), then these values become 9.4% for C3 and 12.3% for C4.

## $C_4$ plants - agronomically desirable traits

Higher photosynthetic capacity/high carbon assimilation, higher growth rate & bio mass production, high nutrient and water use efficiency, biofuel production, other benefits from operating at a lower stomatal conductance might include a greater resistance to gaseous pollutants such as ozone or $SO_2$, reduce the deleterious effects of photorespiration on carbon gain by concentrating $CO_2$, leading to increases in radiation use efficiency and productivity, particularly in tropical climates. Due to less solar energy utilization (Fig. 1) and higher photosynthetic losses (Fig. 2) in C3 plants their is need to manipulate C3 photosynthetic mechanism by converting it to C4 photosynthetic mechanism, because C4 has higher solar energy utilization, less photosynthetic losses along with agronomically desirable traits.

## Strategies to convert C3 to C4:

Improving the quality and quantity of rubisco
Increasing thermotolerance of Rubisco Activase
Increasing $CO_2$ concentration around Rubisco to enhance catalytic rate of Rubisco and to minimize the photorespiration.
Overexpression of C4 genes:

## Improving the quality and quantity of Rubisco

Rubisco (Ribulose 1,5-bisphosphate carboxylase/oxygenase) is the most abundant protein on Earth and it is an essential component of the photosynthetic process of fixing $CO_2$ into organic carbon. In $C_3$ plants it is known to have low catalytic activity, so enhancing the Rubisco performance via quality control and/or quantity control is an obvious target for both increasing photosynthetic performance and nitrogen use efficiency (Yamori, 2013). Recently it has been reported that $C_4$-Rubisco small subunit *(RbcS)* gene was introduced to rice which was derived from sorghum, successfully produced chimeric Rubisco with a greater catalytic turnover rate of Rubisco (*kcat*) in the transgenic rice (Ishikawa *et al.,* 2011). Whitney, *et al.,* (2011) reported that single residues controlling enzymatic properties of Rubisco have been identified and it was successfully engineered to produce greater Rubisco proteins in *Flaveria* species from C3 to C4 catalysis.

## Increasing thermotolerance of Rubisco Activase

Thermotolerance of Rubisco Activase has to be increased to sustain Rubisco Activity under high temperature. The activation state of Rubisco is dependent on the heat sensitive enzyme, Rubisco activase. Kurek, *et al.,* (2007) and Kumar *et al.,* (2009) reported that introduction of a thermostable Rubisco activase into *Arabidopsis* resulted in increases in plant tolerance to heat stress and photosynthetic performance at high temperature. In addition, the thermal stability of photosynthesis was increased slightly when Rubisco activase of maize was overexpressed in rice [Yamori, *et al.,* 2012]. Thus, manipulating Rubisco activase could be a potential target for stimulation of

photosynthesis and especially growth at high temperature.

## Increasing $CO_2$ concentration around Rubisco to enhance catalytic rate of Rubisco and to minimize the photorespiration

Rubisco catalyses net $CO_2$ assimilation in all photosynthetic organisms. Despite this central role, Rubisco is an inefficient enzyme that limits photosynthetic productivity, particularly in plants with the C3 photosynthetic pathway. Rubisco has a slow carboxylation rate (kcat c) and a relatively low affinity for $CO_2$, with a Km for $CO_2$ at ambient $O_2$ (Kc air) close to the $CO_2$ concentration in a C3 leaf mesophyll cell (Galm_es *et al.,* 2014). Rubisco also catalyses D-ribulose-1,5-bisphosphate (RuBP) oxygenation, resulting in the energetically expensive photorespiratory pathway where previously fixed $CO_2$ is lost (Sharkey, 1988).

These features necessitate a large investment in the enzyme (up to 50% of leaf soluble protein) to support adequate rates of $CO_2$ assimilation (Parry *et al.,* 2013). Increasing the operating efficiency of Rubisco and reducing photorespiration are important approaches for improving yields in C3 crop plants (Whitney *et al.,* 2011; Parry *et al.,* 2013; Carmo-Silva *et al.,* 2015; Long *et al.,* 2015; Ort *et al.,* 2015). The operating efficiency of Rubisco in C3 plants could be enhanced by elevating the $CO_2$ concentration in the chloroplast by means of carbon concentrating mechanisms (CCMs).

Possibilities include using components of biochemical CCMs (as in C4 and CAM photosynthesis) and/or the biophysical inorganic carbon accumulation mechanisms from cyanobacteria and eukaryotic algae (von Caemmerer *et al.,* 2012; Price *et al.,* 2013; Meyer *et al.,* 2016).

## Overexpression of C4 genes

Based on (i) the limited factors of photosynthesis in C3 plants and (ii) high photosynthesis efficiency, high rates of biomass accumulation, and high water and N-use efficiency in C4 plants, biotechnologists have long been intrigued by the overexpression of different enzymes of the C4 pathway in C3 plants (Edwards *et al.,* 2001; Leegood, 2002; Häusler *et al.,* 2002; von Caemmerer and Furbank, 2003).

Hence, individual or multiple enzymes (PEPC, PPDK, PCK, NADP-ME and NADP-MDH) of the C4 pathway have been overexpressed in different C3 plants (e.g. tobacco, potato, rice and *Arabidopsis*).

Ishimaru *et al.,* (1998) overexpressed a C4 maize PPDK gene in C3 transgenic potato. PPDK activity in the leaves of transgenic potatoes was up to 5.4-fold higher than that of the control plants (WT and treated control plants. A significant increase in the δ13C value was observed in the transgenic plants, suggesting a certain contribution of PEPC as the initial acceptor of atmospheric $CO_2$.

Their results suggested that elevated PPDK activity may alter carbon metabolism and lead to a partial operation of C4-type carbon metabolism. Zhang *et al.,* (2010) also introduced the intact maize C4-*Pdk* gene into rice (*Oryza sativa* L. *indica* "IR64").

Expression of C4-*Pdk* in most transgenic rice lines resulted in the increase of $CO_2$ assimilation rates compared to untransformed control plants.

Lipka *et al.,* (1999) transformed two potato lines using NADP-ME-cDNA constructs. Increased levels of NADP-ME were found in chloroplasts of transformants.

**Fig.1** Solar energy utilization

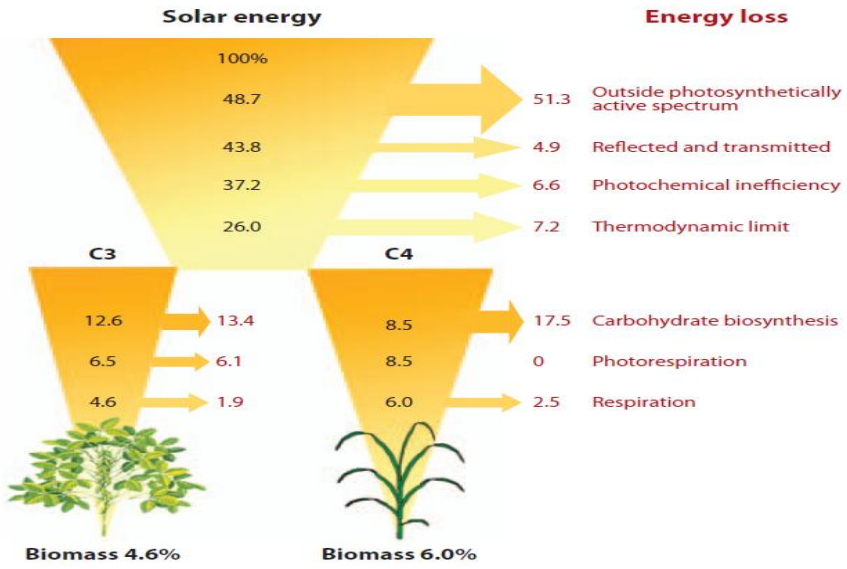


**Fig.2** Photosynthetic loses in C3 crop (rice) in the field

| Process | Cause of loss | Cause and mechanism | Conditions under which loss occurs | Possible remedy for improvement |
|---|---|---|---|---|
| Light harvesting | Poor absorption | Erect upper leaves | Large solar angle at midday | Altered canopy structure |
| | Light saturation | Limitation on $P_{max}$ | High irradiance | Improved acclimation to increase $P_{max}$ |
| | Down-regulation | Slow relaxation of non-photochemical quenching | Fluctuating light intensity | Decreased and/or altered *qE* |
| Electron transport | Photoinhibition | Damage to PSII reaction centre | Severe stress conditions, older leaves? | Improved photoprotection |
| C assimilation | Photorespiration | Rubisco oxygenase | High leaf temperature | Improved Rubisco; $C_4$ photosynthesis |
| | Decline in $P_{max}$ | Stomatal closure/feedback inhibition | Mid-morning in high irradiance | Altered stomatal responses/carbohydrate metabolism |
| | | Leaf senescence | During grain filling? | Delayed leaf senescence |
| Partitioning | Accumulation of stem carbohydrate | Poor remobilization of resources | During grain filling? | Altered internal metabolite signalling |
| Respiration | Loss of fixed carbon | High *LAI* with inefficient lower leaves | Mature canopy; high night temperature | Decreased respiration capacity; improved N economy in lower leaves to reduce *LAI* |

Expression of both genes led to a significantly reduced electron requirement for apparent CO2 assimilation (e/A) at higher temperature. At low temperatures (15°C) 11 electrons per CO2 were assimilated (e/A) in controls, single (PEPC or NADP-ME) and double (PEPC and NADP-ME) transformation. However, when the leaf temperature was raised to 36°C, the electron requirement of the double transformation (15 e/A) was 65% of controls or single transformation (23 e/A). Thus, the temperature-dependent increase in electron requirement was reduced in the double transformation, suggesting a suppression in the oxygenation reaction of Rubisco.

## Challenges associated with placing C4 photosynthesis into C3 leaves

The complexity of C4 photosynthesis indicates that its integration into C3 leaves will be an enormous challenge. Indeed, many domesticated C3 crops, including rice, belong to genera that are deeply embedded in clades consisting only of C3 species [Sage *et al.*, 2011] and so it can be argued that there is some inherent incompatibility between the current genomes of these species and operation of C4 photosynthesis. Additionally, major gaps in our knowledge of the C4 leaf must be addressed. No master regulator(s) has been isolated and loci for many of the transporters associated with metabolite fluxes, modifications to cell biology as well as the specialized anatomy of C4 leaves remain to be identified. The number of genes essential to a functional C4 pathway is large. Existing methods of genetic engineering are probably insufficient for its installation, and the engineering challenge will probably increase as we identify more genes essential to C4.

## The compatibility of C3 leaves with C4 biochemistry

Some characteristics of C4 biochemistry are present in C3 plants. Cells adjacent to veins in tobacco and Arabidopsis use C4 acid decarboxylases to release CO2 from malate [Hibberd and Quick, 2008]. Additionally, some endogenous Arabidopsis genes have BS specificity [Brown *et al.*, 2010]. The ability to accumulate enzymes in a cell-specific manner across diverse C3 lineages implies a pre-existing regulatory mechanism(s) is recruited during C4 evolution. Consequently, the specific site of enzyme expression and the amount accumulated may only need modification rather than generation de novo when evolving C4. The latent ability for C3 genes to be expressed in a C4 manner was recently demonstrated [Brown *et al.*, 2011].

In conclusion, converting a C3 crop to C4 photosynthesis is an extremely challenging goal to maintain a C4 plant in a timely manner to alleviate world hunger. To achieve this Grand Challenge consolidated effort by plant biologist of various expertise include physiology, biochemistry, molecular biology and agronomy would be required to achieve the objective of making C3 plant to C4 type, The extent of our understanding of photosynthesis clearly indicates that enough scope is left for improvement and regulation of this ancient and critical biological reaction to achieve our goals of sustainable food production.

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