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CAM MECHANISM IN ARID PLANTS[#]

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Abstract

Crassulacean acid metabolism is an ecological adaptation of C₃ plants. Since its discovery in 1948 in *Crassula*, almost 33 families with 328 genera and 369 species have been reported to exhibit CAM mode of photosynthesis all over the world and this number is increasing with the new data coming in because of the impact of environmental stress. The world's average global temperature and the drought areas are increasing drastically and this has created a tremendous stress in the survival of the plants and the mode of photosynthesis in particular. Since last 20 years more and more data is pouring in, in the reports of C₃, C₄ intermediates and the facultative CAM. The present work emphasizes that under arid dry conditions more plants once reported for C₃ photosynthesis are expressing facultative CAM nature. This is indicative of the impact of environment change on survival of plants through adapting an adaptive mode of photosynthesis that is facultative CAM nature.

Keywords: Photosynthesis, facultative CAM, Arid region.

[#]General Article

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Introduction

In extreme habitats, plants exhibit versatile photosynthetic pathways in response to environmental variables such as temperature and moisture. One such variation of carbon acquisition, Crassulacean Acid Metabolism (CAM), is often employed by plants in arid regions, where they usually face a "desiccation-starvation dilemma" because they have to acquire enough carbon to survive while minimizing the amount of water loss through stomatal activities and other physiological and biochemical functions. The stomata in the leaves remain shut during the day to reduce evapotranspiration and open at night to collect carbon dioxide (CO₂). It is attractive personification of photosynthetic metabolism for every 24 hours and in all seasons (Black and Osmond, 2003). Strong CAM plants include many long lived, highly succulent desert species from varied lineages, such as the Eponymous (Crassulaceae), cacti (Cactaceae), aloes (Asphodeloideae), and agaves (Agavoideae), but also epiphytes from tropical rainforests including many orchids (Orchidaceae) and bromeliads (Bromeliaceae) (Ianand Erika, 2020)

Origin and Evolution

Some plants in the family crassulaceae are with "Daily acid taste cycle" strongly associated with succulence. Bennet-Clark (1933) used the phrase Crassulacean Type of acid metabolism. Reciprocal daily changes in malic acid and starch under a variety of environmental conditions is reported by Vickery and Pucher (1940). They confirmed that CAM was a very entrained rhythm even when kept in constant darkness, a CAM plant would synthesize starch at the 'correct time-of-day.' To understand CAM photosynthesis, the landmark discoveries were made by Mayers (1875) explaining critical role of stomata and gas diffusive resistance in daily CAM. Initial evolution of weak CAM requires increased flux and therefore stomatal opening during the night. In some CAM species, water limitation leads to daytime stomatal closure (Winter and Holtum, 2014). Coaccumulation of Citric acid with malic acid is reported by Knauff and Arditti in 1969 and Luttge in 1988). In context of this Craynet *et al.*, (2004) assumed that citrate accumulation as an atavism of the evolutionary origin and the CAM trait can revert to C₃ metabolism over evolutionary time. Brautigam *et al.*, (2017) concluded that CAM photosynthesis is a spectrum of C₃ - CAM behavior exists in nature in terms of evolution directly acts on a low flux pathway already in place for amino acid metabolism. A single mutation induces nightly stomatal opening while leaving daytime closure intact is concluded by Costa *et al.* (2015) whereas opening patterns of stomata are completely reversed in strong CAM species is explained by Abraham *et al.* (2016). Time-structured expression of key CAM genes in a C₃ species of *Yucca* suggests that ancestral expression patterns required for CAM may have pre-dated its origin in *Yucca* (Heyduk, 2019).

Biochemistry of CAM

CAM photosynthesis uses the same carbon assimilation pathway as C₄ photosynthesis, but instead of separating the PEP (phosphoenolpyruvate) carboxylation and RUBP carboxylation in space, CAM separates them in night and day time (Davis, 2014) and thereby providing a means of 'turbo charging' RUBISCO mediated C₃ photosynthesis and reducing photorespiration for much of the photoperiod (Borland *et al.*, 2009). The CO₂

fixation co-ordination and optimization along with metabolism during CAM is under control of Circadian clock (Hartwell, 2005) CAM photosynthesis is adapted by a large number of vascular plants in arid regions for water conservation and CO₂ concentration. The nocturnal CO₂ fixation is done by the cytosolic enzyme phosphoenolpyruvate carboxylase (PEPC). The CO₂ is fixed into malate, and stored in the vacuole within the same cell as malic acid serves as a CO₂ reservoir at night and during day time CO₂ re-assimilated by the normal C₃ (Calvin Cycle) photosynthetic pathway (Luttge, 2004). Decker and dewit in 2006, postulated that CAM plants are also succulents and form a significant component of tropical and subtropical environment of arid climate. These plants are relatively rare globally, as they represent a significant fraction of regulation mechanism in some hot, arid environments, perhaps evolved from early hot arid conditions as early as Triassic. CAM plants can effectively save metabolic energy and water during harsh environmental conditions by closing their stomata during the day (Taiz and Zeiger 2010). According to Szarek, (1979) plants which are categorised as CAM group as opposed to the C₃ Calvin cycle pathway or the C₄ dicarboxylic acid pathway, are distinguished from latter groups because: i) a massive circadian variation occurs in titratable acidity of chlorophyllous tissue (ii) Stomatal opening and the carboxylation of exogenous CO₂ are nonautotrophic processes (iii) high δ^{13} values, i.e. -10 to -18 ‰, indicate the coupling of CO₂ assimilation and malic acid accumulation, and (iv) there is long temporal separation of net CO₂ assimilation and net carbohydrate (starch) accumulation. Other criteria have been used for identifying the potential presence of CAM, e.g succulence of photosynthetic tissue, but these may be less diagnostic than the physiological tissue. Feakins (2010) proposed that CAM plants are more enriched by NADPH for lipid biosynthesis is generated more by heterotrophic pathways (probably the PPP) than by photosynthesis. This would be consistent with their slower growth rate during CAM metabolism.

Molecular Mechanism

Photosynthetic gene expression is to some degree circadian controlled in both C₃ and CAM species (Dever *et al.*, 2015). Genes found to be controlled by the clock in CAM-performing *M. crystallinum* encode enzymes involved in photosynthesis, glycolysis, nocturnal CO₂ uptake, decarboxylation, sucrose and starch metabolism (Dodd *et al.*, 2003). The regulation and localization of ME isoforms, PEPC and PPDK have received very limited attention in CAM species and the function of PPDK regulatory protein which is homologue of it has been identified in *Mesebryanthemum crystallinum* remain to be established in CAM operation (Borland *et al.*, 2009). Molecular identity of malate protein is the CAM orthologue of *Arabidopsis thaliana* protein ALMT9 (Aluminium activated malate transporter 9). is reported by Kovermann *et al.*, (2007). The gene that encodes PPCK, the protein responsible for activating PEPC, is expressed at comparable levels in leaves of both C₃ and CAM-performing species of *Clusia* and day / night changes in the expression of PPCK appear to be a consequence of the diel cycling of organic acids and soluble sugars (Taybi *et al.*, 2004).

Adaptation in Photosynthetic Efficiency

The metabolic and morphological features of CAM plants show high biomass production in arid environment. The estimation of CAM can be expressed in 7% of vascular

plant species (Winter and Smith, 1996) many of which dominate the plant biomass of arid, marginal regions of the world. The CAM provides flexibility for modulating carbon gain over the day and night, and control of metabolism growth and productivity. The high water-storage capacity, which translate into an ability to buffer fluctuations in environmental water availability. The CAM tissues on CO₂ supply to the cellular sites of carbon assimilation. This carbon is needs for molecular, physiological and ecological processes.

Source of Bio-energy

CAM plants conserve the more energy as compare to C₃ and C₄. Since, it is an adaptation to arid conditions, often characterized by high temperature, high evaporation, low water capacity (only 20 %) as compared to C₃ and C₄ Plants. They fill important ecological niches in grassland, rainforest and arid ecosystems CAM crops such as *Opuntia*, Agave, Pineapple are particularly in arid and semi-arid regions of the world makes up almost 50% of plant biomass in certain arid and semi -arid region of the world. The potential of CAM plants for food, fodder, biofuel production will only become more significant as dimate uncertainty and tensions over food scarcity increase (Nobel, 1991). It has important component of dryland and tropical ecosystem (Hartzell, 2018) serve as bioenergy feedstocks in semi-arid parts of the world. The photosynthetic efficiency of CAM can equal that of common bioenergy crop and fuel yields from CAM cropping system can be viable for biofuel production (Borland *et al.*, 2009) Masrahi *et al* in 2012 reported CAM permutation and survival of *Carallum* sp. and observed low stomatal diffusive conductance during the entire day and night combined with dampened acidification – deacidification cycles indicate that these three species shift from the obligate CAM physio type to CAM – idling in response to protracted drought during the long dry season. Photoprotection in CAM plants under protracted drought can be attributed to upregulation of the antioxidative response enzyme CuZn-superoxide dismutase (Silvera *et al.*, 2010). CAM behaviour in *Aristolochiabracteolata* Lam. is of adoptive response towards the environment and also justifies the facultative CAM nature because this effect is more profound and significant in unfavourable hot summer season than favourable rainy and winter period (Kadam *et al*, 2012). Devis (2014) reported theoretical and realized energy conversion efficiency of plants using CAM in arid conditions. In arid plants, the productivity is more limited by precipitation and water use efficiency (WUE) than radiation uses efficiency which relies on photosynthesis. The potential for *Agave* as an economically viable source of bioethanol with a zero-waste platform has recently been highlighted in Mexico as well as for the eroded lands of the Great Karoo in South East Africa where the climate and soil are not suitable for the cultivation of other crops (Burger, 2008).

Future Perspectives

Perusal of the literature and critical analysis of the relevant information have revealed that there is need of actual working and use of CAM in arid parts. Water use efficiency which is primary advantage of CAM plants can be utilized for bio-energy potential on arid lands as now days globe temperature range is varying day by day and these plants might successfully exploit in a changing environment. CAM cultivation not only to be extended but also their utilization as terrestrial sequestration of atmospheric CO₂ in arid and semi-arid regions of the world is worth to investigate. Maximum water use



efficiency by CAM plants along with photochemical maximum energy conversion efficiency is useful in bioenergy production such type of work of use of CAM plants biofuel alternative source for common bioenergy crops should be taken into consideration.

References

- Abraham PE, Yin H, Borland AM, Weighill D, Lim SD, De Paoli HC, Engle N, Jones PC, Agh R, Weston DJ, (2016) Transcript, protein and metabolite temporal dynamics in the CAM plant Agave. *Nat Plants* 2: 16178
- Bennet-Clark TA (1933) The role of organic acids in plant metabolism. Part I. *New Phytol* 32: 37–71.
- Black C, Clanton add C Barry Osmond, 2003, Crassulacean acid metabolism photosynthesis: 'working the night shift', *Photosynthesis Research* 76: 329–341, 2003.
- Borland Anne M., Howard Griffiths, James Hartwell and J. Andrew C. Smith, (2009): Exploiting the potential of plants with Crassulacean acid metabolisms for bioenergy production on marginal lands. *Journal of Experimental Botany*, 60 (18): 2879-2896.
- Boxall Dever LV, SF, Knerova J, Hartwell J. 2015. Transgenic perturbation of the decarboxylation phase of Crassulacean acid metabolism alters physiology and metabolism but has only a small effect on growth. *Plant Physiology* 167, 44–59.
- Brautigam Andrea, UrteSchluter, Marion Eisenhut, UdoGowik, 2017, On the Evolutionary Origin of CAM Photosynthesis, *Plant Physiology*, Vol. 174, pp. 473–477
- Burger AK. 2008. Mexico and agaves: moving from tequila to ethanol. <http://www.renewableenergyworld.com/rea/news/story?id¼53265>.
- Clanton C. Black and C. Barry Osmond, (2003): Crassulacean acid metabolisms photosynthesis: 'Working the night shift', *Photosynthesis Research*, 76:329-341.
- CostaJM, MonnetF, JannaudD, LeonhardtN, KsasB, ReiterIM, PantinF, GentyB (2015) Open all night long: the dark side of stomatal control. *Plant Physiol* 167: 289–294
- Crayn DM, Winter K, Smith JAC (2004) Multiple origins of crassulacean acid metabolism and the epiphytic habit in the Neotropical family Bromeliaceae. *Proc Natl Acad Sci USA* 101: 3703–3708.
- Hartwell J. 2005. The circadian clock in CAM plants. In: Hall AJW, McWatters HM, eds. *Endogenous plant rhythms*, Vol. 21. Oxford: Blackwells, 211–236.
- Hartzell Samantha, Mark S. Bartlett and Amilcare Porporato (2018): Unified representation of the C₃, C₄ and CAM photosynthetic pathways with the photo3 model, *Ecological modeling* (384): 173-187.
- Ian S. Gilman and Erika J. Edwards, 2020, Crassulacean acid metabolism, *Current Biology* 30, R51–R63,
- Kadam, M. B., Chavan, S. J. and Murumkar, C. V., 2012, Report of Facultative CAM in *Aristolochiabracteolata* Lam., *Adv. Plant. Sci.*, 25(2), 755-757. ISBN: 097-3586
- Karolina Heyduk, Jeremy N. Ray, Saaranaraj Ayyampalayam, Nida Moledina, Anne Borland, Scott A. Harding, Chung-Jui Tsai, and Jim Leebens-Mack, 2019, Shared expression of Crassulacean acid metabolism (CAM) genes predates the origin of

- CAM in the genus *Yucca*. Journal of Experimental Botany, Vol. 70, No. 22. pp. 6597–6609.
- Knauft RL, Arditto (1969) Partial identification of dark $^{14}\text{CO}_2$ fixation products in leaves of *Cattleya* (Orchideaceae). New Phytol 68: 657–661
- Kovernmann P, Meyer S, Hortensteiner S, Picco C, Scholz- Starke J, Ravera S, Lee Y, Martinoia E. 2007. The Arabidopsis vacuolar malate channel is a member of the ALMT family. The Plant Journal 52, 1169–1180.
- Luttge U (1988) Day-night changes of citric acid levels in crassulacean acid metabolism – phenomenon and ecophysiological significance. Plant Cell Environ 11: 445–451
- Mayer A (1875) Über die Bedeutung der organischen Säuren in den Pflanzen. LandwVersuchsstat 18: 410–452
- Nobel PS, (1991): Achievable Productivities of certain CAM plants: basis for high values compared with C_3 and C_4 , New Phytologist 119, 183-205.
- Sarah C. Davis, Davis S. LeBauer and Stephen P. Long, (2014): Light to liquid fuel: theoretical and realized energy conversion efficiency of plant using Crassulacean acid metabolism (CAM) in arid conditions, Journal of Experimental Botany, 65(13): 3471-3478.
- Vickery HB, and Pucher GW (1940) Organic acids of plants. Ann Rev Biochem 9: 529–544
- Winter K, Holtum JAM (2014) Facultative crassulacean acid metabolism (CAM) plants: powerful tools for unravelling the functional elements of CAM photosynthesis. J Exp Bot 65: 3425–3441
- Yahya S. Masrahi, Turki A. Al-Turki, Osama H. Sayed (2012); crassulacean acid metabolism permutation and survival of *Caralluma* species (Apocyanaceae) in Arid Habitats, Ecologia Balcanica, 4(1): 63-71.

