

Demographic estimation methods for plants with dormancy

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Extended abstract

Demographic estimation methods for plants with dormancy.— Demographic studies in plants appear simple because unlike animals, plants do not run away. Plant individuals can be marked with, e.g., plastic tags, but often the coordinates of an individual may be sufficient to identify it. Vascular plants in temperate latitudes have a pronounced seasonal life-cycle, so most plant demographers survey their study plots once a year often during or shortly after flowering. Life-states are pervasive in plants, hence the results of a demographic study for an individual can be summarized in a familiar encounter history, such as 0VFVVF000. A zero means that an individual was not seen in a year and a letter denotes its state for years when it was seen aboveground. V and F here stand for vegetative and flowering states, respectively. Probabilities of survival and state transitions can then be obtained by mere counting.

Problems arise when there is an unobservable dormant state, i.e., when plants may stay belowground for one or more growing seasons. Encounter histories such as 0VF00F000 may then occur where the meaning of zeroes becomes ambiguous. A zero can either mean a dead or a dormant plant. Various *ad hoc* methods in wide use among plant ecologists have made strong assumptions about when a zero should be equated to a dormant individual. These methods have never been compared among each other. In our talk and in Kéry et al. (submitted), we show that these *ad hoc* estimators provide spurious estimates of survival and should not be used.

In contrast, if detection probabilities for aboveground plants are known or can be estimated, capture-recapture (CR) models can be used to estimate probabilities of survival and state-transitions and the fraction of the population that is dormant. We have used this approach in two studies of terrestrial orchids, *Cleistes bifaria* (Kéry et al., submitted) and *Cypripedium reginae* (Kéry & Gregg, submitted) in West Virginia, U.S.A. For *Cleistes*, our data comprised one population with a total of 620 marked ramets over 10 years, and for *Cypripedium*, two populations with 98 and 258 marked ramets over 11 years. We chose the ramet (= single stem or shoot) as the demographic unit of our study since there was no way distinguishing among genet (genet = genetical individual, i.e., the "individual" that animal ecologists are mostly concerned with). This will introduce some non-independence into the data, which can nevertheless be dealt with easily by correcting variances for overdispersion. Using ramets instead of genets has the further advantage that individuals can be assigned to a state such as flowering or vegetative in an unambiguous manner. This is not possible when genets are the demographic units. In all three populations, auxiliary data was available to show that detection probability of aboveground plants was ≥ 0.995 .

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We fitted multistate models in program MARK by specifying three states (D, V, F), even though the dormant state D does not occur in the encounter histories. Detection probability is fixed at 1 for the vegetative (V) and the flowering state (F) and at zero for the dormant state (D). Rates of survival and of state transitions as well as slopes of covariate relationships can be estimated and LRT or the AIC machinery be used to select among models. To estimate the fraction of the population in the unobservable dormant state, the encounter histories are collapsed to 0 (plant not observed aboveground) and 1 (plant observed aboveground). The Cormack–Jolly–Seber model without constraints on detection probability is used to estimate detection probability, the complement of which is the estimated fraction of the population in the dormant state.

Parameter identifiability is an important issue in multi state models. We used the Catchpole–Morgan–Freeman approach to determine which parameters are estimable in principle in our multi state models. Most of 15 tested models were indeed estimable with the notable exception of the most general model, which has fully interactive state- and time-dependent survival and state transition rates. This model would become identifiable if at least some plants would be excavated in years when they do not show up aboveground.

Our analyses for three analyzed populations of *Cleistes* and *Cypripedium* yielded annual ramet survival rates ranging from 0.86–0.96. Estimates of the average fraction dormant ranged from 0.02–0.30, but with up to half a population in the dormant state in some years. Ultrastructural modeling enables interesting hypotheses to be tested about the relationships of demographic rates with climatic covariates for instance. Such covariate modeling makes the CR approach particularly interesting for evolutionary–ecological questions about, e.g., the adaptive significance of the dormant state.

Previous and foreseeable future applications of CR in plant ecology

Since the paper by Alexander et al. (1997), it has become increasingly clear that CR models may be useful for demographic analysis of plant populations. In the future, we are likely to see increasing use of these methods that were originally developed for animal populations. Here is a summary about all previous applications that I have come across. I am grateful if readers point out to me any titles that I may have missed.

If a reliable way to mark seeds can be devised, CR might indeed provide the analysis tool for tackling one of the ultimate frontiers in plant population ecology: the dynamics of the seed bank. Indeed, the first ever application of CR to plants that I have come across (Naylor, 1972) used a fluorescent dye to mark seeds and a Lincoln–Peterson–type estimator to estimate the seed bank size in an agricultural weed. The application of CR to plants with dormancy has been treated by Shefferson et al. (2001, 2003), Kéry et al. (submitted) and Kéry & Gregg (submitted). Population size, and survival rates of plants whose aboveground states are easily overlooked have been estimated for an elusive prairie plant (Alexander et al., 1997; Slade et al., 2003) and for a tropical savannah tree (Lahoreau et al., 2003). For plot–based plant demographic studies, we have shown previously that (not surprisingly) different life–states may have different detection probabilities, and that this may seriously bias inference from population modelling (Kéry & Gregg, 2003).

It is somewhat astonishing that there still appear to be no applications of CR to the analysis of plant populations and communities. For instance, species richness, patch occupancy, population extinction rates, and species turnover in communities are all still based on adding up the raw data, even though the animal literature has plenty of papers showing more adequate ways of estimating these quantities (e.g., Boulinier et al. 1998; Nichols et al. 1998). I have submitted a note (Kéry, submitted) describing the use of the Cormack–Jolly–Seber model to estimate extinction probabilities for plant populations in a manner exactly analogous to patch occupancy models (MacKenzie et al., 2002, 2003). It is perhaps in plant community ecology where we will see most future applications of CR.

References

(This list contains all plant studies that have used CR, that I have come across by the end of October 2003. There are also a few non–plant papers mentioned in the text.)

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