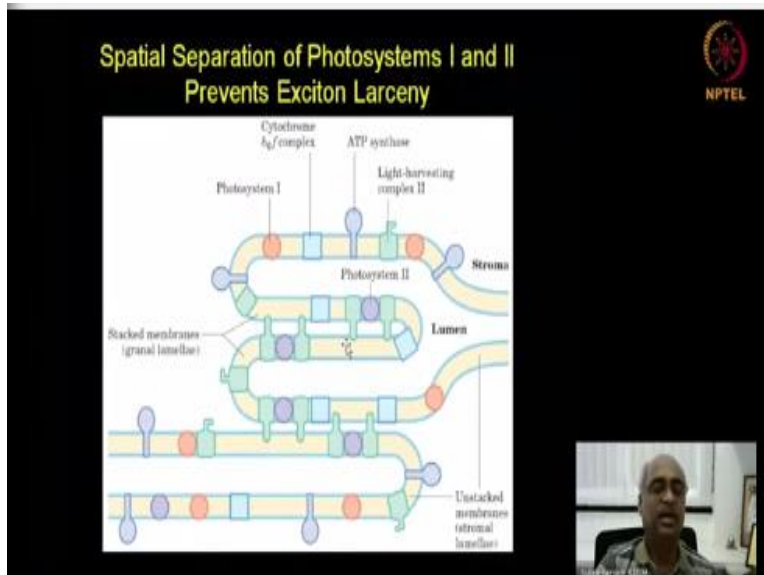


Introduction to Biomolecules
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Lecture-24
Photosynthesis and Carbon Assimilation (Part-2/3)

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Great. So, let us continue the photosynthesis that we were discussing in the last class. So, in the last class we were looking at the z scheme of photosystem II and photosystem I in cyanobacteria and plant chloroplast. So, we saw how the light harvesting system works and how the light harvesting system contains, what are called antenna chlorophylls and from the light absorbed by them the energy gets transferred to neighbouring molecules by a process called exciton transfer.

And that whole array like structures we called as the light harvesting antenna. And then finally from all such molecules you have the energy transfer to the reaction center. So, we saw the reaction center P680 and P700 in photosystem II and photosystem I. So, today what we are going to do is, we are going to see one important regulatory step that happens there and then we will move on to how the electrons that are transferred due to excitation to the electron carriers.

Like for example ubiquinone getting reduce to ubiquinol and then finally to cytochrome b_6f complex and to the next photosystem. So, how the electron lost from the reaction center is

replenished from water, so that is our next discussion. So, then the third we will move on to actually synthesizing a carbohydrate molecule by taking the carbon dioxide. So, that is the carbon assimilation reaction.

So, first let us look at the photosystem I and photosystem II. So, photosystem II say in this diagram what you are seeing in this cartoon. So, this is the stack grana like thylakoid where these are pressed against each other. And while this is at the top or this is at the bottom where they are exposed to stroma, also these sides. So, if you look at the diagram you do not see this photosystem I in the oppressed region.

So, here you do not see and you see photosystem II primarily only in that region and you have this light harvesting antenna that is harvesting the light energy for photosystem II are in close proximity. So, this regulation is required because the energy required like this one photosystem I actually gets excited at wavelength 700 requiring lesser energy than the one that required by the photosystem II which is 680.

So, as a result exciton harvesting by this light harvesting complex can actually be lost to photosystem I more readily to photosystem II. So, these light harvesting antenna could actually be transferring the exciton energy into this one, because this requires less energy than this, because this is excited by wavelength having less energy P700. So, as a result what would happen, if they are randomly uniformly distributed then photosystem II will not get excited frequently.

So, this will be under excited chronically while this will be over excited. So, if this is over excited then the electrons lost from this will not be fulfilled because the electrons lost from this comes from plastocyanin which ultimately gets it from the excited photosystem II. So, to avoid this problem there is a regulatory mechanism that plays a role and that is what is shown by this asymmetric distribution.

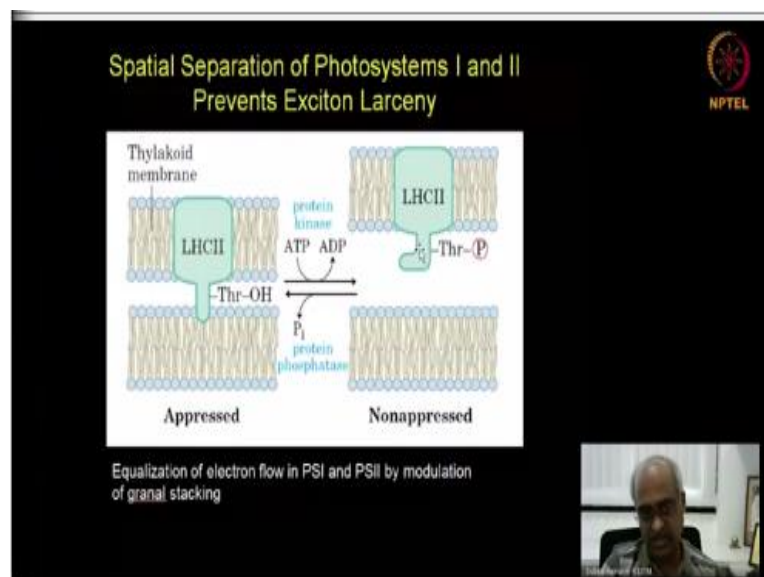
So, the photosystem II is present tightly in a stacked regions of the thylakoid membranes in this grana-like structure. And despite oppressing of these membranes is mediated by the light harvesting antenna of photosystem II itself. And as a result these are immobilized and this

ensures the spatial suppression from photosystem I ensures that the exciton transfer from LHC2 actually goes to photosystem II.

This ensures that the photosystem II is adequately excited. So, when you have bright light with heavy component on the blue region then you have this excited, more frequently than this. And therefore the ubiquinone is reduced to ubiquinol form and reduced ubiquinol form is very readily available. And the electron transfer from this to the next step is therefore needed to be speeded up, because you have more UBH-2 and from that electron should flow via the cytochrome b6f to plastocyanin and to photosystem I.

And if the UBH-2 that is a fully reduced ubiquinone, if its level is very high meaning this system is getting adequate excitation. Then that activates an enzyme as shown in this cartoon.

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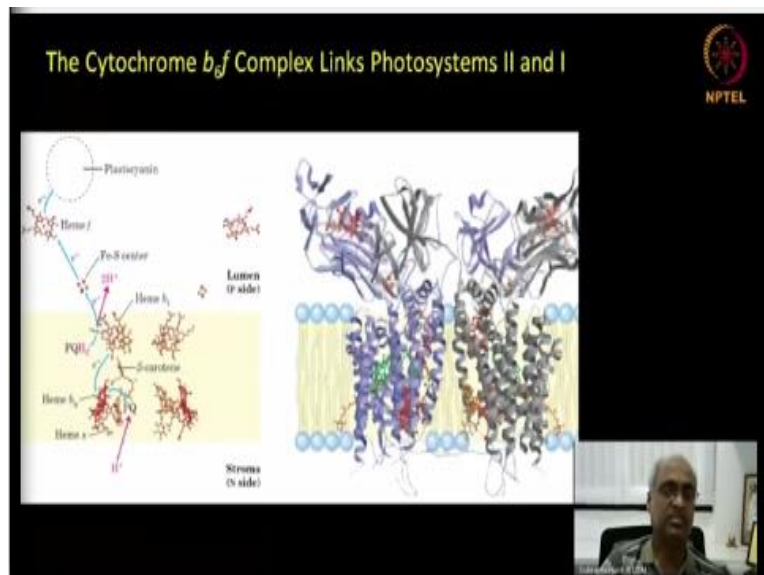
A protein kinase that phosphorylates threonine residue on the LHC2 and that leads to a conformational change such that it is no longer anchored on the other membrane of the thylakoid and it detaches. And when it is detached and this structure is relieved then this is free to go and harvest photons for photosystem I. So, now the UBH-2 fully reduced ubiquinone produced by photosystem II gets consumed by this.

On the other hand, when you have dim light with more components coming from the red region then this will deplete of the reduced ubiquinone and then you will have more oxidized ubiquinone. And the presence of more oxidized ubiquinone drives the opposite reaction by activating this enzyme protein phosphatase. And when the threonine is dephosphorylated then that leads to a conformation change in LHC2 such that it anchors to the adjacent membrane and it gets tightly oppressed.

Then it is locked in position with the photosystem II and whatever little light that it gets the energy absorbed is ultimately used to activating or exciting photosystem II. So, this way depending on the light intensity the light harvesting is regulated such that you have a balanced or optimum production and consumption on the ubiquinone, essentially not consumption of ubiquinone the concern oxidation reduction of ubiquinone to ubiquinol and back.

So, that is how equalization of electron flow in photosystem I and photosystem II is modulated by light itself. So, light ultimately activates these 2 enzymes bright light activates this, dim light activates this. So, this is what they call as larceny, meaning getting siphoned off or photosystem stealing the electrons from photosystem I, stealing it from photosystem II, so that is where they use the term larceny.

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So, that is about the regulation of how electron flow in photosystem I and II happens. So, next let us look at the cytochrome b6f complex itself, which is equivalent to the mitochondrial complex III, so this is again we have already seen this. So, we saw this with the purple bacteria which has only photosystem II and then we saw green sulfur bacteria which has photosystem I. So, there again we saw the electrons from the excited state flow via the cytochrome b6f complex back to the reaction center.

So, and this structure I told you at that time is very similar to the one in mitochondria complex III which oxidizes the fully reduced ubiquinone essentially it is called ubiquinol by transferring electrons to cytochrome f on the mitochondrial inner membrane side. So, where then the cytochrome c moves to the complex IV and transfers the electron there to oxygen there. So, here a very similar structure, so the first part on the left side you see without the amino acids without the protein backbone, we see only the prosthetic groups.

And you have the heme moieties x, so the plastocyanin is the final one, this is a protein, so although the name kind of resembles to the pigments we learnt. But this is a protein, which is functioning like cytochrome c of the complex III in mitochondria. So, electrons finally move to this plastocyanin and plastocyanin transfers to photosystem I. So, before that you have this cytochrome f with this heme f moiety, then the cytochrome b6 itself contains a heme b and an iron sulfur center then you have the heme b h and then another heme called heme x.

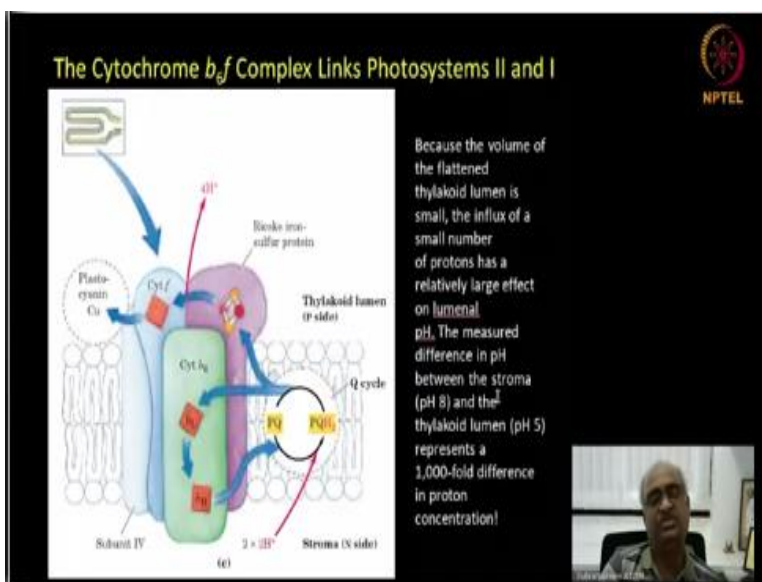
And there is also a beta carotene although we currently do not understand the functional contribution of beta carotene here. And the electron flow diagram is shown by this blue arrow, so this is the reduced form of ubiquinone called ubiquinol. And from there through a Q cycle mechanism that we will see once more in the next slide. But we have elaborately discussed that with respect to complex III in mitochondria.

So, from there electron flows this way and you get the oxidized ubiquinone and then finally to cytochrome this f and from that to plastocyanin. So, this is the part of the electrons here and during this process the conformational changes that happen in this complex due to the electron flow ends up pumping protons across the membrane, just like what complex III in mitochondria

did. And on the right side you have the structure having the protein, so it is a dimeric structure that you see here.

So, this portion on the top on the luminal side of the P side the positive side you are seeing the cytochrome f with the heme f that is shown here, so this one, this structure here. Again the other molecule dimer, so the other heme f is here, this one and the other hemes these heme b, heme x are shown here. And say it forms a canal like structure or a cavern or a valley like structure and that allows the free diffusion of the ubiquinone or ubiquinol in this structure.

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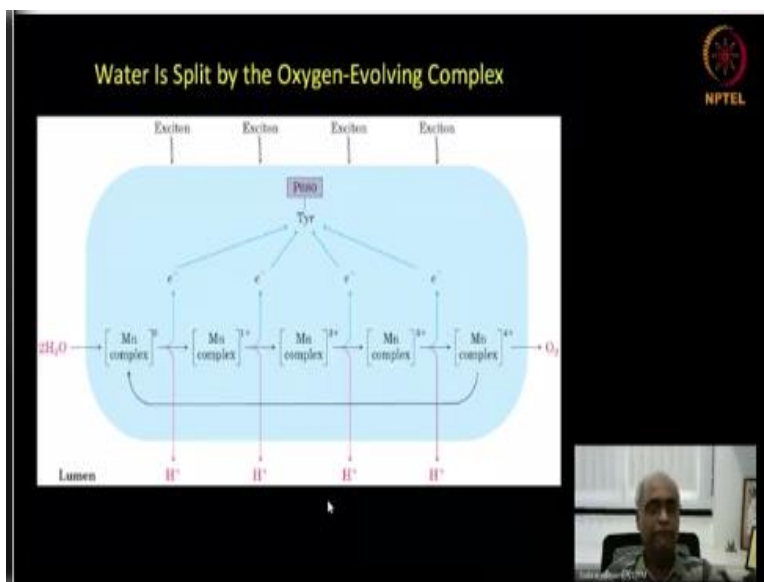
So, this is the Q cycle the very same thing that we saw in a very abbreviated way, there we saw 2 separate UBH reduced QH₂'s binding and how 1 electron goes to cytochrome c and the other one gets cycled back to reduce the semi ubiquinone there was formed due to 1 electron transfer. So, the same thing here again from the fully reduced one, you have 1 electron going via this ion sulfur.

Again this ion sulfur protein to cytochrome f to plastocyanin. So, this is a copper containing enzyme but it is not similar to complex IV in mitochondria. And the other electron via this cytochrome b₆ through these 2 heme moieties go back to reducing that free radical version, the radical version of the partially reduced ubiquinone called semiquinone. And that whole detail is not shown, because we have already seen elaborately.

And a similar Q cycle operates here to ensure 2 electron donations by the fully reduced ubiquinol but transferring only 1 electron at a time to plastocyanin. In this case the this phase, so this area is extremely narrow so compared to the stroma's side when I showed you the chloroplast structure with stacked thylakoid membrane green structures inside orange that you saw. And inside the green is what this space, this lumen, this is really, really small place.

And as a result when the protons are pumped into this by this complex the pH gradient really is about 1000 fold the proton concentration inside the thylakoid lumen is so high, it is pH 5 and outside in the stroma it is pH 8. And therefore there is a 1000 fold difference in proton concentration, sufficient enough for ATP synthesis.

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So, our next main topic in photosynthesis the light reactions part, the first part of photosynthesis is this water splitting by the oxygen evolving complex or water splitting complex, so it is known by both the names. Say essentially the primary thing here what happens is, 4 electrons and 4 protons are taken away from 2 molecules of water. And the 4 protons are pumped into the lumen, so this is the second event of proton pumping that we are seeing.

One, when the excited electron returns rather moves to the photosystem I via the chain of electron carriers in that pathway we just saw that b6f cytochrome pumps protons. And the next

one that we are seeing is the water splitting complex itself and the 4 electrons, so 4 protons are pumped into the lumen and the 4 electrons were taken up. They go into reducing these manganese ions, so manganese can exist in a stable oxidation state between +2 and +7.

So, it can very readily take 4 electrons in one go or it can take 1 electron at a time readily 4 electrons in sequence. And it can also get oxidized by giving out 1 electron at a time or giving 4 electrons at a time. And that flexibility of manganese ion is very smartly co-opted by this water spreading complex. And that is how the 4 electrons were taken away from 2 water molecules are given 1 electron at a time to the reaction center.

If you remember the cartoon that we saw in the last class or the class before that green vertical rectangle like things, when an exciton energy is transferred like 1 photon equivalent is transferred 1 electron is donated by the reaction center, creating the electron pole there, and that is how the charge separation happens. So, it loses only 1 electron at a time and from the electron donor it takes only 1 electron at a time.

But here when you split water into oxygen and protons you get 4 electrons in one go from 2 molecules, when you produce molecular oxygen you end up consuming 2 molecules of water. And these 4 electrons, the reaction center cannot take in one go it will take only one at a time, and that situation is what is very ingeniously handled by the water splitting complex taking the multiple stable oxidation states of manganese ion into good advantage.

And the electrons from the manganese ion is transferred to tyrosine residues on this complex. And so the textbook says the crystal structure solving of this complex was one of the most challenging among crystallizing and solving structures of proteins. And the mechanism has not been fully deduced, so this is the model that is supported by the available experiments and this is what currently we know.

But there are still some nitty-gritty details that needs to be filled. And this tyrosine residue is the one that takes at the electrons and from the tyrosine residue it goes to the next the reaction center that is P680. And this is how from water electrons are transferred into the reaction center. And

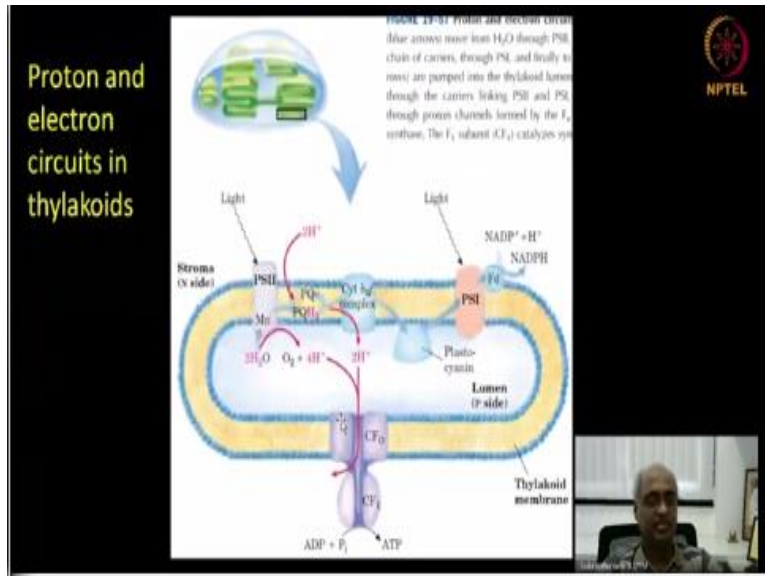
from the reaction center of course it goes via the carriers and finally reducing NADP into NADPH+ H⁺ are hydride transfer.

Like 2 electron, 1 proton transfer happens at the end of the 2 photosystems. So, that is where the electrons have gone, so and the protons have also been taken up when it comes through the ATP synthase. Then you have the reduced equivalence NADPH generated there. And when the protons returning ATP is also produced. So, you have reducing equivalence for the dehydrogenase reactions and then you have the energy to drive the ATP both are available.

So, that it can now readily go and do carbohydrate synthesis. Like in loosely speaking opposite of what we have learned so far through glycolysis and TCA cycle. I am saying loosely because it is not the exact reversal and in the process from water you have the oxygen evolving out. And this is how the atmosphere got its oxygen, from water only you get it, it is not from carbon dioxide.

And similarly we saw in the mitochondria, the electrons coming from the donors like NADH or FADH₂ succinate dehydrogenase reaction, they finally go to reduce oxygen to water, the exact opposite ends up happening in mitochondria. And there carbon dioxide is liberated from glucose kind of molecules. Here the carbon dioxide now we are going to see is going to be used to make glucose kind of molecules.

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So, we will not discuss the ATP synthase in great detail, because it is essentially the same as what we saw in mitochondria. You have the FO subunit oligomycin sensitive subunit, so do not call F not or F 0. And you have this F1 ATPs and the same rotational catalysis, instead of inter membrane space of mitochondria, here you have the thylakoid. And instead of matrix of the mitochondria here you have the stroma of the chloroplast, this open this bluish area.

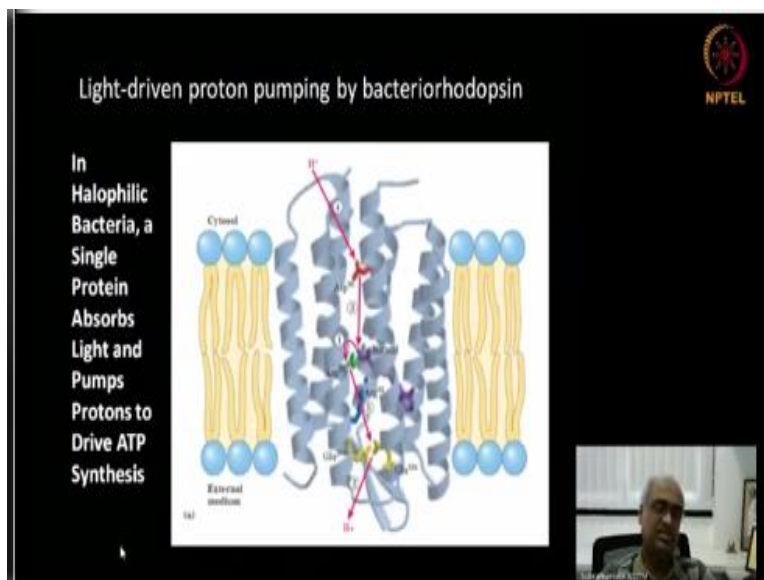
So, this cartoon actually is a summary of whatever we have learnt. So, you have the light reaction, here light exciting and all the antenna all that we know here. And from here you have that b6f pumping proton into this and this is the water splitting complex itself producing protons and evolving oxygen. Then you have it flowing to b6f and from that to plastocyanin, and plastocyanin is exactly like the cytochrome c in mitochondria.

This is again on the surface inside there that is on the inter membrane side; here it is on the luminal side of the thylakoid to photosystem I which again get excited by light as well. And from there the electrons go via ferredoxin to ferredoxin oxidoreductase reduces NADP to NADPH. So, that is where from water the electrons have gone into. So, from here this will be used and combined with the oxygen, carbon dioxide to make the carbohydrates.

And the proton gradient created here by these 2 water splitting complex here and then this cytochrome b6f complex that when it flows down the gradient then you make the ATP. So,

reducing equivalence as well as ATP are produced by the light reactions. So, up to now the light is absolutely essential for these reactions to happen. Essentially we have light energy, now in chemical potential energy. So, this is like the guy standing on the tall diving board, so potential energy is very high. And the required electrons and protons are here.

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A small detour into evolutionary history before we go to the carbon assimilation reactions that is a simpler a proton pump which is directly activated by light. So, there is no such complex thing like this where you have a separation of activation and pumping etcetera. So, this one what it does is, this molecule is called a bacteriorhodopsin, rhodopsin simply because like the protein in our rods and rod cells in the eye in the retina.

So, we already know retinol, retinoic acid, retinaldehyde all that because we have learnt that in term of studying the fat soluble vitamins. So, there I told you the cis-trans isomerism happening in the double bond of the retinol changing from cis to trans activated by light and then that returning back to cis. That alternating the cis-trans isomerism of retinol is used for sensing light in our eye.

A very similar thing here and that is why this is also called a rhodopsin, opsin optical, it is about the light and then this rod cell is probably from where this rhodopsin name comes. So, here very similar thing, only thing is here there is no brain sensing and making an image instead this cis-

trans isomerism happening due to light absorption by this retina is used to alter the confirmation of this protein.

Such that the amino acid side chains end up donating accepting protons and eventually leading to proton pumping. So, the light energy alternate the cis-trans configuration of the retina. And that changes the confirmation of the protein, such that the protein ends up pumping proton. And this is helpful for bacteria living in extreme saline environment. So, the extremely saline environments can have a salt concentration as high as 10^4 molar or 10^5 molar sodium chloride.

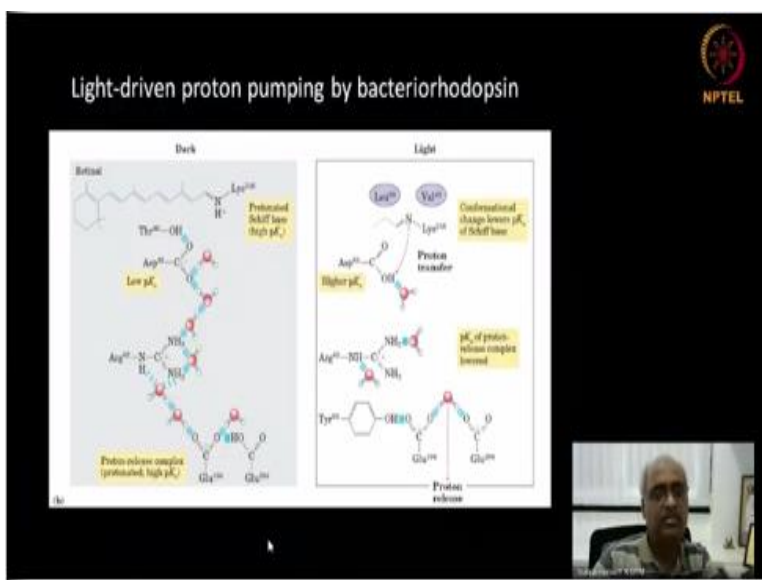
In such a high salt concentration environment, although this bacteria like us uses oxygen and burns fuel like glucose available from the surrounding media to obtain it is ATP and energy requirement. The oxygen availability in such environments is very low. And due to that it supplements it is energy requirements by using this protein and making some ATP synthesis. So, when light directly activates bacteriorhodopsin and pumps proton then you have a proton gradient generated.

And when that proton gradient goes via the ATP synthase, you get some ATP produced. No reducing equivalent, no other carbohydrate synthesis, nothing. A single molecule responding to light and undergoing conformation change pumps proton across and the proton gradient is used to make ATP. So, this is how it supplements the normal oxidative phosphorylation by a means without requiring the oxygen.

So, under low oxygen condition these bacteria benefits by the supplemental ATP synthesis. So, halophilic means salt loving bacteria. So, these are so adapted to the salty conditions, they cannot live in a less salt solution, live alone fresh water. So, there are places on earth, where you have all sides surrounded by mountains. So, therefore whatever little rain that falls on the mountains, they come to the middle bowl like valley and they know water flowing out from there. It never rains to fill the whole bowl and the overflow.

And the water evaporates there itself, and leaving the salt behind. So, the rain falls on the mountains, dissolves the minerals and salts, comes to the valley, forms a lake and when it is summer, the water evaporates but the salt stay there. And in such environments whatever water that remains on that salt they are called the brine b r i n e brine, that is extremely salty water and in such environments you find this bacteria.

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So, as a little bit detail about this proton pumping, this is primarily because we learnt what is proton hopping, this water is slightly ionized and that proton is readily taken up by a water molecule forming a hydronium ion. And since water molecules are hydrogen bonded such protons resulting from ionization through this hydrogen bonding can readily hop instantaneously to long distances.

And that time I told that kind of proton hopping is really very useful for catalysis of the enzyme active site. And here is one such example we see here. So, in this protein, so here this is the retinol molecule and in the dark condition this lysine side chain this protonated shifts base this has a high pKa that is ensured by the protein confirmation. And upon illumination the retinol structure changes, such that the amino acid is positioned closer to another one and that confirmation change leads to reducing the pKa of this group shifts base nitrogen and that readily donates the proton.

Because its pKa value is reduced and therefore even at a lower pH it readily donates a proton. And that via a series of proton hopping shown here, from threonine 89 to aspartic acid 85 and 82 and so on. It comes to the other end of the membrane, so this is the membrane. And finally from when these things undergo conformational change their pKa also changes such that they donate the proton. Only thing is when they donate the proton it is into the cytoplasmic side of the bacterium I through the extracellular side in the periplasmic phase, so that is where it ends up pumping.

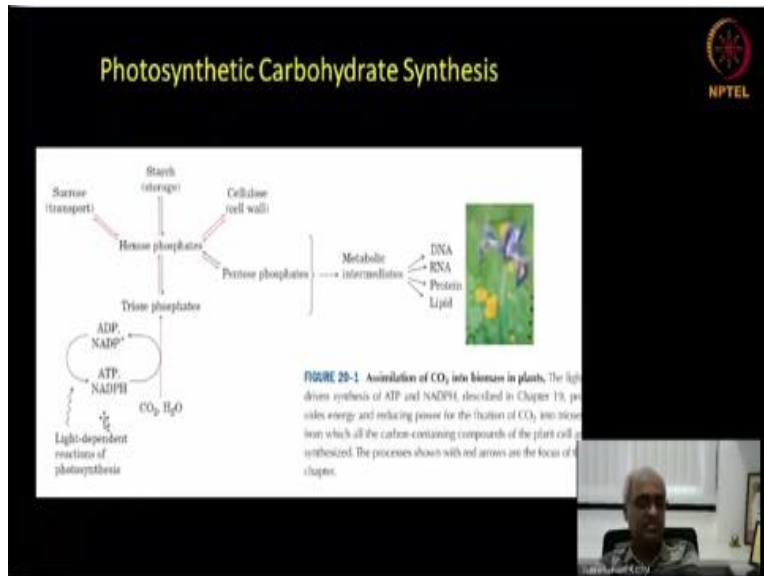
So, between the cell wall and the cell membrane you create a higher concentration of proton and compare to the cytoplasm and when it returns via the ATP synthase that leads to energy synthesis in ATP synthesis. So, the main point here is the conformational change affects the pKa of this group as well as this. And as a result upon illumination the lowering pH leads to proton donation.

And that via these amino acid side chain enabling proton hopping it comes to the other side. And since this one's pKa also is reduced, it readily donates the proton, but that proton is donated into the periplasmic space. Now this proton donated by this needs to be fulfilled and that is done by another amino acid in this case aspartic acid 85. And that eventually takes that proton from the cytoplasmic site.

So, essentially you are pumping from cytoplasm to the periplasmic membrane protons whenever illumination happens, so this is how the bacteriorhodopsin works. So, well before going and studying the photosystem I, photosystem II etcetera, people focused on the bacteriorhodopsin because it is an extremely simpler protein and easy to purify and crystallize, like relatively compared to the other ones.

And so this is one of the light sensitive molecular machines that you encounter. There is one more photolyase that helps in dimer repair in DNA, so that you probably will learn in molecular biology.

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So, that is all about light reactions. So, now we are going to use the reducing equivalence produced in the form of NADPH and the chemical potential energy in the form of ATP. And we are going to hydrolyze the ATP and the energy released will be used to drive the reduction of carbon dioxide into trios phosphates and then into hexose phosphate etcetera. So, that is what is going to happen in the carbon assimilation reaction.

And for this you do not need light; it can happen in the presence as well as absence of light. So, this cartoon gives you an overall view of what is happening, from carbon dioxide and water you have the trios phosphates formed. And from them to hexose phosphates and this may be converted into disaccharide sucrose and that is transported to other parts of the plants, like to root and storing in the roots.

And sometimes in the stem itself, like for example sugarcane that is why sugarcane juice is sweet, because sucrose is there. So, sucrose is the form in which it is transported, so that is an important concept you need to remember. So, the form in which the carbohydrates produced in the leaves are transported to other parts of the plants is in the form of sucrose. And in grains like rice and wheat, barley etcetera or potato, cassava in all of them the storage is starch.

Glucose we know that starch is a polymer of glucose. And for cell wall structure we have cellulose and this one pathway that we did not cover during our carbohydrate metabolism. We

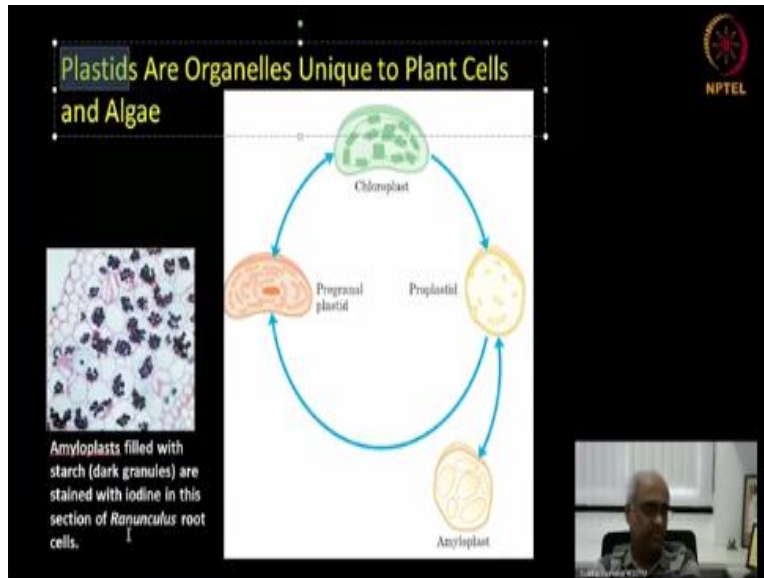
saw glycolysis and we saw a TCA cycle, but there is one more pathway called the pentose phosphate pathway or PPP triple P pathway or HMP shunt in memory or the in honor of the scientist who discovered that pathway.

Say, essentially that pathway, we are not going to go into it, I am briefly telling you what is the essential function of that pathway. That pathway produces pentose sugars from the hexose sugars and the pentose sugars we know are required for nucleic acid production. And other intermediates for protein as well as lipid biosynthesis, so somehow like hexoses can go into this. So, when you look at all of this, you see this, these molecules this and this.

So, entire set of macromolecules are covered, molecules of like whatever we learned are all covered. So, meaning, all of them are produced from carbon dioxide fixation into triose. So, this is why carbohydrate chemistry central in life, so life is actually carbohydrate chemistry. The other molecules are all produced from carbohydrates only that is because the way carbon enters into the system is via carbohydrate formation.

So, now let us look at this, we are not going to learn all of this, so our focus will only be coming up to this. So, we are going to assume via this is self-explanatory we learned, we will understand and also this is the only biochemistry course I am going to learn, so I am not going to cover all the branches and details.

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Before we go into is again what is the stage in which this drama happens? So, that is what we are going to first look at it. So, chloroplast is where all this light reactions, all the green thing, so this is where NADPH production ATP all that is happening. And they are used in the stroma area here and that is where the carbon assimilation reaction related enzymes are located.

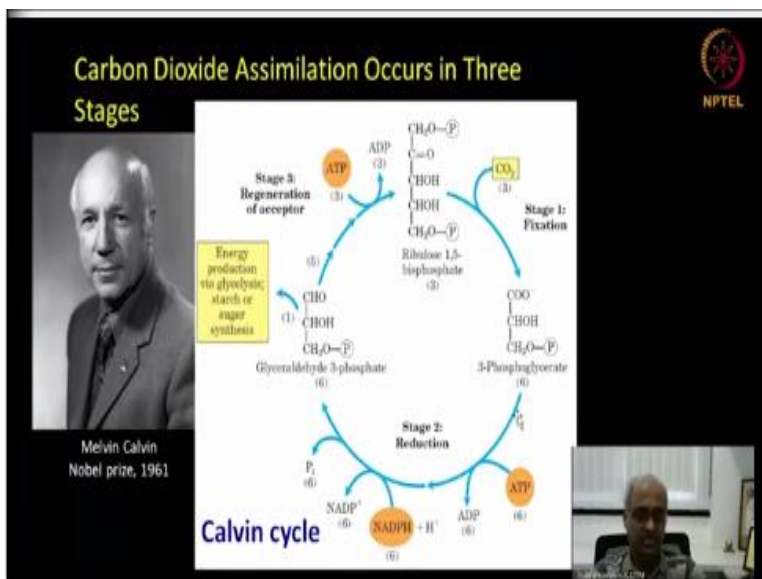
And at the end of this when you produce lot of carbohydrates they are converted into starch. And that leads to conversion of this chloroplast into what are called amyloplasts. Amyloplast do not have this internal membrane structures, these are all broken down and the entire space is used for storing starch. And such starch filled structures these organelles are called plastids, may chloroplast is a plastid here in the title you have the spelling.

So, the plastid filled with the starch and not doing photosynthesis is amyloplast. So, here is the micrograph of amyloplast, iodine stained, iodine binds to starch and you have here the starch granules are shown everywhere here, so this is starch filled. So, this is the kind of plastid you will find for example in potato, potato is not going to have this green chloroplast. And these actually exist in homeostasis which form this exist reflects what organ and what it is function is?

For example, in leaf where photosynthesis happens, they exist in the form of chloroplast, in storage organs they exist in the form of amyloplast. Meaning, these are reversible, these structures an intermediate called proplastid can assemble the grana and they can become

chloroplasts. And chloroplast can lose them and become protoplastids and from there they can go and become amyloplasts. So, this is an intermediate structure called pre-granule plastids, meaning grannum has not formed but the membranal flattened discs have already formed.

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So, this is the overall summary of the carbon assimilation reaction like the way we saw the TCA cycle circle first and then we went into the individual reactions. Similarly this is the overall perspective. So, the scientist who worked out this they were actually 3 of them Belvin, Bosham and Calvin. And in that 3 member group Calvin is the main person, so he got the Nobel prize in 1961 because this is one of the central aspect of biology.

So, this is how carbon enters into the biosphere. So, carbon dioxide in sense should be called inorganic carbon, because it is not part of the living system. So, but carbon in this form like this carbohydrates, they are genuinely products of life and therefore they only are organic compounds, organism derived. So, this inorganic carbon becomes organic carbon by this cycle.

So, this cycle has 3 stages, the first stage is carbon fixation, the carbon dioxide gets incorporated into a pre-existing carbohydrate and this pre-existing carbohydrate used here is this pentose ribulose 1, 5 bisphosphate, ribulose that u l should sound aldolase like fructose. It has the like fructose, it has a ketone group, so this will form chemi ketol if it forms an internal a linkage.

So, ribulose, is phosphorylated in 2 places, so it is ribulose biphosphate, so this 5 carbon compound becomes 2, 3 carbon compounds by taking this carbon dioxide, so this is the fixation reaction. And next there is a reduction reaction, because the end product is 3-phosphoglycerate, this we saw in the reverse order in glycolysis. Glyceroldehyde-3-phosphate became actually that is 1, 3 biphosphoglycerate that is what it forms.

So, that phosphoglycerate is what you are seeing here, in glycolysis it was the opposite direction, so now it is in this way. So, this is a reduction reaction because carboxylic group, aldehyde group, so that is a reduction carboxylic acid to aldehyde group. In glycolysis, we saw aldehyde becoming carboxylic acid and therefore we call it as oxidation, so that is a dehydrogenation reaction as well there.

So, here it is the opposite of that, so therefore we call this reduction, so that is the second step. Third is regeneration of the ribulose biphosphate, therefore the cycle can continue? And to take care of the stoichiometry we begin this way, we begin with 3 molecules of this, so 3 times 5, 15 carbons. And we take 3 molecules of carbon dioxide, so 18 carbons, end up producing 6, 3 carbon phosphoglycerates.

Now of the 6, 5 of them are going to combine, so 5 times 3, 15, so 5 carbon, 3 molecules. The net result is 3 carbon have become 1 glyceroldehyde-3-phosphate which has 3 carbons in it. So, this is the stoichiometry, 3 carbon dioxide are fixed with 3 ribulose biphosphate producing 6 trioses whether you are talking about this or this, 6 of them. Of which 5 are going to make 3 of these pentose and the 1 is the net gain.

And that 1 is going to now form hexose and go into making starch and sugar etcetera. So, we have the fixation step, reduction step and regeneration of the acceptor step. That regeneration step requires the energy in the form of ATP. So, I will stop here, in tomorrow's class we will focus on the fixation reaction, how ribulose-1-biphosphate is converted into 3-phosphoglycerate.