1 Optimal Control Models

[1] Dan Cohen. 1971. Maximizing final yield when growth is limited by time or by limiting resources. *Journal of Theoretical Biology*, 33(2):299–307. tex.isbn: 0022-5193 tex.mendeley-tags: optimal control.

> This paper spells out that you expect selecting for mean yield (arithmetic mean) and a constant environment produce the same effect: you would expect bang bang reproduction. Is there any data on maize/teosinte flowering phenology that I could use for a comparison?

[2] Dan Cohen. 1976. The optimal timing of reproduction. *The American Naturalist*, 110(975):801–807.

> Lindh 2015 summarize this paper as follows: Cohen (1976) showed that with constrained growth, the optimal allocation is to first put all resources to vegetative growth, and at some time switch to put all resources into reproduction until the end of the season. When survival was described instead by a decreasing function, Cohen (1976) also found a bang-bang control; we give an alternative proof of bang-bang control with exponentially decreasing survival corresponding to constant mortality in Methods S1.

[3] David King and Jonathan Roughgarden. 1982. Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length. *Theoretical Population Biology*, 22(1):1–16. tex.isbn: Alphabetical tex.mendeley-tags: optimal control.

> from Johansson 2013: King & Roughgarden (1982a) showed for example that continuing resource allocation after onset of reproduction is optimal when the season length varies between years due to stochastic fluctuations. Similar to our model, the optimal timing of onset of the final, full reproductive stage in their model increases with season length both on a relative and an absolute time scale.

[4] David King and Jonathan Roughgarden. 1982. Vegetative multiple switches between and reproductive growth in annual. *Theoretical Population Biology*, 21:194–204. tex.mendeley-tags: optimal control.

> Optimal control model that shows how multiple switches between vegetative and reproductive growth can be the best strategy. For example, vegetative losses can lead to multiple switches in the model. In the paper, they tag and follow individuals of Plantago and Clarkia. They find that almost all the plants follow a graded control rather than instantaneous switch. They also find that the length of graded control is negatively correlated with start of flowering: plants that flower later show less overlap of vegetative/reproductive growth. The observed mean control is suboptimal (vs. instantaneous switch) while the timing of switch seems optimal. They also explore regarding some of the reproductive biomass as vegetative to capture the potential effect of photosynthesis in flowers. Here are some of their hypotheses for why there is a gradual switch to reproduction: metabolic source-sink relationships (i.e. carbon is allocated in proportion to organ size and floral organs grow with time), selection from unpredictable season lengths, light competition.

[5] David King and Jonathan Roughgarden. 1983. Energy allocation patterns of the california grassland annuals plantago erecta and clarkia rubicunda author. *Ecology*, 64(1):16–24.

> The introduction states that few studies have assessed whether annual plants follow optimal allocation patterns, or tested whether the timing of switch to reproduction is optimal. The authors compare the results of theoretical models with empirical data. The authors describe the theory from their paper on multiple switches, specifying that their assumptions exclude shading by competitors. They describe how vegetative and reproductive losses due to senescence or herbivory are proportional to mass. The model results in an optimal strategy with switching. Austen and Weiss (NP review) recognize that the paper shows how under some conditions "the function relating the timing of a life-history event to fitness is expected to be asymmetric".

[6] Maxine A Watson. 1984. Developmental constraints: Effect on population growth and patterns of resource allocation in a clonal plant. *The American Naturalist*, 123(3):411–426. tex.mendeley-tags: empirical.

> Watson (1984) first proposed a meristem cost as distinct from a resource cost, by showing that the cost of reproductive structures could not account for difference in size between flowering clones and branching clones. This paper proposes that meristem allocation can determine patterns of reproductive allocation. In part, the study is motivated by research showing that vegetative and reproductive modules can 'pay their own [carbon] cost' through photosynthesis. In this study, Watson examines two populations of water hyacinth and assesses patterns of ramet production. She rules out the hypotheses that most carbon allocation takes place early during bud develoment, and that carbon is stored and used during inflorescence production. Instead, she suggests that development constrains resource allocation because meristems are differentiated prior to inflorescence development.

[7] Author D A Pyke. 1989. Limited resources and reproductive constraints in annuals. *Functional Ecology*, 3(2):221–228.

> Considers the role of morphological constraints in determinate and indeterminate reproductive growth. Pyke suggests structural and functional switches between reproductive and vegetative growth. For example, with 'reproductive shutdown', plants with determinate modules stop differentiating flowers while plants with indeterminate modules stop differentiating metamers that produce flowers from axillary meristems. With a 'reproductive-vegetative switch', plants with indeterminate growth can switch from producing reproductive to vegetative metamers while plants with determinate growth would continue to produce reproductive metamers but these would fail to develop (functional abortion).

[8] Monica A Geber. 1990. The cost of meristem limitation in polygonum arenastrum: Negative genetic correlations between fecundity and growth. *Evolution*, 44(4):799–819. tex.mendeley-tags: empirical.

> Study that suggests meristem limitation can generate trade-offs betwene life history traits. Early committment of meristems to reproduction favors high early fecundity but reduces the number of meristems available for later vegetative differentiation, which can later limit meristem availability and thus growth and reproduction. The opposite relationship also holds: early commitment to vegetative growth reduces early fecundity but can increase late growth and fecundity.

[9] G A Fox. 1992. Annual plant life histories and the paradigm of resource allocation. *Evolutionary Ecology*, 6:482–499. tex.mendeley-tags: optimal control.

> Fox describes how allocation models, both with and without assuming an optimal control, generally predict bang-bang control (equivalent to an instantaneous switch). Changing the assumption of these models can lead them to predict multiple switches of a graded control. However, Fox writes that instantaneous-switch allocation patterns are unlikely to occur in many plants. Fox notes Cohen's mention of how development/morphology should couple vegetative and reproductive growth. Three key levers identified by Fox as possibly useful in a model are differentiation of primordia (fast), determination of primordium fate (slow but with a threshold), and expansion of organs. Any of these could act as a 'control' in the control-theoretic sense. Fox suggests treating determination as a bang-bang control for simplification (citing Geber 1990 as an example with multiple switches). This idea intersects with those in Kellogg 2000 and Prusinkiewicz et al. 2007. Fox also suggests using allometric models as a temporary fix: he uses flowering time as a constraint on allometric relationships. He works through solving the optimal control problem and solves for the adjoints but concludes that this particular approach doesn't seem particularly promising (?) as it makes predictions such as that reproductive allocation will decline with time for particular parameters. Here's a nice statement "can we successfully address the interesting ecological and evolutionary questions associated with life history evolution by considering whole-plant resource budgets independently from the developmental rules of plants?" Key would be that a developmentally explicit model is concerned with the biological 'decisions' that affect the carbon budget, rather than the carbon budget itself.

[10] Johanna Schmitt. 1993. Reaction norms of morphological and life-history traits to light availability in impatiens capensis. *Evolution*, 47(6):1654–1668. tex.mendeley-tags: empirical.

> Early allocation of axillary meristems to flowering precludes primary branch formation and might limit later reproduction. Plants from woods population show no variation in branching. Plants from sun population reproduce later and allocate more axillary meristems to branches than flowers but this allocation depends on light availability. Contrast might be that in woods population all individuals receive low light (understory) but that in sun population some individdiduals are shaded out due to competition while others are able to reach the canopy. Plastic response of meristem allocation may thus be a way of adapting to "fine scale heterogeneity in the light environment" caused by neighbors.

[11] Susan A. Dudley and J Schmitt. 1995. Genetic differentiation in morphological responses to simulated foliage shade between populations of Impatiens capensis from open and woodland sites. *Functional Ecology*, 9(4):655–666. arXiv: arXiv:1011.1669v3 tex.arxivid: arXiv:1011.1669v3 tex.isbn: 9788578110796 tex.mendeley-tags: empirical.

> Early mortality selects for allocation to early flowering at expense of branch production. Low light reduces commitment of axillary meristems to branches.

[12] Kathleen Donohue, Dinan Messiqua, Elizabeth Hammond Pyle, M. Shane Heschel, and Johanna Schmitt. December 2000. Evidence of adaptive divergence in plasticity: Density- and site-dependent selection on shade-avoidance responses in Impatiens capensis. *Evolution*, 54(6):1956–1968. tex.mendeley-tags: empirical.

Attempts to infer whether plasticity in flowering time is adaptive. In the woodland site, plasticity in flowering time is maladaptive because there is constant early mortality. In the sun site, plasticity in flowering time is adaptive because variation in density (and associated cue for longevity) may select for plasticity.

[13] Yoh Iwasa. 2000. Dynamic optimization of plant growth. *Evolutionary Ecology Research*, 2(4):437–455. tex.isbn: 1522-0613 tex.mendeley-tags: optimal control.

Reviews study of growth and reproductive schedules by loooking at dynamic optimal allocation of material between organs. Provides summary of early work on optimal timing of switch to reproduction, shoot/root balance models, perennial plants, stochastic environments, and leaf age/chemical defenses. The optimal defense models are interest because they involve a leaf age structure. This may be useful for meristem age structure?

[14] Elizabeth A. Kellogg. A model of inflorescence development. In Katherine L. Wilson and David A. Morrison, editors, *Monocots: Systematics and Evolution*, pages 84–88. CSIRO Publishing, Collingwood, VIC, Australia, 2000.

Describes genetic regulation of meristem indeterminacy/determinacy and meristem fate. This is directly connected to Prusinkiewicz et al. 2007 by Whipple 2017, so I think it's important to cite this. There's a clear explanation of how the genetic mechanisms create iterated developmental patterns that are a template for an array of morphological outcomes. Also includes a verbal algorithm and relation to comparative study.

[15] Kyle W. Shertzer and Stephen P. Ellner. 2002. State-dependent energy allocation in variable environments: life history evolution of a rotifer. *Ecology*, 83(8):2181–2193. tex.mendeley-tags: dynamic energy budget,optimal control.

Reread 'energy allocaiton and life history' - difficult to understand without figures on hand? Steve notes that this may be more useful than the optimal control book he initially recommended that I read. The paper presents genetic algorithms as a possible solution to optimization for energy allocation problems. The alternative methods that they discuss in the paper are dynamic programming and Pontryagin's Maximum Prinicple. I think the latter gets used in the early papers by Cohen and King/Roughgarden. Also note that they are modeling a three way tradeoff, which is what Steve suggested a V/M/R problem would be.

[16] Harmony J Dalgleish and David C Hartnett. 2006. Below-ground bud banks increase along a precipitation gradient of the North American Great Plains: a test of the meristem limitation hypothesis. *New Phytologist*, 171:81–89. tex.mendeley-tags: empirical.

Study of bud banks in perennials. Suggests that bud banks may help plants respond to interannual variation in climate. For example, it suggests that temporal variability in productivity may be related to availability of belowground bud banks. Even with high interannual variability in precipitation (arid systems), absence of a belowground bud bank precludes plants from responding to variability. Intermediate rainfall sites have greater bud banks and are able to respond to that variability. Make connection of dormant pool of meristems to herbivory tolerance/regrowth after damage. Suggest that maintaining a reserve bud population is a bet hedging strategy for species in which it is costly to do so.

[17] Przemyslaw Prusinkiewicz, Yvette Erasmus, Brendan Lane, L. D. Harder, and Enrico Coen. June 2007. Evolution and development of inflorescence architectures. *Science*, 316(5830):1452–1456.

> Models of inflorescence architecture that try to explain diversity of form using various functions for 'vegetativeness'. The models are tested using Arabidopsis lines. Of particular interest is Figure 2 and the description in the Appendix, as well as calculation of how different inflorescence architectures are related to fitness.

[18] Monia S H Haselhorst, Christine E. Edwards, Matthew J. Rubin, and Cynthia Weinig. 2011. Genetic architecture of life history traits and environment-specific trade-offs. *Molecular Ecology*, 20(19):4042–4058. tex.isbn: 1365-294X tex.mendeley-tags: empirical.

> "Regardless of the exact mechanism, the range of expressed plant architectures may vary with reproductive timing and differ across seasonal natural or cultivated populations. It is noteworthy that delayed bolting was significantly or marginally associated with increased axillary branching in all environments." Meristem allocation decisions may produce additional life history tradeoffs.

[19] Jacob Johansson, Kjell Bolmgren, and Niclas Jonzn. 2013. Climate change and the optimal flowering time of annual plants in seasonal environments. *Global Change Biology*, 19(1):197–207. tex.isbn: 1365-2486 tex.mendeley-tags: optimal control.

> from Lindh 2015: Recently, Johansson et al. (2013) applied a [optimal control] model of this kind to predict how the optimal flowering time should respond to changes in seasonal growth conditions. An interesting finding of that study is that 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. energy allocation trade offs are key to interpreting phenological patterns optimal control models typically find the energy allocation schedule that maximizes reproductive output and make predictions that agree with allocation patterns from empirical studies not often applied to understanding variation in response of species shifts in phenology - we ask how plants should optimally change their timing of flowering in response to changes in the seasonal environment. parameters: seasonal production curves, start/end of growing season, peak production date, and temporal slope of production for unimodal production curve, slope of linear production curve, accumulated production emphasize: reproduction is subject to a time/size trade-off and that growth rate undergoes seasonal variation * authors note that comparison to model predictions may require closer inspection of factors affecting productivity (cf. Shitaka & Hirose 1993); productivity is also included in Schaffer 1977

[20] David L. Remington, Pivi H. Leinonen, Johanna Leppl, and Outi Savolainen. 2013. Complex genetic effects on early vegetative development shape resource allocation differences between Arabidopsis lyrata populations. *Genetics*, 195(3):1087–1102. tex.isbn: 1943-2631 (Electronic)\r0016-6731 (Linking) tex.mendeley-tags: empirical.

> Study with Arabidopsis lyrata looking at genetic basis of resource allocation. Consider 3 models: (1) variation in resource acquisition, (2) a switching mechanism, and (3) one where

vegetative development of axillary meristems precludes later reproductive development. Finds relevant QTLs to include ones that have an effect on early vegetative growth, with cascading effects on later vegetative growth and reproductive development. The results support model in which there is a negative relationship between prereproductive branching and the proportion of shoots developing reproductively (consistent with Baker & Diggle, Kim & Donohue). Resource allocation was largely independent of FT. Relative timing of vegetative vs. reproductive growth can have big impact.

[21] Emily Jane Austen. 2014. *The nature of selection on flowering time: Integrating fitness contributions through male and female function.* PhD thesis. tex.mendeley-tags: empirical.

Dissertation that includes Austen et al. 2015.

[22] Emily J. Austen and Arthur E. Weis. 2015. What drives selection on flowering time? An experimental manipulation of the inherent correlation between genotype and environment. *Evolution*, 69(8):2018–2033. tex.isbn: 1558-5646 (Electronic) 0014-3820 (Linking) tex.mendeley-tags: optimal control.

Experimental study that manipulates the correlation between age at flowering and date of flowering to separate the effects of age at flowering, size at flowering, and environment on fitness. Cites: - papers that model energy production rate as function of size: King & Roughgarden 1983, Ejsmond et al. 2010, Weis et al. 2014 - papers that model energy production rate as function of environment: Johansson et al. 2013 - papers that incorporate environmental variation by discounting the value of late season reproductive investment: Ejsmond et al. 2010 Optimal control models don't consider that modular nature of plant development can impose direct constraints on reproductive output. Experimental study looks at: indirect effect of age at flowering (AAF) through phenotype-environment covariance, by correlation with size/condition whereby condition affects the enviroment experienced during reproduction, and direct selection on age Direct selection on age could be the result of decreasing reproductive capacity with later AAF (decreasing branching probability of axial meristems with age). Propose using results of experiment to guide model development, and point Ejsmond et al. 2010. Relevant features include seasonality, productivity as a function of size, and temporarlly varying returns on reproductive investment.

[23] Jannice Friedman, Alex D. Twyford, John H. Willis, and Benjamin K. Blackman. 2015. The extent and genetic basis of phenotypic divergence in life history traits in Mimulus guttatus. *Molecular Ecology*, 24(1):111–122. tex.mendeley-tags: empirical.

Demonstrate that genetic trade-off for survival to flowering and fecundity is a consequence of difference among genotypes in transition from vegetative growth to flowering (across populations). For example, plants from populations that flower early produce few or no stolons compared to plants from populations that flower later. Identify QTLs with effect on stolon number and flowering time that suggest plants can not simultaneously produce many stolons and flower - they cite McSteen & Leyser to indicate that bud activation switches from bottom up to top down across at the floral transition. Genes that impact axillary meristem outgrowth and fate are expected to be key regulators of shoot architecture (eg. MAX3 homologues, FT/TLF1, gibberellins).

[24] Magnus Lindh, Jacob Johansson, Kjell Bolmgren, Niklas L.P. Lundstrm, ke Brnnstrm, and Niclas Jonzn. 2016. Constrained growth flips the direction of optimal phenological responses among annual plants. *New Phytologist*, 209(4):1591–1599. tex.mendeley-tags: optimal control.

> Unexplained variation in response of phenology to increased temperature - some species advance, stasis, or delay. Many optimal control models assume that plant growth is porportional to vegetative mass during growing season. But growth is often constrained (see Paine et al. 2012 on saturating nonlinear growth). Reasons given are: self shading, costs of structural tissue, decreasing local nutrient levels. Unconstrained growth example is algae in a chemostat with abundant resources. Reasons for constrained growth: allocation to nonphotosynthetic structural tissue to avoid self-shading, increase seed dispersal, display flowers to pollinators, competition from neighbors. Growth often related to metabolism "investigate how growth constraints affect optimal flowering time responses to changed environmental conditions" 3 different growth functions calendar & physiological time unconstrained vs. constrained growth flips response of optimal flowering time (delay vs. advance).

[25] Robert I. Colautti, Jon gren, and Jill T. Anderson. 2017. Phenological shifts of native and invasive species under climate change: Insights from the Boechera-Lythrum model. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1712). tex.isbn: 0034-6748 tex.mendeley-tags: optimal control.

> Boechera stricta and Lythrum salicaria exhibit opposite phenological shifts in response to changing climate (Bs - earlier, Ls - no effect on phenology). Paramaterize a resource allocation model with data from Boechera stricta and Lythrum salicaria to understand phenological responses. Two core trade-offs are (1) the switch from vegetative to reproductive growth (eg. rosette growth ends when bolting starts, or apical meristem stops leaf production when flowering starts) and (2) between growth rate and susceptibility to herbivores. Here is a summary of the model: "Growth initially follows an exponential curve with a base vegetative growth rate (r) from an initial seed size (V0) until a threshold size at reproduction (u). At the time of reproductive maturity, vegetative size remains constant and seed production increases following a saturation curve with an upper limit determined by u. The optimum size at reproduction for a given growing season is a balance of time between adding additional vegetative growth and maximizing seed production before the end of the growing season." Model the growing season with 2 sine functions for temperature and soil moisture, and a threshold value for each species. Consider plastic (tracking onset of season) and optimum genetic response (proportional to duration of season). Also account for the effect of herbivory by modeling loss of vegetative and reproductive growth proportional to intensity of herbivory. Consider 2 models: loss to herbivory is the same as the level of investement in defense, or a relaxed constraint that allows a small increase in relative growth rate. Find that environmental differences lead to opposite phenological shifts in response to warming climate. Mostly determined by changes in the length of the growing season. Escape from herbivores has minimal effect in the ecological release model because effect of herbivory is constant loss across season. In the relaxed constraint model, effect of herbivory is to delay flowering and incrase optimal size. Emphasize the following as important environmental variables: "what limits growth and development because those are what determine the onset and duration of favorable conditions for growth, maturation, and offspring production." State that growth rate prior to maturity effects the initiation of growth, threshold size of reproduction, timing of reproduction, and total reproductive fitness. Suggest that future work could look at constraints on growth rate.

[26] Sebastian Gnan, Tom Marsh, and Paula X. Kover. 2017. Inflorescence photosynthetic contribution to fitness releases Arabidopsis thaliana plants from trade-off constraints on early flowering. *PLoS ONE*, 12(10):1–13. tex.isbn: 1111111111.

> Experiment in which authors removed rosette leaves from 15 A. thaliana accessions. Found variation but even most severely affected accessions were able to maintain 35% of their fitness with just inflorescences. Contribution of inflorescence photosynthetic activity to plant's reproductive output can decouple commonly assumed trade-off between age of reproduction and fitness. Variation in growth rate is unlikely to decouple size, age at reproduction, and reproductive output. The correlation between flowering time and rosette size is maintained because variation in growth rate is not associated in a way that compensates for early flowering. In contrast, early flowering plants tend to have slower growth rate. This agrees with Weis et al. who find that variation in growth rate has little effect on shape of selection on flowering time. Early flowering does impose a constraint on plant size, but this does not mean it is appropriate to assume a cost of early reproduction because reproductive structures can pay some of their own cost. Smaller vegetative size does not seem to constrain fitness of B. rapa either.

[27] Clinton J. Whipple. October 2017. Grass inflorescence architecture and evolution: the origin of novel signaling centers. *New Phytologist*, 216(2):367–372.

> Describes the Kellogg 2000 and Prusinkiewicz et al. 2007 studies and how they are connected. Clear description of the use of modeling of vegetativeness, its relationship to TFL/LFY, and how this is connected to the genetics of development. Focused on grasses.

[28] Matthew J. Rubin, Marcus T. Brock, Robert L. Baker, Stephanie Wilcox, Kyle Anderson, Seth J. Davis, and Cynthia Weinig. 2018. Circadian rhythms are associated with shoot architecture in natural settings. *New Phytologist*, 219(1):246–258. tex.mendeley-tags: empirical.

> Field experiment with A. thaliana suggesting that circadian rhythms are associated with branching and thus fruit production. Circadian clock integrates abiotic factors (light, temperature) and regulates several genes associated with branching. Meristem fate is an important determinant of plant architecture. Here, the authors show that quantitative clock variation is associated with branching, independent of flowering time. One possible mechanism of action is auxin, which might be regulated by circadian rhythm. Another result is that the association between flowering time and branch number is not consistent between years. For more on how these may be independent, see Austen et al. 2015. Both meristem number and fate (quiescent, differentiated) are possible levers. Suggests that difference in fate between cauline and rosette meristems reflects 2 different strategies to increase fitness.

[29] Jacob Johansson and Kjell Bolmgren. October 2019. Is timing of reproduction according to temperature sums an optimal strategy? *Ecology and Evolution*, 9(20):11598–11605.

> The authors compare the solution from optimal control models with and without temperature sums to understand whether control of development by temperature is optimal. They include an informative table in their appendix that describes the different scenarios of variability that they explore and how biomass changes over the course of the season.