Effect of census period on qualitative and quantitative dynamics of the perennial model.

Figure 1 is the life cycle of a perennial plant as depicted by censusing all individuals at the end of the growing season during the fall. The associated population dynamics follow

**NF**all(*t* + 1) = **MFall**(*t*)**NF**all(*t*).

where **NFall**(*t*) = (*NS*(*t*), *NA*(*t*))*T*, the vector of seed and adult plant density. The population projection matrix for the fall is

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Figure 1. Life cycle of the annual as depicted when censusing individuals during the fall, just following the end of seed production. Processes include growth, reproduction, and survival during the growing and nongrowing seasons. Adult plants are given by the top dotted line and seeds are along the bottom dotted line. In between are seedlings of first year plants, which join the pool of adults at the end of the census period.

Figure 2 is the life cycle of a perennial plant as depicted by censusing all individuals at the beginning of the growing season during the spring, just prior to germination of plants. The associated population dynamics follow

**NSpring**(*t* + 1) = **MSpring**(*t*)**NSpring**(*t*),

where **NSpring**(*t*) = (*NS*(*t*), *NA*(*t*))*T*, the vector of seed and adult plant density evaluated at the beginning of the spring. The population projection matrix for the fall is

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Figure 2. Same as Figure 1 but represented as the censusing the population in the spring.

**Some Conclusions on the Effect of Census Time**

Inspection of the matrices **MFall** and **MSpring** indicate that the two have the same structure, which is given by

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where *a*, *b*, *c*, *d*,and *e* are all constants. So far, only fecundity and germination are assumed to depend in some way on the density of other factors in the system. **For both census periods, the parameters *a*, *b*, and *e* are identical between models.** *a* = *sShS* it total survival of dormant seeds over one year. *e* = *sAhA* is total survival of adult plants over one year. *b* = *sSh*1 has slightly different interpretations for the two census points. It is the survival of a seed counted in the fall destined to germinate and reproduce in the following year. It is also the survival of a first-year plant times survival of its eventual offspring that same year when seeds are counted in the spring.

**The models differ is in their values of *c* and *d*, which represent survival of individuals that transition between stages**. *c* is the survival of adults that transition to seeds (i.e. fecundity). In the fall model, *c* = *sAhA* = *e*. In the spring model, *c* = *hAsS* is the product of perennial growing season survival and winter seed survival. *d* is the survival of seeds that transition to adults (i.e. maturation). In the fall model, *d* = *sSh*1 is the product of winter seed survival and growing season survival of first year plants. In the spring model, *d* = *h*1*sA* is the product of first year plant survival and adult winter survival.

**The models are identical when *sA = sS*,** that is when seed and adult survival during the nongrowing season are the same. Effectively, differences between survival probabilities of the two stages during the nongrowing season lead to a disparity in the relative density of each stage at each count. If *sA* < *sS*, then the number of seeds relative to adults in the fall will be less than that in the spring. Hence, there are quantitative differences between the predictions of each models, since the proportions of the stages potentially differ between census times.

**Qualitative differences should not exist between the models, provided they each appropriately account for density-dependent effects**. This is the most likely reason why Nick and Amy’s versions of the model differed with the inclusion of overwinter mortality, since Amy assumed some adult survival that affected the number of competing plants, and Nick did not.

**A possible simplest model is**

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where

 = *sShA* is the total survival of dormant seeds throughout the year;

 = *F1b* is the per-capita number of seeds surviving to the next census period of first-year plants, accounting for both mortality of newly produced seeds, mortality of seedlings before seed production, and reduction of fecundity for first-year plants;

= *FhAsA* is the per-capita fecundity of an adult plant, which includes mortality prior to reproduction as well as post reproductive mortality of seeds;

*s*1 = *d* is the fraction of seeds surviving their first year as an adult plant (conditional on germination); and

 = *sAhA* is the survival total yearly survival of an adult plant.

The spring and census models are different representations of this general model. Different choices about the census times only affect the actual values of *s1* and . Since they can be described by the same general model, it follows that all the possible behaviors of the spring and fall census behaviors are present in the general model above.

**Competition as affected by the Census Time**

As the differences between the models are in terms of the actual values of their constants, any differences between models are multiplicative. Hence, the competition coefficients can always be rescaled to include any constant morality differences between the models.

For example, consider that all plants following germination contribute to competition (even if some die during the summer). Then competition is some function of total number of plants weighted by their competitive effects, *f*(α\*total plant density).

When counts of individuals occur in the fall, total competitive effect is



where *α*A is the competition coefficient for an adult present at the beginning of the growing season and *αS* is the competition coefficient for a seedling.

When counts of individuals occur in the spring, total competitive effect is

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Since there is constant survival of adults and seeds over the winter,  and . Thus, the total competitive effect of the population in both census cases is proportional to each other by some constant. Hence, competition effect per-individual is equivalent once accounting for differences in survival, even if population numbers are different.

One might note that, for parameterization purposes, competition coefficients per fall counted individual are smaller than that of spring counted individuals by a factor *s*, which accounts for mortality over the winter before competition occurs. This means an individual adult counted in the fall has a functionally smaller competitive effect than that of the same individual counted in the spring. Thus, so long as competition is written as

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it includes any potential differences in census time between models. For exact equivalence, competition coefficients will need to differ between models.

**Any census time is a special case of the general model M\*, denoted by the stars above. Furthermore, differences between census times influence competition, but may be accounted for in the per-capita competition coefficients themselves.**

These statements hold for any other complexities added to the model in which the constants *a*, *b*, *c*, *d*, and *e* are invariant of population densities.

**Consensus Plant Models**

Plant density is counted in the spring, just prior to germination of both species.

*NA* for annual seed density

*NP* for perennial adult density

*NS* for perennial seed density

Growing season is as follows:

Germination 🡪 competition, growth, and mortality 🡪 reproduction 🡪 overwintering

Assumptions:

**Annual**

Competition affects plant size, not plant mortality

Negligible mortality upon germination

Competitive effect *αA* per seedling (seedling density is *NAGA* = seed density\*germination fraction)

Some overwintering mortality of seeds (likely low)

Equations:



where *GA*(*t*), the germination fraction, is a decreasing function of litter (does not allow for facilitative effects of litter), and *VA*(*t*), plant size at the end of the growing season, is a decreasing function of competition *C* (see definition of *C* below).

**Perennial**

Competition affects plant fecundity

Some mortality of adults and seedlings during growing season, but density-independent

Seeds that germinate in a year can reproduce that year, although fecundity is significantly less than 2nd year plant reproduction

Some overwintering mortality of adult plants and seeds (likely low)

Competitive effect of adult plant is *αP* per adult plant.

Competitive effect of first year plant is *cαP* where *c* < 1 (first year density is *NSGS* = seed density \* germination fraction)

Equations:

**N**(*t* + 1) = **M**(*t*)**N**(*t*)



where *GS* is the germination fraction and is a decreasing function of litter; *F*1 and *F* are fecundities of first-year and more than first year adult plants, respectively, which are decreasing functions of density; *sS* is the survival of seeds over the course of a year; *s*1 is the survival of first year plants; *sP* is the survival of adult plants.

**Litter**

Litter can remain for multiple years but has a decay rate *b*

Litter is proportional to biomass of annual

No contribution of the perennial to litter

Germination is a decreasing function of litter for both species

Competition between plants is independent of litter

Equation:

*L*(*t* + 1) = *aVA*(*t*)*GA*(*t*)*NA*(*t*) + (1 – *b*)*L*(*t*)

where *a* is the conversion of annual biomass to litter and *b* is the fraction of litter from the previous year that decays.

**Competition, *C***

Any reasonable measure of competition should be an increasing function of total growing plant density weighted by the competitive effect of each species, *C* = *f*(*αAGANA* + *αPNP* + *αPcNSGS*), with *f* some monotone increasing function.