Significance of Guard Cells in Photosynthesis, a Mechanism for Food Production in the Form of Carbohydrates in Plants

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Abstract :Plants play an important role in human and animal lifecycles and provide food in the ecosystem which is produced in via photosynthesis that has three constituents of the process – water, light and carbon dioxide. At cellular level in plants, the process of photosynthesis strongly depends on the opening and closing of stomata that is mediated by guard cells. In this article, the guard cells action to control the behavior of stomata, which ultimately affects the production of food in plants, is elaborated.

I. INTRODUCTION

Plants play a very significant role in human life. They provide food in the ecosystem which is produced in plants via photosynthesis. In general, there are three constituents of photosynthesis process – water, light and carbon dioxide. At cellular level in plants, the process of photosynthesis strongly depends on the opening and closing of stomata which is mediated by guard cell. In this article, the guard cells action to control the behavior of stomata which ultimately affects the production of food in plants is elaborated. Guard cells are specified cells those surround each stomata and are found abundantly in the epidermis of leaves and other structure like stem which are associated with gas exchange. These cells are found in pairs and have a space between two adjacent guard cells commonly known as stomata pore. Stomata are adjustable pores which are abundantly found on the aerial organs of the higher plants (Edwards et al., 1998). Guard cells are morphologically deviated from other epidermal cell and are responsible for opening and closing of stomata (Franks &Farqhuar, 2007). Stomata are mostly found on adaxial and abaxial surface of leaves which are known as amphistomatous leaves (Tichà, 1982). While some plants mostly trees have stomata only on the lower surface of the leaves which are known as hypostomatous leaves whereas aquatic plants like lilies have stomatal pores on the upper surface. These types of the leaves are known as epistomatous leaves (Morison, 2003). So, the main function of the guard cell is the regulation of gases exchange between leaves and environment. This article also aims towards the examination of the significance of the guard cells as it linked to syntheses of the food by photosynthesis.

The mechanism of food production in plants is known as photosynthesis. In photosynthesis plants convert light energy into chemical energy in the form of carbohydrates which are synthesized from water and carbon dioxide. Van Niel in 1931 suggested that photo-synthesis observed in plants is actually a redox reaction in which water and carbon dioxide is used to form organic compounds. It indicates that the raw materials for the photosynthesis are the water and carbon dioxide; both are obtained from the environment. Water is absorbed by root hair from the soil and transported to leaves while the carbon dioxide obtained from air through the small pore present on the leaves facilitated by guard cell (Boyer, 1982).

Guard cells play very significant role for the syntheses of biomolecules in plants. Guard cell provides direct and indirect role in carbohydrates syntheses. Sucrose and starch are directly synthesized in guard cells and is known as important role guard cells while they also help mesophyll cell to regulate the process of photosynthesis by opening and closing of stomata because the leaf cuticle is impermeable for water and carbon dioxide. Hence the guard cell plays a central role for the exchanges of gases between environments and leaves (Jones, 1992). The uptake of carbon dioxide into the leaf is compulsory for food production by photosynthesis. Plants normally open their stomata under light or illumination condition and close them in night and high carbon dioxide concentration (Lawson, 2009) but several plants have adaptation to regulate stomatal complex for exchange of gases; one notable example is CAM (when the plants absorb sunlight energy at the day time and use this energy for the fixing carbon dioxide at night time is known as CAM pathway or crassulacean acid metabolism) plants. CAM plants open their stomata in night and close in day for the uptake of carbon dioxide while C3 (if during the fixation of carbon dioxide plants produce PGA (3-phosphoglyceric acid) or 3C acid as the first products is known as C3 pathway. And those plants which have C3 pathway are known as C3 plants) and C4 (When plants instead of going to C3 pathway produces 4 -carbon compound known as oxaloacetic acid (OAA) which is their first product is called as C4 pathway. The C4 pathway is also known as Hatch and Slack pathway when plants open stomata in light and close in dark for the uptake of carbon dioxide (Luttge, 2002).

The internal physiology of guard cell and environmental factors regulate the stomatal complex (Luttge, 2002). In normal condition, opening of pores mediated guard cell is activated by high light intensity, high humidity while closing is mediated by low humidity, high temperature, darkness, and high carbon dioxide concentration (Shimazaki et al., 2007). Hormones like Abscisic acid (ABA) also affect the opening and closing of stomata in CAM plants which commonly open stomata during night and close during day (Weyers& Paterson, 2001). The stomata of lemna spp. (Park et al., 1990) are insensitive to a number of environmental factors while other species are insensitive to various plants hormones (Weyers& Paterson, 2001).

The stomatal response to light depends upon two components; that are photosynthesis-independent component and photosynthesis-mediated component. Photosynthesis-independent component facilitated with blue light action associated with rapidly opening of stomata (Zeiger et al., 2002) involves the activation of H+-ATPase found in plasma membrane (Shimazaki et al., 2007). The other photosynthesis-mediated components are influenced by red light (Messinger et al., 2006). The osmotic potential produced in guard cell due to accumulation of solutes and ions lower the water potential, causing the uptake of the water from apoplast (Willmer&Fricker, 1997). So due to increase in the osmotic potential in guard cells, their size increases which widen the pore between guard cell (stomata) which is responsible for opening of stomata (Franks and Farqhuar, 2007). The closure of the pores between guard cell is reverse mediated by reverse action that is the loss of the solutes and ions (Willmer and Fricker, 1997). The mesophyll photosynthesis and stomatal conductance have strong positive correlation. The correlation between photosynthetic proficiencies in mesophyll cells and guard is also observed (Lawson et al., 2003).

In addition to mesophyll cell, chloroplast is also found in guard cell, (Lawson et al., 2003) which vary in number; range from 10-15 chloroplasts in each guard cell). The chloroplasts found in the guard cell are smaller and less developed than mesophyll chloroplast (Willmer&Fricker) 1997). In most guard cells, chloroplast behave reverse to mesophyll cell by accumulating starch in night and disappear in day but this situation is not for all species as reported by Stadler et al. (2003) the Arabidopsis guard cell accumulate starch during the light period and found free of starch in dark period. Osmoregulatory pathways are essential to understand the significance of guard cell photosynthesis to facilitate mesophyll photosynthesis by stomatal behavior for carbon dioxide uptake. The most usual recognized theory concerning to osmoregulatory function for many years is given by (Lloyd, 1908) known as starch–sugar hypothesis. According to this theory the guard cell contained more starch when stomata closed in night as compared to day when stomata open. This theory based on inter-conversion of starch to sugar, results in alteration in osmotic changes which leads to change in turgor pressure in guard cell. This theory has been most widely accepted for several years (Meidner& Mansfield, 1968).

Another theory which is known as K+-malate2− theory was given by Fischer (Fischer, 1968). This theory was about the osmoregulatory function of guard cell, which replaced the starch–sugar theory by K+-malate2− theory. Schnabl&Raschke, (1980) reported that K+ uptake in guard cells coupled with malate2− or chloride (Cl−) assist for opening of stomata. Usually malate2− is main ion for balancing of K+ but in some species like Allium cepa, chloride ion (Cl−) used as ion for balancing of K+ (Schnabl&Raschke, 1980). ATPase activates assistance to maintain H+ gradient in guard cell which facilitate up taking of K+ in Guard cell (Outlaw, 1983).

There are four basic ways in which chloroplasts of guard cell contribute to stomatal behaviors.

- The electron transport in guard cells produces ATP and/or reluctant used in osmoregulation (Shimazaki&Zeiger, 1985).
- Chloroplasts are involved in blue-light signaling and response (Zeiger, 2000)
- Starch stored in the chloroplasts synthesize malate as a counter ion to K+ (Willmer&Fricker, 1997) or is broken down into sucrose.
- Photosynthetic carbon assimilation within guard cells produces osmotically active sugars (Zeiger et al., 2002).

Willmer&Fricker, (1997) reported that the mesophyll cell consists of 20–50-fold more chlorophyll then the guard cell which result in poor guard cell photosynthesis as compared to mesophyll cell. The small amount of chlorophyll in guard cell means the assimilation rate of carbon dioxide could be one-third to one-tenth that of the mesophyll, so therefore chloroplasts found in guard cell provide a significant energy cradle for those cells which are associated with stomatal behavior to mesophyll photosynthesis. Stomatal behavior is well facilitated with mesophyll photosynthetic CO2 fixation (Mansfield et al., 1990). The association of stomatal behaviors with photosynthesis led to the hypothesis that the function of guard cell associated to mesophyll photosynthetic capacity or guard cell photosynthesis may provide a metabolite signal (Wong et al., 1979). The debate about the role of the guard cell photosynthesis to facilitate the stomatal behavior in relation to demand of CO2 for mesophyll photosynthesis remnants unresolved. The carbon dioxide fixation in Mesophyll assists the Stomatal behaviors (Mansfield et al., 1990). Various studies have suggested a strong association between photosynthesis and stomatal behaviors under CO2 concentration, different nutrients and light intensities (Hetherington & Woodward, 2003). The stomatal behavior and photosynthesis relationship led to the hypothesis which indicate that mesophyll photosynthetic capacity facilitate the guard cell response through mesophyll signals or photosynthesis in guard cell itself may offer a metabolite signal (Wong et al., 1979). The research about guard cell over the past few years has exposed a complex network of signaling pathways and osmoregulation in guard cell (Li et al., 2006).

It is observed that the guard cells have the ability to change mechanism of stomatal opening and closing depending upon the complicated environmental factors. The alteration in mechanism of stomatal behavior depends on the plants species (Zeiger et al., 2002), this flexibility gives guard cell to mediate stomata to regulate photosynthetic activities and plants water status. The latest investigation conducted by Lawson et al., (2008) in (antisense SBPase) plants species suggested that photosynthesis taking place in guard cell or carbon reduction in guard cell play a significant role in stomatal behavior to red light.

Besides described metabolic pathways, other ecological factors also affect the behavior of the stomata. The most important factor is the ambient temperature (temperature of the surrounding environment). The low or cold temperature induces closure of stomata (Allen et al., 2000) through stimulation of cytosolic calcium ion oscillations. On the other hand, high temperature or heat induces opening of stomata, which ultimately leads to high transpiration rate. The high transpiration rate induces again closure of stomata (Schulze et al., 1973). Heat and drought often effect together which lead temperature induced behavior of the stomata. Few other ecological factors like ozone also have deep effect on stomatal behavior mediated by in guard cells. The cope with effects of ozone plants close their stomata via signaling pathway commenced by activation of ROS (reactive oxygen species) in plasma membrane (Song et al., 2014).

The abiotic factors like pathogen attack also induce stomatal closure. Pathogens like bacteria and fungi enter into plants through stomata and reach stomatal cavity.

The recognition of MAMPs (microbe-associated molecular patterns) indications to signaling pathways mediated through OST1-dependent initiation of the S-type anion channels like SLAC1 and SLAH3 which finally causing stomatal closure (Guzel et al., 2015)

The future of the stomatal research will be based on experimental condition like environment and other biotic and abiotic factors which affect the stomatal behavior, osmoregulation solutes and signaling pathways. The recent change towards gene trap lines and application of transgenic and mutant's plants open a new door of prospect to perform advance ways of research to answer many unsolved questions about metabolism of the guard cell. In past the importance was given to mechanism of photosynthesis in mesophyll and guard cell but the oxidative phosphorylation path has been ignored in past. Mutants and Transgenic plants provide a perfect chance to define the role of oxidative phosphorylation pathway in stomatal and response sensory mechanisms. The discovery and development of promoters associated with guard cell will allow manipulation in metabolism of guard cell without disturbance of mesophyll metabolism (Yang et al., 2008). Such system provides credible reports those assist to elucidate association between stomatal conductance and mesophyll photosynthesis. Coupe et al., (2006) stated that molecular genetics techniques like proteomic and microarray technology assist us to identify gene expression patterns of signal transduction pathway associated various environmental stress conditions. Leonhardt et al., (2004) used microarray technology to compare the profile of mesophyll and guard cells.

They concluded that spray of ABA (Abscisic acid) activates many enzymes which are linked with guard cell metabolism, and reduce PEPc transcript (Kopka et al., 1997). Gray, (2005) reported that Transcriptomic analysis also used for identification of transcription factors which is essential for stomatal behavior in darkness and light. The research in past about stomatal behavior is limited to those plants species which are familiar to biologist. So there is the distinct gape in literature concerning grass species and CAM plants. CAM plants are the best intermediates which provide an ideal way to expose CO_2 and light response as well as signaling pathway and specific gene induction. There is a hysterical need to define the order of stomatal behavior and the impact of joint factors on stomatal behavior, and signaling transduction mechanisms.

Although the latest techniques to understand function of guard cell and stomatal behavior have introduced in last century but still many gaps are in our understanding about metabolism of guard cell and its function in stomatal behavior. The application of antisense technology in combination with promoters, mutation in metabolism of guard cell chloroplast together with photosynthesis and stomatal behavior to various factors, provides a key for establishing the significances of these conserved subcellular structures.

Lawson et al., (2012) reported that the best way to improve the crop production is alteration in guard cell physiology which copes with drought stress. The change in the regulatory mechanism of guard cell assets plants to minimize the loss of water via evaporation. But it is also observed that to cope with loss of water by changing behavior of stomata also affects the assimilation of carbon and finally reduced growth (Antunes et al., 2012). Hence it is important to enhance water use efficiency which does not affect the rate of photosynthesis. A well understanding about metabolism of guard cell contributes in discovering new goals for the breeding and management of drought tolerant and high productive crop species.

The role of molecular genetics to investigate the genetic basis of starch metabolism in guard cell is limited. In spite of great struggle of research groups, not enough data is obtained yet about the molecular regulation of starch metabolism (breakdown) in guard cells. But researchers are still struggling to find genetic traits of stomatal behavior, especially the scientist working on crop improvement.

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