

Photosynthesis : CO₂ Fixation Pathway

Hatch and Slack pathway (C₄ Cycle)

Until the discovery of a new pathway of carbon dioxide fixation, Calvin cycle was supposed to be the only cycle for CO₂ fixation. It was in the year 1954, when Hugo Peter Kortschak and his co-workers reported synthesis of 4 carbon organic acid as first stable product of photosynthesis in sugar cane. Australian plant physiologists and biochemists of David North Plant Research centre, Queensland, Australia, M.D. Hatch and C.R. Slack (1966) proposed a complete pathway of CO₂ fixation in sugar cane plants, giving the name Cane type photosynthesis or C₄ cycle. Hence, this cycle is named as Hatch and Slack pathway. This cycle is also known as dicarboxylic acid cycle or the Cooperative photosynthesis. This was reported by a Russian botanist Karpilov (1960) in Maize plants also.

Furthermore researches on different plants, it was found to occur in many plants such as sorghum, *Atriplex*, spp. besides sugar cane and maize, with some differences. This is categorised as follows:-

1. NADP-ME type Sugar cane (*Saccharum officinarum*), Maize (*Zea mays*), *Euphorbia hirta*
2. PCK-type-found in *Panicum guyana*, *Atriplex spongiosa*
3. NAD-ME type

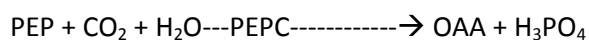
Studies with radio isotopic C¹⁴ O₂ fed sugar cane leaves, it was observed that C¹⁴ O₂ was accepted by Phosphoenol pyruvate (PEP) in the mesophyll cells and then it passed to the bundle sheath cells(BS) in the form of C₄ acids. CO₂ is released in the BS, where it is trapped by Ribulose 1,5-biphosphate operating in C₃ cycle. Therefore, C₄ plants have both the types of carbon fixation –C₃ in the BS cells and C₄ in the mesophyll cells.

Following are different steps of C₄ cycle:-

In mesophyll cell chloroplast-

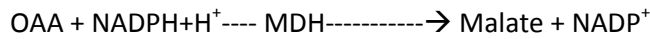
In the mesophyll chloroplasts atmospheric CO₂ is primarily accepted by phospho enol pyruvate (PEP) in contrary to RuBP, as in the case of C₃ cycle.

Carboxylation of PEP is catalysed by the enzyme PEPcarboxylase (PEPC), and as a result a four carbon intermediate Oxaloacetate (OAA) is formed.



OAA undergoes two transformations

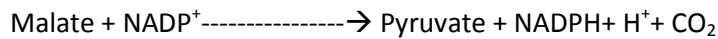
- (i) OAA is reduced by NADPH to produce Malate by the enzyme Malate dehydrogenase(MDH)



Malate is transported to the bundle sheath cell chloroplast-

In bundle sheath chloroplast-

Malate is decarboxylated to pyruvate by the enzyme malic enzyme



In some plants, such as *Panicum maximum* and *Chloris gayana*, aspartate is transported to BS cells and gets converted to OAA, which is converted to Pyruvate releasing CO_2 , by the enzyme PEP carboxylase.

Thus there is release of CO_2 in the BS cells at two steps. CO_2 released is trapped by the RuBP and proceeds for Calvin cycle. Simultaneously the pyruvate formed by the malic enzyme, is transposed back into the mesophyll cells, where it is phosphorylated to produce PEP, the reaction is catalysed by the enzyme phosphate- pyruvate- dikinase.



Thus, there are double pathways of CO_2 fixation in C_4 plants, one C_4 in the mesophyll cells and C_3 in the bundle sheath cells. Hence these plants are also called as efficient plants besides some other reasons.

Structural peculiarities of C_4 plants-

The most unique feature in C_4 plants is the presence of bundle sheath cells (BS), which surround the vascular tissues like floral wreath. These are arranged in one or more layer of thick-walled cylindrical cells in the form of a circle, which is surrounded by many layers of mesophyll cells, hence this anatomy is known as Kranz anatomy (German term, Kranz- wreath). C_4 plants have two types of chloroplast structures (dimorphic). BS cells possess larger chloroplasts, centripetally arranged. They contain starch grains but lack grana. On the other hand mesophyll cells contain normal type of chloroplasts having grana. Presence of dimorphic chloroplasts is evident of two types of biochemical reactions in them.

Detailed studies revealed that the ratio of PSI:PSII activity was three times higher in the BS cells than that in the mesophyll cells. The mesophyll cells are almost three times more active in non cyclic ETS than that of BS chloroplasts.

Chollet and Ogren (1975) recognised three categories of C_4 plants on the basis different metabolic pathways in CO_2 fixation, which are as following:-

1. In sugar cane (*Saccharum officinarum*) and Maize (*Zea mays*), where CO_2 is initially fixed by PEP, producing OAA. OAA is converted to malate, and further malate is transported to BS cells.

2. In *Panicum maximum* and *Chloris gayana*, where aspartate is transported to BS cells in place of Malate. There it is transaminated to OAA which becomes converted to Pyruvate and CO₂ by PEP carboxylase

3. In third group, the aspartate produced in the mesophyll cells is transported to BS cells where it is transaminated and reduced to Malate. The Malate is decarboxylated to form pyruvate and CO₂. This is found in *Atriplex spongiosa*.

Differences between C₃ and C₄ plants

C ₃ Plants	C ₄ plants
1. Calvin cycle is the only CO ₂ fixation pathway	1. Hatch and Slack pathway in mesophyll cells and Calvin cycle in BS cells
2. Less efficient in low level of CO ₂	2. Highly efficient in low concentration of CO ₂
3. The CO ₂ acceptor is RuBP	3. CO ₂ acceptor is PEP
4. Only one type of chloroplast present in all the cells.	4. The chloroplasts of BS cells and mesophyll cells are dimorphic.
5. The first stable product is Phosphoglyceric acid, a three carbon compound.	5. The first stable compound is a four carbon compound oxaloacetic acetate.
6. In each chloroplast, two pigment systems (PSI & PSII) are present.	6. In the BS chloroplasts PSII is absent, therefore these are dependent on mesophyll chloroplasts for supply of NADPH+H ⁺
7. The CO ₂ compensation point is 50-150 ppm CO ₂	7. CO ₂ compensation point is 0- 10 ppm CO ₂ .
8. Photorespiration is present	8. Photorespiration is absent.
9. Net rate of photosynthesis in full sunlight is 15-25 mg CO ₂ per dm ² of leaf area/hour	9. It is 40-80 mg of CO ₂ perdm ² of leaf area/hr.
10. The optimum temp. For this process 10-25 ⁰ C.	10. It is 30-45 ⁰ C. So these are warm climate Plants.

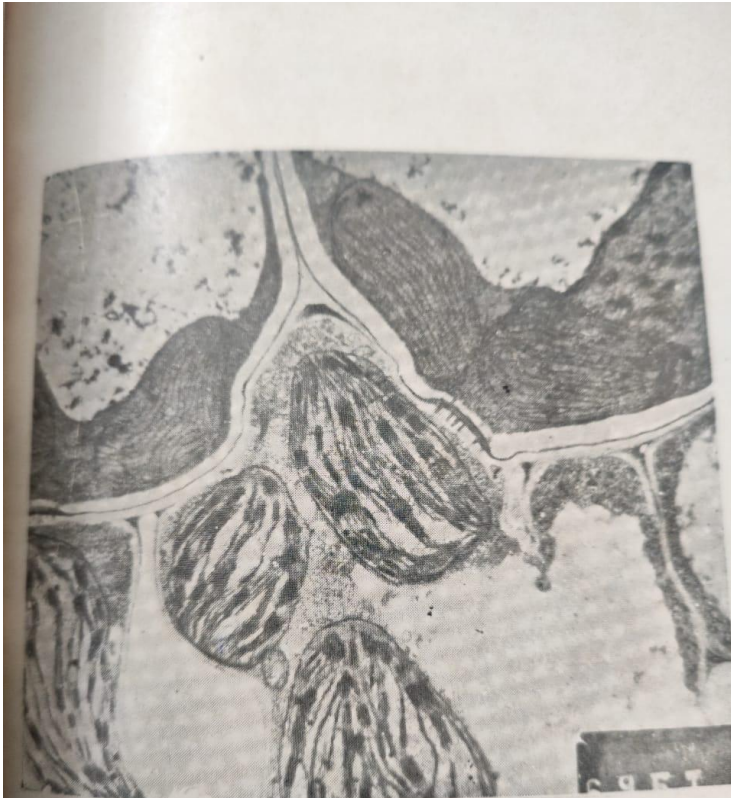


Fig. Plate 12.1. Fine structure of chloroplasts of sugarcane. The upper two cells are bundle sheath cells (grana absent) and the lower cells are mesophyll cells showing well developed grana in chloroplasts. (Courtesy: *Dr. W. M. Laetsch*).

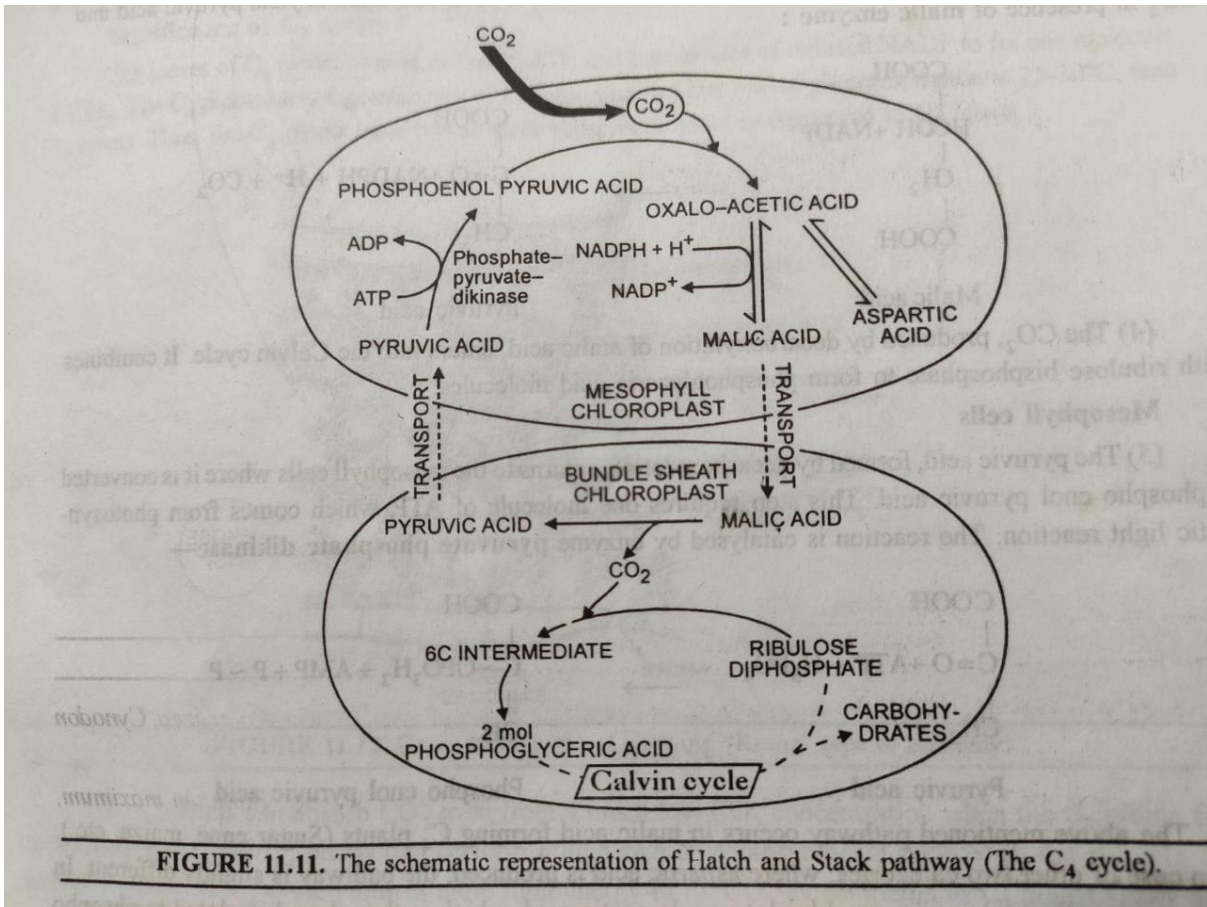


FIGURE 11.11. The schematic representation of Hatch and Slack pathway (The C₄ cycle).