**Notes on terminology for state variables.**

I have been using the following terms in my model: (P) primary meristem, (V) vegetative biomass, (I) inflorescence meristem, (F) floral meristem. I’ve looked back through notes as I was developing the model structure to determine how I developed those categories. My intention was to use the processes with which plant developmental biologists describe plant meristem dynamics to construct the plant architectures that are described by evolutionary ecologists.

I use the term primary meristem to identify the tissue that produces the axes of plant growth. The term is synonymous with primary shoot meristem, or primary shoot apical meristem. The primary shoot apical meristem (SAM) is an embryonic tissue that establishes the primary axis of plant growth. The primary SAM produces leaf primordia with secondary meristems in their axils. Divisions of the primary SAM generate metamers consisting of a node, internode, leaf, and axillary meristem. Axillary meristems are secondary meristems, as they originate from within the embryonic primary meristem. There are two hypotheses about axillary meristem formation—the cells in the axillary meristem might directly consist of cells from the primary shoot am, or the cells in the axillary meristem might reacquire the ability to function as a shoot apical meristem. In either case, the if the axillary meristems are activated they are (for our purposes) functionally equivalent to shoot apical meristems during branching. I thus use primary meristem to label the state variable describing the meristem pool that produces the axes of plant growth and generates metamers.

I use the term vegetative biomass to identify leaves. To understand why I separate this from primary meristems, consider the example of an unbranched plant. For an unbranched plant, a primary meristem division generates one copy of itself and an axillary meristem that remains dormant. In essence, the number of primary meristems remains constant at one throughout the life of the plant. However, the number of leaves grows – each primary meristem division adds a new leaf. So I include a vegetative biomass pool that is separate from the primary meristem pool.

I use the term inflorescence meristem to identify the tissue that is competent to flower. Primary meristems transition to inflorescence meristems before producing flowers. If the plant we are interested in has a determinate inflorescence, the inflorescence meristem produces a floral meristem once it divides. If the plant we are interested in has an indeterminate inflorescence, the inflorescence meristem produces an inflorescence meristem on the main axis and a floral meristem (i.e. a flower) in an axillary position.

I use the term floral meristem to identify flowers. Flowers are produced from inflorescence meristem; even if a plant produces only a single flower on the its primary axis of growth, the primary meristem transitions to an inflorescence meristem before producing a floral meristem.

**Changes.**

Our meeting this week and rereading my notes helps me understand how my choice of language confuses the issues. I think I can keep the same model structure but change the words to better correspond to existing literature. I will describe how the primary and secondary meristems generate the vegetative plant body plan, and then collectively refer to the primary shoot apical meristem and secondary axillary meristems as **vegetative meristems** (formerly primary meristems). To distinguish this from the pool of ‘vegetative biomass’ that I use above, I will use **leaves** (formerly vegetative biomass) to refer to the photosynthetic structures produced by vegetative meristem divisions. I will keep the term **inflorescence meristem** and use **flowers** (formerly floral meristems). This would separate parts of the model that can divide to produce more of themselves (vegetative and inflorescence meristems) from parts of the model that can’t (leaves and flowers).

**Model.**

We want to maximize the objective function

Which means we are looking for the controls that maximize the expected fitness of log(F(t)) when the end of season is uniformly distributed between the time T/2 and T. We follow King and Roughgarden (1982) in using the log of reproduction as our fitness criterion because we are also interested in determining the optimal strategy under variation about the end of the season.

The dynamics of the vegetative meristems (V), the leaves (L), the inflorescence meristems (I), and the flowers (F) are subject to the following differential equations:

The parameter controls the proportion of meristem divisions that generate branches. If , the plant has an unbranched architecture; if the plant has an architecture in which each division produces a branch in an axillary position.

The initial conditions are

We impose the meristem constraints as

We impose the resource constraint as

Finally, there is a constraint on the control *u*,

**Parameter interpretation.**

**Time derivative of leaf number.**

The time derivative of leaf number (*d*L/d*t*) is in units of leaves/day. I’ve found a few studies of leaf production (leaf birth, leaf death, leaf longevity, leaf lifespan) that measure related quantities. For example, Mendez-Vigo et al. (2010) studied the “rate of leaf production” (leaves/day) in *Arabidopsis* and Ackerly et al. (1992) studied the “leaf initiation rate” in two annual plant species.

**Per-capita rate of division by vegetative meristems.**

The per-capita rate of division by vegetative meristems is in units of meristems/(meristem\*day). Following from the description above, the per-capita rate of division by vegetative meristems should be directly related to the rate of leaf initiation. To see this,

The units on the above are

There’s something missing to convert the right-hand side to the units on the left-hand side. I think this is handled by making explicit that each meristem, upon dividing, has a leaf associated with

**Conversion rate of standing biomass.**

The conversion rate of standing biomass has the following interpretation. The product of alpha and leaf number should be equal to the product of the per-capita rate of meristem division, meristem number, and a conversion factor of 1 leaf/meristem.

The resource constraint is written as

For the moment, I focus on the case where there are not yet any inflorescence meristems (I=0). The equation then reduces to

Focusing on the units of the equation, this is

The term alpha, the conversion rate of standing biomass, thus needs to convert between the total leaf number and meristem divisions. If we introduce an additional term on the left hand side of the equation to remind ourselves that each meristem will carry a single leaf, the equation is

The left hand side of the equation then is in units of leaves/day. The term alpha must equate the number of leaves to the rate of leaf production. Following Ackerly (1998), one way to establish this relationship might be to take alpha as the mean net assimilation rate of leaves over the cost of leaf construction. The net assimilation rate of leaves is

The cost of leaf construction is

The term alpha might then be a rate, as shown below

When multiplied by the number of leaves, this is then in the same units (leaves/day), as the left hand side of the equation describing the resource constraint (Equation 1.1). The interpretation is that the left-hand side describes the production of new meristems (and associated leaves) in by multiplying the per-capita rate of meristem production, , and the available vegetative meristems, V. The right-hand side describes the production of new leaves (and associated meristems) in terms of the conversion rate, , and the available leaves, L.

The conversion rate describes how much of the carbon cost of a gram of leaf that each gram of leaf is able to pay (assimilate) per day. For , the net carbon assimilation of a gram of leaf per day is exactly equivalent to the carbon cost of producing a gram of leaf. For , the net carbon assimilation of a gram of leaf per day is less than the carbon cost of producing a gram of leaf, and for , it’s more than the cost.

**References for parameters.**

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| --- | --- | --- | --- | --- |
| **Parameter** | **Range of values** | **Species** | **Measurement** | **Reference** |
| rate of leaf production () | [0.3-1.4] leaves/day; 80 day “season” for a total of 60 leaves | *Arabidopsis* | Divide number of new leaf primordia over a time interval by number of days | Méndez-Vigo et al. 2010 |
| Leaf initiation rate () | [0.25-1.2] leaves/day | *Abutilon, Amaranthus* | Slope of linear regression of plastochron index on time | Ackerly et al. 1992 |
| Net assimilation rate (part of ) | [-0.2, 0.2] g dry mass/(g leaf day) | *Xanthium* | Dry mass of harvested plants | Shitaka and Hirose 1998 |
| Net assimilation rate (part of ) | [0, 0.15] g dry mass/(g leaf day) | *Xanthium* | Dry mass of harvested plants | Shitaka and Hirose 1993 |

If my interpretation of the parameter for rate of leaf production makes sense, I think it should also be related to the plastochron rate along an axis.