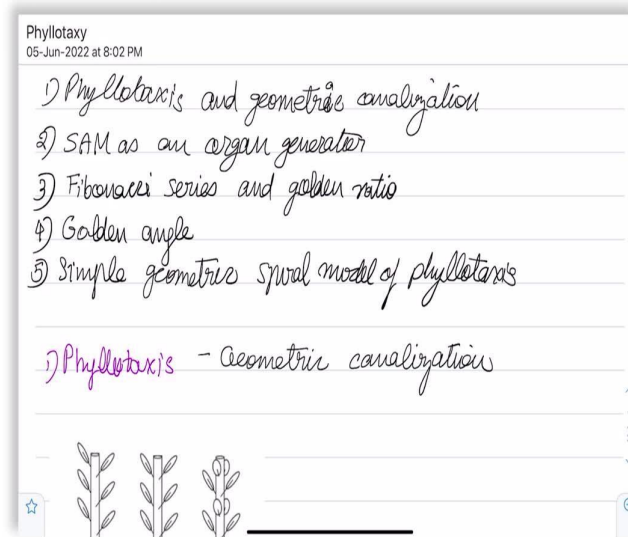


Cellular Biophysics
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Lecture 58
Phyllotaxis Part 1

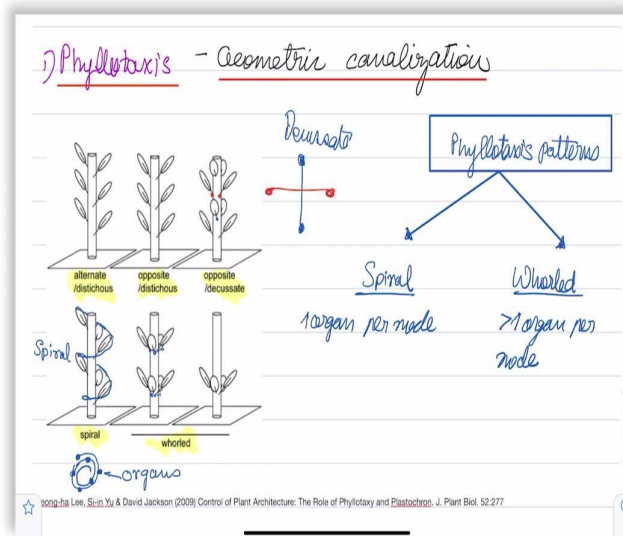
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Hi, in this section, we are going to discuss a fascinating problem in pattern formation and development called phyllotaxy or what you are reading, as phyllotaxis. You will probably some of you will be aware of the fact that phyllotaxis is something that shows up in plants. But I am not sure how many of you are aware that there is a reasonable amount of mathematics and theory that has gone into understanding it.

It combines a mystery that is really truly fascinating because it covers the questions, we are going to cover the questions today in terms of phyllotaxis and geometric canalization, move on to the shoot apical meristem as an organ generator, then touch upon something you learned in high school, the Fibonacci series and something you will have seen in popular writings in maths called the golden ratio. We will briefly touch upon what is the Golden angle, and the fact that it shows up in phyllotaxis, and end with a simple spiral model of phyllotaxis. So, let us get to it.

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What do we mean when we say geometric canalization? So, the idea is that if you look around, and I urge you, so C.V. Raman, C.V. Raman, the Nobel laureate from India once remarked in a speech at IIT Madras for the convocation, that it is important to be in the classroom, but it is also important to wander around the campus, look at the banyan trees, IIT Madras have a lot of banyan trees.

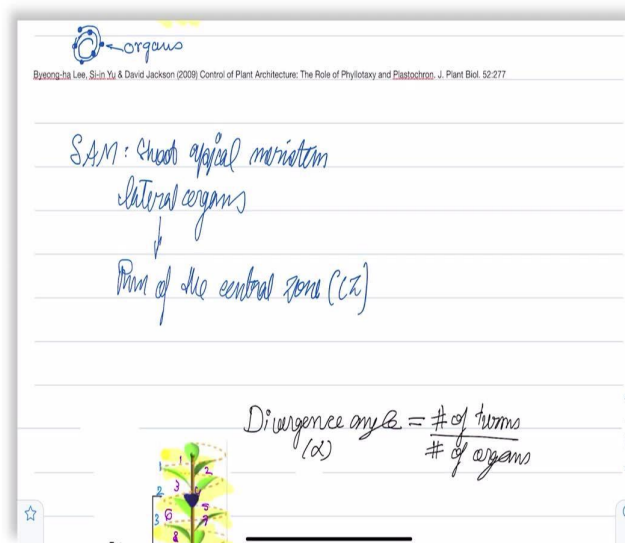
Unfortunately, not all campuses have banyan trees because these days trees cost money to plan to maintain, and observe. His point was to observe nature and as a student to not just learn from the classroom, but to learn from the natural world around you. It does not matter whether you are physics student, biology student, chemistry student, arts student, history student, you learn from nature.

So, broadly, if you look at phyllotaxis patterns, meaning to say the regularity with which leaves organize on a stem, then you will note that broadly you will find an alternate arrangement, sometimes called as distichous, opposite arrangement, meaning to say, or at 180 degrees apart, opposite decussate arrangement which means that two opposite, a pair of opposites, let us say here are followed by a new pair of opposites one level below that are at 90 degrees to the earlier one.

So in a top view, you will see something like this. And in some cases, you are likely to find a spiral which means that the line that can be drawn to connect the leaves as they emerge forms a helical structure around the stem. This is a, you could say, an imaginary model or spiral. And along this spiral so is the emergence of individual organs or leaves, and so on.

Whirled phyllotaxy suggests that at a given node, we will have multiple leaves emerging. So, given this broad classification for the regularity of phyllotaxis patterns, we can divide them into two broad types. One type is spiral and the other type is whirled. Spirals are defined as one organ per node and whirled are greater than one organ per node. The shoot apical meristem is the part where the structures are released, but sticking with the geometry, we need to define a few terms.

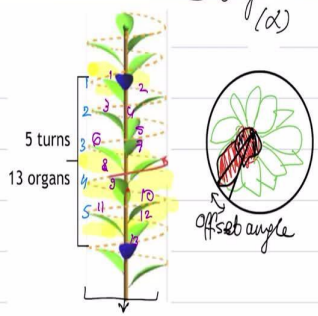
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So, the first term we are going to define is the divergence angle which is the angle between two consecutive organ primordia. The idea is that as the shoot apical meristem forms, it drops off lateral organs along its periphery. This periphery is the rim of the central zone CZ.

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Divergence angle $(\alpha) = \frac{\# \text{ of turns}}{\# \text{ of organs}}$



5 turns
13 organs

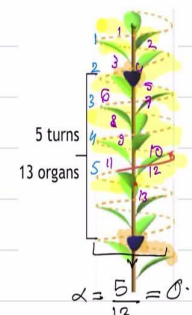
offset angle

$$\alpha = \frac{5}{13} = 0.385 \text{ turns} = 138.5^\circ$$

Ref. $\hookrightarrow \text{Angles} \times 360^\circ$

Godin, Cole & Douady (2020) Development.

Divergence angle $(\alpha) = \frac{\# \text{ of turns}}{\# \text{ of organs}}$

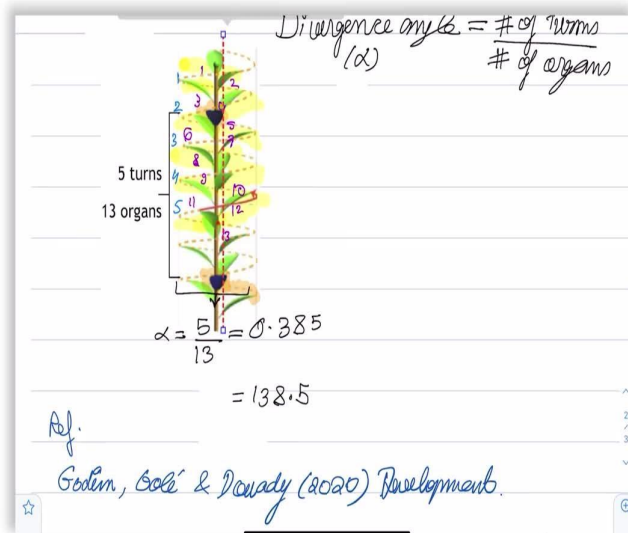
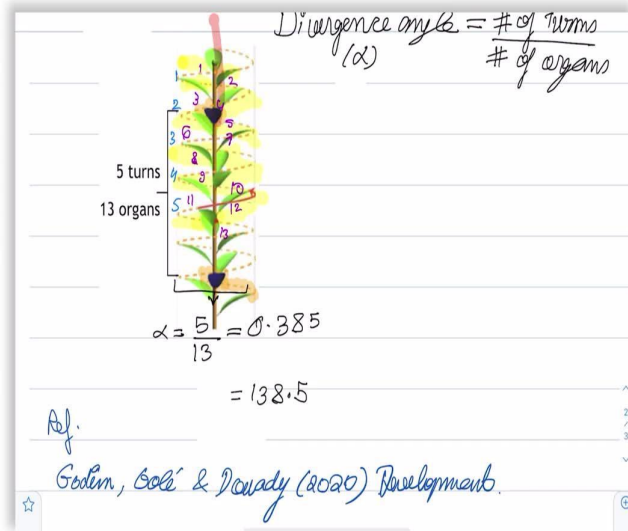


5 turns
13 organs

$$\alpha = \frac{5}{13} = 0.385$$
$$= 138.5$$

Ref.

Godin, Cole & Douady (2020) Development.



So, in such a case the divergence angle is, can be measured experimentally as the number of turns for a given number of organs. One way to calculate this is to take this example that we have taken here from the paper of Godin, Gole and Dwydy from 2020 in the journal Development where they reviewed the theory and geometric ideas that explained this process.

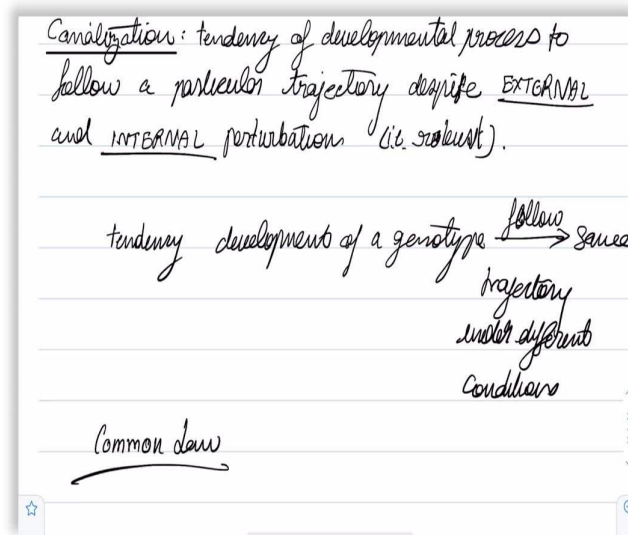
So, what you are looking at is a very simple numbering of the organs with blue, this one we start with the counting or you can start from below, and we go up. So, we say that this spiral starting here makes one turn, touches the blue, goes behind, touches one more, one more, one more, one more, one more, till we can identify another organ that exactly lies at the same angular position.

And one way of knowing it is to do a top projection. So, if you project these leaves, then you should see that the leaf of interest is followed by more leaves 1, 2, 3, 4 so we are numbering

there. As I was saying, count the leaves 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13. Now it is true, if you note a center point and a circle here, then the angle formed by this, the first and the second are offset a little bit or maybe large. And this depends a little bit on the species.

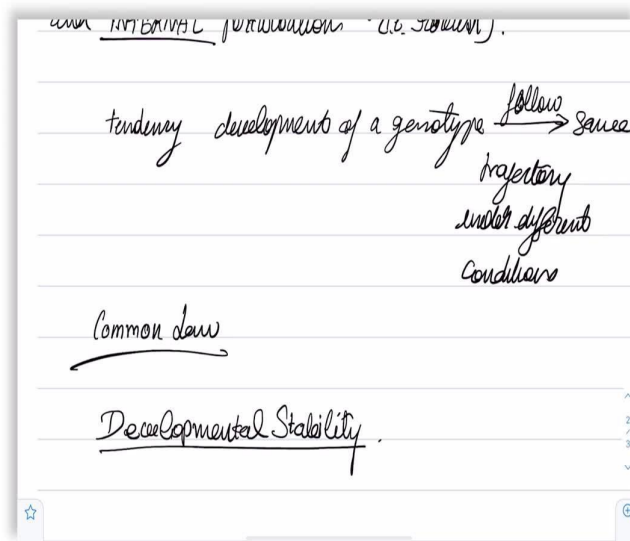
However, we can still calculate an angle that expresses this regularity. And we call this the divergence angle. And by definition, it is the ratio of the number of turns divided by the number of organs that pass through those number of turns. So we get this value which is 5 by 13 which is 0.385, which is in units of turns. So if we want angles, we need to multiply by 360 degrees then we get 138.5 degrees. So just a few terms that we should have clear.

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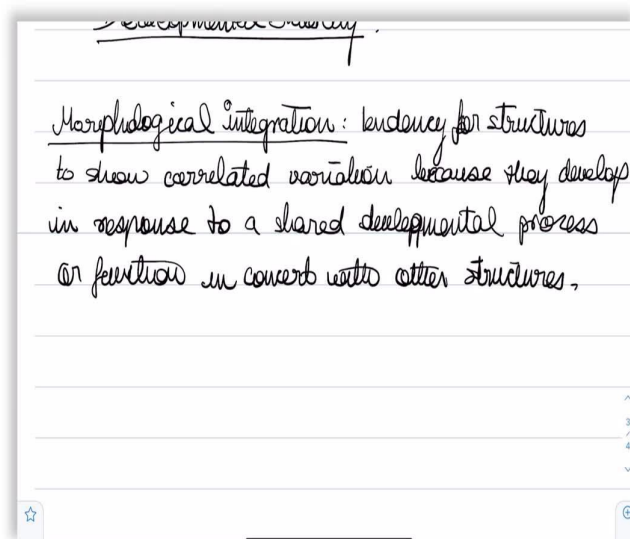
The fact that there is a tendency amongst developing organisms and organs to follow a particular trajectory despite external and internal perturbations, that is it is robust, is called canalization. The idea is that the tendency for development of a specific genotype to follow the same trajectory under different conditions suggests that there is some common law underlying it.

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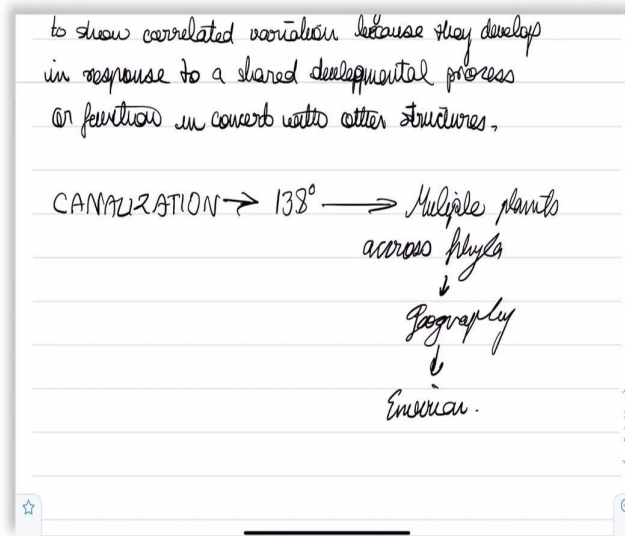
In physics, this would basically be just a mathematical law, but with developmental processes we are so unclear about what is going on that this becomes very hard. This is also sometimes referred to in the biological literature as developmental stability.

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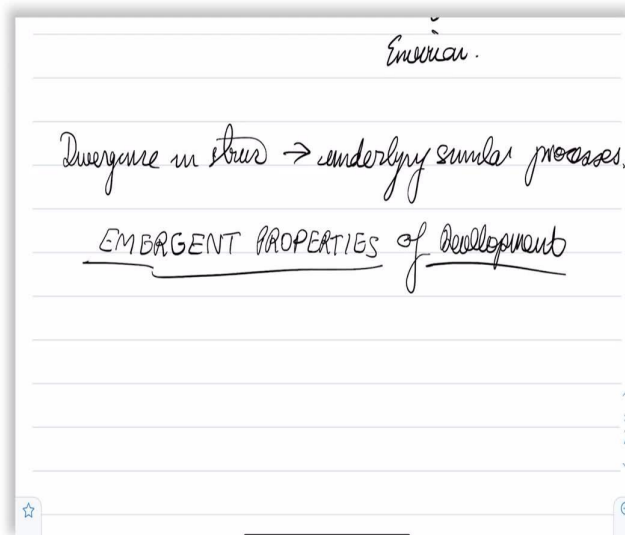
The morphological integration on the other hand is the tendency for structures, biological structures or organs to show correlated variation because they develop a response to a shared developmental process or functioning in concert with other structures. Now, what do we mean by this?

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So, on the one hand canalization means in the case of phyllotaxis that the angle that we talked about earlier of 138 degrees shows up in multiple plants across phyla, geography and environment. This means that there is something unique or conserved across these.

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What you mean by morphological integration? It means that the divergence in these structures has underlying similar processes. These properties canalization, developmental stability and morphological integration, we refer to as emergent properties of development.