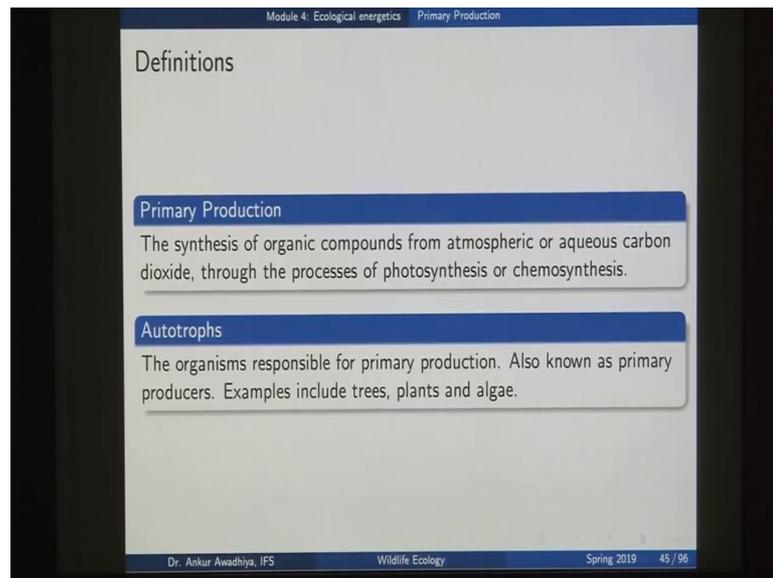


Wildlife Ecology
Prof. Ankur Awadhiya
Department of Biotechnology
Indian Institute of Technology, Kanpur

Lecture – 11
Primary Production

(Refer Slide Time: 00:20)



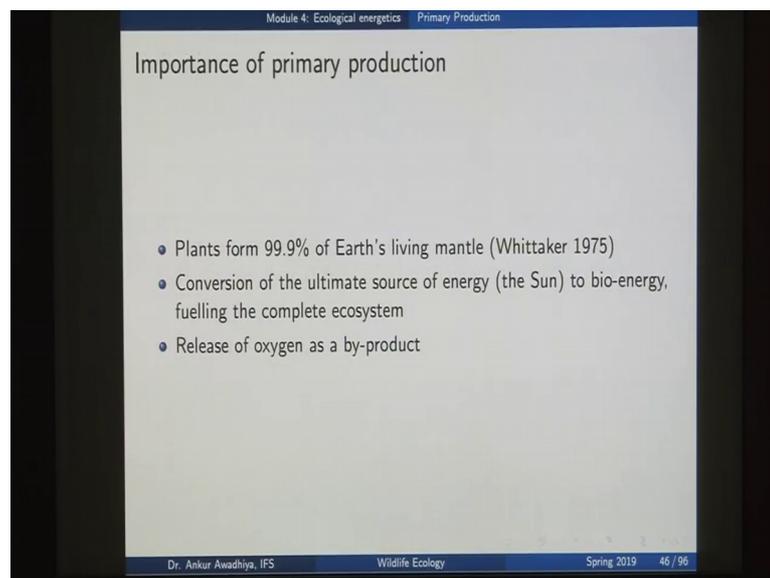
[FL]. Today, we move forward with our discussion on ecological energetics, and look at primary production. So, we look at some definitions. Primary production is the synthesis of organic compounds from atmospheric or aqueous carbon dioxide, through the process of photosynthesis or chemosynthesis. So, here we are looking at the autotrophs or the organisms that are responsible for primary production, as we have seen in one of our earlier lectures. And these are of two kinds they are photo autotrophs or chemo autotrophs.

So, photo autotrophs are those organisms that use light photo is light, auto is self, troph is nutrition. So, with the help of light, they are doing self-nutrition which means that they are fixing up carbon dioxide into organic molecules. Now, these organic molecules such as carbon such as carbohydrates or fats or proteins, and so on, then make up the bodies of these organisms. And these organic molecules are not only required to make up the bodies of these organisms. But, then when these organisms are eaten up, by other organisms which we call as consumers. So, in that process these organic molecules move up in the food chain.

And in with those the energy that was fixed up by the primary producers is also moved up in the food chain. So, primary production which is the synthesis of organic compounds from atmospheric or aqueous carbon dioxide. Now, atmospheric carbon dioxide in situations, where we have the photo autotrophs; that are exposed to the air. And in the case of those photo autotrophs that are or in the case of those chemo autotrophs that are not exposed to the air, but are residing in an aqueous environment or water environment in that case, they also use the aqueous carbon dioxide.

So, examples would be organisms that are living in the oceans, in the rivers, in the different water bodies ponds, lakes, and so on. So, synthesis of organic compounds from atmospheric or aqueous carbon dioxide through the process of photosynthesis or chemosynthesis and the organisms that are doing primary production are autotrophs which are of two kinds, we have photoautotrophs, and the chemoautotrophs. And the examples include trees, plants, algae, and so on.

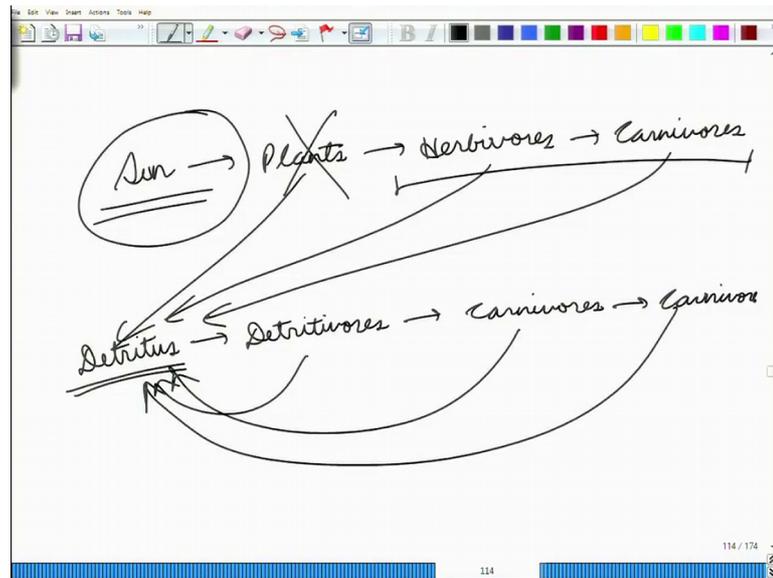
(Refer Slide Time: 02:29)



So, why that important to learn about the primary production, it is important for three main reasons. One plants form 99.9 percent of the earth's living mantle. So, there is this report from the table, which says that 99.9 percent of the earth's living mantle or all the organisms that are living. So, 99.9 percent of those is made up of the autotrophs or the plants, so because they form a very major portion of the ecosystem. So, it becomes extremely important to know about those.

Now, this is also evident if we go to any of our forested areas, so if you visit any forest, you will see so many trees around, but so let less number of animals that are there which is which come which makes this ratio of 99.9 percent. The second reason is that primary production is responsible for the conversion of the ultimate source of energy, which is the sun to biological energy which fuels the complete ecosystem.

(Refer Slide Time: 03:34)



So, in the case of any food chain, when we have so if we talk about sun and the energy goes to the plants, from there it goes to the herbivores, from there it goes to the carnivores. Now, in such a food chain the, the primary source of energy is the sun. And if this portion is not there, if plants are not there, so the rest of the food chain will also collapse.

Now, even in the case of the detritus food chains. So, when we talk about detritus, which is then fed by detritivores, which is then fed upon by carnivores, and then the next higher level carnivore and so on. So, in this case when we talk about this detritus, this detritus is coming from the plants or the herbivores or the carnivores or other parts of this food chain.

So, in this case also, we can trace the ultimate source of energy to the sun. Except in those very few instances in which the source of energy is chemical reactions, when we are starting a food chain through the process of chemo synthesis, through chemo autotrophs. Now, even in that case the conversion of the energy into the biological

molecules in the very first place occurs through the action of autotrophs, which is the same as talking about the primary production.

And the third importance is that it releases oxygen as a by-product. Now, oxygen is required by most of the other organisms to convert these biological molecules into energy, and because this is a by-product of primary production. So, there also it becomes extremely important to learn about primary production.

(Refer Slide Time: 05:28)

Module 4: Ecological energetics Primary Production

Two processes happen in tandem

Photosynthesis

$$6\text{CO}_2 + 6\text{H}_2\text{O} \xrightarrow[\text{Solar energy}]{\text{Chlorophyll, enzymes}} \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2$$

Respiration

$$\text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2 \xrightarrow{\text{Metabolic enzymes}} 6\text{CO}_2 + 6\text{H}_2\text{O}$$

Dr. Ankur Awadhya, IFS Wildlife Ecology Spring 2019 47 / 96

Now, when we are talking about these reactions, there are two processes that are happening in tandem or at the same time. So, in the case of a plant a plant is doing photosynthesis, and it is also doing respiration. Now, in the process of photosynthesis, you have carbon dioxide and water which are being acted upon through the action of enzymes, which are present in the chloroplast. So, chlorophyll is also important here, and they are fixing up solar energy into these sugars. So, here we are talking about glucose, so it is converting carbon dioxide and water into glucose, and is releasing oxygen as a by-product.

Now, most of the cells of the plants, and also all most of the cells that are present in animal bodies are also doing respiration. Now, respiration is a reverse process. In the process of respiration, these molecules that were made by the plants are then burnt to generate energy. So, when we talk about respiration, you just can invert this arrow. So, you will have this glucose plus oxygen in the presence of metabolic enzymes, it is giving

you carbon dioxide and water. And the solar energy that was fixed in the process of photosynthesis is then released in the form of energy molecules such as ATP.

(Refer Slide Time: 06:53)

Module 4: Ecological energetics Primary Production

Definitions

- Gross primary production**
Energy (or carbon) fixed via photosynthesis per unit time
- Net primary production**
Gross primary production - Energy (or carbon) lost via respiration per unit time
- Compensation point**
The equilibrium point for plants where photosynthesis equals respiration

Dr. Ankur Awadhya, IFS Wildlife Ecology Spring 2019 48 / 96

Now, when both of these reactions are act are acting at the same point, we can define three terms. First is the gross primary production. Now, gross primary production is the energy or carbon that is fixed by photosynthesis per unit time.

(Refer Slide Time: 07:09)

$6\text{CO}_2 + 6\text{H}_2\text{O} \xrightarrow[\text{solar energy}]{\text{Chl., enzymes}} \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2$

Photosynthesis - Respiration

120 / 174

So, what we are asking here in the case of gross primary production is when we are talking about this reaction. Now, when we have this reaction, when we are talking about

gross primary production, what we are asking is how much of this carbon dioxide is getting fixed or how much of this energy is getting fixed or how much of these biological molecules are getting formed or how much amount of oxygen is getting released. So, when we ask this question that this reaction is happening, but what is the rate at which this reaction is happening, then we are talking about the gross primary production. The energy or carbon that is getting fixed via photosynthesis per unit time is the gross primary production.

(Refer Slide Time: 08:14)

Module 4: Ecological energetics Primary Production

Two processes happen in tandem

Photosynthesis

$$6\text{CO}_2 + 6\text{H}_2\text{O} \xrightarrow[\text{Solar energy}]{\text{Chlorophyll, enzymes}} \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2$$

Respiration

$$\text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2 \xrightarrow{\text{Metabolic enzymes}} 6\text{CO}_2 + 6\text{H}_2\text{O}$$

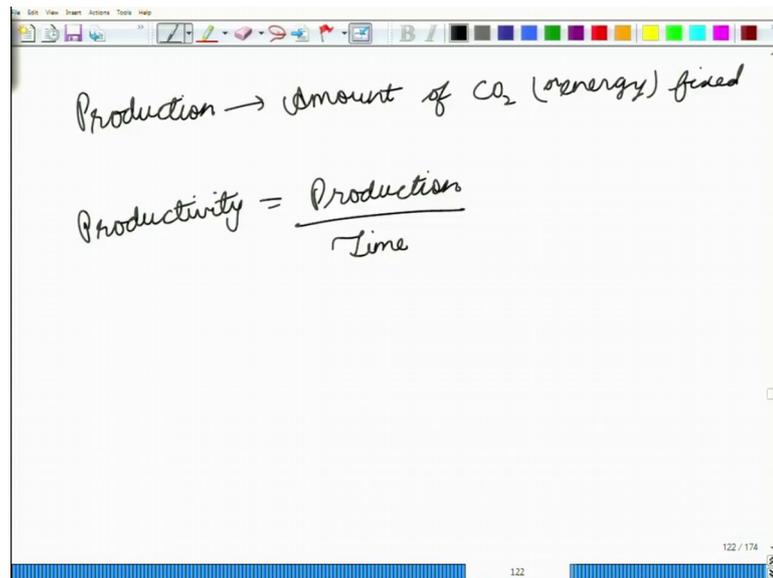
Dr. Ankur Awadhya, IFS Wildlife Ecology Spring 2019 47 / 96

Now, as we saw before there are two reactions happening in tandem. Now, in any plant cell or in those cells that have chloroplast, we are having this process of photosynthesis. And at the same time we are also observing respiration in the whole of the plant. So, so when we talk about photosynthesis some amount of carbon is getting fixed, but then when we talk about respiration some of that carbon is again getting released back.

So, when we are talking about the gross primary production, we are asking about the rate of photosynthesis. But, when we subtract respiration from this, so photosynthesis minus respiration. So, in that case we are talking about the net primary production. So, net primary production is the gross primary production or the energy or carbon that was fixed by photosynthesis minus the energy or carbon that is lost via respiration. And when we express it per unit time, we are talking about the net primary production.

Now, in some of the books we say that when we are talking about gross primary production, it is the energy or carbon that is fixed. And when we talk about gross primary productivity, in that case it is fixation per unit time. So, this is a semantic difference that we see in some literature.

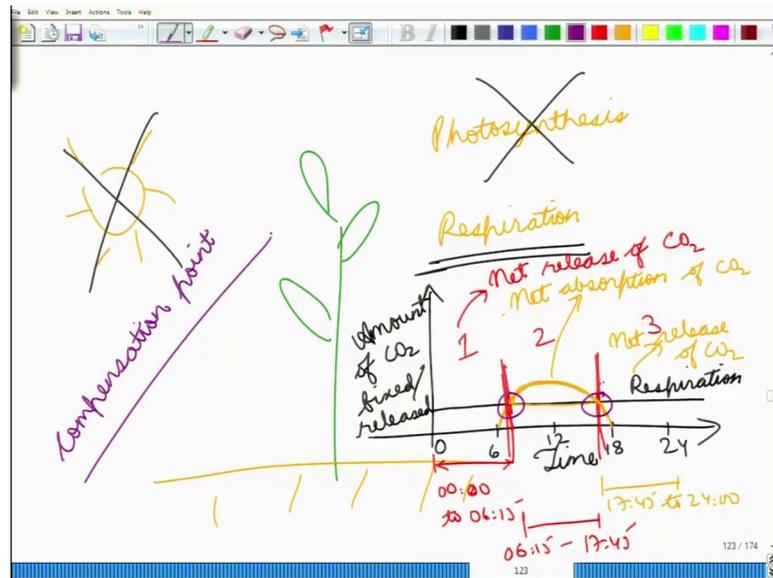
(Refer Slide Time: 09:43)



The image shows a digital whiteboard with handwritten text. The top line reads "Production → Amount of CO₂ (or energy) fixed". Below this, the equation "Productivity = $\frac{\text{Production}}{\text{Time}}$ " is written. The whiteboard interface includes a toolbar at the top with various drawing tools and a status bar at the bottom right showing "122 / 174".

So, when we say production that is amount of CO₂ or energy fixed. And when we say productivity that means, production per unit time, but then there are some books that use these terms interchangeably. So, when we talk about gross primary production, we can also say that we are referring to the energy that is being fixed per unit time. Now, there is this third term called compensation point. Now, compensation point is the equilibrium point for plants, where photosynthesis equals respiration.

(Refer Slide Time: 10:35)



Now, what is compensation point? So, suppose you have this plant, and when you have the sun, then you have two processes that are happening. One is photosynthesis, and the second process is respiration, now this is during the daytime. Now, during the night time, we do not have the sun, and so the photosynthesis stops, and we only have a respiration that is going on.

So, in this case we can say that respiration occurs at all times, whereas photosynthesis happens only in the daytime, only when light is available. Now, if we look at the amount of carbon or the amount of carbon dioxide that is getting fixed, we will find that in the case of food in the case of respiration, you will have a constant amount. So, this is fixed or released.

So, here we have respiration, because that is happening at all times whereas, in the case of photosynthesis, so on the x axis here we have the time. And let us say here you have from 0 hours 6, 12, 18, and 24 hours. Now, 24 hours is the midnight time. Now, suppose the sun rises at around 6'o clock, so in that case the photosynthesis reaction would start at this time. And then or and say let us say that the sun sets at around 6'o clock, and then this would peak at some time. So, this is the amount of carbon dioxide or oxygen that is getting absorbed. And in the case of respiration that would be somewhere below this or something like this. So, here we have respiration.

Now, if we look at this curve, we can divide it into these three regions. Now, region 1, 2, and 3; now, in the first region from 0 hours, till say around 6:15. So, 0000 to 6:15. Here we have a time where the where the carbon dioxide that is released because of respiration is greater than the carbon dioxide that is getting fixed by the process of photosynthesis. So, here we have a net release of carbon or net release of carbon dioxide. In this stage from 6:15 fifteen to say around 17:45 here we see that the amount of carbon that is released in the process of respiration is less than the amount of carbon dioxide that is getting fixed because of photosynthesis.

So, in this section in section-2 will have a net absorption of CO₂. And in this third stage that is from your 17:45 to 24:40 hours. Here again we have a net release of carbon dioxide. Now, in this curve we can delineate two points; one is this, and the second one is this. So, at both of these points, we have the amount of carbon dioxide that is getting released because of respiration is equal to the amount of carbon dioxide that is getting fixed because of photosynthesis. And both of these points go by the name of compensation points.

So, compensation point is the equilibrium point for plants, where photosynthesis equals respiration or the amount of carbon dioxide that is getting fixed by photosynthesis is the amount of carbon dioxide that is getting released because of respiration or in terms of energy the amount of energy that is getting fixed because of photosynthesis is equal to the amount of energy that is being released through the process of respiration.

So, at these two points, the plant is neither absorbing carbon dioxide nor is giving out oxygen. Let us say it is neither absorbing carbon dioxide nor is it releasing carbon dioxide, and it is neither absorbing oxygen or it is release of oxygen. So, these two points as they normally occur during early mornings and late evenings, these two points are known as the compensation points.

(Refer Slide Time: 15:46)

Module 4: Ecological energetics Primary Production

Measurements of production

$$6\text{CO}_2 + 6\text{H}_2\text{O} \xrightarrow[\text{Solar energy}]{\text{Chlorophyll, enzymes}} \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2$$

can be put into energetics terms as:

$$6\text{CO}_2 + 6\text{H}_2\text{O} \xrightarrow[2966 \text{ kJ}]{\text{Chlorophyll, enzymes}} \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2$$

implying that for each mole of glucose produced,

- 2966 kJ of energy is absorbed
- 6 moles of CO_2 is utilised (134.4 litres at standard temperature and pressure⁴)
- 6 moles of O_2 is released (134.4 litres at standard temperature and pressure)

These values can easily be measured to estimate primary productivity.

⁴Since 1982, STP is defined as a temperature of 273.15 K and an absolute pressure of exactly 100 kPa (1 bar)

Dr. Ankur Awadhya, IFS Wildlife Ecology Spring 2019 49 / 96

Now, how do we measure the gross primary production or the net primary production? So, here we have three different methods through which we can measure the amount of energy that is being fixed or the amount of carbon that is being fixed. When we write this reaction $6\text{CO}_2 + 6\text{H}_2\text{O}$ in the presence of chlorophyll enzymes, and solar energy is giving you glucose plus 6 oxygen.

So, in terms of energetics we can ask this question, how much amount of solar energy is required in this process. So, if we compute the amount of solar energy that is required, it comes to around 2966 kilo joules, when you have one mole of glucose that is being produced. So, for each mole of glucose that is being produced, you have 2966 kilojoules of energy that is getting absorbed. 6 moles of carbon dioxide that is getting utilized and 6 moles of oxygen that is getting released.

Now, when we say 6 moles of carbon dioxide, it means 134.4 liters at the standard temperature and pressure, which is defined as 0 degrees Celsius, and a pressure of 1 bar. Now, when we have these values, we can measure the amount of carbon dioxide that is getting fixed by either measuring the rate at which this carbon dioxide is getting utilized.

So, for instance you have a plant you cover it with a glass jar, and you measure the amount of carbon dioxide that is present in the air there. And then throughout the day, you try measuring the amount of carbon dioxide at different points of time. And

when you come to this conclusion that this x amount of carbon dioxide has been utilized, so we can say that x divided by so x moles divided by 6 moles is the amount of glucose in moles that has been produced or in place of measuring carbon dioxide, we can even measure oxygen.

So, we can measure the amount of oxygen that has been released by the plant to make an estimate of the amount of carbon dioxide that is getting fixed or the amount of these biological molecules that are getting synthesized. So, this is a way of measuring, the gross primary production or productivity. Now, in this case if we also include the amount of carbon that is getting released because of the process of respiration, we are measuring the net primary production or productivity.

(Refer Slide Time: 18:04)

Module 4: Ecological energetics Primary Production

Another method

$$6\text{CO}_2 + 6\text{H}_2\text{O} \xrightarrow[\text{Solar energy}]{\text{Chlorophyll, enzymes}} \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2$$

In this process, we may replace CO_2 with labelled, radioactive ^{14}C .
After some time, the complete plant is harvested and the quantity of ^{14}C is measured to estimate the amount of CO_2 absorbed by the plant.
Issue: Some amount of ^{14}C may also get lost during respiration.

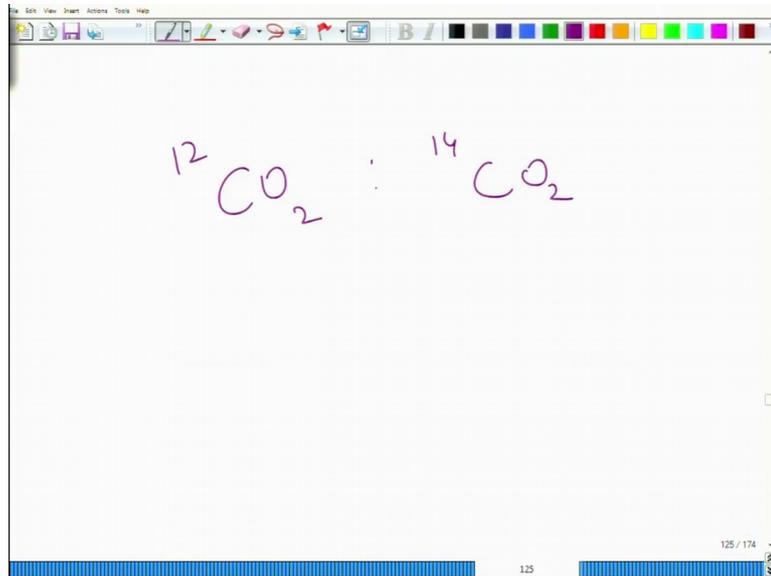
Dr. Ankur Awadhya, IFS Wildlife Ecology Spring 2019 50 / 98

Now, another method is this. So, here we see that in place of carbon dioxide, if we replace it with radioactive carbon dioxide. So, if we replace carbon 12 with carbon 14, then this carbon 14 will also get incorporated in these sugar molecules that are being produced. So, we can put this plant into a chamber in which it is not having our normal CO_2 , but all the carbons in the CO_2 have been labeled. So, they are all carbon 14.

So, in that case we can measure the amount of carbon 14 that is getting incorporated in the plants. And then we can use it to make an estimate of the amount of carbon dioxide that has been absorbed by this plant in the process of photosynthesis. Now, even in this case, because the plant is also doing some amount of respiration. So, some amount of

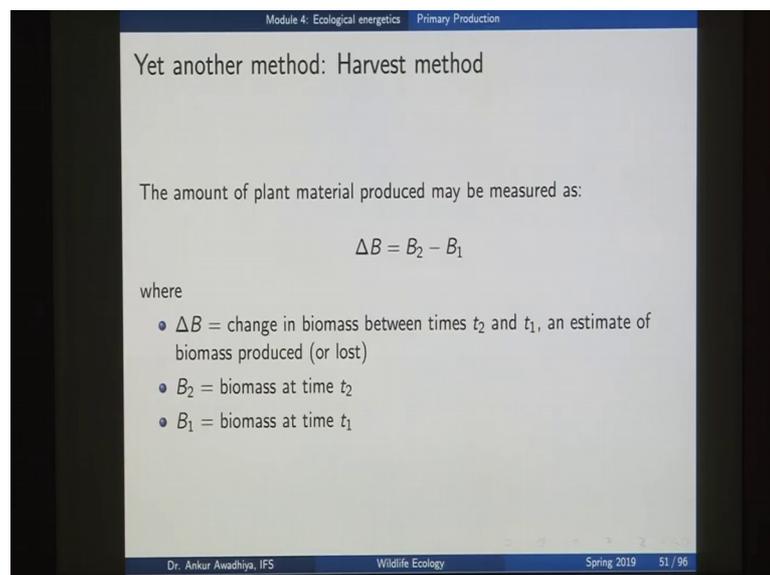
carbon 14 will also be lost. And so in that case, we are measuring the net primary production or the productivity.

(Refer Slide Time: 19:17)



Now, one other variant could be that we are not replacing all of CO₂ with carbon 14, but what we are doing is that we have a mixture of carbon 12 and carbon 14. And then if we know the ratio that was there in the beginning, we can use this ratio as well to figure out the amount of sugars that are getting produced by looking at an amount of carbon 14 that has been fixed in this process.

(Refer Slide Time: 19:39)



Module 4: Ecological energetics Primary Production

Yet another method: Harvest method

The amount of plant material produced may be measured as:

$$\Delta B = B_2 - B_1$$

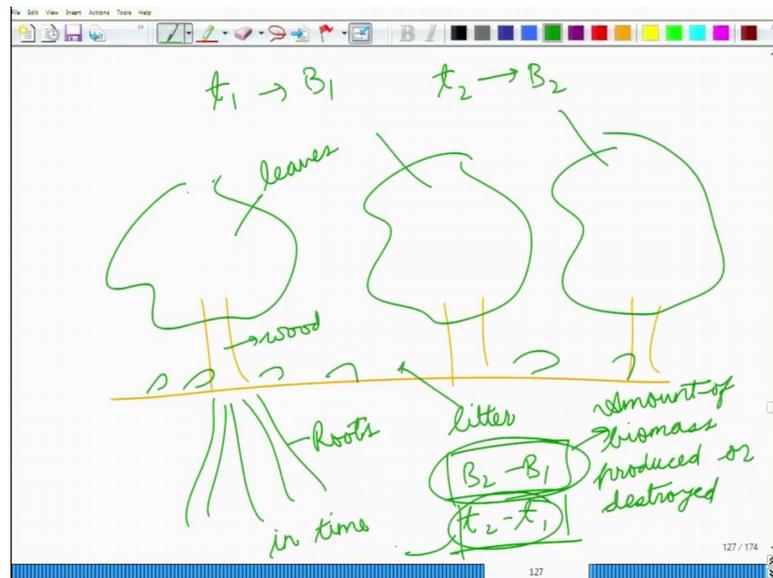
where

- ΔB = change in biomass between times t_2 and t_1 , an estimate of biomass produced (or lost)
- B_2 = biomass at time t_2
- B_1 = biomass at time t_1

Dr. Ankur Awadhya, IFS Wildlife Ecology Spring 2019 51 / 96

Now, the third method which is the easier method and is the most widely utilized method it says that the amount of plant material that is being produced can be measured as ΔB , where B is the biomass. So, ΔB is the change in the biomass between two time periods t_2 and t_1 . And B_2 is the biomass at time t_2 , and B_1 is the biomass at time t_1 .

(Refer Slide Time: 20:11)



So, if we take this difference, so what we are doing in this case is that suppose you have a forest, now in this forest we go there at say time t_1 , and we measure the total amount of biomass that is there in the system. Now, how do we measure the biomass, well we can make an estimate of the total amount of wood that is present, the total amount of leaves that are present. And we can also make an estimate of the total amount of biomass in the form of roots that is present in this forest. So, you add the leaves from this plant this plant, and so on.

And also you can make an estimate of the amount of litter that has gone down. So, let us consists of the dead wood or the decaying wood or the dead leaves that are that have come down. Now, at time t_1 , when you make this measurement of the total amount of biomass that is present in this forest. And you measure that it is B_1 . Now, you go back to this forest, after say one year, and at that time you at time t_2 , you measure the amount of biomass and that is B_2 .

Now, in this period of t_2 minus t_1 , you have a total change of biomass of B_2 minus B_1 , so that is the amount of biomass that has been produced or destroyed depending on

whether it is a positive or negative in time t 2 minus t 1. So, this is the amount of biomass divided that was produce were destroyed, and divided by that the time period of measurement. So, from this as well we can make an estimate of the net primary productivity of this particular forest.

(Refer Slide Time: 22:11)

Module 4: Ecological energetics Primary Production

Efficiency

Efficiency of gross primary production

$$\eta = \frac{\text{Energy fixed by gross primary production}}{\text{Energy in incident sunlight}}$$

Efficiency of net primary production

$$\eta = \frac{\text{Energy fixed by net primary production}}{\text{Energy in incident sunlight}}$$

Dr. Ankur Awadhya, IFS Wildlife Ecology Spring 2019 52 / 96

Now, we can also define the efficiency of production. So, the efficiency of gross primary production is defined as the energy that is fixed by gross primary production divided by the energy in this incident sunlight.

(Refer Slide Time: 22:33)

1000 cal. →

30 cal. are lost due to resp.

$M_{gross} = 40 \text{ cal} \times 100\%$

$= 4\% \text{ } M_{gross}$

$40 \text{ cal} - 30 \text{ cal} = 10 \text{ cal.}$

$M_{net} = \frac{10 \text{ cal}}{1000 \text{ cal}} \times 100\%$

$= 1\% \text{ } M_{net}$

129 / 174

So, what we are asking here is suppose you have a plant, and this plant intercepted say 1000 calories from the sun. Now, when it intercepted this amount of calories, how much was the amount of energy that it was able to fix in the form of the biological molecules, because in this process is well, this will not be a 100 percent efficient process. So, you will also be losing out some amount of energy. Now, suppose this tree got 100 calories of energy, and it was say able to fix 40 calories through the process of photosynthesis.

So, in this case we will define the efficiency of gross production as 40 calories divided by 1000 calories into 100 percent. So, here we will have a 4 percent efficiency, which is the gross efficiency. Now, in place of using this term energy fixed by gross primary production, if we remove the amount that was released back because of respiration. So, we are using the net primary production, so in that case we can define the net efficiency. So, suppose out of this 40 calories, we have a situation in which 30 calories are lost due to respiration.

So, the net amount of energy that gets fixed is 40 calories minus 30 calories is 10 calories. And in that case, we define the net efficiency as 10 calories divided by these 1000 calories in to 100 percent, which is a 1 percent efficiency of net primary production.

(Refer Slide Time: 24:34)

Module 4: Ecological energetics Primary Production

Productivity

Definition

$$\text{Productivity} = \frac{\text{Production}}{\text{Time}}$$

Net primary productivity

$$\text{Net primary productivity} = \text{APAR} \times \text{LUE}$$

where

- APAR = Absorbed photosynthetically active radiation ($\text{MJ} / \text{m}^2 / \text{time}$)
- LUE = Light use efficiency (grams carbon per MJ energy)

Dr. Ankur Awadhya, IFS Wildlife Ecology Spring 2019 53 / 96

Now, we can also define another term which is productivity. And productivity is defined as production per unit time. So, if we say that net primary production for a particular

forest was say 1 ton of biomass that was produced, and that amount of biomass was produced in a period of say 2 years. So, we will say that productivity is 1 ton divided by 2 years, which is 0.5 tons per year, so that is productivity production divided by time.

Now, we can define or we can try to compute net primary productivity using this equation. The net primary productivity is given by APAR multiplied by LUE, where APAR is the absorbed photosynthetically active radiation multiplied by the light use efficiency.

(Refer Slide Time: 25:28)

The diagram shows the following equation and units:

$$\text{Net primary productivity} = \text{APAR} \times \text{LUE}$$

Units for APAR: $\frac{\text{MJ}}{\text{m}^2 \times \text{hours}}$

Units for LUE: $\frac{\text{grams carbon}}{\text{MJ energy}}$

Final result units: $\frac{\text{g C}}{\text{area} \times \text{hr}}$ or $\frac{\text{g C}}{\text{m}^2}$

Additional note: Per unit area.

So, in this case what we are saying is that we are talking about the net primary productivity is given by APAR into LUE. Now, APAR is the absorbed photosynthetically active radiation. So, essentially how many joules of energy or how many mega joules of energy was absorbed per square meter of area, and per unit time say into x hours.

So, if we have say y mega joules of energy that was being that was absorbed by the plants, now this energy is coming from the sun. So, out of the incident radiation, there was five there was y mega joules of energy that got absorbed by the plant, and this is the photosynthetically active radiation. What do we mean by photosynthetically active radiation, when we talk about the whole of the spectrum the VIBGYOR, then the wavelengths that are mostly responsible for photosynthesis come in the blue region, and in the red region. And the other radiations say green, yellow, orange, they are mostly reflected by the plants, they are not used for photosynthesis.

Now, because green is mostly reflected, so this is why the leaves look green in color. So, green is not being used for photosynthesis, whereas the red and blue are being used for photosynthesis. So, we are only considering that portion of the spectrum that is being used, because in the process of photosynthesis, so that is photosynthetically active radiation.

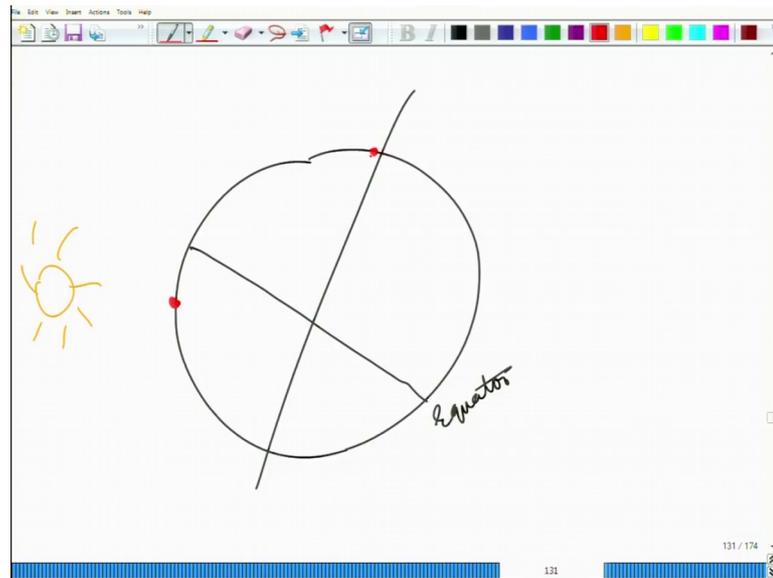
Now, out of that photosynthetically active radiation, the total amount that gets absorbed is the APAR. Now, that photosynthetically active radiation is given in terms of how many mega joules of energy was there per unit time, per unit area, so which is why we have mega joules per unit time, per unit area.

Now, light use efficiency is the efficiency of the plants to use this light. So, in this case what we are asking is the plant was able to absorb, these many mega joules of energy and when these many mega joules of energy were converted into carbon that was fixed. So, here we have the grams of carbon per mega joule of energy. So, in this case, you will have mega joule and mega joule that will get canceled out, and we will have an estimate of the grams of carbon that are being sequestered or that have been converted in the form of biomass per unit area, and per unit time, which is an estimate of the gross primary or the net primary productivity.

So, net primary productivity, we had defined it as x amount of carbon or x grams of carbon that was getting generated per unit time. So, per unit time is say in 1 hour. And in the case of net primary productivity, we can define it for a forest or for any area or we can define it per unit area. So, in this equation we are using this was there in an area of say a square meters.

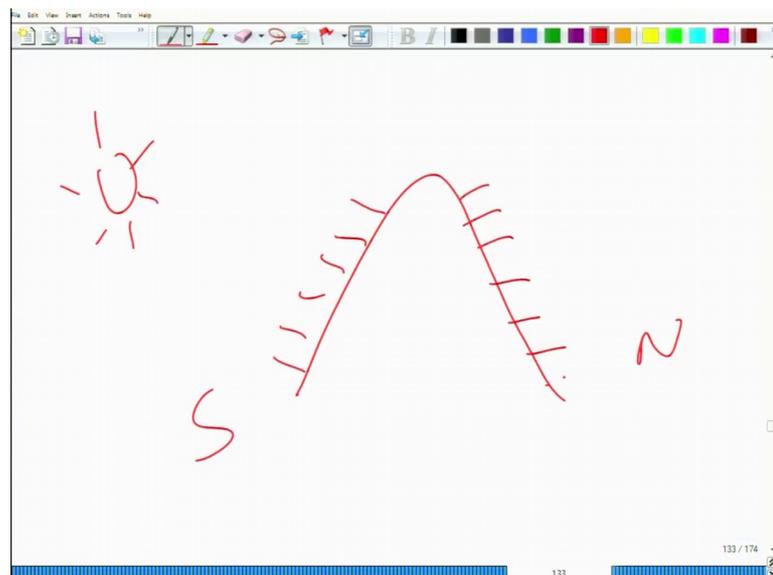
So, in that case we have the net primary productivity that is given by the multiplication of absorbed photosynthetically active radiation multiplied by the light use efficiency. Now, this gives us a way of estimating the net primary productivity for any area on earth, because the absorbed photosynthetically active radiation will depend on how much amount of radiation is actually made available at that particular area.

(Refer Slide Time: 29:47)



So, for instance if we consider the earth, and in this case this is the equator. Now, if we have the sun here, so in this case if you consider a point here, so this point is getting much more amount of sunlight as compared to a point here, because this point is receiving a light that is incident at a very flat angle. So, the amount of photosynthetically active radiation that gets absorbed can be figured out by looking at the latitude of the place that can also be looked at by looking at the aspect of that place.

(Refer Slide Time: 30:37)

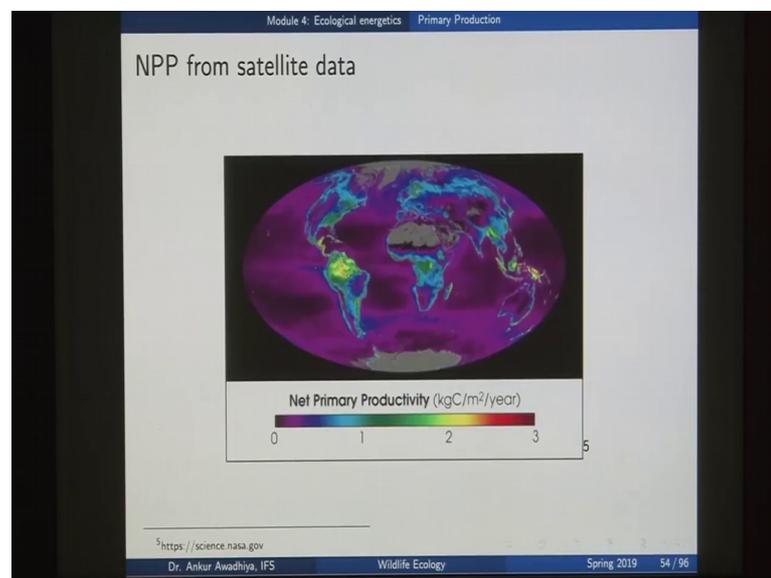


So, for instance in the case of India, if we have a hill and because India is in the northern hemisphere, so we will this is north and this is south. So, in this case the southern aspect gets more amount of sunlight as compared to the northern aspect. So, if more amount of sunlight is getting incident on the southern aspect, so more amount of light is made available to the plants and so more amount of light will be absorbed by the plants.

So, APAR can be discerned by looking at the location of that place, it will also depend on the amount of cloudiness on in that area, because clouds are able to block the sunlight. So, if there are if there is an area that has more amount of clouds in a year, so in that case the APAR will be less.

Now, similarly we can compute the light use efficiency, light use efficiency will depend on different species for instance, it will also depend on the on the fertility of that area or the amount of water that the area has or the amount of nutrients mineral salts that are there in the soil in that particular area, so that makes it possible to model the APAR, and the light use efficiency to make an estimate of the net primary productivity.

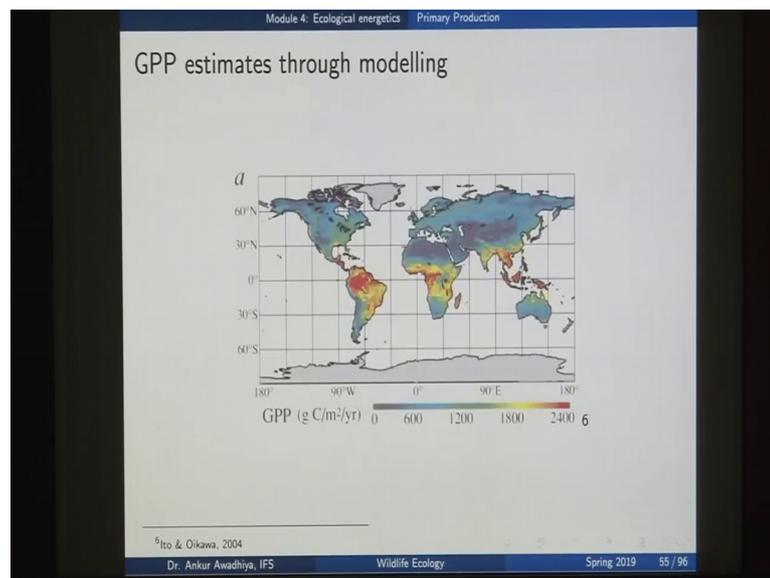
(Refer Slide Time: 31:57)



So, using that we can compute the net primary productivity now, net primary productivity can also be computed using satellite data. Now, in the case of satellite data what we are trying to measure is the amount of chlorophyll that is there per unit area. So, the amount of chlorophyll that is present here if you have more amount of chlorophyll

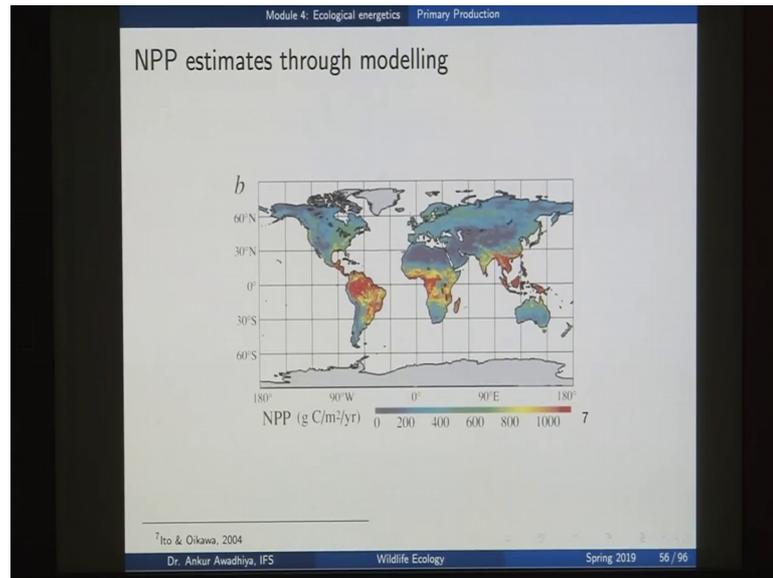
and you know what kind of species are there. So, you can figure out what is the amount of productivity that we can expect from that area. So, we can make an estimate of the net primary productivity of different areas of the earth. And we can also compute the net primary productivity and the gross primary productivity using modeling.

(Refer Slide Time: 32:40)



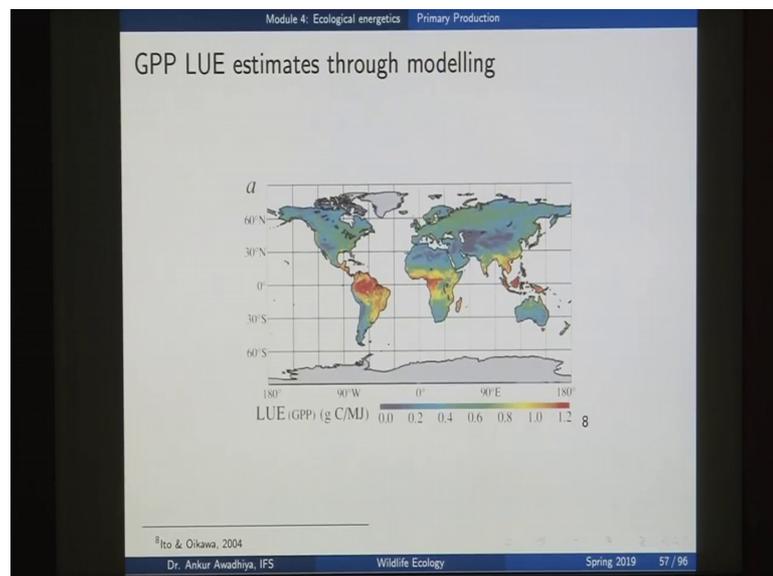
So, this is the gross primary productivity of different areas. And here we can observe that it starts from 0 and goes to 2400. And so these areas are the most productive areas. So, like this area is the Amazonian rainforest. So, these rainforests have a very high amount of gross primary productivity. Now, in comparison these areas so like this is the Sahara desert. Now, Sahara desert will be having a very less amount of gross primary productivity, because you have less number of plants, and you have a dearth of water in that area. Now, most of the areas of Europe will come in a moderate amount of productivity in comparison India has a much higher level of gross primary productivity and so is the Southeast Asian nations.

(Refer Slide Time: 33:37)



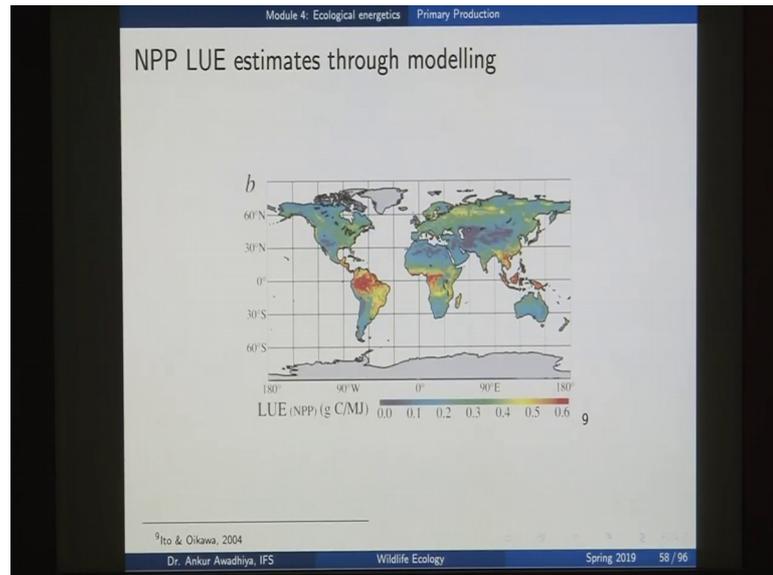
We can also compute the net primary productivity.

(Refer Slide Time: 33:39)



Or we can also compute the things such as the light use efficiency for gross primary productivity and the net primary productivity.

(Refer Slide Time: 33:41)



(Refer Slide Time: 33:46)

Module 4: Ecological energetics Primary Production

What does productivity depend upon?

Productivity is a function of seven variables¹⁰:

- 1 solar constant: the rate at which energy reaches the earth's surface from the sun, usually taken to be 1,388 watts per square metre
- 2 latitude
- 3 cloudiness
- 4 dust and water in the atmosphere
- 5 leaf arrangement
- 6 leaf area
- 7 concentration of CO₂

¹⁰Monteith, J. L. (1972). Solar radiation and productivity in tropical ecosystems. *Journal of applied ecology*, 9(3), 747-766. Chicago

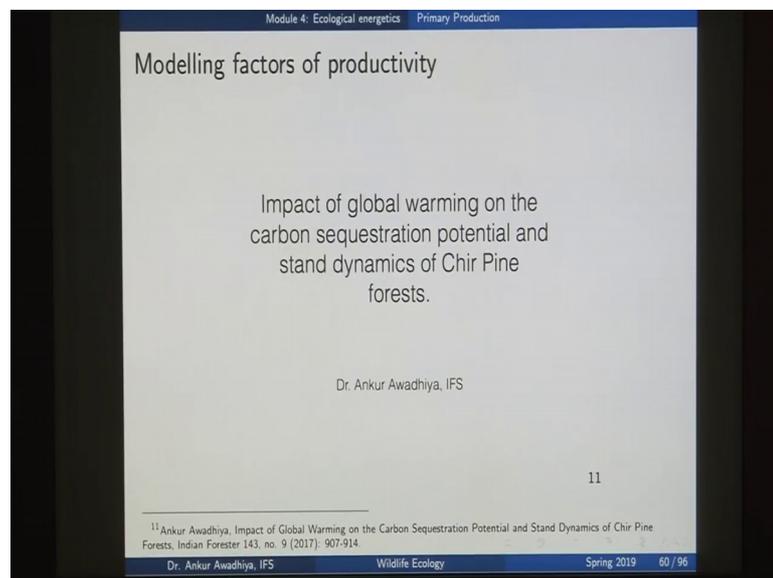
Dr. Ankur Awadhiya, IFS Wildlife Ecology Spring 2019 59 / 96

So, now to recap what is productivity depend on, productivity depends on the solar constant the rate at which energy reaches the earth's surface from the sun. And this is usually taken to be 1388 watts per square meter. So, this is the amount of energy that the sun is giving. Now, we know how much amount of that energy is photosynthetically active radiation. So, we can figure out a proportion of photosynthetically active radiation using the solar constant. Now, this is the energy that is being received by the sun on average, but different areas would be receiving different amounts of energy, depending upon the latitude of that place the cloudiness of that place.

Also the dust and water that are there in the atmosphere, because dust and water will also occlude or block the photosynthetically active radiation that is reaching the plants now, the amount of sunlight that is received by the plant will also depend on the area of leaves that the plant has, and the arrangement of leaves.

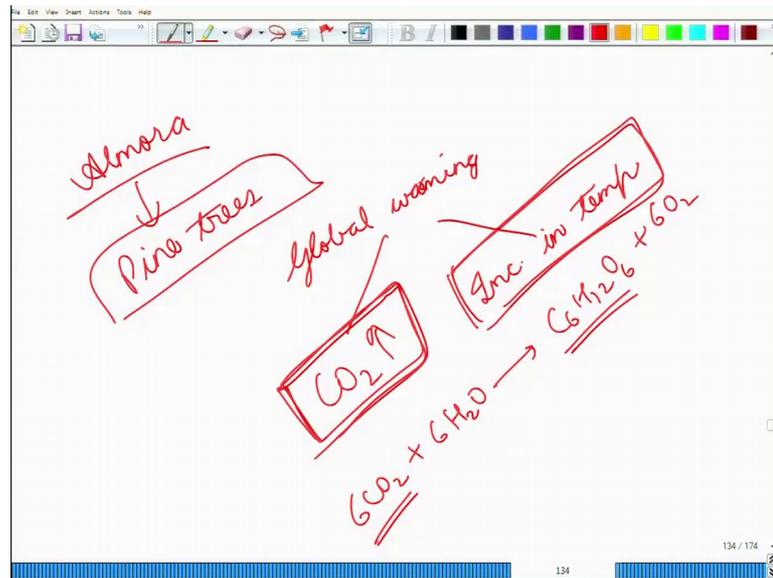
So, the plant needs to have an arrangement that maximizes the amount of radiation that is being intercepted by the leaves. And it will also depend on the amount of carbon dioxide that is there in the atmosphere as will be the amount of water that is being available in that area. Now, using all of these different factors, we can model different factors of productivity.

(Refer Slide Time: 35:10)



So, this is once it is such simulation exercise that we had done, and this was to understand the impact of global warming on the carbon sequestration potential and stand dynamics of Chir Pine forests.

(Refer Slide Time: 35:30)



So, what we did here was that we considered in area and this area was Almora district of Uttarakhand. And in this Almora district we were considering the pine trees. Now, if we have pine trees, and they are at the current ambient conditions. Now, the current ambient conditions means the amount of carbon dioxide that we have in the air at present, and also the location of this place how much what is the latitude of this place, how much is the amount of cloudiness that is there in this place, how much amount of water is there that this area is receiving, what is the level of fertility that the soil have, so those are all the ambient conditions.

Now, we wanted to understand if in the process of global warming, now when we have global warming, there are two things that are happening. One is that we have an increase in the carbon dioxide levels in the atmosphere. And because of that and because of the greenhouse effect, we will observe an increase in an increase in temperature. Now, for in for most of the plants if you increase carbon dioxide, so because in the process of photosynthesis you have carbon dioxide plus water is giving you the sugars and oxygen.

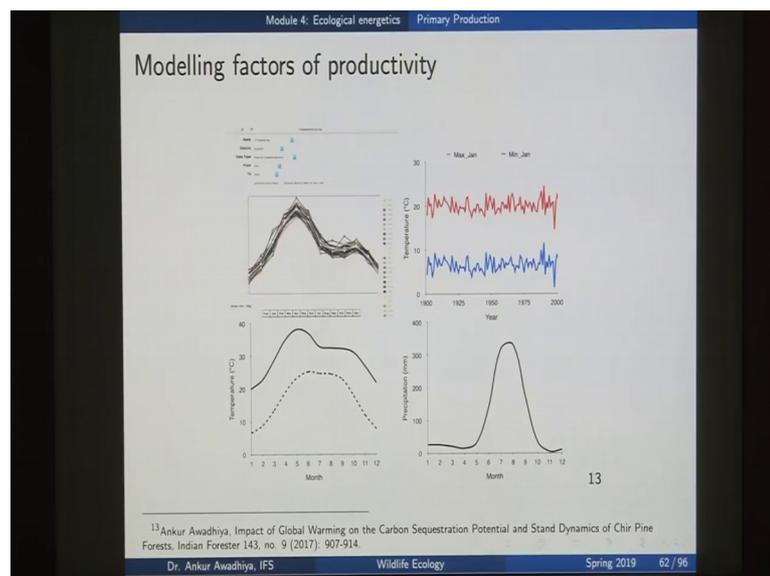
So, if you increase the amount of carbon dioxide, then the amount of production of your glucose or the sugars will increase. So, this will have an impact of fertilization on the plants. Whereas, an increase in temperature might be useful for the plants or it might be help it might be harmful for the plants that would depend on the existing conditions. So, for instance, if you have a banyan tree that is there in Uttarakhand, now banyan tree is

normally found in the tropical area. So, it is a tree that wants to have a higher temperature, but then you have planted it somewhere in Uttarakhand, where it is very cold.

So, in that case if you increase the temperature, so this plant will be more comfortable and it will be much more efficient in absorbing carbon dioxide or sequestering carbon dioxide. On the other hand, if you consider say a pine tree that is planted in Madhyapradesh. So, in that case, your pine tree which is a tree of cold areas has already been put in an area that is extremely warm.

Now, if you increase temperature further, its efficiency will go down even further. So, we wanted to ask that because we have these two processes, carbon dioxide fertilization and an increase in temperature, how would that impact trees in different locations.

(Refer Slide Time: 38:04)



So, for that we began with by looking at different data. So, here we have data of the amount of precipitation that we have, the maximum and minimum temperatures that we have the level of cloudiness that we have in different in the Almorah district and so on.

(Refer Slide Time: 38:19)

Module 4: Ecological energetics Primary Production

Modelling factors of productivity

Other parameters

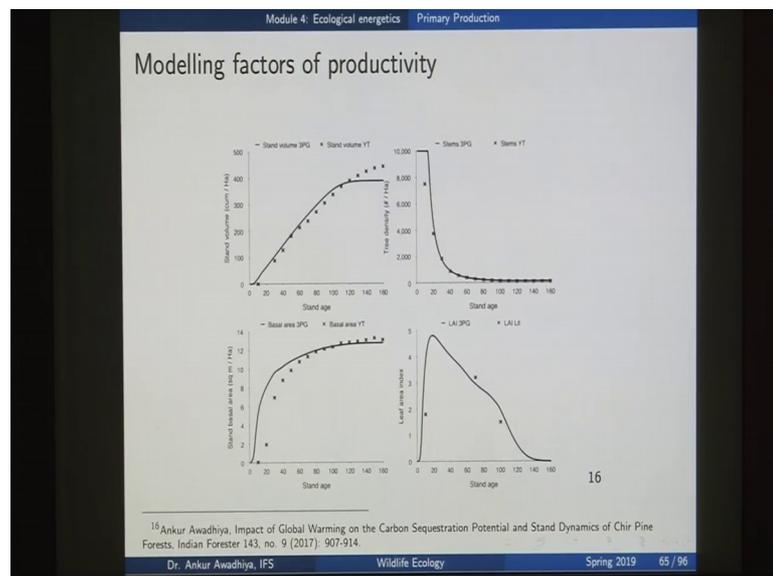
Meaning/comments	Name	Units	Pinus rostrata ¹⁴ Mean ^{0.004} , with modifications
Biomass partitioning and turnover			
Allometric relationships & partitioning			
Foliage:stem partitioning ratio @ D=0 cm	pFS2	-	1.328
Foliage:stem partitioning ratio @ D=20 cm	pFS20	-	0.7
Constant in the stem mass x diam relationship	aS	-	0.084
Power in the stem mass x diam relationship	sS	-	2.7
Maximum fraction of NPP to roots	pR _{max}	-	0.8
Minimum fraction of NPP to roots	pR _{min}	-	0.15
Litterfall & root turnover			
Maximum litterfall rate	gammaF _x	1/month	0.025
Litterfall rate at L = 0	gammaF ₀	1/month	0.001
Age at which litterfall rate has median value	lgammaF	months	24
Average monthly root turnover rate	gammaR	1/month	0.015
NPP & conductance modifiers			
Temperature modifier (T)			
Minimum temperature for growth	T _{min}	deg. C	6
Optimum temperature for growth	Topt	deg. C	22
Maximum temperature for growth	T _{max}	deg. C	35
Frost modifier (FR_{max})			
Days production lost per frost day	VF	days	0.5
Soil water modifier (SW)			
Moisture ratio deficit for L = 0.5	SW _{worst}	-	0.6

14 Ankur Awadhiya. Impact of Global Warming on the Carbon Sequestration Potential and Stand Dynamics of Chir Pine Forests. Indian Forester 143, no. 9 (2017): 907-914.

Dr. Ankur Awadhiya, IFS Wildlife Ecology Spring 2019 63 / 96

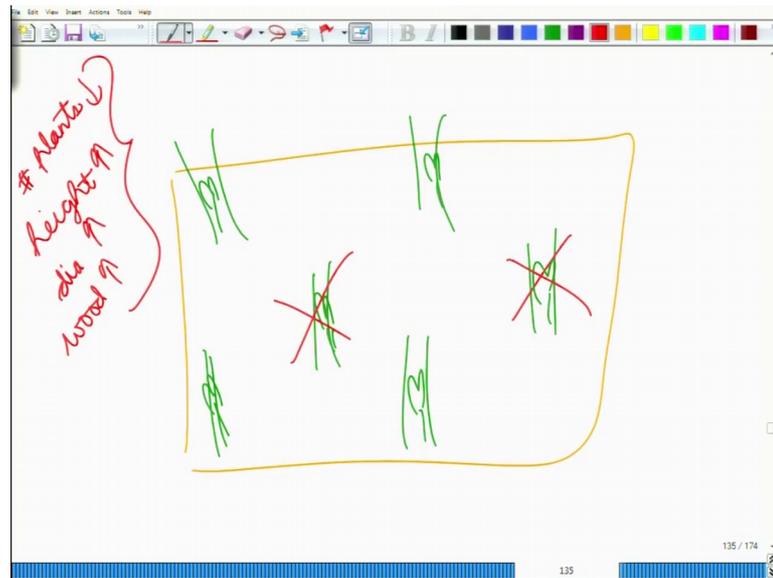
And then we looked at different factors of productivity for the pine trees.

(Refer Slide Time: 38:26)



Then we made that model and then we calibrated it with the existing data. Now, our data is available in the form of yield tables. Now, in the case of a yield table what people have done is that they have gone to the forest, and looked at different trees at different stages of their life.

(Refer Slide Time: 38:49)



So, for instance you have an area that is that is completely free of any plants, and then you plant some pine saplings here. Now, with time these saplings will grow up. So, they will start becoming larger and larger. Now, once that happens, these plants will start competing with each other, and so maybe some of the plants would die off to reduce the density or the number of trees that are available per unit area in this particular piece of land.

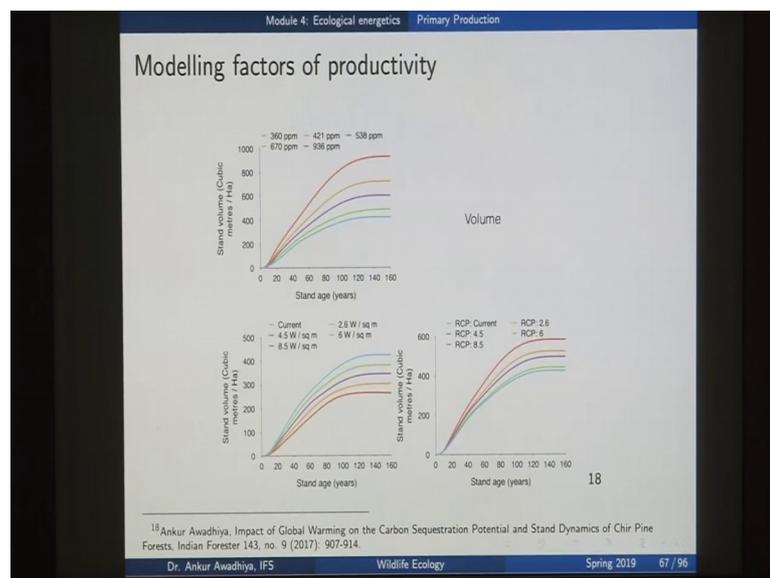
And at the same time when these plants are growing then their height would increase. So, the height increases the number of plants reduces the height increases the diameter also increases the total amount of wood that is there in the plant also increases and so on. So, all these measurements have been done for such stands of pine for different time periods. So, in this case, for instance, here we have the stand volume. Now, this stand volume is the total volume of all the trees that are present in that particular area. And then this stand volume is given as cubic meter of wood per hectare.

Now, if you look at the stand age, so at zero age you do you have only saplings. So, these saplings make up for a very small volume of timber, so that is 0. And then with increasing age this amount increases. Now, these crosses are showing us the actual field values. So, this is from the yield table. And this straight line is showing our modeling results. In this case what we are trying to do is that we are calibrating our model, so that it best represents the existing field situations. So, we have from here we see that there is

a very good correspondence between both of these till say around 110 years, then this one is showing you the number of stems that are there or the number of plants that are there.

Now, when we increase their stand age because different plants are competing against each other, so there would be a number of deaths of plants. So, the number of plants that are there per unit area would decrease. So, here again this is what the model is predicting, and the crosses are what is the actual field situation. So, here also we see that there is a very good correspondence this is about basal area this is about the leaf area index. So, once we have calibrated the model, we can then ask the questions, what is the impact of global warming on volume for instance.

(Refer Slide Time: 41:22)



So, if we look at the volume of this stand and here we differentiated it in two parts. So, the first part is in this case you have an increase in carbon dioxide concentration. So, this is 360 ppm which is the ambient concentration of carbon dioxide that we have considered, so from 360 ppm, 421 ppm, 538 ppm and so on. So, if you increase carbon dioxide, and you keep everything else constant, so you keep temperatures constant. So, if you only increase carbon dioxide, you can see that the stand volume increases. So, this is 360, this is 421, this is 538 and so on.

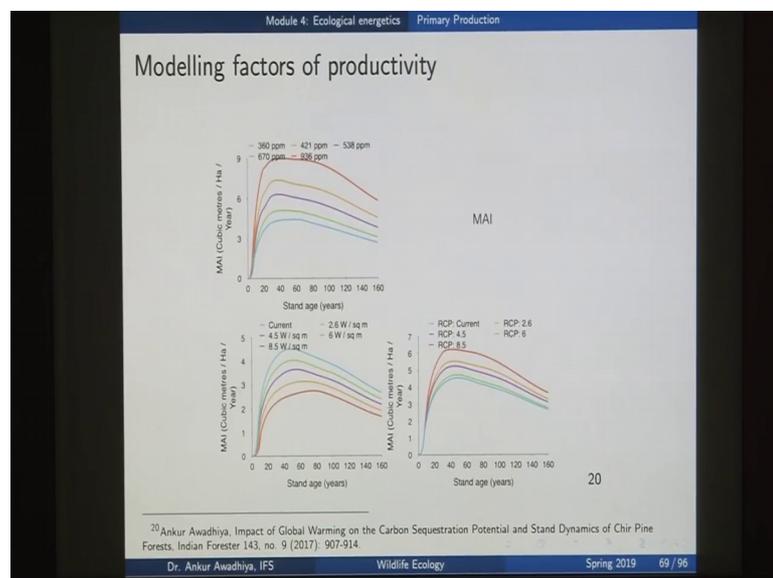
So, with increasing carbon dioxide concentration the stand volume will increase. So, this is an impact of the carbon dioxide fertilization. Whereas, if you keep the carbon dioxide

constant and you only increase the temperatures, so in that case the stand volume goes on decreasing with different levels of global warming. So, these are the standard scenarios that have been used. So, they go by the name of representative concentration pathways, and these representative concentration pathways are the standard scenarios through which we model different levels of global warming.

And then if you do both of these things together, you increase carbon dioxide, so that is the fertilization effect, and you increase the temperature which is harmful to the plants if you do both of these. So, in this particular case, we can see that the stand volume increases. So, the increase between the current representative concentration pathway, and RCP of 2.6, which means an effective global warming of 2.6 watt per square meter.

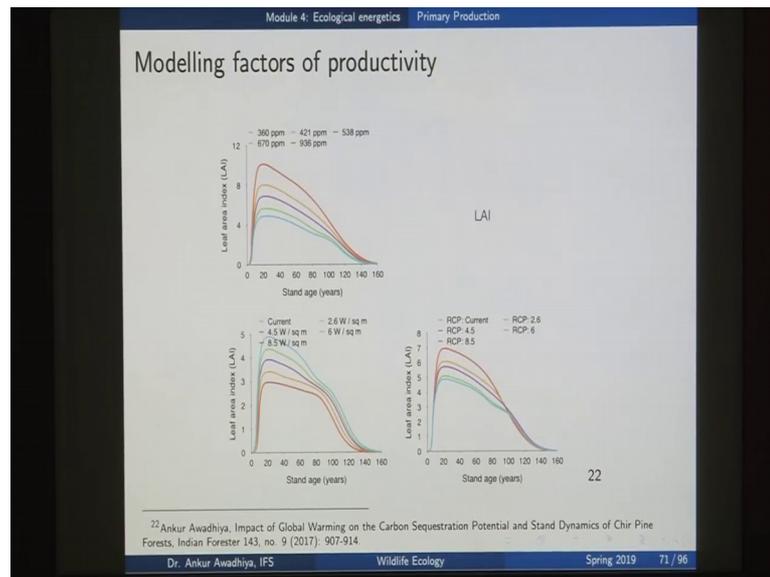
So, in that case, the difference is negligible, but then with increased amount of global warming there would be an increase in the stand volume. So, by using these modeling equations, we can discern what would be the impact of different scenarios. The impact of increasing carbon dioxide, the impact of increasing temperature and the combined impact.

(Refer Slide Time: 43:30)



Now, we can also look at things such as the mean annual increment of the plants.

(Refer Slide Time: 43:34)



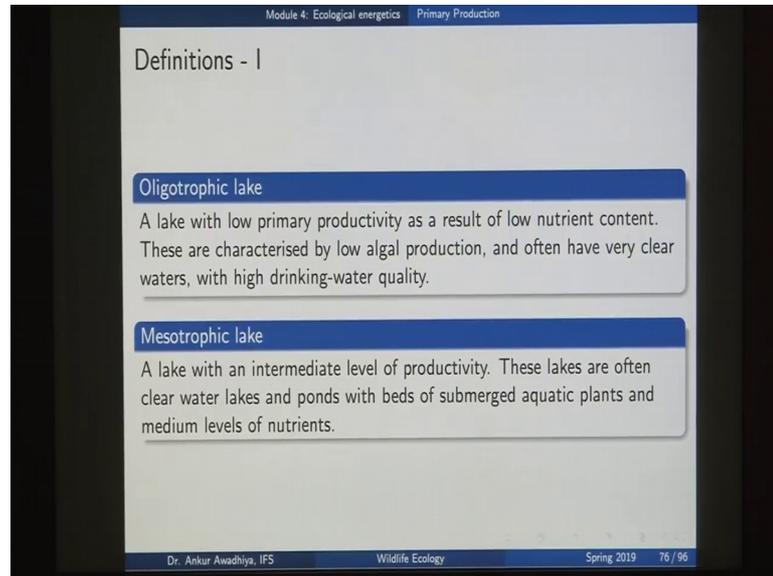
Or things like the leaf area index that is there in the stand or the gross primary productivity or the amount of carbon sequestration that we have. Now, this curve is important, because it is showing us that as the stand progresses in its age, the total amount of carbon that has been sequestered it increases to a maximum and then it starts decreasing.

Now, why does it start decreasing after a while because your stand has become so old that there are a number of trees that are dying off they are shedding off their leaves, they are shedding of their branches. And when that happens these branches, and these leaves get decomposed they get they get degraded, and the carbon dioxide is released back into the atmosphere. So, we see that dry matter releases a peak reaches a peak and then it starts decreasing.

So, essentially if you are managing your forests for maximum amount of carbon sequestration, this is the point where you should cut your trees, so that you have the maximum amount of carbon that has been sequestered away. Now, in this case we can observe that currently if we have if currently we should cut our forests at say around 105 years because that is the point where your amount of carbon sequestration as back has reached the maximum point, now with global warming that would reduce.

So, this is a very significant finding in place 105 years we will have to say cut your trees at around 70 years. So, all these kinds of predictions can be made through modeling because we are using all these equations of production and productivity.

(Refer Slide Time: 45:11)



Now, moving forward now we move at some other definitions. Now, any area would be productive when it is providing all the necessary conditions for the plants to thrive. So, for instance, in the case of Almora, when we were looking at these Chir Pine forests, so these plants require water, they require carbon dioxide, they require different amount of mineral nutrients, they require some amount of fertilizers that are available naturally so like they will require concentrations of nitrogen, phosphorus, potassium and so on.

Now, does an area provide these nutrients, and to what extent is one way through which we define the trophic status of a particular place. So, for instance, in the case of lakes, we can have an oligotrophic lake. Now, oligo is less and trophic is the level of productivity. So, oligotrophic means you have a lake that has a low primary productivity as a result of low nutrient content.

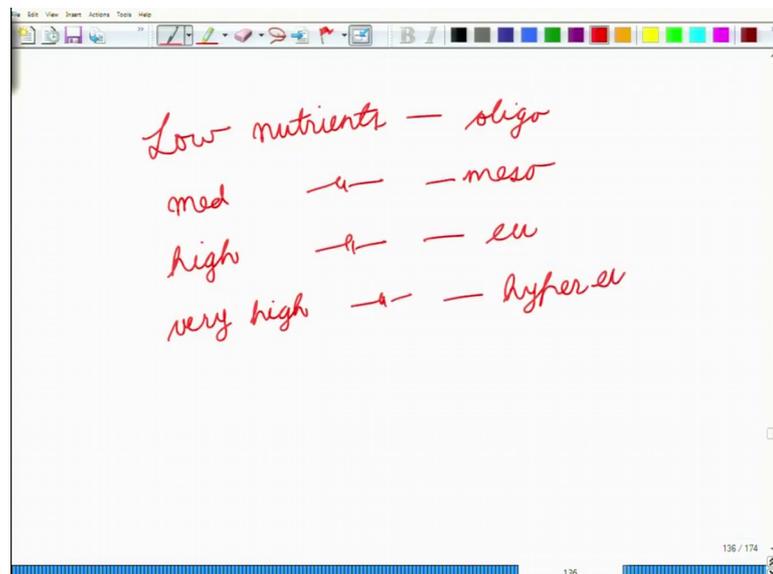
So, because you do not have these minerals, nitrogen, phosphorus, potassium or because your lake is in a place where it is not getting sufficient amount of sunlight or if it is in a place that is so cold that it does not allow any plants to thrive. So, you will have a situation of oligotrophic lake.

But in most situations, we observe that this is because of a low nutrient content. Now, a low nutrient content can happen if you have for instance a glacial lake. Now, in the case of a glacial lake, you have a glacier that is melting. Now, how do glaciers form the glaciers form because of snow deposition. Now, snow is practically pure water.

So, when you have snowfall in an area, when you have a glacier, it does now it does not have a very high amount of mineral salt content inside it, because it is practically pure water. And when this glacier melts and it forms a lake, so that lake also has a very less amount of different minerals. So, it has very low amount of nitrogen, phosphorus, potassium, calcium and so on. Now, if that is the situation the lake will not be able to support a heavy plant growth. So, you will have a an oligotrophic lake with a low amount of primary productivity. So, these are characterized by low algae production, and often have very clear waters with high drinking water quality.

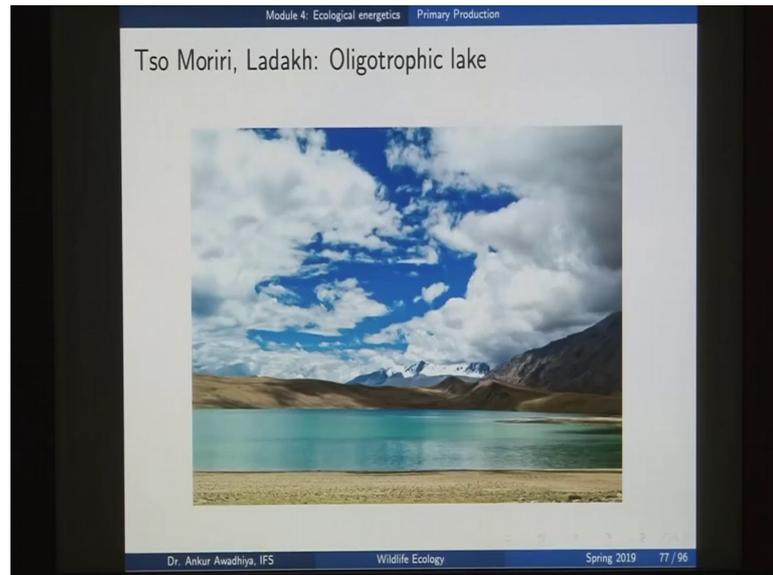
Now, from oligo we move to mesotrophic lakes. So, meso is something that is in between. So, a meso trophic lake is an is a lake with an intermediate level of productivity. These lakes are often clear water lakes and ponds with bits of submerged aquatic plants and medium level of nutrients.

(Refer Slide Time: 48:00)



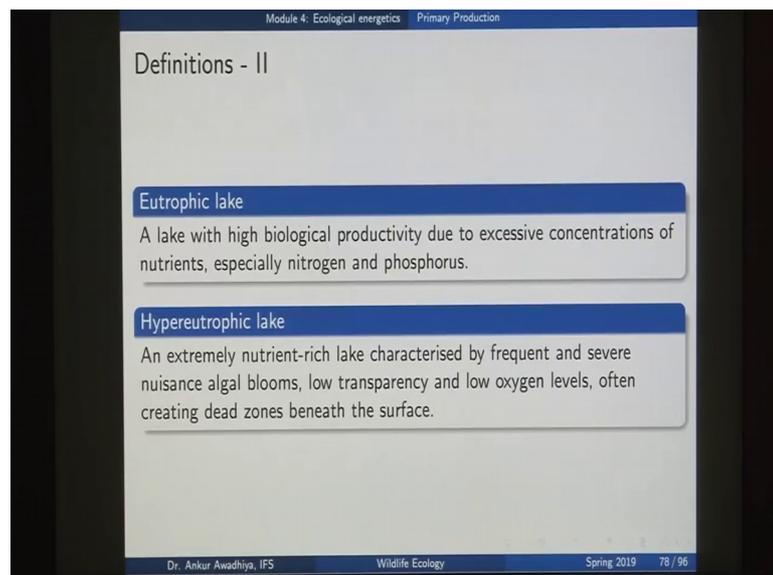
So, we have low nutrients which is an oligo trophic lake, you have medium nutrients that is a mesotrophic lake. So, this is an example of an oligotrophic lake.

(Refer Slide Time: 48:16)



Tso Moriri lake in Ladakh. So, in this case, you can observe that there is hardly any plant growth or hardly any algae growth that we are observing here. Now, why is this lake an oligotrophic lake, because it is getting its water from the glaciers. Now, from oligo and mesotrophic lakes, then we have high amount of nutrients. If you have a high amount of nutrients, then you will have a eutrophic lake eu means good.

(Refer Slide Time: 48:45)



So, eutrophic means good productivity. A lake with high biological productivity due to excessive concentrations of nutrients especially nitrogen and phosphorus. So, essentially

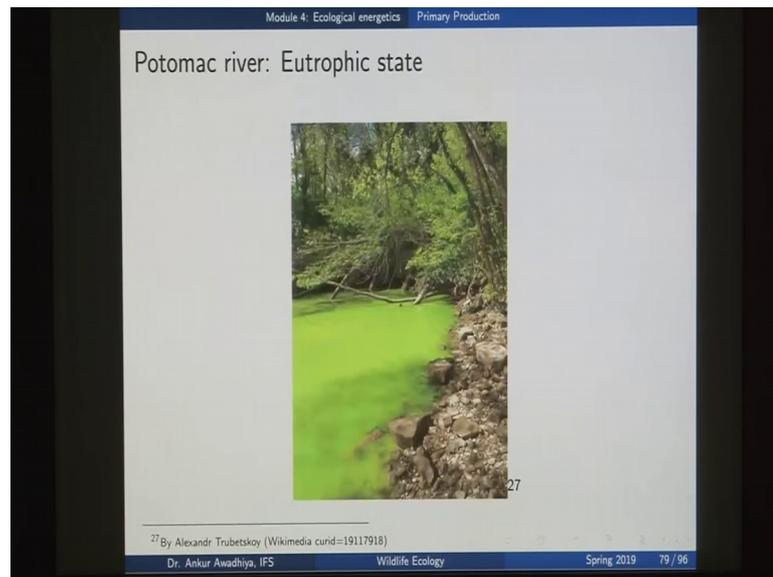
you have a lake and you are putting in more amount of nutrients and so you have more amount of plant growth. Now, why do we have more amount of nutrients there, this is possible if for instance the lake is getting waters that are coming because of runoff from agricultural fields.

So, in the agricultural fields, you have put a very heavy dose of fertilizers and when there is a rain. So, these fertilizers are getting washed down and they are also reaching the lake. So, in that case you have a lake with a high concentration of the nutrients because of which there is a high productivity. So, we call it in oligotrophic lake, we will call it our eutrophic lake.

And then if we have a very high level of nutrients, then you will have a hyper eutrophic lake hyper is excessive. So, this is excessive good productivity lake. An extremely nutrient rich lake that is characterized by frequent and severe nuisance algal blooms, the amount of algal blooms is so high that it is becoming a nuisance.

Low transparency and low oxygen levels, why low oxygen levels because once you have these heavy number of plants they will also die after a while, and when they die off there the tissues will get decomposed, and during this process of decomposition you will have oxygen consumption by the microorganisms. So, you will have very low oxygen levels. And the oxygen levels are so low that this lake now does not support any amount of animal life. So, it often creates dead zones beneath the surface. So, this lake only has algae, it does not have anything else.

(Refer Slide Time: 50:37)



So, this is an example. So, this is a portion of the Potomac River which is in the eutrophic state. And in this case there is so heavy algae will growth here that it has become a hypertrophic lake or a eutrophic lake.

(Refer Slide Time: 50:51)

Module 4: Ecological energetics Primary Production

Table: Trophic classifications

Trophic Class	Trophic Index	Chlorophyll ($\mu\text{g} / \text{litre}$)	Phosphorus ($\mu\text{g} / \text{litre}$)	Secchi depth (m) ²⁸
Oligotrophic	< 30 – 40	0 – 2.6	0 – 12	> 8 – 4
Mesotrophic	40 – 50	2.6 – 20	12 – 24	4 – 2
Eutrophic	50 – 70	20 – 56	24 – 96	2 – 0.5
Hyper-eutrophic	70 – 100+	56 – 155+	96 – 384+	0.5 – < 0.25

²⁸Secchi depth is a measure of transparency or turbidity in a water body. The more the depth, the clearer is the water. The less the depth, the more turbid is the water in the water body.

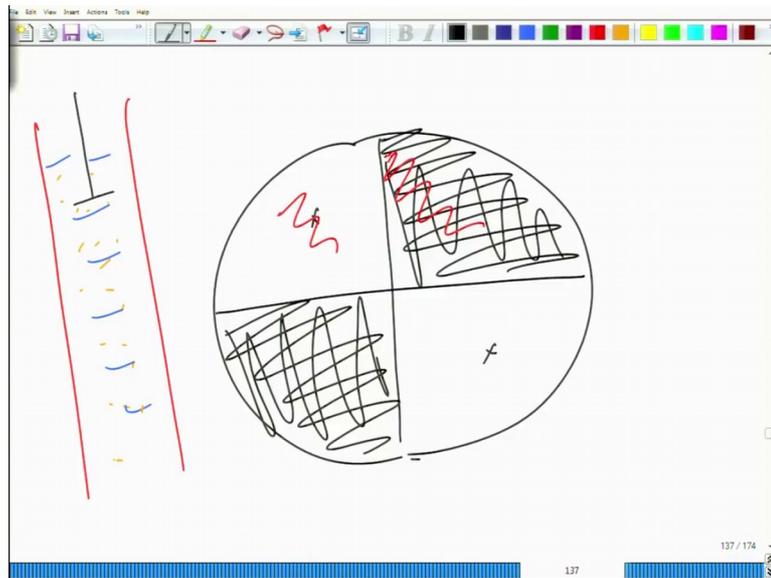
Dr. Ankur Awadhya, IFS Wildlife Ecology Spring 2019 80 / 96

Now, we can also look at different other characteristics of these lakes. So, we can have a look at trophic index. Now, trophic index is the amount of productivity that we have in this lake. So, when we move from oligo to meso to eutrophic to hyper eutrophic, the

amount of productivity increases. The amount of chlorophyll also increases because you have more number of plants, so more amount of chlorophyll.

The amount of phosphorus is typically also large which is supporting these heavy plant growth. And the secchi depth, now secchi depth is an indication of the amount of turbidity that is there in the lake. So, secchi depth is a measurement of transparency or turbidity in the water body. The more the depth the clearer is the water.

(Refer Slide Time: 51:40)



So, what happens in the case of a secchi depth is that you take a disk which is around 30 centimeters in diameter, and then this disk is having these four portions, both of these are black in color. So, this is black portion, and then there are two areas that are white in color. So, you have this disc. You attach this disc to a rod, so it will be attached like this, and then you lower this disc in the water.

So, when you are lowering this disc in water, you are now wanting to measure what is the depth at which you are not able to see this black part as a black part and the white part as a white part, so that if this disk is there on the surface you can very clearly see the black and the white portions. But then as you increase the depth and if there is turbidity in the water, so in that case it will become more and more difficult to see black part as black and white part as white.

So, the depth at which you are unable to make out which part is black and which part is white that is known as the secchi depth. Now, if you have more amount of turbidity in water, so if you have this water column and if you have say very less amount of turbidity. So, if you have a very less amount of turbidity you have put your secchi disc at this depth as well, and you are able to see white as white, and black as black. But then if you have a heavy amount of turbidity in this water, in that case you will bring your secchi disc till this depth and you would not be able to see black as black and white as white.

So, in this case what we are observing is that in the case of an oligotrophic lake because this is a clear lake with very low turbidity so secchi depth is very high it is greater than 3 meters. And as you move onto hyper eutrophic lakes it becomes as less as 25 centimeters. So, these are the differences between these different lakes. Now, the next question is when we talk about these levels of productivity and these amounts of nutrients that are available, how do these nutrients get into the lake.

(Refer Slide Time: 53:46)

Module 4: Ecological energetics Primary Production

Sources of nutrients

- 1 rivers bringing sediments
- 2 bird droppings
- 3 upwelling in oceans
- 4 dust clouds, etc.

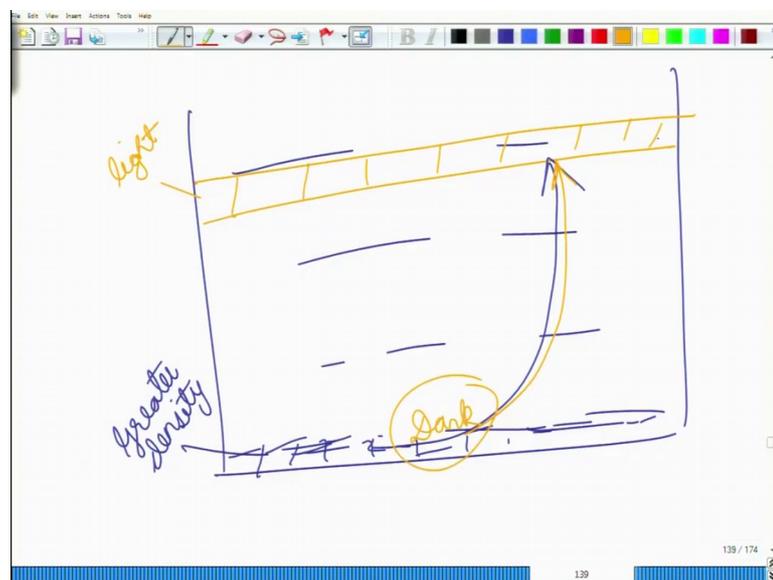
*Credit: Jacques Desclotres, MODIS Rapid Response Team, NASA/GSFC.

Dr. Ankur Awadhiya, IFS Wildlife Ecology Spring 2019 81 / 96

So, the sources of nutrients can be many and of these some are rivers that are bringing sediments. Now, when we say sediments if you have a rock, a rock has a number of mineral salts inside. And when that rock breaks apart and when it converts itself into sediments, and these rivers are bringing sediments. So, all those mineral salts are also brought along with the water. So, rivers that are bringing sediments are one source of nutrients.

The second source is bird droppings. Now, what happens is in the case of birds if you have birds that are feeding on fishes for instance. So, they ate fishes and the nutrients that were there in the fish, they are getting absorbed during the process of digestion, but not all the nutrients get absorbed. So, when that happens some amount of nutrients are then released along with the fecal matter, so that also becomes a source of nutrients. At the same time when we look at bird droppings they also have a heavy amount of uric acid. Now, uric acid is also nitrogen range, so there that also becomes a source of nutrients.

(Refer Slide Time: 55:00)



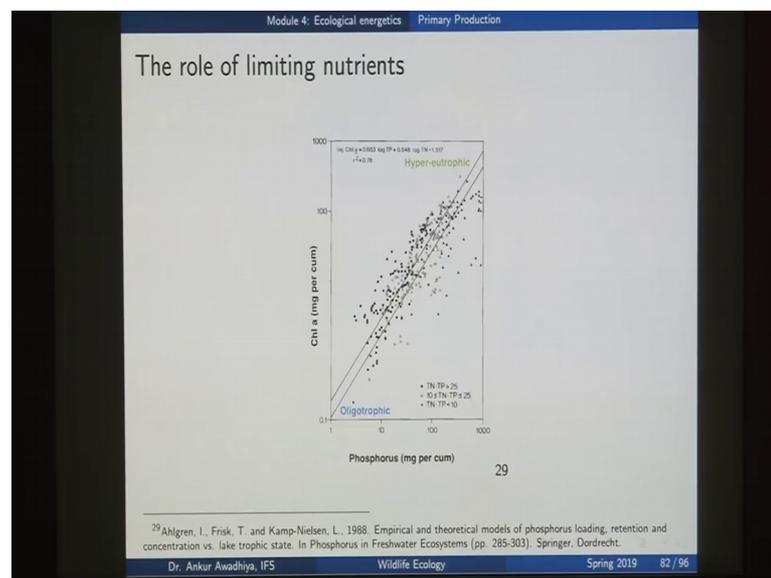
Upwelling in oceans now what is upwelling. So, if you have an ocean, so let us consider that this is a column of the oceans. The bottom portion of water is at a greater density, greater density because it is cooler, and also because it is very much rich in salts. So, if you add salt to water, the density increases. And if you add that water in a water column, then this salt rich water will get to the bottom.

Now, you have rivers that are bringing sediments, and when these rivers are reaching the seas, so these sediment rich waters are now getting to the bottom. Now, upwelling is a situation in which because of some process this water rises up. So, if this water rises up, so it will bring all these different sediments and all these different mineral salts along with it to the top, so that becomes a source of nutrients that is made available to the plants.

Now, why was it not available to the plants at this depth, it was not available to plants, because this in the case of an ocean only the this top layer is able to get light from the sun, and this bottom portion is dark. So, when it is dark, then plants are not able to survive there they are not able to use these nutrients. But only when these nutrients come up to the top, and they reach this zone that is photosynthetically active, so in that case they are able to use these nutrients.

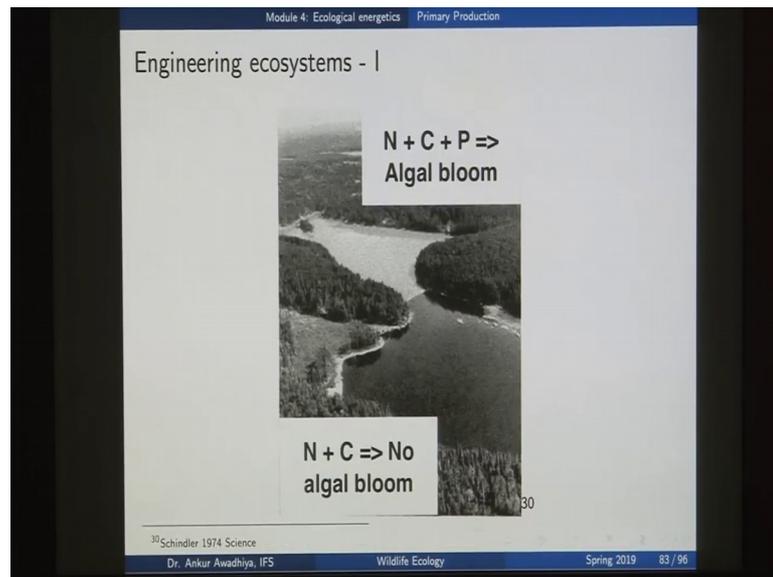
Another source of nutrients is dust or cloud and so on. So, for instance here we are observing an area that is close to Africa. And here we see that there is wind that is taking all of this dust to the ocean. So, when this happens along with the dust quite a lot amount of nutrients also gets passed into the oceans.

(Refer Slide Time: 56:53)



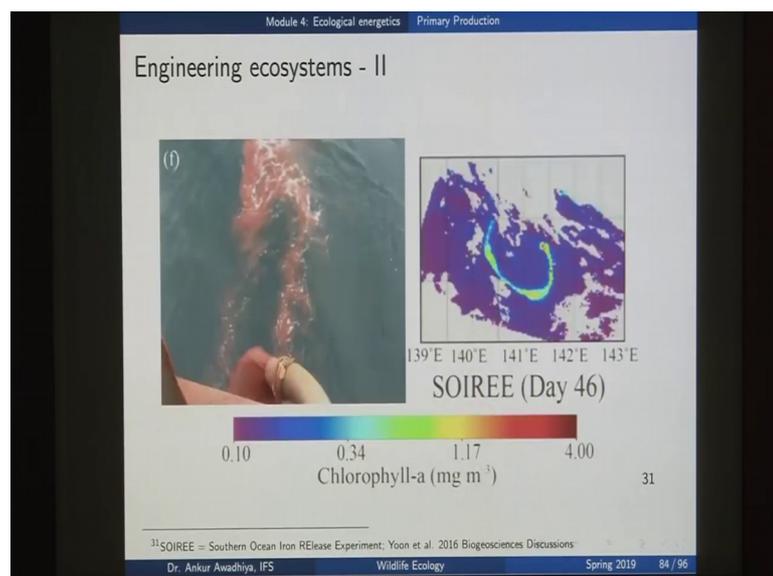
And it is important to note which nutrients are there in a water body because that permits us to engineer these water bodies. So, for instance, here we have a graph where the x-axis is showing the phosphorus concentration, and the y-axis is showing the chlorophyll concentration. So, in a number of lakes it has been observed that with an increased amount of phosphorous, the amount of chlorophyll a increases, which means that in these lakes phosphorus is as the limiting nutrient. If you increase phosphorus, you will move this lake from an oligotrophic lake to a eutrophic or a hyper eutrophic lake.

(Refer Slide Time: 57:30)



And this was also shown in one of the experiments. So, in this experiment, there was a lake that was divided into two portions with a barrier here. And then in both the regions you added nitrogen, you added carbon, and nothing happened and in one portion you added phosphorus; and in the other portion you did not add phosphorus. So, the portion where you have phosphorus you see a very heavy algal bloom which is telling us how we can increase the productivity of this particular lake.

(Refer Slide Time: 57:59)



In the case of oceans, iron is a nutrient that is available in less quantities. So, there was this experiment which goes by the name of Southern Ocean Iron Release Experiments, SOIREE. So, in the case of SOIREE there were ships that released iron salts and when that happens. So, this is the root of one such ship. And here we can see that the amount of chlorophyll has increased in these regions. Now, why is that important that is important, because if you have more amount of chlorophyll, if you have more amount of primary productivity so along with primary productivity this is also acting as a source of carbon sequestration.

So, if we want to circumvent global warming, so in that case we can put some amount of or we can seed the oceans with some amount of iron, so that the algal increase in their numbers the phytoplanktons increase in their numbers and the amount of carbon dioxide and more and more amount of carbon dioxide gets sequestered from the atmosphere, and is dumped into the oceans. So, this makes these experiments tell us that we can also engineer ecosystems to our advantage.

So, in this particular lecture we looked at primary productivity, we defined gross primary production, net primary production, productivity light use efficiency and so on. And we looked at how all of these concepts can be made use of in modeling to understand the current situation of different ecosystems and also to predict what is going to happen because of global warming. And then we also looked at how we can engineer ecosystems to our advantage if we say want to increase the amount of plants that are there in an ecosystem, how we can put in nutrients, how we can seed it with nutrients and so on. So, that is all for today.

Thank you for your attention. [FL]