REVIEW ARTICLE

Review on structural, physiological and biochemical adaptat on of C4 plants in desert area

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The C4 plants perform the Calvin cycle in the bundle sheath cells of the leaf veins. They are specifically adapted to photorespiration. These plants are adapted to hot and dry weather conditions and even their stomata open during the day and subsequently close during the night in the absence of light. C4 plants have a distinctive leaf anatomy which means Kranz anatomy, with chloroplast-rich bundle-sheath cells, it performs a gas-tight cylinder surrounding the vascular bundle. The C4 photosynthesis is an adaptation of the C3 pathway that overcomes the limitation of the photorespiration, improving photosynthetic efficiency and minimizing the water loss in hot, dry environments.

Key Words: *Bundle-sheath; Biochemical; Calvin cycle; C4 plants; Photorespiration*

INTRODUCTION

According to Rozentsvet et al., C4 plants are in which the CO_2 is first fixed into a compound containing four carbon atoms before enter into the Calvin cycle of photosynthesis. The name of C4 plants is given due to this four-carbon molecule that is the first product of carbon fixation [1]. In case of C4 plant CO_2 is first bound to a phosphoenol-pyruvate in mesophyll cell resulting in the formation of four-carbon compound which is called oxaloacetate. These four-carbon metabolites act as a means of carbon transporting molecules between mesophyll cells and bundle sheath cells. Among land plants, C4 species have been found to date only in angiosperms and with about 7500 species in 19 families [2]. Although C4 plants represent only a small portion of the world plant species, accounting for only 3% of the vascular plants, they contribute about 20% to the global primary productivity because of highly productive C4 grass-lands [3]. Most of them are grasses followed by sedges and dicots. According to Edwards et al., of these 19 families the grasses (the monocot, family Poaceae) has the largest number of C4 species, followed by sedges (family Cyperaceae) comprised roughly 79% of the total number of C4 species. Among the dicots, family Chenopodiaceae has the largest number of C4 species. The total number of known C4 species is very low, currently about 3% of angiosperm species. However, C4 species have an effect on global productivity that is disproportionate to the number of species exhibiting C4 photosynthesis. Their origins were due to an ecological shift from moist tropical forest to drier and more open woodland or savannah habitats. Therefore, they are dominating all tropical and subtropical grasslands as well as most temperate grasslands in warmer regions of the world [4]. As a result, C4 plant seems to be a key adaptation to one of the most important ecological transitions in the evolutionary history of grasses which ultimately enabled the assembly of the tropical grassland biome [5]. Compared to ecologically similar C3 plants, C4 plants generally exhibit higher photosynthesis rates and have higher efficiencies of light, water, and nitrogen use at low CO_2 and elevated temperature in warm to hot environments [6]. These improvements in photosynthetic performance appear to have greatly enhanced the fitness of C4 grasses in low latitudes, salinized soils, and temperate regions with hot summers and some growth season precipitation such that C4 plants often dominate these landscapes [7]. Ecologically specialization of these plants for hot, dry and saline landscapes could select for carbon conservation mechanisms such as re-fixation of photorespired CO_2. C4 plants are rare to absent in cold environments. Subjects that C4 plants can offer smaller benefits at low temperatures under high light conditions, so that C4 plants can colonize cooler regions following the acquisition of cold adaptations, increasing the ecological diversity within C4 groups. According to Sage et al., some plants with C4 metabolisms that show cold adaptation still require warm Periods during the day in order to exist in cold habitats. In consequence, C4 species are poorly competitive against C3 photosynthesis and they mostly grow in subtropical/tropical environments. Plants in this group include some of the world´s most productive crops like maize (*Zea mays*), sugar cane (*Saccharum officinarum*), sorghum (*Sorghum bicolor*), Bermuda grass (*Cynodon dactylon*) a wide variety of tropical pasture grasses and most of the world's worst tropical weeds such as crabgrass and nutgrass [8].

General objective

The main objective of this review paper is to search evidence about the adaptive mechanism of C_4 plants in desert environment

Specific objective

- To identify different structural, physiological and biochemical adaptation used.
- To distinguish the most commonly used adaption mechanisms used by this plant.
- To identify different environmental stress which affect C4 plants.

Impact of environmental stress on C4 plants

According to Chelli-Chaabouni environmental stresses affect negatively plant growth, productivity, reproductive capacity, and survival ship. It may result from abiotic factors including drought, salinity, extreme temperature, inadequate or excessive light conditions, ozone, pollution, and radioactivity. It can also be caused by biotic factors resulting from plant interaction with other organisms such as insects, fungi, bacteria, viruses, plant competition, and allelopathy. The occurrence of one abiotic stress may affect the plant functioning mechanisms through the induction of several interrelated changes at the structural, anatomical, physiological, and biochemical levels. However, the effect of extra-optimal environmental factors on plant growth and development is not necessarily harmful [9]. Speed at which the stressful factor installs as well as the intensity and duration of stress determines the beneficial or injuring effect of stress. Hence, the gradual physiological

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adjustments induced by the slow increase of stress may protect plants from inhibition of growth and/or injury resulting from suddenly imposed stress.

Plants are literally rooted in one place and therefore are easy prey for herbivores and suitable for climate change. They are often exposed to various abiotic environmental stresses [10]. Global climate change is result increases daily, annual and seasonal mean temperature. Temperature and other environmental variations have a direct impact on plant growth and it is major determining factors in plant distribution. Since humans rely on plants directly and indirectly knowing how well they're able to withstand and/or acclimate to the new environmental order is crucial [11]. Literatures indicate that C4 plants are directly affected by drought which is occurred due to high temperature and elevated CO_2 concentration in their natural environment. These and others like low rainfall, salinity and high intensity of light cause water stress. He explained that C4 photosynthesis is highly sensitive to water stress. With declining leaf water status, stomatal conductance decrease rapidly in order to prevent water loss and low intercellular CO_2 concentrations present due to decrease stomata conductance. When stomata conductance is decrease leaf temperature increase and causes enzymatic denatured and photosynthesis decrease as a result molecular oxygen decrease and reactive oxygen species like hydrogen per oxide increase.

Environmental adaptation of C4 plants

When C4 plants subjected to environmental stresses including water deficit, drought, salinity, and her-bivory attacks, needs to reallocate energy in a way allowing stress adaptation but also to maintain growth and productivity. These latter functions are closely related to water movements within the plant which are supported by vascular tissues [12]. Plant controls gaseous exchanges and water loss mainly by the regulation of stomatal movements. To reach these vital objectives, plant responds by the activation of many metabolic processes controlling photosynthesis, ion homeostasis, and plant hormone signaling that may alter gene expression. These reactions are usually expressed at both phenotypic and genotypic levels [13].

Adaptations are any organism character that helps an organism to survive long enough to reproduce more successfully in its changing environment. As all living things change to fit their environment, plants also protect themselves, by evolved various structural, biochemical, physiological and molecular mechanisms to withstand such various environmental stresses. These adaptations affect the plant's vegetative growth, reproductive development, yield and quality [14]. Like other organisms, plants, must perceive environmental signals *via* specific receptors/sensors, which then activate various signaling pathways. These involve various plant hormones, secondary messengers, transcription regulators and signal transducers these receptors then trigger a plant to prepare response by making modification of cellular or metabolic activity, including regulation of the expression of specific genes. These plants use various adaption mechanisms in order to survive in their environment [15]. Like other plant C4 plants use different adaptation mechanisms to increase their survival on their existing environment. They use structural, physiological as well as biochemical adaptations.

Structural adaptation of C4 plants

The major feature that determines the structural adaptation is concerned with leaf as it is the principal site of gaseous exchange, photosynthesis, biochemical reactions including defensive mechanisms and metabolic activities [16]. According to Bacelar et al. structural adaptations of C4 plants when exposed to various biotic and abiotic forms of stress such as heat, water deficit, drought, salinity, wounding, and pathogen attacks, might include an increase in wax Cuticular thickness, which have reflectance ability plays a major protective role against high radiations in drought conditions and UV-B harmful radiations due to the stratospheric ozone layer damage and epidermis of leaf, stomatal movements *i.e.*, the disruption of stomatal conductance by stress affects directly gaseous exchanges that are mainly related to photosynthesis (CO_2) and photorespiration (O_2). A reduction of size and density of epidermal cells and xylem and greater cell wall lignification, dense root systems, thickened cell walls, and small leaf areas are various traits that plants use in resisting stress have been considered as structural adaptation of C4 plants. These anatomical and morphological modifications reflect a better control of water loss through cuticular transpiration in water deficit conditions. C4 plants are characterized as having Kranz-type leaf anatomy, with two structurally and biochemically specialized photosynthetic cell types, mesophyll and bundle sheath, that function coordinately in carbon assimilation [17]. Most C4 plants have a distinctive leaf anatomy (Kranz anatomy) which is characterized by the presence of special bundle sheath parenchyma cells around the vascular tissue of the leaf [18]. The word Kranz means "wreath" or "ring". Kranz anatomy is a specialized structure in C4 Plants where the mesophyll cells are clustered around the bundle-sheath cells in a ring-like fashion. The number of chloroplasts in the bundle-sheath cells is more than the mesophyll cells. In this case the mesophyll cells are not differentiated into palisade and spongy parenchyma. Vascular bundles are surrounded by layers of radially arranged parenchymatous cells. The sheath appears like a wreath, hence called Kranz (wreath) anatomy that can be viewed as a structural compromise which restricts water loss and also permits efficient CO_2 fixation. As was stated earlier that a feature of Kranz anatomy is the existence of a solid cylinder consisting of the vascular tissue and the large bundle sheath cells (Figure 1).

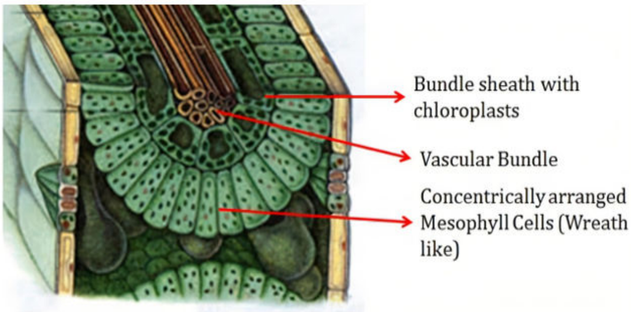

Figure 1) *Kranz anatomy*

According to Laetsch these thick-walled bundle sheath cells do not have air spaces between them, and a C4 plant leaf is really composed of rows of these cylinders.

Along with the arrangement of the mesophyll and bundle-sheath cells, most C4 plants have dense vein spacing and a low mesophyll to bundle-sheath cell ratio and the distance between mesophyll cell and bundle sheath is short [19]. This cell arrangement enhances metabolite cycling and ensures that all mesophyll cells are in contact with a bundle-sheath cell. The number of chloroplast present in bundle sheath is more than in mesophyll cells (Figure 2). Due to this, C4 photosynthesis requires spatial separation of distinct metabolic functions between discrete mesophyll and bundle-sheath cells of the leaf. Presence of unique leaf anatomy in C4 plant is advantageous over C3 plants. Some of the advantage of having kranz leaf anatomy in C4 plants is: first, provide a perfect site for CO_2 fixation and raises the concentration of CO_2 in the bundle-sheath, second sufficient to saturate Rubisco with CO_2, because Bundle sheath cells are surrounded by thick cell walls containing suberins and other hydrocarbons that limit the diffusion of CO_2 to confine it within the cells. This allows the C4 cycle to metabolically concentrate CO_2 in the bundle sheath cells where Rubisco functions. Third, in this case the mesophyll cells are not differentiated into palisade and spongy parenchyma. Vascular bundles are surrounded by layers of radially arranged parenchymatous cells. The sheath appears like a wreath, hence called Kranz (wreath) anatomy, helps in preventing or to eliminate photorespiration and it enables the CO_2 fixation twice with the C4 plant with the help of the bundle sheath cells. These aid the C4 leaves or the whole plant to save up or store CO_2 with them for longer. This also helps to carry out photosynthesis even if there is lower level of CO_2 in the environment.

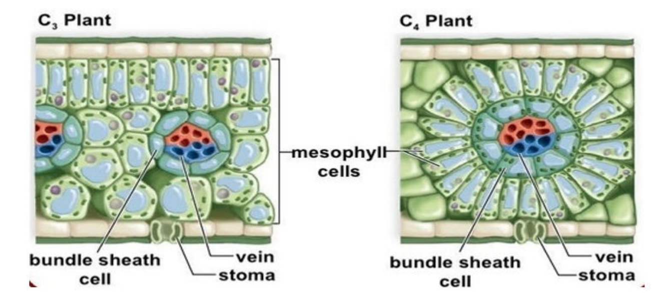

Figure 2) *Chloroplast distribution in C4 vs. C3 plants*

LITERATURE REVIEW

Physiological adaptation

Vascular plants perform many ecologically significant functions. Physiological adaptation of C4 plants combined with stomata closure plays a key role in the reduction of water loss and the maintenance of cell turgor in C4 plants subjected to osmotic stress conditions. However, stomata closure leads to a reduction of gaseous exchanges through the leaves and a diminution of plant photosynthetic activity due to a reduction of CO_2 entry. In these conditions, C4 plants optimize carbon uptake due to the presence of two types of cells [20]. C4 plants are four carbons organic acid forming plant species, and therefore plant physiologists would lump them into a single adaptive syndrome based on their photosynthetic characteristics. Physiological adaptation is an internal body process to regulate and maintain homeostasis for plants to survive in the environment in which it exists. Examples include photosynthesis, respiration, growth rates, abscission layer formation (deciduousness), seed and bud dormancy, sprouting (apical dominance).

Induce photosynthesis

All plants ingest atmospheric carbon dioxide and convert it into sugars and starches through the process of photosynthesis but they do it in different ways. The specific photosynthesis method used by each plant class is a variation of a set of chemical reactions called the Calvin cycle. These reactions impact the number and type of carbon molecules a plant creates the places where those molecules are stored and most importantly for the study of climate change a plant's ability to withstand low carbon atmospheres, higher temperatures, and reduced water and nitrogen.

Some plants have supplemental or alternative pathways like C4 pathway that increase the efficiency of photosynthesis in either intense light or arid conditions. The C4 photosynthetic pathway has evolved as one physiological adaptation to high photo respiratory pressures resulting from various combinations of stresses which include low atmospheric CO_2 concentration, high temperature, aridity and/or salinity. C4 photosynthesis is a physiological process resulting from a series of biochemical and anatomical modifications of C4 Plants. The stomata are partially close at day time in order to reduce water loss and atmospheric carbon oxide does not enter inside leaf as a result, low intercellular CO_2 concentrations in their bundle sheath cell. In order to increase this low level carbon dioxide concentration and thereby increase photosynthesis, they use mesophyll cell as site of initial carbon fixation rather than bundle sheath cells. According to Lara and Andreo they use the following procedures to increase the concentration of carbon dioxide. First, in mesophyll cells: Pyruvate+ATP+H_2O give Phosphoenolpyruvate (PEP)+AMP+Pi. An enzyme called PEP carboxylase binds CO_2 to Phosphoenolpyruvate (pep) even at very low concentration CO_2 (binds it much better than RUBISCOco binds CO_2); PEP carboxylase catalyzes: PEP+CO_2 give oxaloacetate (4-C, compound). Second, Oxaloacetate +NADPH+H+give NADP$^+$+malate (usually). Third, Malate is then sent to bundle sheath cells, in these cells: Malate+NADP+give CO_2+ pyruvate +NADPH+H+. Pyruvate is sent back to the mesophyll cells to continue the cycle and Carbon dioxide greatly increases in bundle sheath cells and allowing the C3 pathway to proceed in those cells (look Figure 3). When the level of carbon dioxide concentration increase in bundle sheath a major problem which is observed in the C3 cycle that is the enzyme Rubisco catalyzes two competing reactions carboxylation and oxygenation. The oxygenation reaction directs the flow of carbon through the photo respiratory pathway and this can result in losses of between 25% and 30% of the carbon fixation is completely solved by C4 pathway.

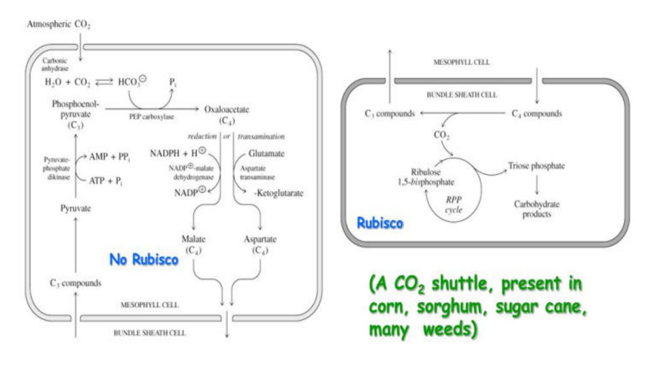

Figure 3) *The C4 pathway*

Photo-respiratory pathway occurs when Rubisco adds O_2 to RuBP rather than a CO_2 (the oxygenase function of Rubisco). This is most likely under conditions of low carbon dioxide concentration and high oxygen concentration. The product of this pathway cannot be used in the C3 cycle, some byproducts are broken down in part into CO_2 and H_2O; organic material is lost from the system, and no energy is captured (no ATP are produced; in fact, some are consumed) called photorespiration because it occurs in the light and consumes O_2, while producing CO_2 and H_2O. Photosynthetic pathway is one of the main causes of growth rate variation among plant species. C4 photosynthesis has allowed plants to grow faster by increasing carbon uptake compared to the ancestral C3 photosynthetic pathway. By concentrating CO_2 around Rubisco and suppressing photorespiration through a coordinated set of anatomical and biochemical modifications, photosynthetic rate and efficiency can be enhanced at high temperatures and low intercellular CO_2 in these plants.

DISCUSSION

Reduce photorespiration

C4 plants are commonly found in warm-to-high temperature environments, such as tropical grasslands, where photo respiratory rates would be high in C3 plants. C4 plants have doubled water-use efficiency of C3 plants because photosynthesis can operate at low intercellular concentrations of CO_2 and hence lower stomatal conductance. Nitrogen-use efficiency is also improved because Rubisco is used more efficiently due to the suppression of photorespiration. Photorespiration is a wasteful pathway that competes with the Calvin cycle. It begins when Rubisco acts on oxygen instead of carbon dioxide. Photorespiration is therefore wastes energy and decreases sugar synthesis because it uses active sites of enzyme, it consumes RuBP, the recovery of carbon in phosphor-gylcolate consumes ATP, it reduces carbon gain and dissipates photosynthetic energy.

Under high temperature potential photosynthesis in C3 plants is suppressed by oxygen as much as 40%. Because Rubisco has a higher affinity for O_2 when temperatures increase. The extent of that suppression also increases under stress conditions such as drought, high light and high temperatures. Rubisco is an inefficient enzyme. It has a slow catalytic turnover rate and about half the soluble protein in leaves is Rubisco, making it the most common protein in nature. Rubisco reacts not only with CO_2 but also O_2, leading to photorespiration, a process that wastes assimilated carbon. It catalyzes both oxygenation and carboxylation reaction and the ratio of oxygenation to carboxylation by Rubisco is depends upon the relative concentrations of CO_2 and O_2 and oxygenation increases as the temperature increases. Therefore, a selection pressure on plants to reduce the rate of photorespiration by means of CO_2 concentrating mechanisms, so as to improve their carbon economy. C4 plant solve this problem by mechanisms that concentrate CO_2 at the carboxylation site compensating for the relatively low affinity of Rubisco for its substrate and allowing acclimation to a wide range of CO_2 concentrations by increasing its concentration and by reducing oxygen competition to bind with Rubisco and there by prevent photorespiration.

Biochemical adaption

The biochemical and enzymatic activities of C4 plants may change under stressful conditions. Biochemical are chemicals either organic or in organic produced by living organism. Especially plants use secondary plant compounds which are synthesize within a plant body that are often used in plant defense, but not produced *via* primary metabolic pathways such as photosynthesis or respiration that are necessary for life. Due to the defensive nature of secondary compounds, they are mostly toxic to other organisms. They release toxins or poisons for defenses against herbivore, releasing antifreeze proteins to avoid freezing in cold environments and synthesize chemical for temperature regulation. From these toxic compounds, many of which are used by humans as flavorings, spices, herbals, dyes, preservatives, medicines, and recreational drugs. In the case of C4 plants biochemical adaptive mechanism is used to minimize the loss of photosynthetic carbon through photo-respiration. According to Tipple and Pagani C4 plants possess a series of biochemical reactions prior to the Calvin-cycle that convert aqueous bicarbonate (HCO_3) into a sequence of organic acids that are ultimately converted back to CO_2 and used to produce carbohydrates *via* the Calvin-cycle. Organic acids are involved in numerous metabolic pathways in all plants. These plants have four-carbon carboxylic acids as the first product of carbon fixation which plays essential roles as photosynthetic intermediates. These are oxaloacetate; malate and aspartate are substrates for the Calvin cycles that reinforce the CO_2 concentrating mechanism of C4 photosynthesis. Oxaloacetate is the immediate, short-lived, product of the initial CO_2 fixation and it is rapidly converted in to malate or aspartate depending on the C4 photosynthetic pathway enzymatic sub-typein C4 leaf mesophyll cells. These organic acids are delivered to the sites of carbon reduction in the bundle-sheath cells of the leaf and they are decarboxylated torelease CO_2 used to make carbohydrates and three-carbon organic acids (pyruvate). Pyruvate is returned to the mesophyll cells used to regenerate Phosphoenolpyruvate (PEP) which serves as CO_2 initial acceptor. An important outcome of the C4 Calvin cycle is increase the concentration of CO_2 around ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) in the bundle sheath to levels at least 10-times higher than those of the surrounding atmosphere. This result in C4 plants requiring less Rubisco for carbohydrate production than C3 species, which translates into increased nitrogen-use efficiency. Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) the primary CO_2-fixing enzyme in plants, has poor kinetic properties. Most importantly, Rubisco has a low ability to discriminate between molecular CO_2 and O_2. In addition C4 plants have a special protein within their mesophyll cell called PEP Carboxylase. The role of PEP Carboxylase in C4 plants is a biochemical advantage that enhances the accumulation of CO_2 around Rubisco, thereby enabling these plants to assimilate atmospheric carbon dioxide with very high efficiency. Study by Maranville and Madhavan suggests that PEP Carboxylase and enzymes associated with phosphoenolpyruvate synthesisare significant factors in maintaining relatively high photosynthesis under nitrogen stress in case of Sorghum.

Studies show that enzymes incorporated into the C4 plant have important roles. For example, PEP carboxylase is important in stomatal function, pH balance, nitrogen assimilation, carbohydrate metabolism and osmotic regulation. No new enzymes appear to have been required in the evolution of C4 metabolism. Instead, expression of existing biochemistry is modified so that activities of certain enzymes (PEP carboxylase, pyruvatePi dikinase, decarboxylating enzymes) are enhanced, whereas for others such as Rubisco, changes in the spatial pattern of enzyme expression occur.

C4 plants have been traditionally grouped into three biochemical subtypes depending on the major decarboxylation enzymes used. These are NADP-malic enzyme (NADP-MEsubtype), NAD-malic enzyme (NAD-MEsubtype) and phosphoenol-pyruvate carboxykinase (PEP-CKsubtype). Each C4 subgroup possesses particular structural features, biochemically and physiology and also differences in the mechanism used to regenerate Phosphoenol-pyruvate (PEP), the substrate of PEP-carboxylase in mesophyll cells (Figure 4). PEP Carboxylase (PEPC) in the mesophyll cytosol fixes bicarbonate, generate from CO_2 by Carbonic Anhydrase (CA) and produces Oxaloacetate (OAA). OAA is reduced to malate in the mesophyll chloroplasts by NADP-Malate Dehydrogenase (NADP-MDH). Malate is transported to the bundle-sheath *via* the plasmodesmata and decarboxylated in the bundle-sheath chloroplast by NADP-Malic Enzyme (NADP-ME). The released CO_2 is fixed by Rubisco in the Calvin cycle. PEP is regenerated from pyruvate by pyruvate, Pi-dikinase (PPDK) in the mesophyll chloroplast.

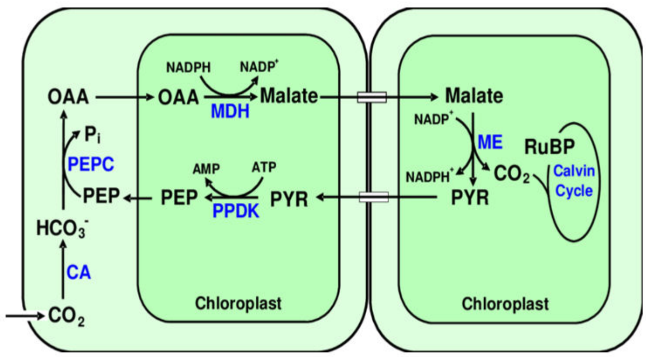

Figure 4) *The concentrating mechanism in an NADP enzyme type C4 plant sugarcane*

Accumulating evidence indicates that many C_4 plants use a combination of organic acids and decarboxylases during CO_2 fixation and the C_4-type categories are not rigid rather the ability to transfer multiple organic acid species and utilize different decarboxylases has been suggested to give C_4 plants advantages in changing and stressful environments as well as during development, by facilitating the balance of energy between the two cell types involved in the C_4 pathway of CO_2 assimilation.

CONCLUSION

Several structural, physiological, and biochemical changes occur during C4 plant development. As C4 plants develop, they show usually an increase in carbon/nutrient balance and carbon storage capacity as well as greater accessibility to water, nutrients, and sunlight but also a decrease in growth rate, root/shoot ratio, photosynthesis, stomatal conductance, and metabolic activities. C4 plant adaptation to stress requires the reallocation of energy in a way allowing the activation of the mechanisms of adaptation and maintaining growth and productivity. When soil water resources are low small openings usually on the underside of the leaves called the stomata close to reduce the loss of water from the plant. This also reduces the incoming carbon dioxide as plants absorb carbon dioxide through these same stomata. Without carbon dioxide plants cannot photosynthesis and growth halts (stops). When a plant is wilting it has reached this point. Some plants have adapted to overcome this. The C4 plants are able to close stomatal pores in order to reduce water loss whilst still obtaining carbon dioxide thereby maintaining photosynthesis in hot and dry conditions. Plants that normally live in dry, hot climates have adapted different ways of initially fixing CO_2 prior to its entering the Calvin cycle. As I have seen and read different articles and books C4 plants have a series of structural, physiological and biochemical modifications to adapt such environment. They are plants in which carbon dioxide is first fixed into organic compounds which have four carbon atoms during photosynthesis in light independent reaction. C4 photosynthesis is the operation of a carbon dioxide concentrating mechanism in their leaves and the first step of C4 photosynthesis occur in the mesophyll and involve the hydration of carbon dioxide into bicarbonate which reacts with phosphoenolpyruvate with the aid of phosphoenolpyruvate carboxylase to produce oxaloacetate (a 4-C acid), hence the terms C4 plants and C4 photosynthesis derives. Oxaloacetate is converted into other C4 acids (malate, aspartate or alanine) which diffuse into the bundle sheath cells where they are decarboxylated, releasing enough carbon dioxide for fixation by Rubisco to synthesis carbohydrate. As a result, they have higher photosynthetic efficiency and low photorespiration relative to C3 plantsunder high light and temperature. Hence, C4 plants are ecologically dominance in open, hot and arid environments. Gnerally C4 plants possess total functional properties related to the fixation of atmospheric CO_2 that occurs in mesophyll cells with PEP (phosphoenol piruvate kinase) carboxylase leading to the formation of C4 acids that further become a carbon source in the Kalvin cycle in vascular bundles' sheath cells. In accordance with the enzyme catalyzing decarboxylation in these cells, three biochemical types of C4-plants are distinguished: NADPH malate dehydrogenase, NAD malate dehydrogenase, and PEP carboxykinase.

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