Resources and development jointly shape life history evolution in plants

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1 Introduction

- The interplay between development and ecology is the basis for evolutionary change [evolution is the control of development by ecology (van Valen)]

    - A central tenet of life history theory is that selection maximizes fitness by favoring trait combinations that optimally balance different parts of the life cycle (Cole (1954); Lande and Arnold (1983)).

    - Theoretical and empirical studies typically assume that organisms must allocate a limited pool of resources to competing functions such as growth versus survival. Fox (1990) states this assumption is shared by approaches of reproductive effort, dynamic optimization, and evolutionary demography. Quantitative genetics assumes that there are correlations among components of life history but focuses on genetic and phenotypic correlations.

    - From early papers that used optimal control theory to study life history evolution, authors have suggested incorporating development into the models (Cohen (1971); Fox (1992a); Schaffer et al. (1982)). However, no such models have yet been developed.

- Multiple lines of evidence support the association between life history and architecture

    - Adaptive radiations on oceanic and sky islands demonstrate association between life history and morphology in shift from annual/herbaceous to perennial/secondary woodiness Nürk et al. (2019)

    - Developmental biology: studies demonstrate how maintenance of active apical or axillary meristems changes architecture and life history. Includes comparisons such as mutant lines of model plants, comparisons of genes between annual/perennial relatives (Ponraj and Theres (2020); **?**)

    - Evolutionary ecology studies in the field demonstrate the role of branching in life history as well; examples include ecotypes of Mimulus guttatus (Baker and Diggle (2011); Baker et al. (2014); Friedman et al. (2015)), Erysimum populations across an elevation gradient (Kim and Donohue (2011))

    - <mark>Identify studies that demonstrate the presence of heritable genetic variation in bud differentiation/organ identity</mark>. For example, potentially could include Baker et al. (2014); Bonser and Aarssen (1996); Huang et al. (2013); **?**); **?**); **?**); **?**. Could also cite crop studies (e.g. Hardy et al. (1998))

- Various lines of evidence exist that point to constraints of development on life history evolution that should inform optimization studies

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- Experiments that show genetic covariance/correlation of flowering time and meristem number/tiller number. We have data from plants from different habitats (e.g. Geber (1990); Schmitt (1993)), from RILs (e.g. Haselhorst et al. (2011)), from the result of selection experiments (e.g. Mitchell-Olds 199x?). Also Duffy et al. (1999); Friedman et al. (2015); Kudoh et al. (2002); van Tienderen et al. (1996); Watson (1984) Diggle 1993, Gardner and Latta 2008, Latta and Gardner 2009, Austen et al. 2014, Rubin et al. 2018

- Studies of development with mutants/knock-outs in Arabidopsis that show that modifying flowering time genes (e.g. tfl) has an effect on the number of meristems, establishing that there is pleiotropy (Bradley et al. (1997); Karami et al. (2020), Melzer et al. 2008, Baumann et al. 2015)

- We have studies focusing on developmental stages (e.g. Baker and Diggle (2011)).

- Parker and Smith (1990) describe how comparative studies and quantitative genetics can be used in conjunction with optimization to understand phenotypes. Specifically, they suggest that quantitative genetics can be used to identify constraints that are relevant for optimization models. Comparative methods can then be used to test the predictions of those models. Here's a quote: "discovery of a genetic covariance can indicate presence of a developmental constraint that must be taken into account when formulating an optimization model". Experiments and interspecies comparisons can also help discover these constraints.

- Plant growth and development

  - Plants grow and reproduce via meristems, tissues that are made up of undifferentiated cells and are analogous to stem cells in animals (reviewed in McSteen and Leyser (2005); Wang et al. (2018)).

  - Individual meristems can grow vegetatively, become an inflorescence meristem, or remain undifferentiated. Each vegetative meristem may generate additional meristems with the potential to differentiate into one of these three types. A meristem that differentiates into an inflorescence can no longer grow vegetatively. The onset of flowering thus prevents future vegetative growth at the level of individual meristems.

  - Limiting the number of meristems available for differentiation and reproduction can thus produce tradeoffs: a plant with that allocates most of its meristems to reproduction now will not be able to allocate those meristems to reproduction later (Geber (1990); Schmitt (1993); Watson (1984)).

- Theory and models identify consequences of variation in season length on resource allocation decisions

  - For a fixed season length (no variability), a bang-bang control maximizes arithmetic mean fitness (Cohen (1971))

- For a uniform distribution of season length (highly variable), the optimization problem becomes one of maximizing geometric mean fitness. In this case, simultaneous allocation to vegetative and reproductive growth can be part of optimal strategy (King and Roughgarden (1982*a*)).

- Using an evolutionary algorithm and examining intermediate variability in season length (between fixed and uniform distribution), the authors find that steepness of gradient relates to the amount of variability in the environment (Wong and Ackerly (2005)).

- A study that examines the production of workers versus sexual individuals in annual eusocial insects suggests that high levels of environmental variability are required to promote a graded control; they propose that realistic levels of environmental variability in season length are unlikely to be sufficient to do so (**?**).

- Variations on the basic form of the model explore the effect of mortality (Cohen (1976)), nonlinear (**?**) or seasonal production functions (Fox (1992*b*); Schaffer et al. (1982)), tissue loss (King and Roughgarden (1982*b*)), storage (Chiariello and Roughgarden (1984)), or constrained growth (citation needed).

- More thoughts? Overview of model types that address connection of life history and timing or reproduction. Specific benefits of optimal control. Original models have been extended and enriched. I think this should be reduced to 1-2 concise paragraphs that also address other modeling approaches that have been used to study this kind of problem (evolutionary algorithms; Wong and Ackerly (2005)) and why we chose to use optimal control theory.

- Branching modifies plant architecture and contributes to temporal patterns of resource allocation and reproduction

  - A model of development demonstrates that season length and variability determine the optimal morphology of an inflorescence. (Prusinkiewicz et al. (2007)). Ideas presented in this confirmed in tomato by a study demonstrating that inflorescence architecture is determined by rate of meristem maturation (Park et al. (2012)).

  - Variety of evidence associating variation in branching with environment: branching and altitude (Milla et al. (2008)), bud banks increase with productivity in perennials (**?**)

  - Developmental programs differ among plants in terms indeterminate versus determinate flowering, and how is that related to resource allocation patterns

  - Developmental genetics identifies independent/related basis for flowering time, leaf production, and growth rate. Review to determine what these studies state about the relationship among these variables (e.g. Karami et al. (2020); Méndez-Vigo et al. (2010); Remington et al. (2013); Serrano-Mislata et al. (2016); Taylor et al. (2019); **?**); **?**); **?**)

Life history theory is a framework for understanding how evolution generates and responds to tradeoffs among growth, survival, and reproduction over the course of an organisms' life cycle. A central tenet of life history theory is that selection maximizes fitness by favoring trait combinations that optimally balance different parts of the life cycle (Cole (1954); Lande and Arnold (1983)). Theoretical and empirical studies typically assume that organisms must allocate a limited pool of resources to competing functions such as growth versus survival. While this may be an appropriate assumption for animals, plants are modular organisms.

Plants grow and reproduce via meristems, tissues that are made up of undifferentiated cells and are analogous to stem cells in animals (reviewed in McSteen and Leyser (2005); Wang et al. (2018)). Individual meristems can grow vegetatively, become an inflorescence meristem, or remain undifferentiated. Each vegetative meristem may generate additional meristems with the potential to differentiate into one of these three types. A meristem that differentiates into an inflorescence can no longer grow vegetatively. The onset of flowering thus prevents future vegetative growth at the level of individual meristems. Limiting the number of meristems available for differentiation and reproduction can thus produce trade-offs: a plant with that allocates most of its meristems to reproduction now will not be able to allocate those meristems to reproduction later (Geber (1990); Watson (1984)).

In plants where reproduction is fatal (monocarpic plants), plants must balance their investment in and the timing of growth and reproduction because both processes draw on a shared set of resources. Theoretical models of life history evolution typically represent this as a trade-off in energetic investment. However, plant development is modular and can constrain future energetic allocation to growth or reproduction.

The hypotheses I've written turn explicitly to developmental patterns. I think that the question has become more about the relationship between development and the environment than it was when I originally wrote this introduction. It would be helpful to have theory about

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Fox (1990) discusses experiments with Eriogonum demonstrating that patterns of reproduction are the product of growth and development.

1.1 Questions

- Questions for an unbranched plant with a determinate inflorescence (1-dimensional model with a switch time only)

    - ...

- Questions for a branched plant with a determinate inflorescence

    - Are plant life histories more sensitive to meristem or resource constraints in face of variability in season length? When season length is variable, branching creates variation in meristem number that in turn supports simultaneous growth and reproduction, and may be a a strategy that reduces variability in fitness.
    - How do meristem and resource constraints shape life history? Meristem and resource constraints will both influence fitness; the optimal strategy will be determined by the relative magnitude of the rate of meristem divisions and resource use efficiency.

- Questions about optimal control

    - I will use the models to determine whether including differentiation and growth of meristems reduces the likelihood of obtaining a strategy with an instantaneous switch (Cohen (1971)). Put another way, are graded allocation strategies optimal when vegetative and reproductive growth are coupled Fox (1992a)?
    - I will look at the control strategies of decisions (e.g. meristem division) and the cumulative impact on control of resource budget. Do the control strategies of meristem decisions (e.g. bang-bang) translate to resource budgets (also being bang-bang?) (Fox (1992a))?
    - I will ask when plants are more likely to be resource versus meristem limited. Specifically, I will focus on how the optimal strategy changes with increasing levels of environmental variation; are plants likely to be meristem limited in scenarios with high levels of uncertainty about season length in order to maintain the ability to capitalize on those longer seasons? (Salomonson et al. (1994); Schemske (1980); Stebbins (1974); Wyatt (1982))

- Questions about the optimal strategies under different allocation rules

    - What is the best strategy when there are no meristems?
    - What is the best strategy when the rates are the same but there are meristems?
    - A model of resource allocation decisions will inevitably produce trade-offs that are the result of resource limitation. Will a model of meristem allocation decisions inevitably produce trade-offs that are the result of meristem limitation?

- Distinguish meristem versus resource allocation as the trade-off shaping life history evolution.

    - Geber, Fox, Lehtila and Larsson
    - Define conditions for meristem vs. resource limitation.
    - Set up boundary conditions or test cases that demonstrate meristem vs. resource limitation.

- Does including development lead to bang-bang control or graded allocation, and how does this depend on development mode?

    - Hypotheses: Cohen, King and Roughgarden, Fox, Iwasa
    - Recover optimal controls.
    - Compare results to the strategies from the Cohen or King and Roughgarden models.

- Explore the effect of environmental variation on flowering time via development.

    - Hypotheses: Prusinkiewicz et al. (2007); Stebbins (1974); Wyatt (1982)

- Predictions about season length and variability in season length

    - I expect that longer seasons favor branching (Geber (1990)).
    - As the end of the season becomes more unpredictable, it might become advantageous to have multiple branches, some of which can produce flowers and others which might still be producing leaves (Geber (1990)).
    - I also expect this effect to be less pronounced for plants which produce inflorescences than single flowers (Bonser and Aarssen (2006)), as inflorescences should provide additional flexibility in how many flowers to produce per reproductive meristem (Bonser and Aarssen (2006); Salomonson et al. (1994)).
    - "a particular plant morphology is the product of developmental decisions about the number and types of metamers, and thus branches produced. Is carbon availability critical to such decisions, and if so, at what level of morphological organization is its availability assessed?"

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- Developmental decisions are made so as to maintain a positive carbon balance within a physiological unit (Watson and Casper (1984)). When reproductive and vegetative branch formation compete for the same meristems, the development of reproductive branches will reduce the number of vegetative branches that can form (Watson (1984)). Even if reproductive branches may be able to support themselves, forming them may reduce ultimate carbon balance because they are unlikely to contribute excess assimilate. Life history theory for animals does not apply to plants - the assumptions are not valid for plants where elaborating the aboveground structure can pay for its own cost. "predictions about a plant's behavior in different environments will vary according to the time period in which carbon availability acts as a developmental constraint, the degree to which translocation of assimilate is architecturally constrained, and the extent to which structures differ in their capacity to be carbon-autonomous." (Watson and Casper (1984)).

- Flowering in plants is correlated with rosette size - does this reflect the availability of stored assimilate to support maturation of the inflorescence OR does it reflect the development of sufficient leaves to support the inflorescence with current assimilate?

- Predictions in terms of model parameters

  - When does flowering start? This asks when plants start allocating meristems to reproduction, or when plants start producing inflorescence meristems. In the model for determinate inflorescences, this would be when $p(t) < 1$. In the model for indeterminate inflorescences, this would be when $p(t) - q(t) < 1$ or $q(t) > 0$.

  - How quickly do plants commit resources to flowering? This asks whether there is an instantaneous or graded allocation to reproduction.

  - How do allocation strategies respond to different levels of interannual variation? How does the optimal control shift with increasing variance in season length?

  - How do optimal strategies respond to different rates of division in primary and inflorescence meristems, β_1 and β_2? For example, what is the optimal control for different levels $\beta_1 < \beta_2$ (primary meristems divide more slowly than inflorescence meristems), $\beta_1 = \beta_2$ (primary and inflorescence meristems divide at equal rates), or $\beta_1 > \beta_2$ (primary meristems divide more quickly than inflorescence meristems)?

  - What is resource limitation in these models? What is meristem limitation in these models?

  - Which developmental mode favors meristem limitation? MAG suggest that determinate development should favor meristem limitation because the meristem can be consumed by a floral meristem while indeterminate development can always keep growing.

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- When are resource allocation models appropriate for understanding the developmental decisions that plants make? When are resource allocation models insufficient for understanding the developmental decisions that plants make?

- More predictions about flowering time and meristems

  - Early flowering reduces meristem number and late flowering increases meristem number.
  - Environmental risk (e.g. dry habitats) promote the evolution of annuals and early flowering. This could be an interspecific comparison (within genera) or intraspecific (populations in riskier habitats flower earlier).
  - Annuals derive from perennial ancestors (phylogenetic).

1.2 Overview of dynamic optimization (assumptions, predictions, goals)

Life history theory typically assumes that trajectories of growth and reproduction are shaped by resource allocation decisions. Descriptions of development (Figure ?? and ??) highlight how growth and fecundity depend on meristem production. Models that do not explicitly represent resource and development can not distinguish between the origin of tradeoffs. See White et al. (2016) for a complementary perspective on sources and sinks in plant growth and Körner (2015) for a review on how sinks might often limit plant growth. Fox (1992a) suggests allometric models are not sufficient and models that incorporate development will be necessary.

A key assumption of the classic models is that plants are making allocation decisions about carbon, which is assumed to be the limiting resource. Although this assumption has been extended to include other nutrients, plant development complicates the picture. Because plants have modular structures, vegetative and reproductive growth are coupled insofar as plant architecture limits the total potential number of flowers or inflorescences. More generally, whether a plant is in a vegetative or reproductive phase is the product of decisions about the fate of primary or axillary meristems. This perspective aligns with a

source-sink perspective on plant growth that suggests potential photosynthesis is not the sole determinant of plant growth but that plant growth is instead a balance of source (photosynthate) and sinks (maintenance, organ production, etc.) Körner (2015); White et al. (2016).

A shared assumption of reproductive allocation models, dynamic optimization models, and evolutionary demographic theory is that demographic parameters are themselves parts of organisms (Fox (1990), p 1420). However, the representation of organisms in these models is nonetheless an abstraction. In particular, they treat growth and reproduction as independent components of an organism's life history to which some fraction of a limiting resource can be allocated. (Fox (1990), p 1407) outlines three key points to why its important that development couples reproduction and growth for understanding how plants respond to drought. First, the models above assume that the reproduction and growth are independent. Second, developmental coupling is invariant among populations suggesting similar responses to the environment.

Modifications to original models include varying functions for productivity and reproduction (e.g. seasonal pattern, overlap or not), tissue loss and maintenance costs, multiple organs, allocation to storage, different types of survivorship curves, allometric relationships of reproductive to vegetative mass, and environmental stochasticity. The value in these models comes from an ability to explore how allocation decisions respond to different assumptions about variables such as resource use or variability in season length.

- Cohen 1971: derives bang-bang control; maximizes arithmetic mean yield; does not derive analytical solution for maximizing geometric mean

- Cohen 1976: constant environment, maximize arithmetic mean, ... [what are key conclusions here?]; also considers describing survival by a decreasing function and finds bang-bang

- Vincent and Pulliam 1980: analyzes Cohen 1971, generalizes the model; considers

2 photosynthate production functions (linear + nonlinear, saturating), both predict bang-bang; also analyzes optimal leaf toxin allocation

- Schaffer, Inouye, Whittam 1982: seasonal variation in photosynthesis/storage

- King and Roughgarden 1982: introduces random variation in season length; maximizes geometric mean fitness; builds on C71; obtains graded control, basis for Fox 92, Lindh 16

- King and Roughgarden 1982: includes tissue loss (herbivory); Rathcke and Lacey (84) claim as accurate

- Chiariello and Roughgarden 1982: includes tissue loss (herbivory), seasonal variation in assimilation/storage

- Fox 1992: modifies photosynthate production function to be time-varying (with a peak) and looks at different survivorship curves

- Fox 1992: reviews assumptions of resource allocation models; develops allometric model (cf Lindh 2016); suggests development needs to be incorporated

- Shitaka and Hirose 1993:

- Johansson et al. 2013: "the seasonal distribution of productivity (e.g. temperature and precipitation) can affect the size and even the direction of the optimal response of the flowering time to certain types of environmental change, such as increased productivity or increased season length" (Lindh et al. 2016), "assumed that plant growth rate is proportional to the vegetative mass during the growth season" (Lindh et al. 2016)

- Lindh et al. 2016: modifies KR82 by making growth exponential, logistic, or WBE (general constrained or allometric); also in appendix shows bang-bang control with exponentially decreasing survival corresponding to constant mortality

2 General approach

- Describing plant development and branching using differential equations

  - Various authors have proposed considering plants as a population of subunits (e.g. White (1979)).
  - Plant architecture can be described using L-systems (Prusinkiewicz et al. (2007)) but here we do not explicitly represent branching but rather the population of plant parts that result from branching. This is analogous to an approach modeling cell divisions using differential equations (Itzkovitz et al. (2012)).

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- We developed differential equations that capture the basic processes of plant develop-
ment

  - Assumed key step limiting steps were review (Fox (1992*b*))
  - Followed dichotomous characterization of inflorescence development (Kellogg (2000)
  - Key transition was from producing vegetative to inflorescence meristems, as sug-
gested by developmental studies (e.g. Bradley et al. (1997)).
  - Interpretation of conversion efficiency is based on physiological interpretation
(Ackerly (1999))
  - Interpretation of per-capita rate of meristem division is based on plastochron
index

We took the following approach to solving the problem outlined above. First, we sought
to develop differential equations that capture the basic processes of plant development that
are relevant to our questions. To accomplish this goal, we reviewed existing literature on
plant development, models of plant development. Second, we specified the optimal control
problem and goals. This step included defining Hamiltonian for cases with and without
state variable constraints. Third, we solved the optimal control for the case without state
variable constraints. We took this step in order to develop intuition about the system and to
determine initial conditions for the numerical solution. Finally, we implemented a numerical
algorithm to obtain solutions to the optimal control problem.

Here, we apply these ideas to develop a system of ordinary differential equations that
describes the dynamics of plant development and constrains growth by the availability of
photosynthate. This approach places the allocation decisions at the level of meristems (de-
cisions about meristem fate) and leaves flexibility about much these decisions are limited
by photosynthate. In classic models, any quantity of vegetative biomass can support unlim-
ited primary meristem divisions which can in turn contribute to unlimited number of floral
meristems.

Resource limitation generates negative correlations between growth and fecundity within
a life stage because both compete for resources. In a situation where resources are limited,

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we might expect to see trade-offs that are the result of resource allocation decisions (we wouldn't see these decisions when resources are not limited).

Meristem limitation generates positive correlations between growth and fecundity within a life stage because both depend on meristem production. In a situation where meristems are limited, we might expect to see trade-offs that are the result of meristem allocation decisions (we wouldn't see these decisions when meristems are not limited).

Goals: connect vegetative branching, inflorescence development, trade-offs, and flowering time. Distinguish meristem versus resource limitation as the trade-off shaping life history evolution. Explore the effect of environmental variation on flowering time via development. Does including development lead to bang-bang control or graded allocation, and how does this depend on development mode.

3 Models of plant development

The description of plant development that I give here should be directly connected to a figure demonstrating the different types of divisions that I base the model on. The file basic-inflorescence in the notes folder should be helpful for this. I think I need to make the case that the interplay between meristem and resource allocation are well-represented by two basic developmental decisions: whether or not the plant branches, and whether the inflorescence is determinate or indeterminate. I will try to marshal: (1) a brief overview of research on genetics of development, (2) role of these processes in shaping plant morphology, (3) life history arguments.

Development in flowering plants can be characterized as a series of decisions at the meristems Kellogg (2000). The primary shoot divides at the shoot apical meristem (SAM) and produces additional primary shoot meristems (main branch) and axillary meristems (AM), each of which is subtended by a leaf. The axillary meristems can develop into an

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axillary branch or remain quiescent. Each axillary branch has similar dynamics as the primary shoot meristem (though potentially at different rates). The shoot apical meristem is converted to an inflorescence meristem (IM) through internal or external signals. In turn, inflorescence meristems give rise to floral meristems (FM).

In plants with determinate inflorescences, the inflorescence meristem is eventually converted to a terminal flower, which consumes the meristem. Tomato is an example of a plant with a determinate inflorescence and sympodial growth Park et al. (2012). In plants with indeterminate inflorescences, the inflorescence meristem only produces flowers at axillary positions. *Arabidopsis* is an example of a plant with an indeterminate inflorescence and monopodial growth Bradley et al. (1997).

The 'rules' characterizing plant development have been used to model the evolution of inflorescence architecture Prusinkiewicz et al. (2007). The meristem dynamics that underly inflorescence architecture are also likely involved in organizing branching architecture Park et al. (2012). Lindenmayer systems (L-systems) are a grammar that is capable of reconstructing the branching architecture of various organisms (e.g. algae, bacteria, plants). L-system statements highlight the overlap in decision rules that determine branching in vegetative and reproductive growth.

Cohen (1971) identified development as a factor that could help explain why an instant switch in allocation from vegetative to reproductive growth is rarely observed. Development connects growth and reproduction, and constrains how plants can shift allocation to reproduction Fox (1992a). Life history models for plants have not included developmental processes, which may limit their applicability and interpretation Fox (1992a). For example, it may be easier to test the predictions from models that separate meristems and biomass. Also, models that do not represent development can not determine whether allocation patterns are the result of selection on developmental decisions or resource allocation directly. The broader issue here is whether resource-based models can adequately represent plant

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life histories, or whether it is necessary to include development to describe the biological processes underlying life histories Fox (1992a). need to work on this paragraph

I first describe resource allocation models Cohen (1971); King and Roughgarden (1982a). I then describe how I represent meristem and resource allocation in models for plant life histories. These models are developed from ideas in Fox (1992a); Itzkovitz et al. (2012); Kellogg (2000); Prusinkiewicz et al. (2007). First, I write models for plants with determinate inflorescences. Next, I write models for plants with indeterminate inflorescences.

4 Determinate inflorescences

In plants with determinate inflorescences, the shoot apical meristem forms a terminal flower and an axillary bud Bartlett and Thompson (2014). In tomato, the primary shoot meristem converts to a floral meristem and a sympodial inflorescence meristem; this pattern is iterated to form the inflorescence Park et al. (2012).

I describe the developmental decisions in a plant with determinate inflorescences using three types of divisions (Figure ??) Itzkovitz et al. (2012). First, a primary meristem can divide at the shoot apical meristem to give rise to two primary meristems: the main branch and an axillary bud. These divisions generate a vegetative, branching architecture. Second, a primary meristem can divide at the shoot apical meristem to give rise to an inflorescence meristem and a floral meristem. These divisions end vegetative growth and mark the transition from vegetative to reproductive growth along an axis. Third, an inflorescence meristem can divide into an inflorescence meristem and a floral meristem. These divisions are the only possible fate for inflorescence meristems. Using these categories assumes that there is no terminal division into two floral meristems. The end of season terminates flowering. This assumption is somewhat unrealistic because some plants do stop flowering.

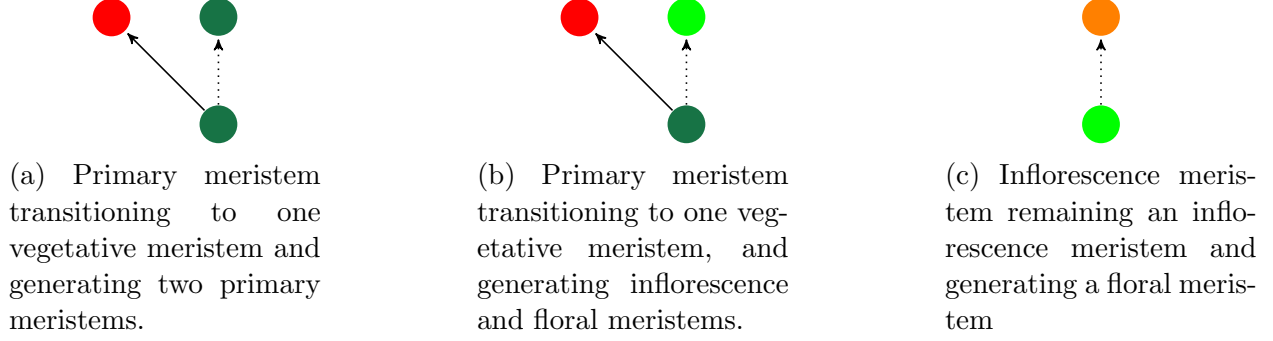I use these types of divisions/transitions to summarize the meristem dynamics for plants

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(a) Primary meristem transitioning to one vegetative meristem and generating two primary meristems.

(b) Primary meristem transitioning to one vegetative meristem, and generating inflorescence and floral meristems.

(c) Inflorescence meristem remaining an inflorescence meristem and generating a floral meristem

Figure 1: Meristem transitions in plants with determinate inflorescences.

(a) Primary meristem transitioning to one vegetative meristem and generating two primary meristems.

(b) Primary meristem transitioning to one vegetative meristem, and generating inflorescence and floral meristems.

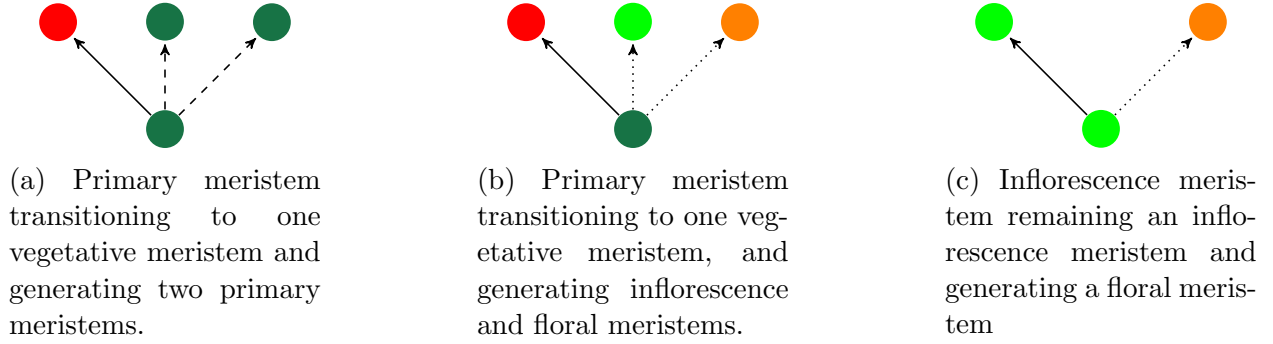(c) Inflorescence meristem remaining an inflorescence meristem and generating a floral meristem

Figure 2: Meristem transitions in plants with determinate inflorescences.

with determinate inflorescences in a system of equations with constraints (Equation 1 and 2) and a state diagram (Figure 3). In this model, P, V, I, and F are the populations of primary, vegetative, inflorescence, and floral meristems, respectively. Primary meristems divide at a rate β_1. Inflorescence meristems divide at a rate β_2, and are thus converted to floral meristems at a rate β_2. Each division by an inflorescence meristem produces one inflorescence meristem and one floral meristem. The probability that a primary meristem divides into two primary meristems (branch and axillary meristem) and a vegetative meristem is given by the control function, $p(t)$. The probability that a primary meristem divides into a vegetative meristem, inflorescence meristem, and a floral meristem is given by $1 - p(t)$.

To summarize Figure 3, panel (A) occurs proportional to the number of primary meristems at a rate $\beta_1 p(t)$. Panel (B) occurs proportional to the number of primary meristems at a rate $\beta_1(1 - p(t))$. Panel (C) occurs proportional to the number of inflorescence meristems

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442 at a rate β_2.

The goal of this optimization problem is to maximize F. The variable in the model is T, the length of the season. The model is described by the following system of differential equations:

$$\dot{P} = 2\beta_1 p(t)P - \beta_1 p(t)P - (1 - p(t))\beta_1 P$$
$$\dot{V} = \beta_1 p(t)P + (1 - p(t))\beta_1 P$$
$$\dot{I} = \beta_1(1 - p(t))P$$
$$\dot{F} = \beta_1(1 - p(t))P + \beta_2 I \tag{1}$$

subject to

$$0 \leq p(t) \leq 1$$
$$0 < P$$
$$0 \leq I$$
$$0 \leq F \tag{2}$$

443 The equation $\dot{P} = 2\beta_1 p(t)P - \beta_1 p(t)P - (1 - p(t))\beta_1 P$ describes how primary meristems
444 that divide into two primary meristems add to the pool P in proportion to size of the pool
445 of primary meristems. These divisions also add to the vegetative meristem pool V. The
446 process here is that a primary meristem unit becomes a vegetative meristem, and gives rise
447 to two new primary meristems. Primary meristems are lost from the primary meristem pool
448 when divisions give rise to inflorescence and floral meristems.
449 The equation $\beta_1 p(t)P + (1 - p(t))\beta_1 P$ describes the dynamics of the vegetative meristems.
450 Primary meristems contribute to the vegetative pool when primary meristems propagate.
451 The transition from primary to vegetative meristems is a proper flow. Primary meristems
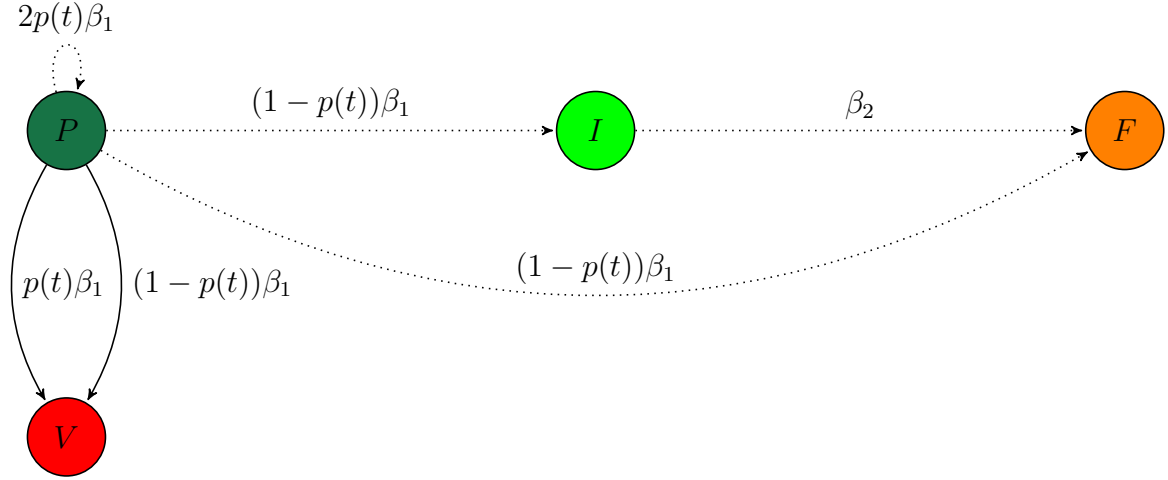
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Figure 3: State diagram describing the dynamics for plants with determinate inflorescences.

also contribute to the vegetative pool when primary meristems divide into inflorescence and floral meristems. This is also a flow.

The equation $\dot{I} = \beta_1(1 - p(t))P$ describes the dynamics of the inflorescence meristems. Primary meristems contribute to inflorescence meristems when they; this happens with probability $1 - p(t)$ and proportional to the primary meristem pool P.

The equation $\dot{F} = \beta_1(1 - p(t))P + \beta_2 I$ describes the dynamics of the floral meristems. Primary meristems contribute to floral meristems with probability $1 - p(t)$ and proportional to the primary meristem pool P. Inflorescence divisions also contribute to floral meristems and occur proportional to the size of the inflorescence meristem pool.

4.1   Model description

Qualitatively, this model describes the accumulation of primary meristems through division at the shoot apical meristem (SAM). Without further modification to the model, all primary meristems have active SAMs (can produce further primary meristems through division). Primary meristems that are converted to inflorescence meristems or floral meristems can not revert to primary meristems. Inflorescence meristems divide and produce inflorescence

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and floral meristems, but can not produce more vegetative axillary meristems. For values of $p(t) = 0$, plants produce vegetative, inflorescence, and floral meristems in proportion to the available primary meristem pool.

There are two rates in the model: the rate of primary meristem division and the rate of inflorescence meristem division. High rates of primary meristem division (β_1) correspond to morphologies with short internodes (e.g. rosettes) or high levels of branching. Low rates of primary meristem division correspond to morphologies with long internodes and low levels of branching. High rates of inflorescence meristem division (β_2) correspond to tightly packed inflorescences. Low rates of inflorescence meristem division correspond to spaced floral meristems.

In this model, committing a primary meristem to flowering consumes the branch. The process produces a terminal flower and inflorescence meristem; this structure can be iterated but can't revert to producing primary meristems. This should show up in the model because the decision for total asymmetric branching ($p(t) = 0$) will convert primary meristems to inflorescence and floral meristems. This means that once all meristems are committed to flowering, the only way in which reproductive biomass (i.e. floral meristems) will get added is by division of the inflorescence meristems.

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4.2   Equations

The optimal control problem we are interested in is

$$\max_{u} \int_0^T \log(F(t))dt$$

$$\text{subject to } \dot{P} = 2\beta_1 p(t)P - \beta_1 p(t)P - (1 - p(t))\beta_1 P$$

$$\dot{V} = \beta_1 p(t)P + (1 - p(t))\beta_1 P$$

$$\dot{I} = \beta_1(1 - p(t))P$$

$$\dot{F} = \beta_1(1 - p(t))P + \beta_2 I$$

$$0 < P, \ 0 \le V, \ 0 \le I, \ 0 \le F,$$

$$0 \le p(t) \le 1, \ 0 \le q(t) \le 1.$$

If we set β_1, β_2 to be functions of vegetative biomass, we write the system of equations:

$$\dot{P} = 2[q(t)V]p(t)P - [q(t)V]p(t)P - (1 - p(t))[q(t)V]P$$

$$\dot{V} = [q(t)V]p(t)P + (1 - p(t))[q(t)V]P$$

$$\dot{I} = [q(t)V](1 - p(t))P$$

$$\dot{F} = [q(t)V](1 - p(t))P + [1 - q(t)]VI \tag{3}$$

The Hamiltonian here is:

$$H = \log(F) + \boldsymbol{\lambda}^T[P \ V \ I \ F] \tag{4}$$

$$= \log(F) + (PV(2\lambda_1 - \lambda_3 - \lambda_4)\,p + (P - I)\,V\lambda_4 + PV(\lambda_3 + \lambda_2 - \lambda_1))\,q + IV\lambda_4 \tag{5}$$

If season length is uniformly distributed over, season length factors out of the objective function. The objective function is independent of the control . For this problem, the

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optimality condition is

$$\frac{\partial H}{\partial p} = PV(2\lambda_1 - \lambda_3 - \lambda_4)q = 0 \text{ at } u^*$$

$$\frac{\partial H}{\partial q} = PV(2\lambda_1 - \lambda_3 - \lambda_4)p + (P - I)V\lambda_4 + PV(\lambda_3 + \lambda_2 - \lambda_1) = 0 \text{ at } u^*. \tag{6}$$

The transversality condition is

$$\lambda_1(T) = \lambda_2(T) = \lambda_3(T) = \lambda_4(T) = 0. \tag{7}$$

The adjoint equations are

$$-\frac{\partial H}{\partial P} = \dot{\lambda}_1 = -(V(2\lambda_1 - \lambda_3 - \lambda_4)p + V(\lambda_4 + \lambda_3 + \lambda_2 - \lambda_1))q$$

$$-\frac{\partial H}{\partial V} = \dot{\lambda}_2 = -(P(2\lambda_1 - \lambda_3 - \lambda_4)p + (P - I)\lambda_4 + P(\lambda_3 + \lambda_2 - \lambda_1))q - I\lambda_4$$

$$-\frac{\partial H}{\partial I} = \dot{\lambda}_3 = V\lambda_4 q - V\lambda_4$$

$$-\frac{\partial H}{\partial F} = \dot{\lambda}_4 = -\frac{1}{F} \tag{8}$$

5   Indeterminate inflorescences

In plants with indeterminate inflorescences, the inflorescence meristem only produces flowers at axillary positions. For example, in *Arabidopsis* the primary shoot meristem converts to an inflorescence meristem that bears floral meristems in axillary positions Bradley et al. (1997).

I describe the developmental decisions in a plant with indeterminate inflorescences using four types of divisions ((Figure **??**). First, a primary meristem can divide at the shoot apical meristem to give rise to two primary meristems: the main branch and an axillary bud. These divisions lead to a vegetative, branching architecture. Second, a primary meristem can divide at the shoot apical meristem to give rise to a primary meristem and an inflorescence meristem:

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a branch and an inflorescence. These divisions produce either (1) an axillary inflorescence or (2) an inflorescence along the main branch and a vegetative, primary meristem that can continue branching. Third, a primary meristem can divide at the shoot apical meristem to give rise to two inflorescence meristems. Fourth, an inflorescence meristem can divide to give rise to an inflorescence meristem and a floral meristem. Inflorescence meristems have a single fate: they produce a branch with floral meristems in axillary positions.

(a) Primary meristem transitioning to one vegetative meristem and generating two primary meristems.

(b) Primary meristem transitioning to one vegetative meristem and generating primary and inflorescence meristems.

(c) Primary meristem transitioning to one vegetative meristem and generating inflorescence meristems.

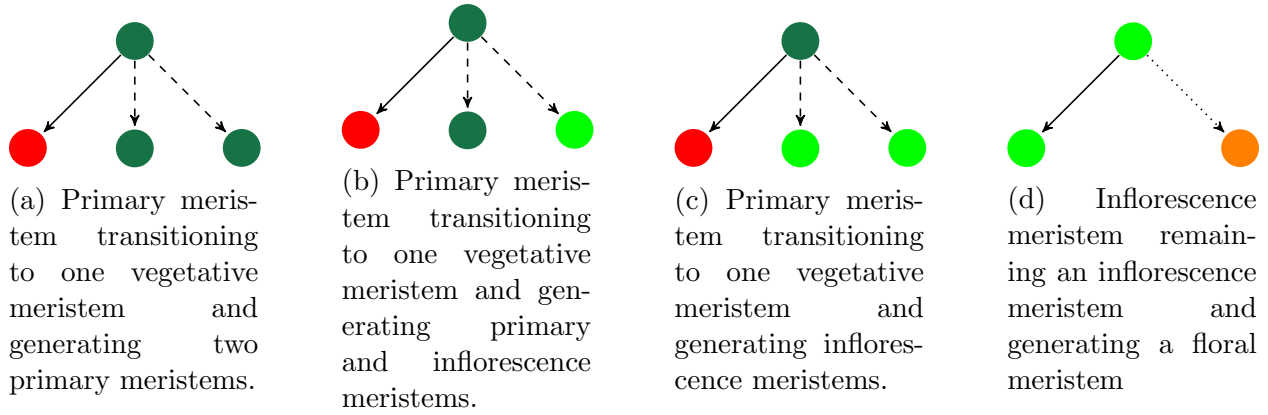(d) Inflorescence meristem remaining an inflorescence meristem and generating a floral meristem

Figure 4: Meristem transitions in plants with indeterminate inflorescences.

I use these types of divisions/transitions to summarize the meristem dynamics for plants with indeterminate inflorescences in a system of equations with constraints (Equation 13 and 15) and a state diagram (Figure 5). In this model, P, V, I, and F are the populations of primary, vegetative, inflorescence, and floral meristems, respectively.

5.1 Description of diagram

The division shown in Figure ??A occurs at rate $\beta_1 p(t)$. The rate is the product of β_1, the ..., and $p(t)$, the probability with which the division shown in Figure ??A occurs. It results in the net gain of one primary meristem and gain of one vegetative meristem. The differential

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equations corresponding to this are:

$$\dot{P} = 2\beta_1 p(t)P - \beta_1 p(t)P = \beta_1 p(t)P$$

$$\dot{V} = \beta_1 p(t)P$$

$$\dot{I} = 0$$

$$\dot{F} = 0 \tag{9}$$

The division shown in Figure **??**B occurs at a rate $\beta_1 q(t)$. The rate is the product of β_1, the ..., and $q(t)$, the probability with which the division shown in Figure **??**B occurs. It results in the gain of one vegetative meristem and the gain of one inflorescence meristem. The differential equations corresponding to this are:

$$\dot{P} = 0$$

$$\dot{V} = \beta_1 q(t)P$$

$$\dot{I} = \beta_1 q(t)P$$

$$\dot{F} = 0 \tag{10}$$

The division shown in Figure **??**C occurs at a rate $\beta_1 r(t)$. The rate is the product of β_1, the ..., and $r(t)$, the probability with which the division shown in Figure **??**C occurs. It results in the net gain of two inflorescence meristems, gain of one vegetative meristem, and

the loss of one primary meristem. The differential equations corresponding to this are:

$$\dot{P} = -\beta_1 r(t) P$$

$$\dot{V} = \beta_1 r(t) P$$

$$\dot{I} = 2\beta_1 r(t) P$$

$$\dot{F} = 0 \tag{11}$$

The division shown in Figure ??D occurs at a rate β_2. It results in the net gain of one floral meristem. The differential equations corresponding to this are:

$$\dot{P} = 0$$

$$\dot{V} = 0$$

$$\dot{I} = 0$$

$$\dot{F} = \beta_2 I \tag{12}$$

The full system of differential equations for the system thus becomes:

$$\dot{P} = \beta_1(p(t) - r(t)) P$$

$$\dot{V} = \beta_1(p(t) + q(t) + r(t)) P$$

$$\dot{I} = \beta_1(q(t) + 2r(t))$$

$$\dot{F} = \beta_2 I \tag{13}$$

I assume that

$$p(t) + q(t) + r(t) \leq 1 \tag{14}$$

505 Because they are probabilities, the controls $p(t)$, $q(t)$, and $r(t)$ are constrained on $[0, 1]$. The

506 difference between controls (e.g. $p(t) - r(t)$) is not constrained and can be negative. For

507 example, when the probability of division into two inflorescence meristems is greater than

508 the probability of division into two primary meristems, the value of $\dot{P} < 0$ and corresponds

509 to a decrease in the size of the primary meristem pool. If all primary meristem divisions are

510 like in Panel A, $\dot{I} = 0$. If $p + q + r < 1$ at any point, than it's beneficial to increase p.

The goal of this optimization problem is to maximize F. The variable in the model is T, the length of the season. The model is described by the system of differential equations above 13 and subject to

$$0 \leq p(t) \leq 1, \ 0 \leq q(t) \leq 1, \ 0 \leq r(t) \leq 1,$$
$$0 < P, \ 0 \leq V, \ 0 \leq I, \ 0 \leq F \tag{15}$$

511 I also tried to summarize the dynamics in a state diagram:

512 The equation $\dot{P} = \beta_1(p(t) - q(t))P$ describes how primary meristems that divide into

513 two primary meristems add to the pool P, and primary meristems that divide into two

514 inflorescence meristems subtract from the pool P.

515 The equation $\dot{I} = \beta_1(1 - p(t) - q(t))P + 2\beta_1 q(t)P + \beta_2 I$ describes how primary meristems

516 contribute to inflorescence meristems when they divide asymmetrically (i.e. do not divide

517 into two primary meristems or into two inflorescence meristems); this happens with proba-

518 bility $1 - p(t) - q(t)$ and when they divide into two inflorescence meristems with probability

519 $q(t)$. Because the primary meristem divides into two inflorescence meristems, the value is

520 doubled in the equation. Finally, inflorescence divisions occur proportional to the size of the

521 inflorescence meristem pool.

522 The equation $\dot{F} = \beta_2 I$ describes how inflorescence meristems divide proportional to the

523 size of the inflorescence meristem pool. Each division produces a floral meristem.
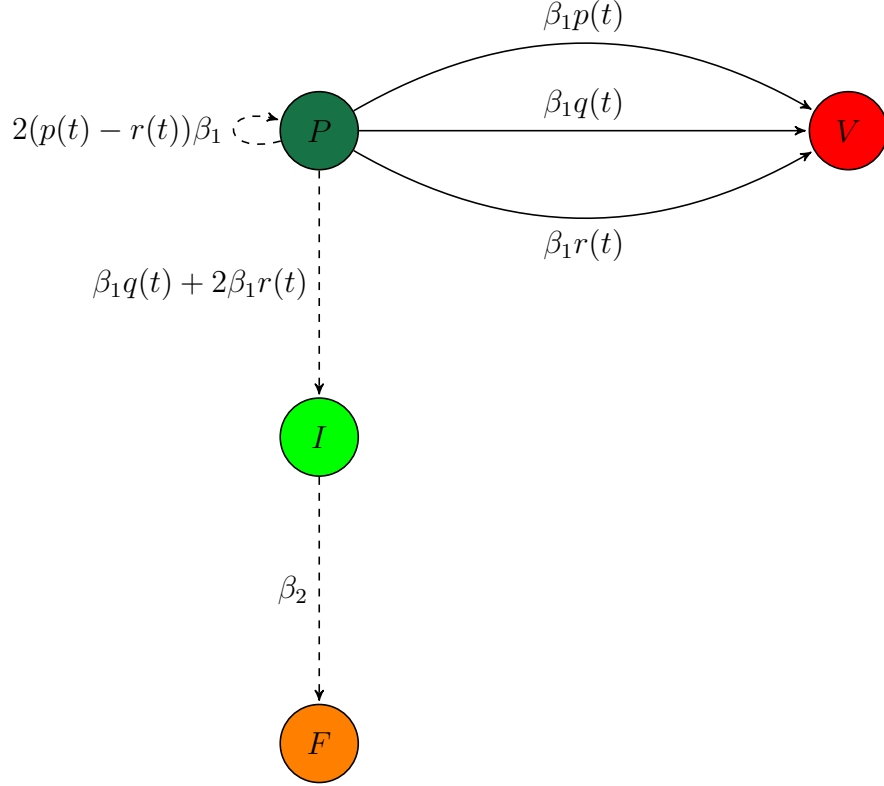
Figure 5: State diagram describing the dynamics for plants with indeterminate inflorescences.

5.2   Model description - NEED TO UPDATE

Qualitatively, this model describes the accumulation of primary meristems through division at the shoot apical meristem. Without further modification to the model, all primary meristems have active SAMs (can produce further primary meristems through division). Primary meristems that are converted to inflorescence meristems can not be reverted to primary meristems. These inflorescence meristems can divide and produce floral meristems but can not produce more axillary meristems with the potential to produce more inflorescence meristems. For values of $p(t) = q(t) = 0$, plants produce both primary and inflorescence meristems.

There are two rates in the model: the rate of primary meristem division and the rate of inflorescence meristem division. High rates of primary meristem division (β_1) correspond

to morphologies with short internodes (e.g. rosettes) or high levels of branching. Low rates of primary meristem division correspond to morphologies with long internodes and low levels of branching. High rates of inflorescence meristem division (β_2) correspond to tightly packed inflorescences. Low rates of inflorescence meristem division correspond to spaced inflorescences.

Another point that I need to elaborate on is how vegetative pools and meristem pools are related. See Korner 2015 for one opinion, as well as Fatichi for a complementary view. Some way of modeling this as source/sink dynamics (cf. Neubert?)

5.3 Optimal control problem and goals

5.4 Analysis of optimal control problem

5.5 Numerical algorithm

6 Results

6.1 Optimal strategies

I will use the models to determine whether including differentiation and growth of meristems reduces the likelihood of obtaining a strategy with an instantaneous switch Cohen (1971). Put another way, are graded allocation strategies optimal when vegetative and reproductive growth are coupled Fox (1992a)?

6.2 Development patterns

I will ask when plants are more likely to be resource versus meristem limited depending on their relative propensity for branching and resource use efficiencies. Specifically, I will focus on how the optimal strategy changes as the probability of branching and resource use efficiency varies jointly.
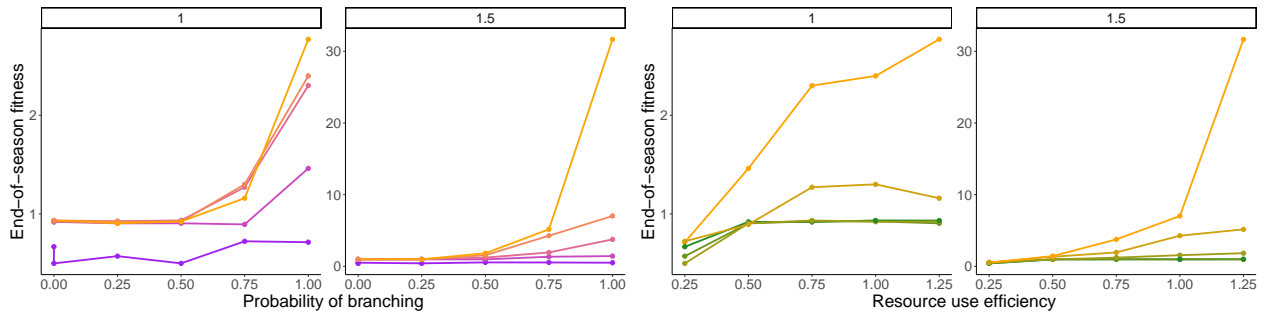

Steve and I have discussed that the degree of resource or meristem limitation would be best analyzed in terms of sensitivities, rather than the end-of-season fitnesses I have presented above.

6.3 Environmental variation

I will ask when plants are more likely to be resource versus meristem limited. Specifically, I will focus on how the optimal strategy changes with environmental variation; are plants likely to be meristem limited in scenarios with high levels of uncertainty about season length as a result of selection for the ability to capitalize on longer, if infrequent, seasons?

In resource-only models (e.g. King and Roughgarden (1982a)), increasing variation in season length increases the proportion of the season in which the singular, graded control is optimal.
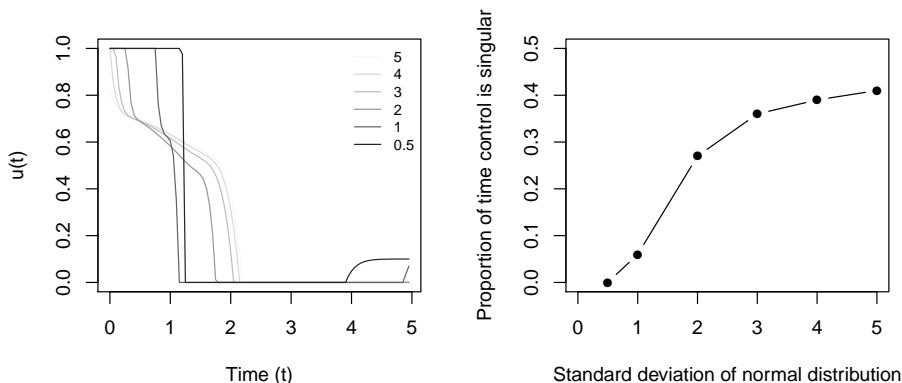
Below, I've included a plot of how end of-season fitness changes as a function of season length under a uniform distribution of season lengths for varying probabilities of branching.
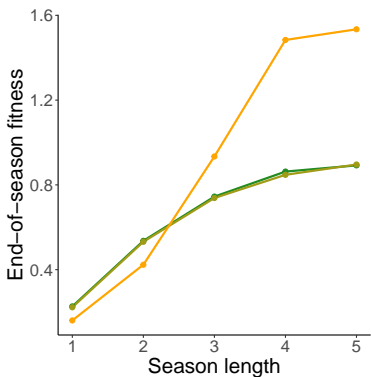
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Supplementary material

Background for hypotheses.

Explanation of key papers that motivate the hypotheses in this manuscript. The document describes results from these papers that are relevant to understanding and interpreting the data in this manuscript. Link to document: . . .

Numerical methods.

Description of numerical methods used to solve the optimal control problems. Includes outline of algorithm and code for a generic version of the optimal control problem. Link to document: . . .

Resource allocation model.

Explanation of models representing plant life history as a resource allocation problem, and analysis of how these models connect to the ones presented in this manuscript. Link to document: . . .

Analysis of optimal control problem.

Presents an analysis of the optimal control problem. Link to document: . . .