# **Hypotheses for Chapter 2**

Below, I describe a number of hypotheses about the relationship between resource and meristem limitation, and how these are likely to be modified by developmental program, inflorescence form, branching, and environmental variation. I am interested in the following axes of variation:

* Developmental form: Plants range from indeterminate to determinate growth. In plants with a determinate growth form, the apical meristem terminates in an inflorescence. In plants with indeterminate growth form, the axillary meristems can produce inflorescences.
* Inflorescence form: Plants have a wide array of inflorescence forms but I will contrast plants with a single flower with inflorescence (racemes, cymes). I choose this particular comparison because it places inflorescence form on a continuum from a single floral structure to a floral structure with multiple, reiterated floral structures that develop over time.
* Branching: Plants are modular and the reiteration of each metamer generates a leaf and axillary meristem. The axillary meristem can remain quiescent, branch, or flower. Variation in the dynamics of axillary meristems contributes to the diversity of plant architectures. I focus on contrasting plants without the capacity for branching with plants capable of branching. This again creates a continuum.
* Environmental variation: There are many axes to environmental variation. Literature suggests two are particularly relevant to the relationship of vegetative and reproductive allocation: resource availability and season length/variability in season length/predictability.

## Development and inflorescence patterns

1. To what extent does plant developmental pattern control the expression of life history strategies and reproductive schedules? For plants with determinate growth, the initiation of flowering along a branch terminates vegetative growth. We predict that plants with determinate growth will delay flowering and deploy branches to increase fitness under long seasons and high resources. Flowering will track changes in season length to guarantee reproduction before the end of the season. Because early flowering will reduce the number of axillary branches allocated to growth, we expect this will also reduce the net reproductive output.

How does development structure life history?

For a given developmental pattern, under some axis of environment variation [season length, resource availability], what’s the optimal reproductive schedule/switch for that developmental pattern?

For a given environment, what is the optimal developmental program? The last set of questions are the most interesting [Monica]; reason is that I’m explicitly building a life history model that includes development in it. We’re often interested in what’s the optimal life history strategy, and that depends on the environment. But if I’m including development the question becomes what’s the optimum pattern of development for a given environment. Are patterns equivalent?

1. Plants with determinate growth will flower early and at small sizes in unpredictable environments; branching from axillary meristems will increase fitness in long seasons. For plants with indeterminate growth, flowers in axillary positions do not terminate vegetative growth along an axis. Plants can continue to switch between producing leaves or flowers. However, the production of a flower comes at the cost of producing a branch capable. Early flowering will directly reduce the number of vegetative branches produced by a plant, but guarantee reproduction in environments with unpredictable season length. Plants with indeterminate growth will also flower early and at small sizes in unpredictable environments; however, both flowering and branching at axillary positions can increase fitness in long seasons. [e.g. **Watson 1984, Geber 1990, Shemesh and Novoplansky 2012**]
2. Does the morphology of reproductive structures modify life history strategies and flowering schedules? We expect that reproductive structures in which flowers are produced sequentially (e.g. racemes or cymes) provide plants with flexibility in how many flowers they produce per reproductive meristem relative to plants with a single flower per inflorescence. All else being equal, the ability to modify reproduction by regulating flower production on an inflorescence will limit the fitness benefit of additional branches. Broadly, we expect that the association between developmental pattern, season length, and life history strategy is modified by the inflorescence pattern. Specifically, we predict that determinate growth and single flowers will favor a delay in flowering and plastic growth strategies that can take advantage of good conditions and increase reproductive output via branching. Determinate growth and racemes will make it possible for plants to flower and adjust reproductive output by modifying the number of flowers on an inflorescence via continued allocation to reproduction (corresponding to plasticity at the level of inflorescences). Regardless of inflorescence pattern, we expect that indeterminate growth will favor a strategy in which flowering starts early and flowers along branches throughout the lifespan of the plant (corresponding to a bet hedging strategy). [e.g. Stebbins 1974, Wyatt 1982, Bonser and Aarssen 2006, Prusinkiewicz et al. 2007, Shemesh and Novoplansky 2012]

## Environmental variation

1. How do season length and predictability affect the optimal branching strategy? We expect that both season length and predictability will modify the optimal life history strategy. For example, we predict that longer seasons favor branching plants that are able to produce more branches that support more flowers will have higher fitness than plants that have fewer branches (all else being equal). When season length is predictable (regardless of length), plants will be able to time their development to match flowering and resource allocation to reproduction. However, when conditions change between meristem development and flowering, retaining meristems will become important: either those meristems will be unused in a short season (a cost) or will be available for development in a long season (a benefit). We expect that developmental patterns will shape how plants respond to increasing unpredictability in season length.. [e.g. **Geber 1990**, **van Tienderen et al. 1996**].
2. How do resource availability and season length interact to shape the optimal strategy? We expect that resource availability modifies whether flowering delays are beneficial in longer seasons. With low resource availability (low growth rates), we expect that early flowering does not impose a cost: the fitness of plants flowering early and late may be similar because low resources may not support many additional meristems. As resource availability increases, we expect that early flowering will be costly because it misses out on the opportunity to deploy axillary meristems and produce more flowers in long seasons. Specifically, this cost will manifest in terms of not having sufficient meristems to produce axillary branches. We expect that this effect will be strongest for plants with determinate growth patterns. [e.g. **van Tienderen et al. 1996, Bonser and Aarssen 2006**]

## Resource allocation and acquisition

1. Does flowering time regulate resource allocation independently of resource acquisition? In plants, flowering time has at times been conceptualized as a trait that modifies resource allocation independently of acquisition (e.g. **Cohen 1971,** **Van** **Noordwijk and de Jong 1986, Mitchell-Olds 1992a,b**). But the onset of flowering likely modifies not only where resources are allocated but also patterns of resource acquisition: flowering at lower nodes reduces the total number of meristems available for vegetative growth as well as the the number of meristems available for continued vegetative growth. We expect that this relationship varies across growth forms (determinate, indeterminate) and inflorescence types (single flower, inflorescence). Specifically, we predict that flowering time controls resource allocation independently of acquisition in unbranched, determinate growing plants. In these cases, flowering controls allocation by switching from vegetative to reproductive growth. We expect that developmental patterns modify this prediction. Especially early in life, patterns of axillary meristem development determine potential vegetative and reproductive growth. These allocation patterns may contribute to resource acquisition independent of flowering time. These differences will likely be most evident in branched plants with indeterminate growth.

## Patterns of selection – drop this section

1. Does selection on flowering time reflect direct selection on flowering time, or direct selection on branching and indirect selection on flowering time? To ask about selection on the traits in our models, we can follow Schaffer et al. 1982 and Fox 1992; they solved for optimal strategies and then compared how fitness changed with suboptimal strategies. They interpret the sensitivity of fitness to changes in the strategy as corresponding to the expected strength of selection on the trait in question. We are specifically interested in understanding how changes in flowering time versus branching affect fitness. We might jointly vary flowering time and branching to ask how departures from optimum flowering time or branching affect fitness, and consequently how strong selection on either trait would be. Two examples of questions we could ask are the following:
   1. Is selection for early flowering likely to be the result of direct selection on flowering time, or the outcome direct selection on branching and indirect, correlated selection on flowering time? (e.g. **Taylor et al. 2019**)
   2. Does selection act on different components in plants with determinate versus indeterminate growth forms? **Torstensson and Telenius 1986** propose that in plants with indeterminate growth where axillary shoots can produce flowers or shoots, selection can act on the balance of meristems producing shoots or flowers. They propose that in plants with determinate growth where apical and axillary meristems have distinct functions, selection acts on the time of reproduction and rate of shoot formation. We predict that if compare suboptimal fitness strategies in determinate versus indeterminate growth patterns, the former will have steep paths through timing of reproduction and the latter will have steep paths through the relative rates shoot and flower production.