*Int.J.Curr.Microbiol.App.Sci* (2017) *6*(3): 1567-1574

International Journal of Current Microbiology and Applied Sciences
*ISSN: 2319-7706* **Volume 6 Number 3 (2017) pp. 1567-1574**
Journal homepage: http://www.ijcmas.com

**Review Article** https://doi.org/10.20546/ijcmas.2017.603.180

# $C_4$ Photosynthesis and Biomass

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**ABSTRACT**

2016 marked the 50th anniversary of the discovery of Hatch-Slack pathway, more popularly known as the $C_4$ photosynthetic pathway in sugarcane leaves. Since then, there had been a significant development in understanding the $C_4$ syndrome and its evolutionary background. $C_4$ photosynthesis produces almost a quarter of the world's entire primary productivity, despite having merely a few plant lineages to compete with. This clearly depicts the extraordinary capacity of the system to effectively trap carbon and converting it into plant biomass. It's not a surprise that $C_4$s represent some of the major crops in the world. This paper discusses the capacity of $C_4$ photosynthesis, its advantage and limitations in producing plant biomass for the sustainable energy future of our planet.

**Keywords**

Biomass crops, $C_4$ Photosynthesis, Bioenergy

**Article Info**

***Accepted:***
22 February 2017
***Available Online:***
10 March 2017

## Introduction

2016 marked the 50th anniversary of the discovery of Hatch-Slack pathway, more popularly known as the $C_4$ photosynthetic pathway (von Caemmerer *et al.*, 2017; Furbank *et al.*, 2016; Sage *et al.*, 2016) in sugarcane leaves (Hatch and Slack, 1966). With the changing scenario of modern day civilization, energy availability is increasingly becoming a crucial issue. Currently most of the developed nations rely on fossil fuel sources for energy, which are non-renewable, limited in supply and convert the fossilized carbon reserves into carbon di oxide, which acts as a greenhouse gas, responsible for global warming. But the future energy sources have to be sustainable and renewable, cost-effective and efficient, safe and easy to harvest (McKendry, 2002; Chum and Overend, 2001). The first sign of an alternate and more sustainable source of energy dates back to 1970s, when America faced the first fossil oil crisis, which resulted in a spike in oil prices that led to the first push for the development of renewable energy (Karp and Halford, 2010).

Biomass is the most common form of renewable resource that is abundantly used in the developing nations but not so much in the industrially developed nations (McKendry, 2002). According to the current estimate, biofuel and wastes supply 10.2% (or 50 EJ) of the total energy need of the world (Key World Energy Statistics, 2015; International Energy Agency, 2011), which is the single largest renewable energy source today (Field *et al.*, 2008; International Energy Agency, 2011). And by 2050 they will supply as much as 27% of transportation fuel of the world (International Energy Agency, 2011). The Rio United Nations Conference on environment and development (1992), the renewable intensive global energy scenario (RIGES) suggested that, by the year 2050, about 50% of the current primary energy consumption and 60% of the electricity in the world would be from renewable sources of which biomass is a significant part (McKendry, 2002; Field *et al.*, 2008; Berndes *et al.*, 2003).

## Biomass

Biomass is a term for all organic materials that are produced by plants on a renewable basis (International Energy Agency, 2011). Green plants convert sunlight into plant material (biomass) through photosynthesis (McKendry, 2002). Biomass is a source, indigenous to most countries and the diversification of which will lead to a more secure supply of energy. Biomass is a very important part the world economy. Apart from energy production, about 60% of the needed process energy in pulp, paper and forest products is supplied by biomass (Chum and Overend, 2001). Biomass production has environmental benefits, such as reduction in emission of Green House Gases (GHG), reduced eutrophication of local water bodies and reduced use of harmful agricultural chemicals and side by side generating employment (McKendry, 2002; Berndes *et al.*, 2003). Plants take up $CO_2$ from air and convert it into biomass. Thus, using biomass as fuel releases only the carbon that was already in the air. Also, the underground plant biomass decomposes and adds to the soil carbon pool thus giving a carbon negative equilibrium. The term biomass energy can refer to any source of heat energy produced from non-fossil fuel origin like crop residues (haulms of grain legumes, stalks of maize, sorghum and millets, straw from rice, wheat, barley and oat), energy crops, timber from forests, animal waste and municipal waste (International Energy Agency 2011; Field *et al.*, 2008; Fischer *et al.*, 2001). The search for a sustainable substitute for fossil fuel has stimulated research into bioenergy crops (Purdy *et al.*, 2013). Energy crop production on surplus agricultural land has a potential contribution of 0–88 $EJy^{-1}$. Crucial factors determining biomass availability for energy are: 1. The future demand for food, depending upon the population growth and the future diet; 2. world-wide adaptation of food production system over the next 50 years; 3. Forest and energy crops productivity; 4. Improved use of bio-materials; 5. availability of degraded and marginal land and 6. Conversion of surplus agricultural land into forests and permanent pastures (Hoogwijk *et al.*, 2003; Yamamoto *et al.*, 2001).

## Dedicated energy crops

As pointed out previously, any crop can be considered as a source of biomass. However, a ‘dedicated bioenergy crop’ refers to nonfood crops that are solely grown for biomass production (Karp and Halford, 2010). For a dedicated energy crop the following criteria must be fulfilled, the feedstock must: 1. Be easily and reliably transformed in useful forms of energy; 2. Have dense tillering; 3. Have high energy per unit of dry matter; 4. Be available throughout the year; 5. Favor the cost of production and delivery; 6. Be a source of renewable energy; 7. Be tolerant to biotic and abiotic stress; 8. Not compete with the arable crop production; 9. Environmentally secure (McKendry, 2002; Purdy *et al.*, 2013; Matsuoka *et al.*, 2014). Major biomass energy crops may include

Sorghum, Maize, Reed canary grass, Miscanthus, Sugarcane (Sims *et al.,* 2006), Switch grass and newly developed 'Miscane' (Burner *et al.,* 2015; Science 2.0, news article, 2015; Chen and Danao, 2015). It is very crucial to select an appropriate energy crop, for best adaptation, benefit and restoration of degraded land (McKendry, 2002; Hoogwijk *et al.,* 2003).

## Photosynthesis and its types

Photosynthesis is an engine that functions under sunlight by interaction of $CO_2$ in the air and water and production of carbohydrates that are the building blocks of biomass. Photosynthesis converts only a mere 1% of total sunlight to stored chemical energy (McKendry, 2002). But virtually it is the source of all of the energy available on this planet's biosphere. Photosynthesis is operative in two stages, a Light reaction that is light-dependent but temperature-independent and a Dark reaction that is light-independent but temperature-dependent.

There are three broad photosynthetic categories exist based on the pathway of carbon fixation, these are, $C_3$, $C_4$ and CAM. $C_3$ Pathway, as explained by Calvin and co-workers, involves RuBP (Ribulose bis-phosphate Carboxylage/Oxygenase) as the main $CO_2$ fixing enzyme. In these species the first product of $CO_2$ fixation is a 3- carbon Phospho Glyseric Acid (3-PGA) molecule, hence the process is named as $C_3$ (Calvin Nobel Lecture, 1961).

From 1954 to 1966, the Calvin cycle was known to be the only pathway of Carbon fixation in plants, till Hatch and Slack in 1966 discovered another carbon fixation pathway that was distinctly different from the Calvin pathway, previously known (Hatch and Slack, 1966). They showed that this pathway uses Phosphoenol Pyruvate (PEP) Carboxylase enzyme, instead of RuBP-Carboxylase. The PEP, a three carbon compound, is carboxylated into three four-carbon acids (Oxaloacetate, Malate and Aspertate), hence, the pathway is named as $C_4$. These acids eventually transported into bundle sheath cells and converted into Pyruvate, releasing one carbon molecule, that produces 3-PGA and the Calvin cycle is operative (Gardner *et al.,* 2003; Sage *et al.,* 2011).

These two pathways have some distinct differences like:

1. $C_3$ species lack chlorophylls in vascular bundle sheath cells, while the $C_4$ does. This typical anatomy of $C_4$ plants is called the *Kranz* anatomy.
2. The principle carboxylating enzyme in $C_3$ species is RuBP carboxylase, while in $C_4$, it is PEP-carboxylase.
3. PEP-Carboxylase has a greater affinity to $CO_2$ than RuBP-Carboxylase and this is the reason behind the lower $CO_2$ compensation point (the concentration of $CO_2$ at which the $CO_2$ produced by respiration exactly matches the amount of $CO_2$ fixed by photosynthesis) in $C_4$ than $C_3$.
4. Plants with $C_4$ pathway have a higher photosynthetic rate than $C_3$ plants, especially under higher temperature and light intensity. This is because the $C_4$ plants lack photo-respiratory $CO_2$ loss.
5. $C_4$ species only have 10% of RuBP-carboxylase than $C_3$ species. Whereas, $C_3$ plants apparently lack PEP-Carboxylase.
6. $C_4$ plants have a greater light, water and nitrogen use efficiency than $C_3$ plats. (Gardner *et al.,* 2003; Iglesias *et al.,* 1986; Kellogg, 2013; Sage, 2004; Sage *et al.,* 2014; Heckmann *et al.,* 2013; Muhaidat *et al.,* 2007; Sage and Kubien, 2003; Byrt *et al.,* 2011).

A third type of photosynthesis exists in some succulent species like, Pineapple, Sisal, Prickly pear etc. that is called the

Crassulacean Acid Metabolism (CAM). This pathway is generally operative in dry and low moisture conditions, in which the plant absorbs the $CO_2$ by opening the stomata only at night. The $CO_2$is fixed by the plant into four carbon compounds by using PEP-Carboxylase. During the day the plant injects the four carbon acids to feed the operative Calvin cycle and produce necessary carbohydrates. This is a highly specialized physiological mechanism by which the plants escape drought and reduce moisture loss (Gardner *et al.*, 2003).

## The evolutionary history of $C_4$

Arguably $C_4$ photosynthesis evolved about 30 Mya (Million years ago) from $C_3$ ancestors (Sage, 2004; Sage *et al.*, 2014; Heckmann *et al.*, 2013; Osborne and Sack, 2012; Taniguchi *et al.*, 2016). Today's $C_4$ plants are the results of convergent evolution that occurred independently in more than 60 plant lineages (Sage *et al.*, 2011; Sage *et al.*, 2014; Heckmann *et al.*, 2013; Pearcy *et al.*, 1981; Tipple and Pagani, 2007). The driving force behind this evolutionary change is traced back as the sudden drop in atmospheric $CO_2$ during the Oligocene period (Oligocene $CO_2$ drop) (Sage, 2004; Sage *et al.*, 2014; Heckmann *et al.*, 2013; Osborne and Sack, 2012; Tipple and Pagani, 2007), in combination with some specific environmental conditions, such as drought, high temperature and high light intensity (Sage, 2004; Sage *et al.*, 2014; Heckmann *et al.*, 2013; Sage and Kubien, 2003; Tipple and Pagani, 2007). Thus majority of the $C_4$ vegetation is dominant on arid and semi-arid tropics.

## Role of photosynthesis in biomass production

Among these three natural carbon fixation mechanisms, $C_3$ species is operative in most of the plant species on Earth. A mere 3% of all the species on the planet have $C_4$ photosynthetic mechanism, although producing about a quarter (23%) of primary productivity (total biologically fixed carbon) (Heckmann *et al.*, 2013; Kellogg, 2013). Only about 65 to 70 known lineages (90 genera from 18 angiosperm families with about 7500 species) are $C_4$ among all the plant species, In contrast to 30000 CAM and 250000 $C_3$ species (Sage *et al.*, 2014; Pearcy *et al.*, 1981; Sage and Zhu, 2011). But among these few, there are several of the world's major crops, including Maize, Sorghum, Pearlmillet, Finger millet, Sugarcane, *Miscanthus*, Sudan grass etc. Notably these plants have higher biomass productivity than their $C_3$ counterparts.

## The $C_3$/$C_4$ debate

As the population of humans is increasing, food and energy security is becoming a concern. Currently global agriculture is at its spatial maxima, the only way of increasing production is by improving the biomass productivity of the crops. Today, majority of the food (in terms of grain) and energy (in terms of crop residues) is supplied by $C_3$ crops (Taniguchi *et al.*, 2016), but time has come to optimize the $C_4$ source and harvesting the system's immense capacity to produce high biomass, to mitigate the increasing global demand for food and energy (Zhu *et al.*, 2010).

In recent times humans have significantly modified the environment, that are, 1. changes in atmospheric composition (rise in global $CO_2$ level), 2. Global warming (due to emission of GHGs), 3. Change in natural landscape by human interference, 4. Eutrophication due to nitrogen leaching, and 5. Introduction of exotic species that later became invasive. Among these changes, may lay the debate over the advantage of $C_3$ or $C_4$ crop species. Rise in atmospheric $CO_2$ may provide a benefit to $C_3$ plants over $C_4$ but rise in temperature has a clear-cut benefit for $C_4$ photosynthesis, especially under high light and low moisture conditions (Heckmann *et al.*, 2013; Sage and Kubien, 2003; Taniguchi *et al.*, 2016; Pearcy *et al.*, 1981; Tipple and Pagani, 2007). Sage and Kubien (2003) argued that even in elevated $CO_2$ levels, $C_4$ plants can show a significantly higher rate of net $CO_2$ assimilation after proper 'photosynthetic adjustment' (Sage, 1994; Sage and Kubien, 2003; Sage, 1994). The tool for land use change for human benefit has historically been the use of fire. Humans burn local landscapes to establish habitat, and this phenomenon affects towards the advantage of herbaceous $C_4$ species (Sage *et al.*, 2016). Nutrient enrichment has a positive advantage towards the $C_3$ species especially in the temperate climate. But, plants at elevated $CO_2$ enrich soil carbon by adding root exudates and leaf, root and stem litter, which are of high C:N ratio due to higher atmospheric $CO_2$ and may limit N availability, that can act as an advantage towards $C_4$ crops. $C_4$ species being more nutrient efficient can grow in a nutrient deprived condition better than the $C_3$ species. Lastly, as far the bio invasion is concerned; many $C_4$ plants are noted bio-invaders (Sage *et al.*, 2016; Sage and Kubien, 2003).

## $C_4$ Advantage

$C_4$ photosynthesis is undoubtedly the most efficient form of photosynthesis on terranean Earth, due to its greater nutrient, water and radiation use efficiency along with the ability of maximizing the $CO_2$ fixation and suppressing the deleterious photoinhibition process (Sage *et al.*, 2011; Taniguchi *et al.*, 2016; Sage and Zhu, 2011; Moore *et al.*, 1987). By suppressing photorespiration, a $C_4$ machinery has 40% greater ability of converting sunlight into biomass than $C_3$. The yield of most productive $C_4$ species are 40-50% higher than that of the most productive $C_3$ species (Monteith (1978; Long (1999)). Hence, $C_4$ species prove to be excellent bioenergy crops. Maize, Sorghum, *Miscanthus*and sugarcane are the leading examples of biomass producers in the world.

## Limitations of $C_4$

$C_4$ photosynthesis has its limitations that restrict our effort to broaden the boundary of crop production. And the major limitation is environment, specifically low temperature. $C_4$ plants commonly inhabit the warm and dry tropical areas that receive ample sunshine and occasional drought. Although having an apparent advantage under tropical conditions, $C_4$ species are less productive in cooler climates (Sage and Zhu, 2011; Lukatkin *et al.*, 2012). This reflects in the list of leading crops in the world where, only two – maize and sugarcane out of 12 leading crops listed, are $C_4$. And only 5, among about 150 crops listed by the United Nations Food and Agricultural Organization in their 2008 productivity tables, represented $C_4$ crops (that are, Maize, Sugar cane, Sorghum, Fonio and Millet group) (Sage and Zhu, 2011).The world's forests are principally $C_3$ indicating the clear lack of woody perennials among the $C_4$ lineages (Sage *et al.*, 2016). But this disadvantage is not absolute as there had been many reports of successful adaptation of many $C_4$ crops under cool temperatures that produce a large biomass. Miscanthus, sorghum and sugarcane are a few among them (Wang *et al.*, 2008a; Głowacka *et al.*, 2015; Wang *et al.*, 2008b; Beale *et al.*, 1999; Illinois news bureau 2015; Ebrahim *et al.*, 1998; Naidu *et al.*, 2003; Purdy *et al.*, 2013; Ercoli *et al.*, 2004; Yu *et al.*, 2004).

In a concluding note, photosynthesis is the single most driving force of nature that is responsible for fulfilment of all food, feed and energy need. The $C_4$ machinery, despite its limitations, has a clear advantage over $C_3$ which broadens the scope of research in these crops. The yield advantage and their capability to produce significant biomass under resource limited environments, make them an undoubtable choice for the sustainable energy future of the world.

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**How to cite this article:**

Suraj Kar, Rakesh Kumar, Parveen Kumar, Magan Singh, Pooja Gupta Soni, Govind Makarana, Deepa Joshi and Manish Kushwaha. 2017. $C_4$ Photosynthesis and Biomass. *Int.J.Curr.Microbiol.App.Sci.* 6(3): 1567-1574. doi: https://doi.org/10.20546/ijcmas.2017.603.180