Resources and development jointly shape life history evolution in plants

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Transcript for the talk recorded by Gregor-Fausto Siegmund for the 2021 Evolution conference.

Slide 1

Transcript: Hello my name is Gregor Siegmund and I'll be talking with you about how *Resources and development jointly shape life history evolution in plants*.

I'm actively working on how to present these ideas, and so would love to hear your thoughts. In addition to chatting at the panel, I would encourage you to reach out to me over email!

Slide 2

Transcript: I'll start by proposing that theory and practice around understanding the evolution of life histories is often framed in terms of energy. For example, trade-offs might emerge because organisms draw on a limited pool of resources to grow or reproduce.

Slide 3

Transcript: Consider the evolution of flowering time in an annual plant. In this graph, I'm illustrating this by showing the relationship between the rate of development and flowering time. Plants that transition to flowering quickly and at an early age avoid the risk of mortality but don't reach large size, while plants that transition late and at an older age have time to accumulate resources but risk mortality.

Extra note: You might expect to see this pattern if variation in life history strategies among plants is determined by genes associated with resource allocation rather than acquisition; in this case genes that control the transition from vegetative to reproductive growth.

Slide 4

Transcript: This trade-off manifests as a positive correlation between time to flowering and size at flowering. Plants that flower early have few leaves, and plants that flower late have more leaves. Leaves are capable of photosynthesis so by growing large the plant is adding the capacity to support reproduction; but, the plant is risking mortality in the time it takes to survive to flowering.

The main point here is that the trade-off between time of and size at reproduction is expected to emerge because of competing energetic benefits and costs.

Slide 5

Transcript: Let's step back for a moment and consider how plants develop.

During vegetative growth, plants repeatedly add a basic vegetative unit consisting of an internode, node, and axillary bud. This happens through division and differentiation of cells in the *meristems.* I'm focusing on the shoot apical meristem which gives rise to aboveground organs. The action at this apical meristem produces the vegetative unit, which I'm showing you a caricature of here.

Each node is accompanied by an axillary bud that is subtended by a leaf. The axillary bud has a few possible fates. First, it can remain 'quiescent' and simply hang out in limbo. Second, it can differentiate to produce a branch. Finally, it can differentiate into an inflorescence or flower.

Slide 6

Transcript: I'm now going to show you a cartoon of how development might play out for plant that does not have branches.

What you see at first is the repeated, iterated addition of a new node and leaf. The "axillary buds" in this plant don't differentiate and so the plant retains only a single axis of growth. After a few vegetative modules have been added, the vegetative meristem differentiates into an inflorescence meristem. This in turn becomes a flower and terminates growth.

This last point is key – once vegetative meristems acquire an inflorescence or floral fate, there's no going back.

Transcript note: Throughout the talk, I represent vegetative meristems in dark green, leaves in red, inflorescence meristems in light green, and flowers in orange.

Slide 7

Transcript: Things get more complicated when the axillary buds of the plant differentiate into branches. In turn, these branches add vegetative modules. Each branch is effectively a new axis of growth and reproduction.

Slide 8

Transcript: The cartoon I'm showing you now emphasizes that branching creates variation in the number of meristems.

The plant grows quickly, adding leaves. But by branching it's also increasing the number of vegetative meristems that can acquire different fates. Each of those meristems could add more vegetative modules or acquire a floral fate and contribute to reproduction.

Transcript note: To summarize: plants grow through the addition of vegetative modules; branching creates variation in the number of these modules; the transition to flowering terminates vegetative growth along an axis.

Slide 9

Transcript: Returning to the level of life histories, meristem dynamics also contribute to patterns that we would not expect if resources alone constrained growth and reproduction. Indeed, empirical work following meristems throughout development suggests that life histories in plants *are* shaped by both meristem and resource constraints.

For me, one of the most accessible distinctions is the prediction that meristem limitation generates positive correlations between growth and reproduction at a given age while resource limitation generates negative correlations. Growth and reproduction both depend on meristem availability – more meristems allows plants to add vegetative modules and flowers – while growth and reproduction compete for resources.

Slide 10

Transcript: Energetic arguments and development thus propose two distinct sets of constraints on the evolution of plant life histories. We have empirical examples that both of these are relevant for plants. I think that developing more theory about this topic could help contextualize and generalize existing examples.

In practice, I'm framing this as a question about how meristems and resources jointly shape life histories in plants. The first step in this project has been to develop a model that expresses plant growth and reproduction explicitly in terms of meristems and resources. With that model in hand, I'm addressing topics that fall under the umbrella of two bigger questions.

Slide 11

Transcript: First, how do meristem and resource constraints shape life history? Without a baseline understanding of when each constraint is important, it's challenging to generalize about their relative strengths or conditions under which one or the other might be predominant. In particular, I'm interested in using the model to explore how these two constraints complement or oppose each other.

Slide 12

Transcript: Second, are plant life histories more sensitive to meristem or resource constraints in face of variability in season length? When the length of the season varies, delaying reproduction exposes plants to the costs and benefits of waiting to flower. Branching might allow plants to reduce variability in fitness by simultaneous growth and reproduction.

To address these questions, we're examining the relative importance of meristem and resource constraints on fitness. The approach follows from previous work that applies optimal control theory to the study of life histories. In the next few slides, I'll dig into the model a bit.

Slide 13

Transcript: Ultimately, the goal is to analyze different combinations of meristem and resource constraints to find the strategies that maximize the geometric mean fitness of an annual plant.

Slide 14

Transcript: The first step was to develop a model that explicitly represents meristem and resource dynamics. A series of differential equations describes the plant life history through time. Whereas classic life history models based on resources considered two pools – one for vegetative biomass and one for reproductive biomass – I've represented the dynamics in terms of vegetative and inflorescence meristems, and the associated leaves and flowers.

Slide 15

Transcript: The plant's propensity for branching is controlled by a single parameter. In this case, I'm assuming the branching pattern is fixed, but one could also imagine an extension of this in which branching responds to environmental cues.

Slide 16

Transcript: I then include three variables, u, beta1 and beta2, that function as 'controls' on plant development. These are three parameters that vary over time and correspond to decisions that the plant makes about producing vegetative versus inflorescence meristems and about rates of meristem division. These controls are what is actually being optimized to change the plant's life history strategy.

Slide 17

Transcript: Finally, I impose the meristem and resource constraints. You can think about these constraints as setting boundaries on the dynamics of the plant. The meristem constraint places a cap on how quickly new meristems can be added, and the resource constraint states that all meristem divisions can't use more resources than the leaves can produce.

Slide 18

Transcript: This slide shows the optimization problem in its details. I'm putting this all up at once in case anyone decides to pause the recording here. We're approaching this problem computationally rather analytically. I'd love to talk about this more when I have some more concrete results in hand.

Slide 19

Transcript: I want to wrap up by returning to the broader picture of how meristem dynamics contribute to phenotypic variation in plants. I've focused on axillary branching during vegetative growth. But meristem dynamics generate a host of other life history patterns, and bringing the lens of evolutionary ecology to bear on these phenomena could help illuminate their function.

Slide 20

Transcript: Thank you for taking the time to watch and listen. I'd love to hear from you if you have any thoughts on what I've talked about today, or to chat about any of the topics below! I also want to acknowledge my coauthors and committee members, Monica, Steve, and Anurag Agrawal, and their lab groups for help in thinking about this. They've been incredible resources and supportive throughout this project.