

**Plant Developmental Biology**  
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**Lecture - 03**  
**Characteristics of Plant Growth and Development - II**

Welcome to the second lecture of Characteristic of Plant Growth and Development. So, if we recall in the first lecture we have discussed the primary growth, primary growth and development, secondary growth and development, lateral growth and development. The axis along which the growth and development occurs, the points or the region of the plants where the meristematic activities are positioned and how they are maintained and coordinated during the process of plant growth and development.

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**Characteristics of Plant Growth and Development**

- **Plastic development:** Adaptability to prevailing environmental condition
- Example: couch grass (*Agropyrum repens*)
- Underground shoot- long internodes, scale leaves  
& adventitious roots
- Aboveground shoot- short internodes, true leaves  
& no root

The diagram illustrates the plastic development of couch grass. It shows two parts: an underground shoot and an aboveground shoot. The underground shoot has long internodes, scale leaves, and adventitious roots. The aboveground shoot has short internodes, true leaves, and no roots. Labels include: Three leaf blades, transition leaf, short internode enclosed in leaf sheath, scale leaf, nodes with adventitious root and lateral branch, and long internode.

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So, now we will continue this lecture of characteristic of plant growth and development with another characteristic of plant development which is Plasticity. It is extremely important for the plants; considering the fact that plants are sessile in nature. They cannot move from one place to another place which means that they have to face all the environmental disturbance or all the environmental condition just by standing at one place. And, to cope with this change in the environment they have adopted a very nice mechanism and which is plastic in nature.

So, the plasticity is basically an adaptability to prevailing environmental condition. I will take couple of example for it and you will appreciate how developmental plasticity is adopted or it is acquired by the plants.

If you take this example, this is couch grass. In the couch grass basically it's shoot grows below the ground as well as above the ground. And, what happens when the shoots are growing underground. Underground means it has a very different environmental condition than the above ground. Underground the light intensity is less, oxygen availability and other factors which are very different than the above ground.

You can see when the shoot is growing underground it has a developmental program which is giving rise to long internode, and leaf like structure which is called scale leaf and more important that at every node you can see lot of adventitious root development.

So, there is a developmental program which is going on here already, but once this growing shoots reaches the ground; once it is coming outside the ground it switches its developmental program. There is a change, the first thing what happens is that now it start making short internode.

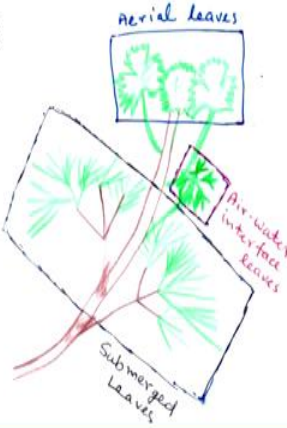
So, the internode length is reduced to do that it has to change; it's the basic program of developmental biology. And, another thing that now there is a formation of true leaf blade like structure. And also this shoot at the node it is no longer making the roots. So, what are the changes it has to do developmentally?

It has changed its program for making long internode to the short internode. It has major changes in their program of the leaf development. Now, the leaf is different and more when it was underground it was having active developmental program for adventitious root development. But, once it is coming above ground it has to shut down the program of adventitious root development.

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### Characteristics of Plant Growth and Development

- **Plastic development:** Adaptability to prevailing environmental condition
- Example: water crowfoot (*Ranunculus aquatilis*)
- Submerged leaves-
- Air-water interface leaves-
- Aerial leaves-



The diagram illustrates the morphological plasticity of the water crowfoot (*Ranunculus aquatilis*). It shows a central stem with three distinct types of leaves: 1) Aerial leaves, which are small and green, growing above the water surface. 2) Air-water interface leaves, which are larger and have a fan-like shape, growing at the water surface. 3) Submerged leaves, which are also fan-like but have a different shape and are located below the water surface. The diagram is labeled with 'aerial leaves', 'air-water interface leaves', and 'Submerged Leaves'.

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This is another case of developmental plasticity. If you look water crow foot which is an aquatic plants. And, it grows in a way that a portion of these plants are submerged in the water, then a portion which is at the surface or at the interface of water and air and then a certain a part of this plant is aerial which is outside. And, that is why this plant makes three types of leaf.

The leaves which are submerged they have a very different morphology, they have a very different structure, they have a different function. If you see these which are basically at the surface of air and water or at the interface of air and water its morphology is very different than this one and the aerial leaves they are totally different. So, this is one example where the developmental programs are being changed depending on the environment.

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### Characteristics of Plant Growth and Development

- **Cell fate determination:** instructed by ancestors or neighbors
- **Lack of cell migration**
- **Cell lineage and position**
  - Cell-intrinsic (lineage-dependent)
  - Cell-extrinsic (position-dependent)

① Lineage based mechanism  
Information for specification

② Position based mechanism

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Next characteristic feature of plant development is how cell fate is determined. So, if you remember a previous class where we have discussed that the first step of organogenesis or differentiation is cell fate specification or identity of a cell or specifying identity, how this is possible? In animals this is widely known that the cell lineage is playing a very important role which means that the ancestors of the cell, the cell which is giving rise to the daughter cells they are also passing the information for its identity.

But, in case of plant you will realize that there are some mechanism of lineage dependent development, but which is restricted. And, the major developmental fate is defined by position dependent mechanism which means that the cell fate is determined by mostly by the neighboring cells, who is next to the cells, not entirely by the ancestors.

This is important because in case of plants the cell migration is not occurring; during animal development cell migration plays an important role in the development. Whereas, in case of plant due to presence of a very rigid cell wall, very tightly glued cell wall the plant lack the cell migration which means that the neighboring cell in case of plant development is going to play a crucial and very important role.

So, if you look that the information which is helping for a cell to take it's a proper fate it can be either cell intrinsic or cell extrinsic. Cell intrinsic means, is it lineage dependent or extrinsic means it is position dependent. If you look this schematic diagram if it is a lineage based mechanism then what happens if consider this is cell A, this is cell B; they

are may be next to each other. But, cell A will already have its own information for a specification, B will have another information for the specification. And, the cells which are being generated from the A, they will carry this information from the ancestor. So, this descendants cells or the daughter cells they are going to take the identity or the fate as instructed by their parent cell.

But, if this is position based mechanism then the parent cells they do not have any information for specification. They just divide and give rise the daughter cells, now the daughter cells which are next to each other they pass the information. So, this cell might get information from this cell and this cell might get information from this cell. And, based on that they define or they decide what is my relative position in the body and that helps them to take the identity and one way of doing it is the clonal analysis.

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**Characteristics of Plant Growth and Development**

➤ **Lineage vs. Position Analysis**

- Clonal analysis  
(heritable visible markers such as pigment mutants)
- Chimera analysis  
(two or more distinct cell population)

Irradiated Early      Irradiated Late

Meristematic cells  
SAM  
Sectorial chimera  
The same plant later in development

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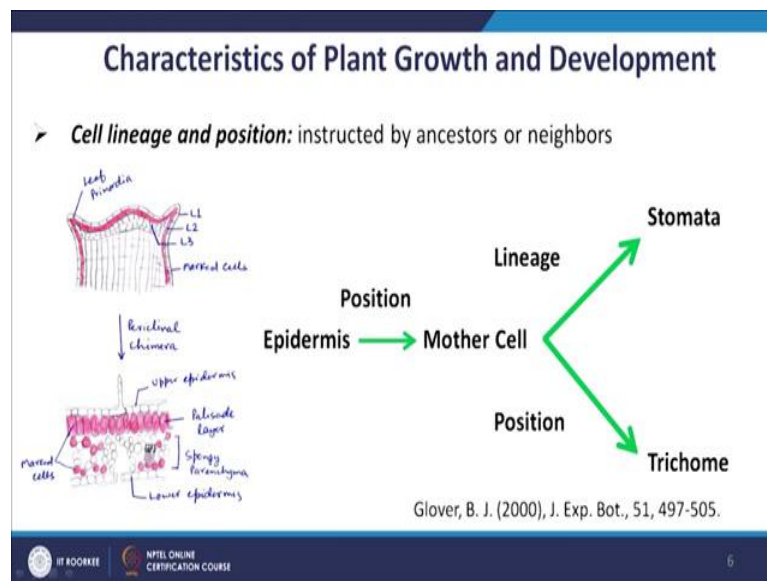
So, in clonal analysis what we do we use a heritable visible marker such as pigment mutants. So, for example, any part of the plant and mutagenize them or you expose them for some kind of mutagen and try to find out a mutant where, some cells lack some kind of pigments, let's assume chlorophyll. If you take this leaf and irradiate them at early stage what you see that you might find a cell here which is losing the pigment. And, then later on at the mature leaf if you see there is a patch of cells which are losing the pigment.

But, if you take this leaf and irradiate at the later stage when the development is quite complete then you see that these patches are relatively smaller in size. So, what this tells? This tells that through the clonal analysis you can actually identify the lineage and the cells which are coming from the lineage. So, there is a strong correlation between lineage as well as the position of it.

Another way of detecting or checking this is chimera analysis. So, chimeras are a kind of plant which might have two or more distinct cell population.

So, if you take this example so, let us assume that this is top view of a plant and it has a sectorial chimera. So, one small portion or sector of this growing meristem has certain marked cells and others they are unmarked cells. And, if plants which are coming from this meristem, if you look them you can clearly see that some regions of these plants which are coming from these cells they are the marked one. And, these two experiments using these two experiment you can actually trace out the lineage of a particular cell.

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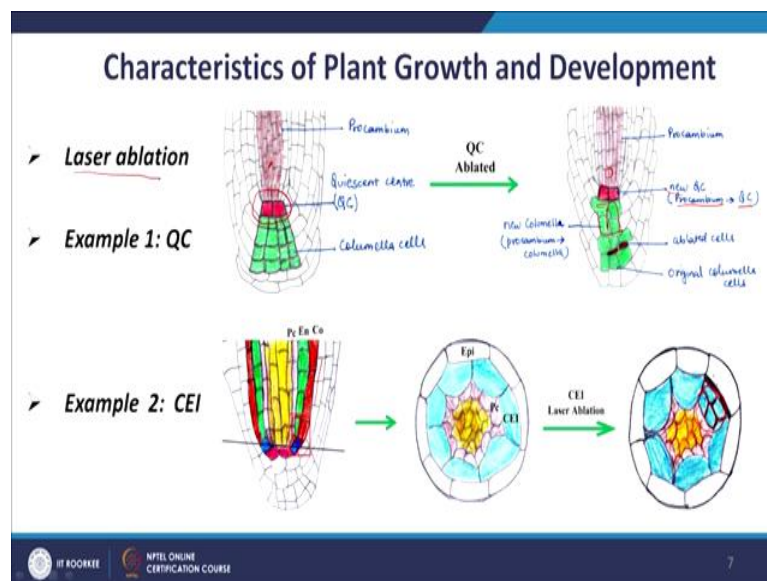
Another kind of chimera is periclinal chimera. So, it is known that the meristem the shoot apical meristem it has basically three layers: layer L 1, L 2, L 3. And, it is known that epidermis which is the outermost layer of any organ it derives from the L 1, and L 2 usually gives a cell layer which is beneath the epidermis. So, if you mark the L 2 cell layers and then study the anatomy of the mature leaf which is coming from here; what you could see that the cell layers which is beneath the epidermis they have the marked

cell. But, apart from that there are other cells as well which are away from these cells, they have also got the marked cell property.

In case of epidermis it was observed that both the mechanisms functions. The differentiation of epidermis is position dependent as well as the lineage dependent. In the leaf epidermis there are three types of cells, pavement cells and the cells which are going to make stomata or the cells which are going to make trichome.

And, what has been seen that from epidermis to mother cell formation it is mostly contact dependent/ position dependent. But, the mother cell which is responsible for the stomata it is lineage dependent. Once the cell fate is determined it will follow the lineage and it will make the stomata whereas, the trichome development is basically adopting position dependent mechanism.

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Another very important technique which can be used to actually distinguish whether cell fate is determined by lineage or by position is laser ablation. So, laser ablation is a technique through which you can very specifically, targeted way kill some cell and then you look what happens to that cells.

So, first example if you take I am going to kill this or if you kill the cell which is called quiescent cell center. So, this is a typical apical root apical meristem; in root apical meristem these cells are very important cell. Why? Because, they pass the information

and maintain the stem cell niche in the root apical meristem. So, all the cells which are directly in contact with QC they have meristematic capability and what happens if you kill this QC or if you laser ablate this QC?

So, if you look here this is procambium cells; what happens if you kill this QC through the laser ablation? Some cells of the procambium they come at the place of QC and then they make new QC. What it means? It means that the fate or identity of procambium is now changed to the QC identity. And, if this happens here the cells which are in this region they originally were also procambium cells. They change their identity and then they make new columella cells which is typically present below the QC.

So, if you look here so, there is a change of the identity this suggests or this tells that the information is not lineage dependent. The fate the new fate determination or new QC or new columella they are taking a new fate depending on their position, not what was their initial programming or what was their information inside it. Similarly, another very important tissue if you look here in the root tip here this is QC; in QC these are the cells which are called initial cells. These are the cells which are meristematic cells and in case of root there are different cell layers. So, cell layers are like epidermis, cortex, endodermis pericycle and vascular cells.

And, what is important here that each cell; each initial cells they give rise to one layer of the cells, particularly here. If you look this initial cell it will give like this cell layer, but there is one cell which is here. If you look this cell this is initial cell because it is in direct contact with the QC and this cell actually eventually give like two layers. So, the layer of cortex and layer of endodermis they are originated from a single initial.

And, this initial is called cortex endodermis initial. So, what happens this initial first it divides, divides and then it makes a kind undergoes periclinal division. And, this periclinal division give rise to two cells parallel cells and one cells then it continues making endodermis another cells it start making cortex.

But, what is important here if you laser ablate this CEI what you see? What we see that the cells which are in the pericycle, this is the inner pericycle layer the cells they basically are getting pushed in and they are taking the place of CEI. And, what happens when they take this place they undergo the process of a periclinal cell division. And, the cells which are outside they now switch their identity and they become cortex



endodermis initial; whereas, the cell which is inside they retain its capability or its identity as pericycle cells.

So, both of these experiment suggest that the new cell fate is not inherited or it is not coming from the mother cell. But, it is getting acquired depending on the place of the cell where this cell new cell is positioned.

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### Characteristics of Plant Growth and Development

➤ **Positional Signals:**

- **Morphogen:** Auxin, gradient & maxima
- **Receptor-mediated signaling:** Secreted ligands and membrane-associated receptors

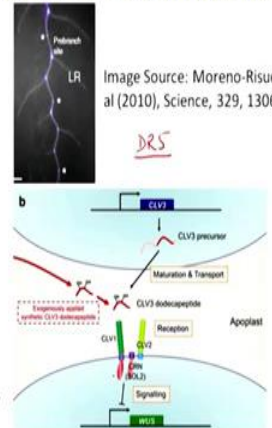


Image Source: Moreno-Risueno et al (2010), Science, 329, 1306-11.

Image Source: Miwa et al (2009), J Plant Res, 122, 31-39.

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If position is very important in case of plant growth and development what are this positional signal,? how a particular cell realize or how a particular cell acquire a particular identity? how it gets the information from the neighboring cells? And, there are certain mechanisms which has been identified the first mechanism is morphogen. Morphogen are the signaling molecules which basically is responsible for providing a cell fate or providing identity. And, one of such molecule very important molecule is auxin, auxin is a plant hormone.

The auxin distribution is very important, it is being transported in the polar manner and there is a formation of gradient. So, auxin distribution, biosynthesis, storage, everything is important. And, the distribution of auxins some places it makes gradient which means that the some cells they always get high amount of auxin, some cells they get low amount of auxin. Not only presence or absence of auxin, but critical amount of auxin is very important for switching on a certain developmental program. And, another thing which is important with respect to auxin is its concentration.

So, some developmental programs are switched by auxin, once auxin reaches a particular amount of concentration which we call auxin maxima. So, if you look this picture, this picture has luciferase marker, but this luciferase marker is driven under DR 5 promoter. DR 5 promoter is a promoter which has auxin response element which means that it is responsive to auxin hormone. So, wherever auxin response is there this promoter will be active. And, you can clearly see a correlation that different regions of the developing primary roots they have a very high amount of signals as compared to other regions and this is called auxin maxima.

And, another important thing if you make a correlation you see that this lateral roots are coming from this region wherever there is high level of auxin or wherever there is auxin maxima. So, this tells that somehow the auxin maxima is correlated with the lateral root development which means that it might be responsible to initiate lateral root development or the program which is specific for the lateral root development. How it is doing? It might be activating some set of genetic network. Where it is activating? It might be activating in some of the cells which is competent of giving lateral root primordia; so, one mechanism which is through morphogen.

Another mechanism; why a particular cell acquires a particular fate is typical receptor mediated signaling. This example we will discuss in detail when we will see shoot apical meristem maintenance or root apical meristem maintenance. Here there are some receptors in one cell which is CLAVATA 1 and 2 here. And, there are some signaling molecules which is secreted by the neighboring cells. And, this neighboring cell they secrete some signaling molecule which is received by the receptors and then these receptors they initiate genetic developmental program So, the second mechanism of acquiring a special fate, position dependent special fate is through this mechanism.

Third and very important mechanism in case of plant is molecular trafficking. So, as I said that the plant cell wall are very rigid, it is very tightly glued. Plant cannot move from one place to another place, their position is fixed during the development. Then how they communicate, and, to break the barrier of communication plant has developed of wonderful way of cell to cell communication which is called symplastic cell to cell communication.

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### Characteristics of Plant Growth and Development

- **Positional Signals:**
- **Molecular trafficking:**

Short- & long-distance trafficking

Mobile molecules- Proteins, RNAs etc.

Image Source: Nakajima et al (2001), Nature, 413, 307-11;  
Scheres et al. (2002), The Arabidopsis Book, e101; 1-18.

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And, this can help in the short as well as long distance trafficking. Trafficking means, there are lot of molecules, signaling molecules in forms of protein, in forms of messenger RNA, in forms of micro RNA and, they have been shown that they are being generated at one place and they are moving to the another place. The movement can be short distance, just next to the neighboring cell or even they can move through the transport system to a long distance.

So, how this happens? If you take this example this is a protein which is called SHORTROOT protein, it is a transcription factor very important transcription factor. Here is the transcriptional fusion construct for SHORTROOT, here is the translational fusion construct.

What do you mean by transcriptional fusion construct? So, when you take promoter of SHORTROOT and put GFP downstream it. Wherever this promoter is active GFP will be expressed and you can see the signal.

But, in translational fusion what you are doing, you are taking SHORTROOT promoter, you are taking *SHORTROOT* gene and you are just removing the stop codon and translationally fusing with GFP. So, you are basically fusing SHORTROOT protein with the GFP.

So, here what you can do? The first thing is that the promoter will ensure the domain of expression and this protein will ensure the localization of the SHORTROOT protein alongwith the GFP.

And, if you compare these two what happens in the transcriptional fusion, just the transcriptional domain where the gene is getting transcribed you can see the signal.

In a root tip it has layer called endodermis and an entire layer of vascular tissues. In transcriptional fusion you can see signal is only in the vascular tissues which means that SHORTROOT promoter is actively transcribing only in the vascular tissues. But, when you track the protein, SHORTROOT protein using translational fusion what happens that the proteins are present in the vascular tissue, but they are also present in the endodermis.

Another interesting thing you can see here that in endodermis protein is localized to the nucleus. So, from where this protein is coming? One thing is clear from here that there is a protein mobility. SHORTROOT protein which is getting synthesized in the vascular tissue it is moving to the endodermis because in endodermis transcription is not happening. So, gene is not getting expressed in the endodermis, the endogenous gene is not getting expressed, but protein is present. And, then we know that this is happening through a very very special structure in case of plant which is plasmodesmata.

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**Characteristics of Plant Growth and Development**

- **Positional Signals:**
- **Molecular trafficking:**

Plasmodesmata

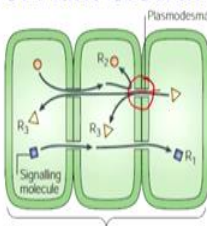


Image Source: Lucas & Lee (2004), Nat Rev Mol Cell Biol, 5, 712-26.

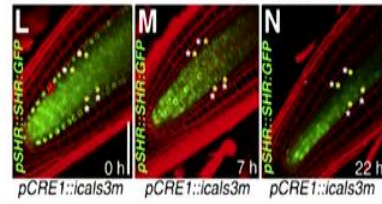


Image Source: Vaten et al. (2011), Dev. Cell, 21, 1144-55.

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Plasmodesmata are the nanopores which is between two cells and they are providing a path, a symplastic path through which molecules can move from one cell to another cell. But, there are a lot of question, is the movement free? No, the movement through the plasmodesmata is highly regulated. So, only those molecules can move through the plasmodesmata which are supposed to move. Those molecule which are not supposed to move they cannot move because, if everything moves from this cell to this cell and everything moves from this cell to this cell then both the cell will lose their own specific identity.

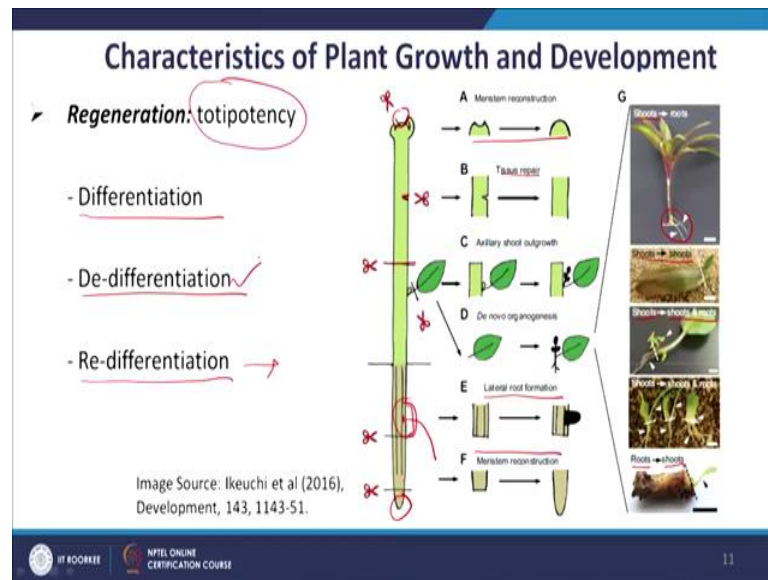
So, both the cells they are ensuring their specific identity, but at the same time they are allowing certain molecules to move from each other from one cell to another cell. And, this is a unique and important feature which plant cells has acquired during the process of development and playing very important role in plant and growth and development.

We will cover this in detail in the later classes, but if you look this picture here SHORTROOT protein is moving through the Plasmodesmata? and how it has been tested? So, there is a mechanism through which what you can do, you can actually block the plasmodesmata between endodermis and the vascular tissues.

So, as in the previous slide I showed you that these proteins are the SHORTROOT proteins are being made or being transcribed and translated in the vascular tissues and then protein is moving to the endodermis. If somehow we block the plasmodesmata which is present in the cell wall between endodermis and the vascular tissue we could block the movement. And, this is what you can see here, when we block this plasmodesmata you can clearly see that the SHORTROOT protein signals are disappearing from the endodermis. Look here it is completely disappeared after 24 hour of blocking plasmodesmata.

So, this clearly tell that the critical or very important transcription factor, SHORTROOT protein is basically getting moved or getting trafficked from one cell to another cell specifically through plasmodesmata.

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Another important characteristic feature of plant growth and development is totipotency. What it means? Every cell in the plants in principle they have a capability that they can undergo the process of cell division, cell differentiation, de-differentiation and they can make plant. And imagine why this is so, important? Again I would say that plants are sessile they cannot move. So, they have to have a mechanism or robust mechanism that under adverse condition, if they lose everything and retain some kind of living cells they should revert back and they should propagate back.

So, this slide if you look here there are some natural mechanism of regeneration and this regeneration mechanism there is a genetic program, there is a regulatory program for this process. So, if somehow the root tips or shoot tips are damaged in a plant or if you cut them what happens? You know that the apical meristems are positioned in the shoot tips and the root tips. If they are lost there is a mechanism plant has acquired a mechanism that they can actually reconstitute, reconstruct the meristem. This is because of their regeneration capability.

Next if there is a tissue damage, again plant has a mechanism through which they can repair the damage. This is again getting activated through the process of regeneration

One thing which I discussed in previous class was the apical dominance. So, when plant is primarily growing then there are axillary meristem, axillary meristems are specified, but their growth is inhibited. Because, plant first want to ensure a certain amount of

growth, particularly they want to transit to the reproductive phase, they want to ensure first successful reproduction. And, then the signal is being transmitted and lot of axillary branches start growing.

But, what happens if you cut the plant from here, they immediately sense it and since this is cut in the differentiated region; if you cut in the meristematic region they can reconstitute the meristem. But, if you cut the region which is fully differentiated, it is difficult for them to fully reconstitute the meristem. But, what they do they immediately activate its axillary meristem and they started making the branches. So, axillary shoot out growth is now getting activated.

Another very important thing is de-novo organogenesis. So, this is a property of plant cell. If you take any part of the plant, which typically we are using in the process of tissue culture which we called explant. And, if you take this plant and activate a proper genetic program, you can generate a full plants or full plantlets. For examples you can take shoot and you can induce the root; you can take shoot and you can induce the shoot.

Similarly, you can take shoot and you can induce both shoot and root, you can take the root and you can induce the shoot. So, what it tells that it tells that there are the genetic program, if you give a proper signal, if you give a proper information or proper hormonal combination you can eventually activate a full and proper developmental program for the shoot development as well as root development.

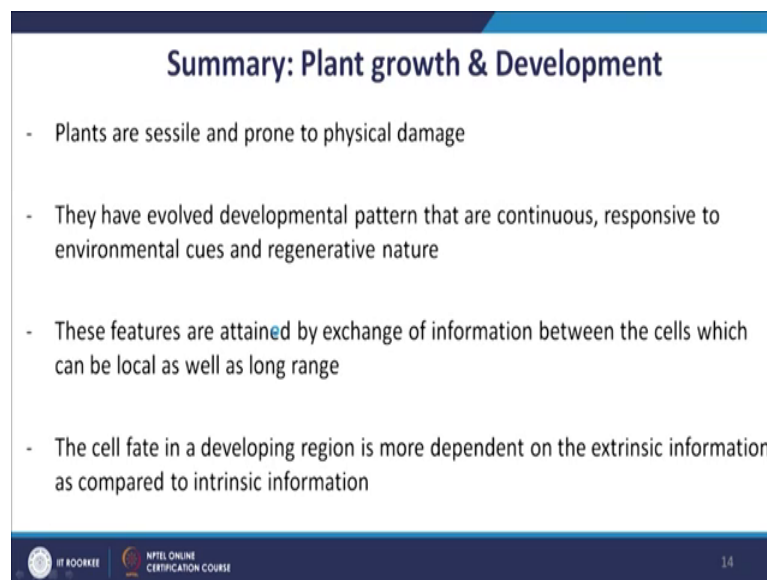
Another important developmental program which occurs is the lateral root formation. So, as I said when plant is growing in the apical and basal axis it is growing by using its apex or shoot apical meristem and root apical meristem. But, once these tissues they are entering in the region of differentiation there is a new meristem which is getting generated somewhere here. And, this meristem they acquire a capability and they make lateral root primordia and then they eventually they make lateral roots coming from here.

So, what happens there is difference from apex. At the apex the meristems are specified as a meristem and they remain as a meristem. So, they are undergoing only the process of cell division. But, here what is happening that at fully differentiated cells they are undergoing the process of de-differentiation, through which they are losing their existing identity and they are acquiring new identity. First the meristematic identity and then later

they undergo a new round of differentiation program or totally new differentiation program and now they are making a new organ or a new tissue.

So, the plants they also have this capability that even though if they are differentiated they can initiate if proper signal is given if required, they can undergo the process of de-differentiation and they can undergo the process of re-differentiation.

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**Summary: Plant growth & Development**

- Plants are sessile and prone to physical damage
- They have evolved developmental pattern that are continuous, responsive to environmental cues and regenerative nature
- These features are attained by exchange of information between the cells which can be local as well as long range
- The cell fate in a developing region is more dependent on the extrinsic information as compared to intrinsic information

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So, if we summarize all the characteristic feature of plant growth and development. So, what we have seen? We have seen that plants are sessile and they are actually very prone to the physical damage. And, that is why they have evolved a developmental pattern that are continuous, responsive to the environmental cues and regenerative in nature. These features are attained in large mostly by exchange of the information between the cells which can be local as well as long range. And, the cell fate in the developing region is more dependent on the positional cues as compared to the lineage information.

So, we will stop here and we will discuss in next class.

Thank you very much.