Introduction to Biomolecules
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Lecture-25
Photosynthesis and Carbon Assimilation (Part-3/3)

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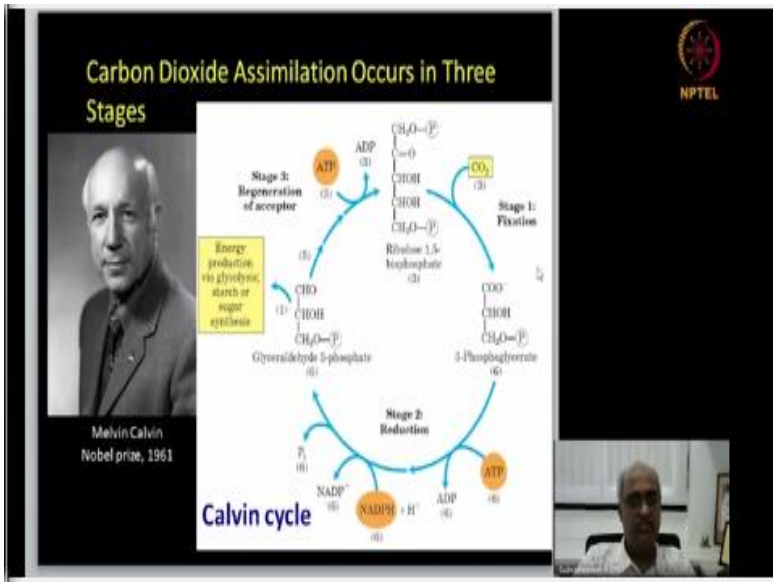

We finished the light reactions and at the end we understood that the end of light reaction the products are reduced equivalence in the form of NADPH and then the proton gradient which leads to the formation of ATP. So, now we are going to look at how this is used to fix the carbon dioxide which is inorganic form of carbon into the carbohydrates**.** So, basically how are we making carbohydrates from carbon dioxide that is in the air?

So, this was figured out by Melvin Calvin and then Benson and Barson 3 of them, so one Nobel Prize in 1961. So, this has 3 steps, it is the 3 stages; the first one is the fixation, like carbon dioxide getting incorporated into an already existing pentose, ribulose 1, 5 bisphosphate, ribulose indicates the presence of keto group like fructose. And the next one is the resulting molecules the molecule will be 3-phosphoglycerate, for every one of ribulose of bisphosphate which is 5 carbon and when you add one more you have got 6.

So, you make 2 trioses and this is in the carboxylic acid form and the next stage is the reduction of that to the aldehyde form that is glyceraldehyde-3-phosphate. So, these are actually the reactions of glycolysis, very similar enzymes, so this will not be difficult for us. We just need to place this in the overall context of understanding flow of carbon in the biological system. And the third is the regeneration of the entry molecule which is the ribulose 1, 5 bisphosphate.

So, to balance the stoichiometry, yesterday I told you the cycle starts with 3 molecules of this and therefore 3 carbon dioxide, so you end up getting 6 phosphoglycerate and after reduction 6-glyceraldehyde-3- phosphate out of the 6, 1 is the net gain, balancing the 3 carbons entered in the form of carbon dioxide. And the other 5 are converted into 3, 5 carbon sugar, this ribulose 1, 5 bisphosphate that is the entry.

And that regeneration requires ATP**,** for every molecules ribulose produced you have 1 ATP hydrolyzed, therefore for 3 of them 3 ATP. So, today we are going to spend significant amount of the time focusing on this stage I fixation. So, this entire cycle is called Calvin cycle in honour of the scientist who elucidated this pathway.

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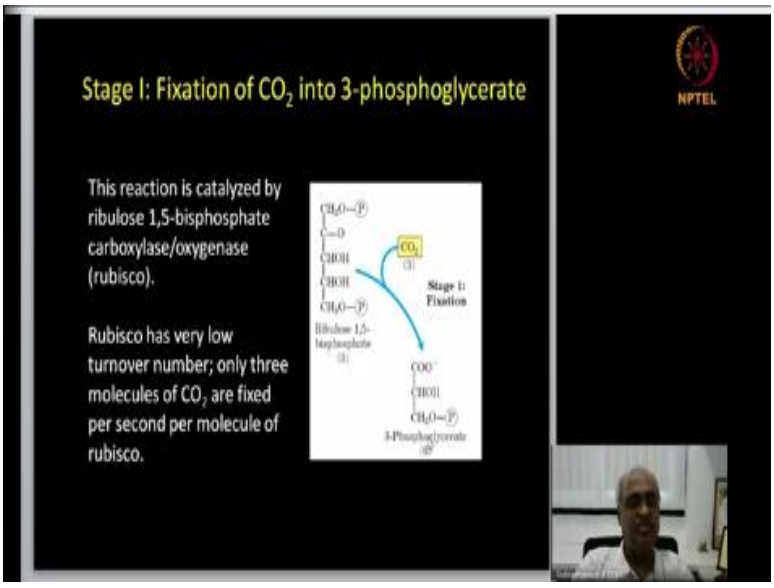

So, this is the stage I, ribulose 1, 5-bisphosphate becoming 3-phosphoglycerate. So, this is catalyzed by an enzyme called ribulose 1, 5-bisphosphate carboxylase oxygenase, because it does both reactions. And we simply call it as rubisco**,** most other people call this enzyme rubisco,

so if you refer to it by rubisco, I will be happy enough. But this is not that complicated, it is a long name but it is very easy it carboxylates this, because carbon dioxide is fixed and it is actually an oxygenation reaction as well, so it is oxygenase. And this enzyme has a very low turnover**,** only 3 molecules of carbon dioxide if you compare this with enzymes like peroxidase, catalase etcetera; they are like several hundred thousand molecules per second they catalyze.

Whereas here the turnover number is low and as a result the chlorophyll has large number of rubisco molecules to enable sufficient carbon dioxide fixation. So, due to this rubisco is the most abundant enzyme in the biological system**,** so enzymes do not exist anywhere anyway. So, rubisco is the most abundant of all enzymes, like cellulose is the most abundant carbon material on earth. So, we look at how this enzyme does this catalysis.

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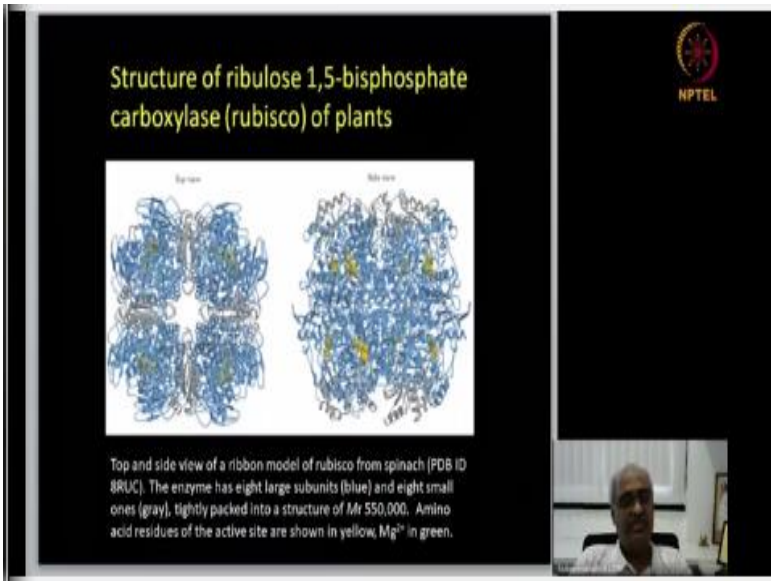

So, this is this enzyme structure, so you are only seeing couple of views. So, you have a top view where you are seeing the 4 blue coloured structures and then this grey. So, these are the different subunits, 4 large subunits the blue coloured one and 4 small subunits that are the grey coloured one**.** And the active site residues are coloured yellow and visible through this ribbon model. And from the side when you look at it this is the view you get**.**

So, this has 8 large subunits or from one side you are seeing only 4, and 8 small subunits. So, the other 4 subunits are below this, you can see in the side view. So, you see 2 here and the other 2

are on the other side, and similarly below which is not seen here 2 more and the other 2 are on the other side. So, 8 large subunits and 8 small subunits, it is a humongous enzyme 550,000 molecular weight.

And you see magnesium green here and that is the main component in the catalysis, so we will see that as we go along. So, I was emphasizing during our journey along with the electrons the importance of the vitamins we saw niacin, we saw flavin, then we saw thiamine, we saw pantothenic acid, we saw biotin, all that we saw along the way as part of enzyme catalysis**.** And equally importantly metal ions play a role, so we have seen heme moiety in cytochromes and there you have ion-ion.

Then in the fourth complex in mitochondria the cytochrome c, NAD, oxidoreductase enzyme. So, there we have cytochrome aa3 and they have copper cofactor. So, we have seen ion, we have seen copper, then we saw manganese in water splitting complex, yesterday, where the stable multiple oxidation states of manganese allows acceptance of 1 electron at a time 4 electrons comfortably and then donating 1 electron at a time 4 electrons**.**

So, we saw manganese, and today we are going to see the importance of magnesium in the catalysis of rubisco. So, all these we call them from a nutritional point micronutrients**,** carbohydrates, lipids, proteins being the macronutrients. So, these micronutrients you will ensure sufficient intake when you have mixed varieties of vegetables, a plant food in your diet**.** So, that is why you should not rely only on french fries or pizza or burger as the only source of food, you have to eat variety of food.

Normally our traditional meal whether south Indian or north Indian ensures you have variety of vegetables going in, in all 3 meals and that ensures you have all of these.

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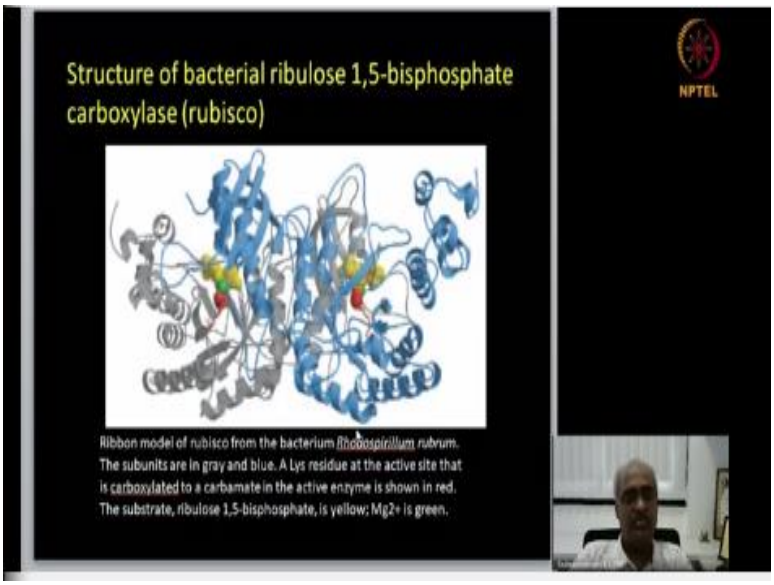

So, this is a simpler version of the same enzyme found in bacteria**,** Rhodospirillum rubrum here shown. So, this is the ribbon model where it is very similar as if you have only a dimer here, so the blue 2 of them and grey 2 of them. With, so you have the magnesium here and this is an important lysine residue that plays a role and this is the ribulose 1, 5-bisphosphate substrate, the yellow colour one. So, this is a lysine that is in carbamoyl form in the side chain of the enzyme that plays an important role in the catalysis, so all of that coming in a next couple of slides**.**

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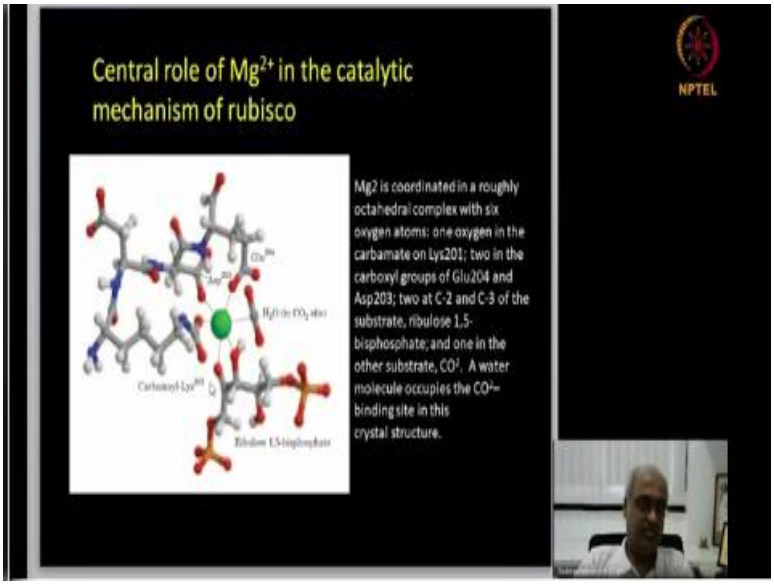

So, here a close-up of this region, particularly focusing on the magnesium. So, here you see magnesium coordinated with atoms actually oxygens from the substrate. Here 2 bonds the substrate, one more with another substrate, normally it is carbon dioxide in the actual catalysis;

here for crystallization they have used water. And then this is again from the enzyme side chain you have a glutamic acid and aspartic acid and this is the carbamoyl lysine, this red one**.** So, this is in an octahedral complex forming 6 coordinations with the side chains and the substrates**,** 3 with the side chains and 3 with the substrates. So, this is the active site structure of rubisco.

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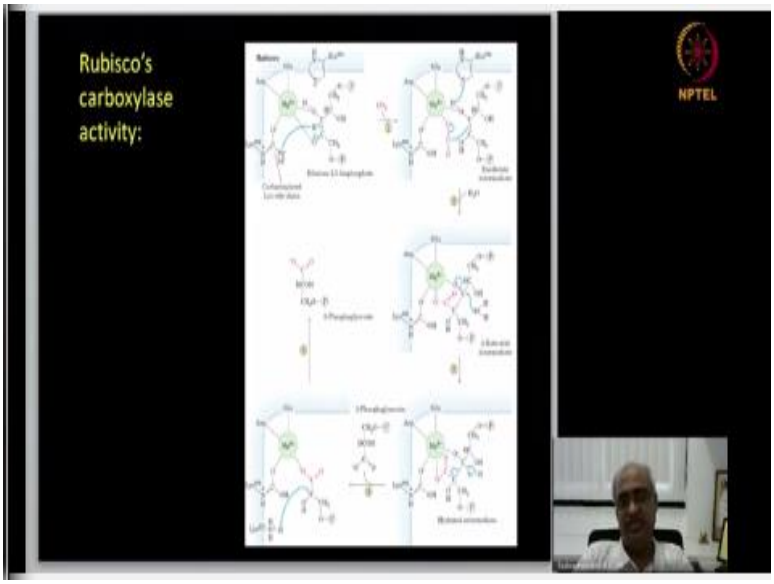

And this shows the reaction mechanism. So, here this as you show this blue shaded area is the acting site of the protein the enzyme here. Here are those residues and this histidine we did not see in the previous one, because the previous one is only focused on how magnesium is coordinated. But for catalysis this nitrogen becomes important and that is why that is shown here. And this is the carbamoyl side chain carbamoyl is NH 3 COH is carbonic acid.

Here the lysine side chain, NH 2 is in carbamoyl form with this carboxylic group. And so this one abstracting a proton from the substrate, so this is the ribulose bisphosphate and abstracting a substrate from this again pay attention to the carbonyl group that is why it is ribulose that is functioning here and not ribose. So, this the chemistry of carbonyl group that we learnt early on. So, those are our core principles those chapters at least that one particular chapter where we considered the 5 different kinds of reactions that we repeatedly encounter in biology.

And some of the cofactor reactions like thiamine pyrophosphate, how it functions, Lipoic acid, how it functions. So, those kind of things you should revise multiple times and remember them,

they are basically the core of the biochemistry concepts that you are learning. So, this is helping this to easily loose proton, remember the carbon adjacent to carbonyl group due to electron delocalization and resonance stabilization here becomes carbanion.

So, this is more acidic than a carbon like this carbon, so therefore it readily loses the proton and this shifts there. And this takes that proton and it becomes a hydroxyl group. So, you have 1 hydroxyl group here and another hydroxyl group that is going to form here and a double bond here. A typical enediol structure, so that is what you are seeing here. So, the abstracted proton is here one, and then here you have the other one and you have the double bond, so this is the enediol intermediate.

So, that allows carbon dioxide to be coordinated with the magnesium here and now you see these acts as a general base catalysis. And that aids in the electron transfer in these forms. And so this double bond is where this is broken and this carbon is going to attach to this particular carbon and the double bond is going to shift to this side. And that leads to a keto acid intermediate**.** So, this is taken as the alpha and this is the keto acid and there you have this carboxyl group attached, and that is why it is acid**,** keto acid formation.

So, this carbonyl group enabled that to initiate this reaction of course magnesium and those coordination and this nitrogen all of that matters. But in the substrate molecule this carbonyl group is the crucial to initiate all of this. And now hydration of this double bond shifts this bond out and then you have this cleavage happening, releasing the first phosphoglycerate**,** so this is the hydrated version.

So, the double bond is reduced to OH and then here you have the other OH**.** Then shifting of these bonds enabled by these linkages leads to cleavage of the bond here and this becomes double bond. So, this becomes a carboxyl group, so therefore it is phosphoglycerate that is released. And the remaining second one the proton originally abstracted from this lysine, but now another lysine's amino group provides that proton and it is stabilized and released as the next 3-phosphoglycerate.

So, this is the reaction mechanism of rubisco**.** The most abundant enzyme and the enzyme that makes all our food**,** so this is how our food actually starts it is journey from air, carbon dioxide, this is the way it ends up becoming 3-phosphoglycerate. And from there it is as they say rest is history, you already know what can happen to 3-phosphoglycerate. Reverse reaction that we saw in glycolysis will be glyceraldehyde 3 phosphate and glyceraldehyde 3 phosphate by isomerization can become dihydroxy acetone phosphate.

And if glyceraldehyde 3 phosphate and dihydroxy acetone phosphate, they join, they can become fructose 1, 6-bisphosphate and then you all the way go back to glucose. So, those are ready for us to understand. So, this formation is what is new and important here, so this is how carbon dioxide enters into the system. So, although I said no more mechanisms but this is one important mechanism, so please pay attention and understand this and remember this well**.**

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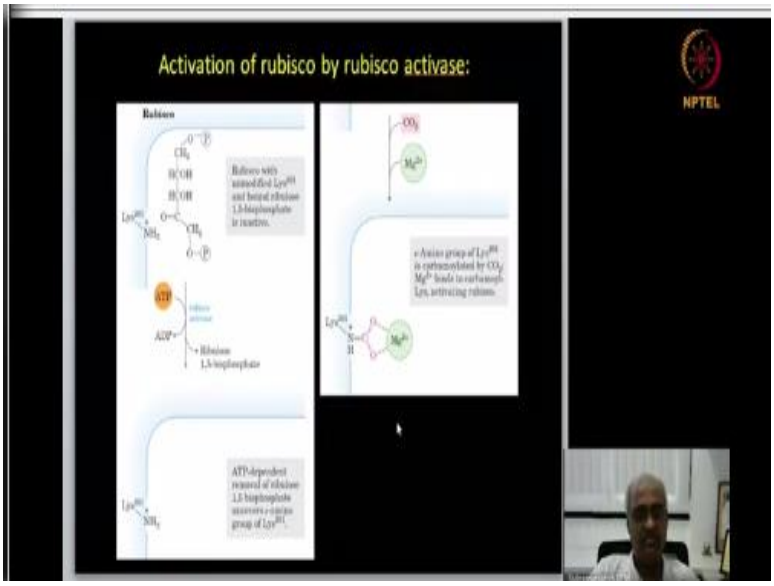

So, one extra detail with respect to rubisco. So, normally rubisco remains completely in an inactive form**.** So, this is activated by an enzyme called rubisco activase, so this is inactive primarily because it is tightly bound with the substrate and that prevents carbamylation of this amino group of the lysine. And in the presence of ATP, rubisco activates expels this out and allows the binding of carbon dioxide and magnesium to form the carbamoyl lysine here**.** So, this is tightly regulated by light and availability of ATP and NADPH etcetera.

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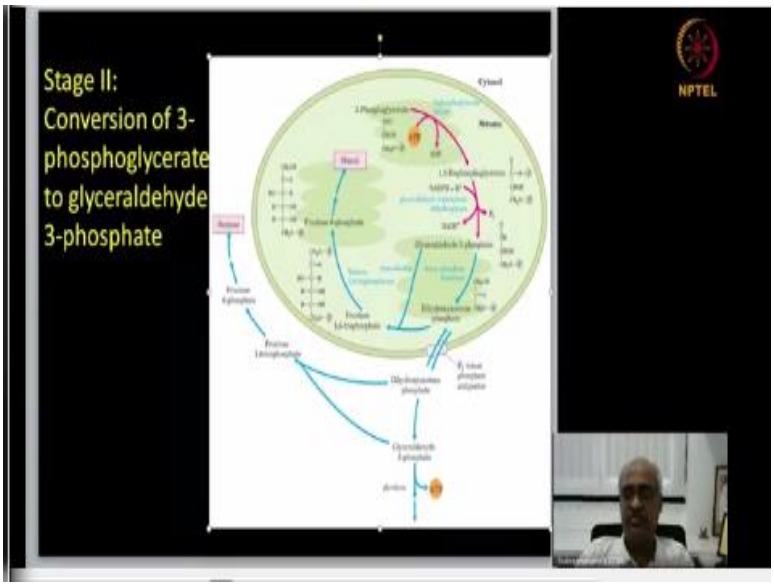

So, now we go to the second stage where it is the reduction of the phosphoglycerate to glyceraldehydes-3-phosphate. So, that you can see here, again I will try to blow it up, remember this whole thing is happening in the stroma of the chloroplast, these light green background is the grana each one having thylakoid flat and disks stacked up. So, this is exactly reversal of what we saw in glycolysis, and again the dehydrogenation step in the opposite direction as we saw in glycolysis produced is glyceraldeyde-3-phosphate.

And similar enzyme but present in chloroplast, isomerase, triose isomerase produces dihydroxyacetone phosphate by rearranging bonds in glyceraldehyde-3-phosphate. And 2 of them can combine and form fructose 1, 6-bisphosphate, again same steps in the reverse in as in glycolysis. And this is a new enzyme, fructose 1, 6-bisphosphatase; this is not there in glycolysis, because there it is the opposite direction where you have a kinase phosphorylating it, PFK phosphofructokinase-1.

So, this is the opposite of that fructose-6-phosphate. Then isomerization to glucose and then you have starch and finally this gets filled with starch. And as I told you yesterday, then it will become amyloplasts chloroplast becomes amyloplast when it fills with a lot of starch. So, this is one fate for the carbon dioxide that entered this root and another one is it may be transported out via this inorganic phosphate triose phosphate anti-porter and the dihydroxy acetone phosphate

that comes out again isomerization to glyceraldehydes-3-phosphate and this might get into glycolysis to produce ATP.

This is what happens in the leaves to generate energy for the leaves function itself. But at the same time these are combined to form the fructose bisphosphate and to form sucrose fructose then isomerization to glucose, then glucose fructose disaccharide is sucrose. And this sucrose is the form in which carbohydrate is transported in plants from the photosynthetic organs such as leaves to other parts of the plant body. So, the transport form of carbohydrate is sucrose**,** so that is why the stem saps are sweet.

If you take a grass and you take the inter nodal region, the stem of the grass and if you chew it you will find it is sweet, that is primarily because sucrose produced in the leaves is being transported to roots, stems and other parts of the plants. So, remember the transport version of the carbon dioxide fixed by the chloroplast is sucrose. And the long term storage is starch which is stored within the chloroplast and the chloroplast becomes amyloplast.

And to sustain the activities of the leaves the glyceraldehyde-3-phosphate which came out as dihydroxy acetone phosphate enters into glycolysis and TCA cycle to produce energy. So, this is the second step the reduction of the glycerate to glyceraldehyde. Third step is actually to regenerate, so that is coming in the next one.

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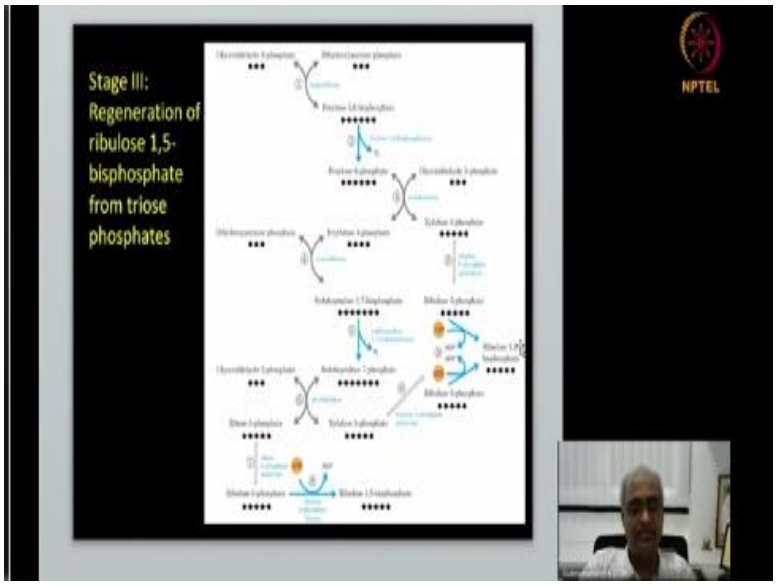

So, this one again I will make big and then we will go step by step, this will look complex but it is actually not complex, already familiar ones, steps. So, the idea is we ended up producing glyceraldehyde 3-phosphate**,** so let me go back to the diagram and come back to this. So, we understand 3-carbon dioxide fixed into 3 ribulose bisphosphate producing 6 glyceraldehyde-3-phosphate.

So, we have net gained 1 glyceraldehyde-3-phosphate and the remaining 5 must combine 3 carbon like triose must combine to make this pentose and how is that done is what is our current slides focus, this one. So, here the main enzymes are these transaldolases and transketolase**,** so the transketolase is an important enzyme whose mechanism we are going to have a look at in the next slide, quite simple but important.

So, here you have glyceraldehydes-3-phosphate and dihydroxy acetone phosphate 3 carbon integrates by this, making the 6 carbon fructose bisphosphate. And the phosphatase makes the removes 1 phosphate giving you the fructose 6 phosphate, this is a irreversible reaction, strongly exergonic due to this hydrolysis of the phosphate group and therefore it goes only in this direction.

Then from here, so this is a keto group and 2 carbons above the keto group is transferred to a aldose, this is glyceraldehyde is an aldehyde 1 and that is why it is called transketolase**,** the

enzyme and the product is, so this aldose becoming ketose and then it produces the remaining part of this is the aldose again, the translocates, the keto group and therefore it is called transketolase.

So, you have 6 + 3, so you have got 9; out of the 9 you make 1, 4 and 1, 5, so the numbers are correct, that is the third step. Transaldolase, here the aldehyde group is transferred converting this into and ketose and then the second step is removing the phosphate, third step is again the transfer of the carbons from a ketose to an aldose. And the fourth step is another dihydroxy acetone phosphate combining with this 4 carbon erythrose phosphate, transaldolase reaction, the same enzyme as that.

Making the 7 carbon unique molecule that you will not encounter outside chloroplast and this enzyme sedoheptulose 1, 7-bisphosphatase is unique to chloroplast. And this is again like this an exergonic irreversible reaction making sedoheptulose-7-phosphate and this molecule via another transketolase reaction, then one more glyceraldehydes phosphate entering. First one we saw then second one and third one here and that produces 2 pentoses, 1 aldose and 1 aldulose, keto sugar**.**

And these molecules isomerize gain of phosphate to become ribulose 1, 5-bisphosphate. For example here this (()) (27:00) 5 phosphate by an epimerase becomes ribulose. And that gets phosphorylated again seriously endergonic reaction requiring ATP hydrolysis, unidirectional again. So, the unidirectional ones are shown in blue forming the ribulose 1, 5-bisphosphate. And a very similar same reaction an epimerase and this kinase reaction converts xylulose formed here to this, these are identical molecules of the same steps.

So, now you almost see a cycle here and this ribose bisphosphate, isomerization to ribulose in aldose becomes aldulose and the kinase makes ribulose bisphosphate, so this is 9. So, the same numbers are shown when the reactions are the same, so similarly 8, 8 here**.** So, you have 1, 2, 3, 4, 5, 6, 7 and 8 and 9th step ends up producing ribulose bisphosphate. So, here I am not going to ask for structures the slide itself does not have the structures, but you need to have a kind of the understanding of the stoichiometry of how the carbons are jumbled by taking 2, 3 carbon sugars initially and then adding 1.

So, essentially 3 trioses going through the series of cyclical reactions end up producing this pentose sugar. And this pentose sugar now has been regenerated; it can go for the stage I which is carbon fixation.

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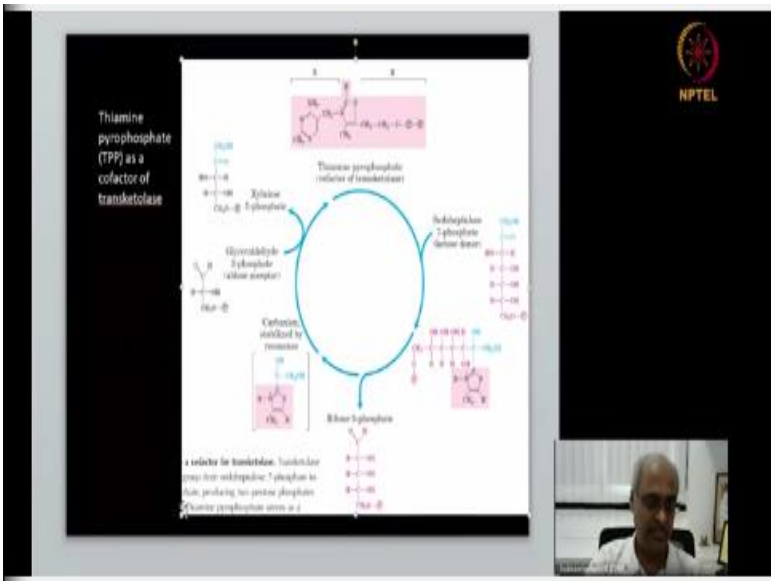

So, now we will focus a little bit on the transketolase enzyme, because this enzyme we will not probably study too much biochemistry encounter elsewhere, but this is an important group transfer reaction. So, therefore I want to go through it in some detail, not great detail but some detail. So, this molecule is very familiar to us, we have spent lot of time with this thiazolium group and this carbon being acidic and can readily become carbon ion.

So, we saw this in pyruvate dehydrogenase complex, where it carries the pyruvate 2 carbons as hydroxyethyl form of the acetaldehyde group from the pyruvate. Very similar thing it does here, the 2 carbon groups of keto sugars it takes up. So, here you have the reaction where you have the entry of sedoheptulose-7-phosphate the ketose. We are looking at that particular step**;** we are essentially looking at this transketolase**.**

So, this is our substrate here and this is the other substrate. So, you have the glyceraldehydes-3-phosphate, so this we will come later. So, first let us begin with this, so sedoheptulose-7-phosphate from that these 2 are going to be carried on this carbon. So, here it is not

hydroxyethyl, because you have 2, hydroxyl groups in this. And so this double bond, this carbon is what is added to the thiazolium carbon.

Again this is aided by this is carbonyl group. So, now from here, so see we are really not looking into the mechanism, we are only getting an understanding of just the major transfers only. So, this bond is cleaved into an aldehyde and then this is as an anion carried and this is stabilized by this thiazolium electron sink, remember the concept electron sink that we have learnt. The conjugated double bonded ring structures helping temporarily juggling the electron among themselves and stabilizing these kinds of unstable structures.

And this now then is transferred to glyceraldehydes-3-phosphate forming xylulose 5-phosphate. So, essentially this keto group is now transferred to an aldo sugar, making that into a keto sugar, so that is why it is called transketolase. So, this is how this transketolase transfers these 2 carbons to glyceraldehyde making xylose-5-phosphate. So, this is the importance of thymine pyrophosphate, thymine remember is one of the B complex vitamins, it is deficiency cause this beriberi and which is fatal, so that is this reaction**.**

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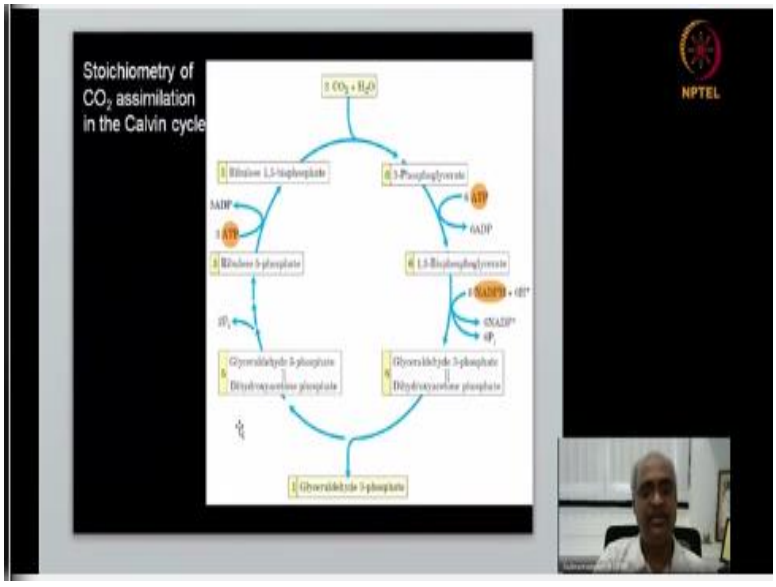

Next is budget calculation**.** So, which I actually did it in the very first cycle itself, what is the psychometric relationship here? So, 3 carbons with 3 ribulose bisphosphate, so the numbers are highlighted here and this is the net gain, 5 of them we saw that large chart how they end up

becoming ribulose 1, 5-bisphosphate. So, this budget calculation includes the ATPs that are produced or consumed.

So, here you see the 6 ATP is consumed and then 6 NADPH, reducing equivalent, these are all equivalent of consuming food. Because we are doing a synthetic reaction, this is anabolic reaction; we are not in catabolism anymore. So, therefore the energy produced, remember, this was produced by the proton gradient created in the thylakoid membrane. And this you remember at the end of the photosystem I, the electrons are transferred to NADP and that is reduced to NADPH.

So, that is how via these inputs going in and this is the net output**.** So, this is the summary of photosynthesis and carbon assimilation reactions. So, there are a lot of small sub branches and special pathways and shunts etcetera which we are not getting into, because I know we do not have that kind of a time in an one course biochemistry in a 4 year program. And if you are very much fascinated by these, I would advise you to read the other portions in learning at, the ones that I am not covering**.**

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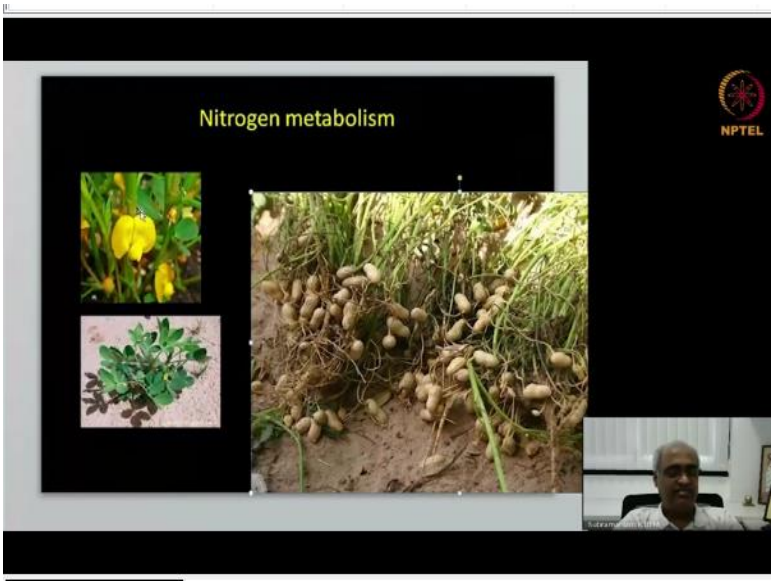

So, that brings us to the conclusion of our discussions of how carbon, hydrogen, oxygen do their dances in the living system**.** This energy for this dance is coming from sun, so as long as sun's energy falls down on the earth, you have these molecules dancing, transporting electron

continuously in a cyclical fashion**.** So, from water electrons are taken and the oxygen is evolved and then later those electrons flowing through that carbohydrate molecules.

And finally come to mitochondria and reduce oxygen into water again**,** so that is the electron circuit. And to make the electrons flow this way the sun's energy makes the carbon, hydrogen, oxygen molecules to keep arranging, rearranging in the manner in which we saw**.** So, this is the core path we have seen, we have not looked at the side branches, that is how I would like to view fatty acid biosynthesis and catabolism also.

So, if we have time we will get into fatty acids, otherwise the core of biochemistry you have learnt through whatever we have learned so far. Except that we have focused only on 3 elements so far, carbon, hydrogen, oxygen. Now we are going to the fourth important molecule, so in the order of abundance also this is the fourth one which is nitrogen**.** So, you would have seen this plant, this is groundnut**,** if you follow American English this is peanuts, so in India we call groundnut, this is the groundnut plant and this is the close-up of it is flower.

So, this shaped flower is a Fabaceae family member or legumes and these plants are absolutely pivotal for the nitrogen metabolism among the living organisms that we have. So, we will see that one step at a time. So, this is the aerial view of the plant and from the branches it has root like structures going into the soil and in the soil you have the seeds**.** The pod and if you open the pod you will find it mostly 2 seeds occasionally you may have 1 seeded 1 or 3 seeded ones, but mostly 2 seeded ones. And what is special about them? We will see as we go along and this is one example, so this is an oil seed.

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And here you go more of them, variety of pulses or lentils, if you speak Hindi dhals or if it is tamil it is paruppu**,** varieties of these. These are 30% dry weight protein source**;** this is the primary source of protein as long as you depend on them for your protein you are in good shape**.** If you forage elsewhere for protein then you will also get saturated fat and along with the troubles.

So, these are the main producers of the nitrogen containing compounds. So, proteins have amino acids and there you have nitrogen, so that is actually where we need the nitrogen. So, these plants, here is the spelling for that word they belong to Fabaceae, this is the botanical name of the family Fabaceae including this. And these are bulk of the crops that we grow, Fabaceae plants and vegetables are primarily Solanaceae family. And then the starch comes from the Gramineae**,** the grass relatives like rice, wheat, barley, oat etcetera.

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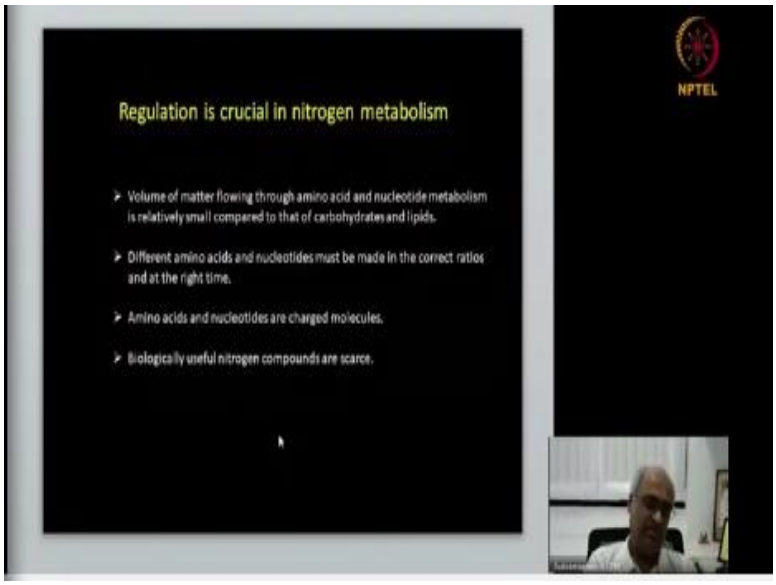

So, before we begin on the Fabaceae plants and why they are important in nitrogen metabolism etcetera. We need to remember these 4 bullets; they are really important regarding nitrogen metabolism. So, the first point is the volume of matter the bulk flow through these pathways that we are going to learn is really low compared to the bulk flow through carbohydrate and lipid metabolism.

They are the main things; bulk of the matter is in the form of carbon, hydrogen, oxygen without phosphorus or nitrogen**,** so those are the carbohydrates and lipids. And different amino acids and nucleotides, remember purine, pyrimidine, they have nitrogens; they are actually called nitrogenous bases. They must be made in correct ratios and at the right time, so if you want to make a protein with 300 amino acids and out of the 20 amino acid if you are deficient of only one amino acid you are not going to make the 300 amino acid of protein**.**

Let us say you have 19 amino acids and the missing amino acid is lysine, in translating an mRNA if the third triplet is for lysine and if you do not have lysine, that is it, you are not going to add the 4th, 5th and so on. So, it is all are none phenomena, so you need all the amino acids at the right ratio at the right time to make the right proteins, same is the case with nucleotides. And a third point is amino acids and nucleotides are charged molecules**,** so these are phosphates attached and therefore they are significantly acidic molecule.

And these have amino group and carboxyl group both are charged molecules. And when you are playing with charged molecules you cannot have too much of them, then you will create electrochemical gradients. So, therefore this needs to be tightly regulated and the nitrogen can be recovered and recycled and as a result the nitrogen compounds are scarce, the atmosphere has 70% nitrogen.

But it is triple bonded extremely stable structure and therefore they are not readily available in the usable form in biological systems. So, the biologically usable nitrogen is very scarce and therefore the nitrogen metabolism is tightly regulated and very efficiently scavenged and recycled again and again. So, this is to break the mix that you need to eat a lot of proteins, it is really not true.

The amino groups can be scavenged and recycled by fixing into carbohydrates and amino acids can be remade in our body**.** So, you really you need proteins but not a whole lot, so for these 4 reasons the nitrogen metabolism is tightly regulated, because the flow is very less and therefore you need to regulate correctly appropriate things at the appropriate time. Similarly correct ratios are important and it is an all or none and therefore again it has to be very tightly regulated to make the right things all at the right time.

Then you do not want charge gradients there and therefore again another reason why it should be regulated and resource is very scarce, so you need to judiciously use. So, these are the 4 reasons why this metabolism is, lot more fine tuned and regulated relative to the other 2 carbohydrates and lipids. They themselves are regulated as well, this is even more stringently regulated, that is all. So, I will stop here and in the next class we will look at why leguminous plants are important and how the nitrogen triple bond is broken and fixed in the biological system?