

Survival costs of adult dormancy and the confounding influence of size in lady's slipper orchids, genus *Cypripedium*

Richard P. Shefferson

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Adult whole-plant dormancy is a phenomenon in which a perennial, herbaceous plant does not sprout for one or more years. Although previous studies have noted a cost of dormancy to survival, none have accounted for the potentially confounding influence of size variation on this relationship. I asked whether the probabilities of dormancy and survival in dormancy-prone plants vary with size, possibly creating the appearance of a life-history tradeoff between survival and dormancy. I censused sympatric populations of three lady's slipper orchid taxa, *Cypripedium parviflorum*, *C. candidum*, and *C. × andrewsii*, in an 11-year study (1994 to 2004) at Gavin Prairie, Illinois, USA. Annual dormancy and survival trends were modeled using Cormack-Jolly-Seber mark-recapture analysis, while stage-specific survival and stratum-transitions (i.e. probability of transitioning among stages conditional upon survival) were modeled with multi-strata mark-recapture analysis. Annual dormancy probabilities and transition probabilities to and from dormancy varied synchronously among taxa, while trends in survival did not. Both survival and dormancy varied with number of sprouts in the previous year, positively in the case of the former and negatively in the case of the latter. Accounting for plant size in this way eliminated any variation in survival by life-history stage, with dormant plants surviving at the same rate as non-dormant plants of the same size. Transitions among stages did not vary with plant size. My results suggest common climatic cues to dormancy, and suggest caution in inferring costs of dormancy from studies in which plant size is not controlled, as such costs may be artifacts of smaller plants being more dormant-prone and less likely to survive.

R. P. Shefferson (dormancy@gmail.com), Dept. of Integrative Biology, Univ. of California, 3060 VLSB No. 3140, Berkeley, CA 94720, USA. Present address: Forestry and Forest Products Research Inst., Microbial Ecology Laboratory, 1 Matsunosato, JP-305-0044 Tsukuba, Japan.

Adult whole-plant dormancy is a condition in which a mature plant foregoes sprouting and photosynthesis during the growing season (Lesica and Steele 1994). It occurs in many plant families, including the Asclepiadaceae, Asteraceae, Liliaceae, Orchidaceae, Ophioglossaceae and Ranunculaceae (Epling and Lewis 1952, Lesica and Steele 1994, Alexander et al. 1997, Morrow and Olfelt 2003, Miller et al. 2004). It has been noted almost exclusively in studies of single populations, with common trends and qualities generally ignored so far.

Dormancy can occur often in wild populations, with up to 70% of a population dormant per year and 11 consecutive years of dormancy per plant noted in the literature (Rydlo 1995, Kull 2002), and can correlate with weather variables, suggesting climatic cues (Shefferson et al. 2001, Kéry et al. 2005). Dormancy may result in costs to adult survival because wild plants experiencing dormancy more often also have higher mortality rates (Shefferson et al. 2003), potentially resulting in disproportionately negative consequences

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to fitness relative to the fitness consequences of costs to reproduction (Silvertown et al. 1993, Sæther and Bakke 2000). However, dormancy has been studied little, and though it occurs somewhat commonly in perennial herbs, its life history context is still obscure.

The observation of tradeoffs and costs can be confounded by differing levels of resource acquisition and partitioning among individuals (van Noordwijk and de Jong 1986, de Jong 1993). In many woodland herbs, resource storage may confound the observation of tradeoffs among life-history traits, including costs of reproduction, as stored carbohydrates are often used to make up for resource shortfalls imposed by costs of reproduction and resource reserves are often directed to the growth of new sprouts (Zimmerman and Whigham 1991, Vallius 2001, Whigham 2004). Observation of tradeoffs in orchids in particular may be further confounded by mycorrhizal interactions, which provide germinating seeds, protocorms, and seedlings of orchids with all of their carbon requirements and either stop or continue to provide carbon later in life (Alexander and Hadley 1985, Taylor et al. 2002). In clonal plants that maintain physiological connections among their ramets, resource acquisition also varies with the number of interconnected ramets, hereafter referred to as clonal plant size. As clonal plants grow root systems, they produce clonal offspring that spread into the surrounding environment, increasing resource acquisition from a more heterogeneous area and reducing mortality risk (Pitelka and Ashmun 1985, Snow and Whigham 1989). Increased plant size associates with increased flowering (Gill 1989, Primack and Stacy 1998, Gregg 2004), and may even result in increased pollination (Snow and Whigham 1989). In turn, positive correlations among plant size, survival, and reproduction often occur as a result (Harper and White 1974, Verburg et al. 1996).

It has been suggested that dormancy varies negatively with plant size in at least some clonal plant species (Primack and Stacy 1998, Shefferson et al. 2005a). Dormancy may thus be more likely in smaller plants, which are more likely to be sensitive to environmental stochasticity (Wijesinghe and Hutchings 1997). Therefore, the observation of survival costs to dormancy may actually be due to a lack of accounting for size variation among plants in demographic analyses. In this study, I explore the relationships among dormancy, survival, and plant size using sympatric populations of two lady's slipper orchid species and their hybrid. First, I asked whether survival and dormancy probabilities among the three taxa varied with plant size in the previous year. I then asked whether the survival of plants in particular life-history stages and transitions to other stage classes from dormancy were dependent on previous plant size. The genus *Cypripedium* was used because it has been

subject to more studies dealing explicitly with dormancy than any other genus.

Methods

Study species and site

Sympatric populations of three long-lived terrestrial lady's slipper orchid taxa, *Cypripedium candidum* Muhl. ex Willd., *C. parviflorum* Salisb., and their hybrid, *C. × andrewsii* Fuller nm. *andrewsii*, were censused from 1994 to 2004 in a 3-ha wet meadow in Gavin Prairie Nature Preserve, Illinois, USA (42°23'N, 88°8'W). In Lake County, Illinois, flowering occurs annually from mid-May through mid-June, with *C. candidum* and *C. × andrewsii* generally flowering a few days earlier than *C. parviflorum* (Swink and Wilhelm 1994). Ramets grow from adjacent nodes as little as 0.5–1.1 cm apart and may eventually split and separate, resulting in vegetative reproduction (Curtis 1954, Kull 1987, Kull and Kull 1991). A typical rhizome may have as many as 20 annual increments of growth, with the oldest increments decaying at the end of the rhizome (Kull and Kull 1991).

Field methods

I censused a total of 982 *C. parviflorum*, 77 *C. candidum*, and 17 *C. × andrewsii* individuals over the course of the study, in mid- to late May each year. Censusing involved locating each physiologically interconnected, individual orchid (also referred to as a "clonal fragment"), composed of all sprouts within 20 cm of each other, and mapping it relative to a fixed stake located in each patch, then recording its life history stage (i.e. vegetatively sprouting, hereafter referred to as 'vegetative', or flowering if at least one sprout was in flower) and the number of sprouts of each stage as an estimator for the number of size per clonal fragment (Shefferson et al. 2001, 2003). These census methods were justified by a low density of sprouts at the site (2.40 ± 0.06 sprouts m^{-2}), with 94.5% of all censused orchids composed of fewer than five sprouts in every year of the study. Detection of non-dormant clonal fragments within each growing season at this site approached unity, with estimated detection rates of 1.000 ± 10^{-5} for vegetative and flowering orchids previously identified, and previously unidentified orchids detected at rates of 0.810 ± 0.061 and 0.977 ± 0.022 for vegetative and flowering clonal fragments, respectively (Shefferson et al. 2001, 2003). I re-censused all flowering clonal fragments in late July to August of 2000 to 2004 to estimate the impacts of herbivory and poaching on the demography of these

populations, but found that only 18 plants “disappeared” in this five-year interval.

Mark–recapture methods

Cormack–Jolly–Seber mark–recapture analysis

I first conducted a Cormack–Jolly–Seber (CJS) mark–recapture analysis to estimate overall trends in apparent survival (ϕ_i), defined as the probability of surviving from year i to year $i+1$ corrected for dormancy and incomplete detection, and the probability of resighting (p_{i+1}), defined as the probability that an individual surviving the interval from year i to year $i+1$ is also observed in year $i+1$ (Lebreton et al. 1992). Because the probability of detecting previously observed clonal fragments that were alive and not dormant in each year approached unity at this site, I estimated the probability of dormancy (d) as the complement to the probability of resighting (i.e. $d=1-p$, per Shefferson et al. 2001). First, a resighting history input file was created in which presence aboveground was coded as a binary variable. Plant size was included as a series of individual covariates, calculated per plant for each year of the study as the number of sprouts per plant (0 to 8, with all plants with >8 sprouts classified as 8 due to low numbers), divided by 8 to standardize to the interval 0–1. This input file was analyzed in program MARK under the “recaptures only” analysis option (White and Burnham 1999), with 18 groups (corresponding to the 12 patches, two of which had three taxa, and a further two of which had two taxa), 11 years of study (1994–2004), and 10 individual covariates (corresponding to clonal fragment size in 1994–2003).

Analysis began with the construction of a global model, in which apparent survival and resighting varied by a size + ([taxon \times patch] \times time) interaction (subscript ‘sz’ for size, ‘s’ for taxon, ‘p’ for patch, and ‘t’ for time; model abbreviated as $\phi_{sz+((s \times p) \times t)} p_{sz+((s \times p) \times t)}$). Because this model includes individual covariates, no test of overdispersion could be performed (White and Burnham 1999). Parameters were reduced to create further models using a design matrix, with all combinations and interactions of patch, taxon, time, and size tested (White and Burnham 1999). Apparent survival was reduced first, followed by resighting, and lastly by apparent survival again.

Multi-strata mark–recapture analysis

I next conducted a multi-strata (MS) mark–recapture analysis in order to separate life-history stage-based effects from size-based effects in demographic parameters. Here, I estimated the probability of stratum-specific survival (S_i^j), defined as the probability that an individual alive and in stratum j in year i survives to time $i+1$, and stratum-transition (Ψ_{i+1}^{jk}), defined as the

probability that an individual surviving to year $i+1$ moves from stratum j in year i to stratum k in year $i+1$, where “stratum” refers to life-history stage (White et al. 2002). I first created a resighting history input file in which presence was coded by life history stage as “F”, “V”, or “0”, depending on whether the plant was flowering, vegetative, or unobserved, respectively. Plant size was added to this file as before. This data set was analyzed in program MARK under the “multi-strata recaptures only” option, with 11 years, three groups (corresponding to taxa), three life-history strata (F, V, and D, for flowering, vegetative, and dormant, respectively), and 10 individual covariates.

Analysis began with the construction of a global model, in which survival varied with plant size, taxon, and life history stage (subscript ‘l’, for life-history stage), and stratum-transition parameters varied by plant size, time, taxon, and specific stratum-transitions (subscript ‘m’, for stratum-transition; e.g. transition from flowering to vegetative; model abbreviated as $S_{sz+(l \times s)} \Psi_{m \times (sz+(s \times t))}$). Previous plant size was modeled as a covariate only in transitions from dormancy to vegetative sprouting, from dormancy to flowering, and from vegetative sprouting to flowering. Resighting (p_{i+1}^k), defined as the probability of observing an individual that survived the interval from year i to year $i+1$ and transitioned to stratum k in year $i+1$, was fixed to 1.000, 0.977, and 0 in all models for the flowering, vegetative, and dormant stages, respectively, per empirically derived detection rates from a previous study on the first seven years of *C. parviflorum* census data (Shefferson et al. 2003). Annual variation in stage-based survival is not always estimable in multi-strata analyses with unobservable life-history stages, and so was not tested (Kéry et al. 2005). Parameterizations were reduced in survival first, followed by stratum-transition terms, and lastly by survival again.

Model selection and parameter estimation

Models were ranked by sample size-corrected Akaike information criterion (AICc) values in both analyses. The model with the lowest AICc value was considered the best-fit model, although all models ≤ 2.0 AICc units were considered equally parsimonious. Akaike weights were estimated in order to ascertain the strength of particular parameterizations. β -parameters from the best-fit models in both analyses were used to derive estimates of apparent survival, stage-specific survival, dormancy, and stratum-transition across a range of previous plant sizes, per the logit link function (White and Burnham 1999). Likelihood ratio tests were used to test specific hypotheses about the importance of previous plant size and the kinds of variation among demographic parameters.

Results

Dormancy trends

The longest observed dormant period was seven years, observed in two *C. parviflorum* plants, but all lengths of dormancy periods up to this maximum were also observed, and *C. candidum* and *C. × andrewsii* went dormant for up to six and three years, respectively. At least 44.4%, 40.0% and 52.9% of all sampled *C. parviflorum*, *C. candidum*, and *C. × andrewsii* plants experienced dormancy during the 11 years of the study. Annually, an average proportion of 0.375 ± 0.032 , 0.338 ± 0.031 , and 0.405 ± 0.029 of the *C. parviflorum*, *C. candidum*, and *C. × andrewsii* populations were dormant, respectively, and each taxon had an average of 1.65 ± 0.05 , 3.46 ± 0.13 , and 3.09 ± 0.35 sprouts per plant, respectively (Fig. 1).

Previous plant size was a significantly positive covariate of resighting, and hence a negative covariate of dormancy (likelihood ratio test, LRT, of model 2, $\phi_{sz+p+t} p_{sz+(p \times s)+t}$ vs model $\phi_{sz+p+t} p_{(p \times s)+t}$: $\chi^2_1 = 55.86$, $P < 0.0001$; Table 1). CJS modeling resulted in the following function to estimate resighting:

$$\text{logit}(p) = 0.223 + g + t + 0.251z \quad (1)$$

where p is resighting, g varies by both patch and taxon (range for *C. parviflorum* patches is -0.131 to 1.630 , for *C. candidum* patches is 0.619 to 1.597 , and for *C. ×*

andrewsii patches is 0 to 1.798), t varies by year (range: -1.642 to 0), and z refers to clonal plant size in the previous year (number of sprouts, from 0 to 8). Previously small or dormant plants were most likely to be dormant in the current year, at a probability approximately four times higher than of plants with eight or more sprouts in the previous year (Fig. 2). All of the top ten models suggested parallel variation among taxa, patches, sizes, and time, suggesting a high degree of sprouting synchrony among patches and taxa (Fig. 1, Table 1).

Apparent survival trends

The best-fit and next most parsimonious models both suggested that apparent survival covaried significantly positively with plant size in the previous year (LRT of model 1, $\phi_{sz+(s \times t)} p_{sz+(p \times s)+t}$ vs model 3, $\phi_{s \times t} p_{sz+(p \times s)+t}$: $\chi^2_1 = 5.71$, $P = 0.017$; Fig. 2, Table 1). CJS modeling resulted in the following function to estimate apparent survival:

$$\text{logit}(\phi) = 0.829 + s + t_s + 0.128z \quad (2)$$

where ϕ is apparent survival, s varies by taxon (*C. parviflorum*: 0 , *C. candidum*: 12.667 , and *C. × andrewsii*: 12.835), t_s varies by year and taxon (range for *C. parviflorum* is 0 to 4.245 , for *C. candidum* is -13.660 to 4.384 , and for *C. × andrewsii* is -13.837 to 9.047),

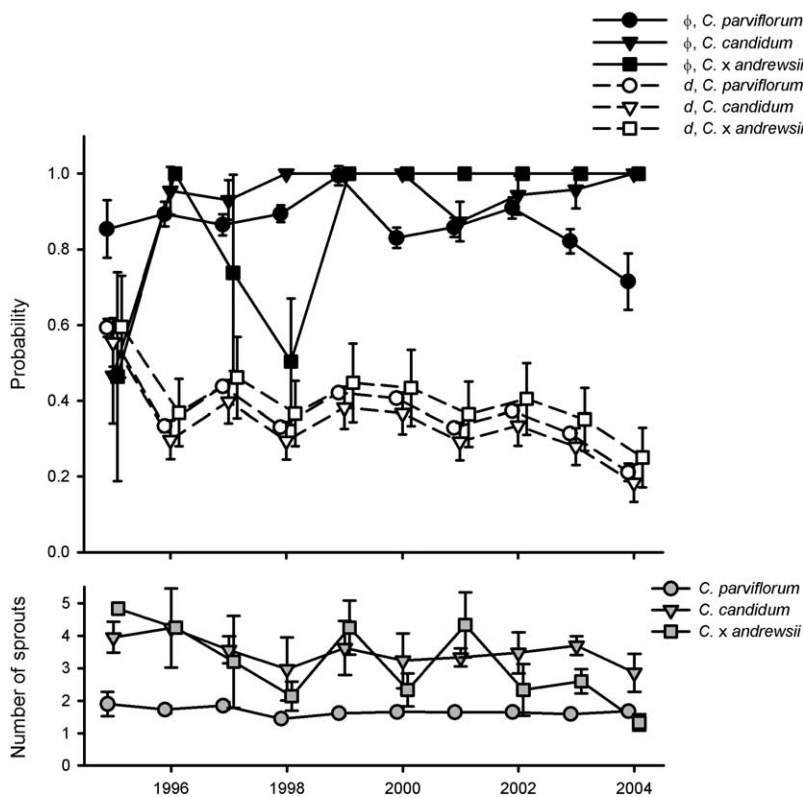


Fig. 1. Annual probabilities of survival (ϕ) and dormancy (d), and average number of sprouts per clonal fragment per year, for *C. parviflorum*, *C. candidum*, and *C. × andrewsii* at Gavin Prairie, Illinois, USA, censused from 1994 to 2004. Apparent survival (ϕ) and dormancy ($d = 1 - p$, where p = resighting) are from the best-fit model of a Cormack-Jolly-Seber mark-recapture analysis in program MARK (White and Burnham 1999; Table 1).

Table 1. Modeling apparent survival (ϕ) and resighting ($p = 1 - d$) probabilities for *Cyripedium parviflorum*, *C. candidum*, and *C. × andrewsii*, censused at Gavin Prairie, Lake County, Illinois, USA, from 1994 to 2004, using Cormack-Jolly-Seber mark-recapture analysis in program MARK. The best ten models are presented. $\Delta AICc$ is calculated as $AICc_i - \min(AICc)$, where i refers to the model, and w refers to the Akaike weight for each model using $AICc$, where support for the model is given on a scale of 0 (no support) to 1 (full support, rendering all other models completely unlikely). K refers to the number of parameters. Model symbols denote variation by taxon (s), patch (p), plant size (sz), and year (t). The best-fit and most parsimonious models are presented in boldface.

Model	Apparent survival	Resighting	K	Deviance	$\Delta AICc$	$w \leq$
1	sz+s × t	sz+(p × s)+t	58	7407.4	0	0.487
2	sz+p+t	sz+(p × s)+t	49	7426.5	0.54	0.373
3	s × t	sz+(p × s)+t	57	7413.1	3.64	0.079
4	sz+(p × s) × t	sz+(p × s)+t	55	7419.4	5.82	0.027
5	p+t	sz+(p × s)+t	48	7434.4	6.36	0.020
6	(p × s)+t	sz+(p × s)+t	54	7424.0	8.32	0.008
7	sz+s+t	sz+(p × s)+t	40	7453.8	9.42	0.004
8	s+t	sz+(p × s)+t	39	7459.7	13.22	0.001
9	sz+p × t	sz+(p × s)+t	139	7249.6	13.41	0.001
10	sz+t	sz+(p × s)+t	38	7462.7	14.23	0.001

and z is as before. Mean apparent survival rates were high among all taxa, but lowest for previously small or dormant plants (Fig. 2). Apparent survival did not vary in parallel among taxa (LRT of model 1, $\phi_{sz+(s \times t)}$ vs model 7, ϕ_{sz+s+t} vs model 7, $\phi_{sz+(p \times s)+t}$: $\chi^2_{18} = 46.42$, $P < 0.001$, Table 1), suggesting that mortality may be linked to different factors among these taxa.

Stratum-based survival trends

Survival did not vary significantly by stage in multi-strata mark-recapture analysis, suggesting no cost of dormancy (LRT of model 13, $S_{sz+1} \Psi_{m \times (s+t)}$ vs model 12, $S_{sz} \Psi_{m \times (s+t)}$: $\chi^2_2 = 3.09$, $P = 0.213$, Table 2). However, plant size was a significant factor in multi-strata survival analysis (LRT of model 11, $S_{sz+s} \Psi_{m \times (s+t)}$ vs

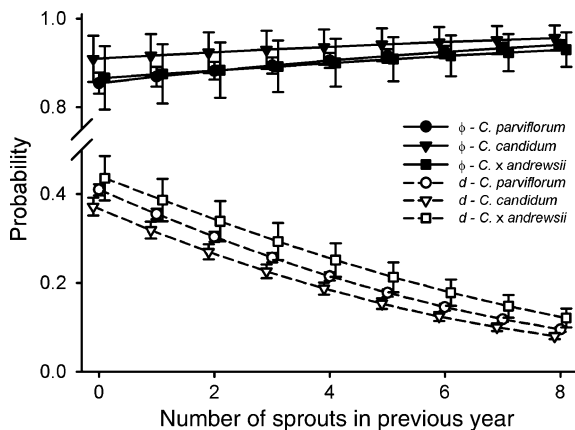


Fig. 2. Annual probabilities of survival (ϕ ; solid symbols) and dormancy (d ; open symbols) as functions of the number of sprouts a clonal fragment grew in the previous year for *C. parviflorum* and *C. candidum* in patch X, and *C. × andrewsii* in patch Alc, at Gavin Prairie, Illinois, USA, censused from 1994 to 2004. Parameters are from the best-fit model of a Cormack-Jolly-Seber mark-recapture analysis in program MARK (White and Burnham 1999; Table 1). Functions used are given in the text as Eq. 2 and 3.

model 20, $S_s \Psi_{m \times (s+t)}$: $\chi^2_1 = 27.29$, $P < 0.001$, Table 2). Without incorporating plant size, modeling suggests a large cost of dormancy to survival – under such circumstances apparent survival is estimated at 0.758 ± 0.014 for dormant plants but 1.000 ± 0.001 for vegetative and flowering plants (model 15, Table 2). Furthermore, the lack of an interaction between size and stage suggests that dormancy is not necessarily more likely to incur a cost in smaller than larger plants (Table 2). However, a lack of equal sample sizes among plant taxa may preclude observation of such size-covarying costs.

Transition probabilities

All models with any support suggested that annual stratum-transitions varied in parallel among taxa, but previous plant size was not a significant factor (LRT of model 16, $S_{sz+1} \Psi_{m \times (sz+(s+t))}$ vs model 13, $S_{sz+1} \Psi_{m \times (s+t)}$: $\chi^2_3 = 1.18$, $P = 0.758$; Fig. 3, Table 2). Lack of variation with size here contrasts with the results of CJS modeling, and suggests that either there were rather strict size-based differences among life-history stages but not within life-history stratum-transitions, or that there was a lack of power in this multi-strata analysis to show size gradients within stratum-transitions. Transition probabilities were significantly additive among taxa and time (LRT of model 13, $S_{sz+1} \Psi_{m \times (s+t)}$ vs model $S_{sz+1} \Psi_{m \times t}$: $\chi^2_{12} = 70.61$, $P < 0.0001$; Table 2), suggesting common cues among taxa for flowering and dormancy. Trends among mean transition probabilities varied among taxa, with *C. candidum* plants generally staying within the same stage from year to year while vegetative *C. parviflorum* and both vegetative and flowering *C. × andrewsii* plants generally transitioned to dormancy (Table 3). Furthermore, flowering *C. parviflorum* plants were more likely to transition to dormancy than to vegetative sprouting (Table 2), suggesting that a large proportion of flowering plants may suffer either lower resource inputs or higher reproductive costs.

Table 2. Modeling stage-specific survival (S) and stratum-transition (Ψ) likelihoods for *Cypripedium parviflorum*, *C. candidum*, and *C. x andrewsii*, censused at Gavin Prairie, Lake County, Illinois, USA, from 1994 to 2004, using multi-strata mark-recapture analysis in program MARK. The best ten models are presented. $\Delta AICc$ is calculated as $AICc_i - \min(AICc)$, where i refers to the model, and w refers to the Akaike weight for each model using $AICc$. K refers to the number of parameters. Model symbols denote variation by taxon (s), stage (l), stratum-transition (m), plant size (sz), and year (t). The best-fit and most parsimonious models are presented in boldface.

Model	Survival	Transition	K	Deviance	$\Delta AICc$	$w \leq$
11	sz+s	m × (s+t)	76	11076.4	0	0.316
12	sz	m × (s+t)	74	11080.6	0.06	0.306
13	sz+l	m × (s+t)	76	11077.5	1.14	0.179
14	sz+l+s	m × (s+t)	78	11073.6	1.34	0.162
15	l	m × (s+t)	75	11084.4	5.91	0.016
16	sz+l	m × (sz+(s+t))	79	11076.4	6.23	0.014
17	l+s	m × (s+t)	77	11082.2	7.84	0.006
18	sz+(l × s)	m × (s+t)	82	11081.2	17.30	0.001
19	l × s	m × (s+t)	81	11089.2	23.24	0.001
20	s	m × (s+t)	75	11103.7	25.21	0.001

Discussion

With plant size taken into account, support for a survival cost to dormancy disappeared in these three

lady's slipper taxa. Because dormant plants cannot photosynthesize until they "re-appear", such plants must be obtaining and/or utilizing carbon underground. Carbohydrate reserves, stored from previous years'

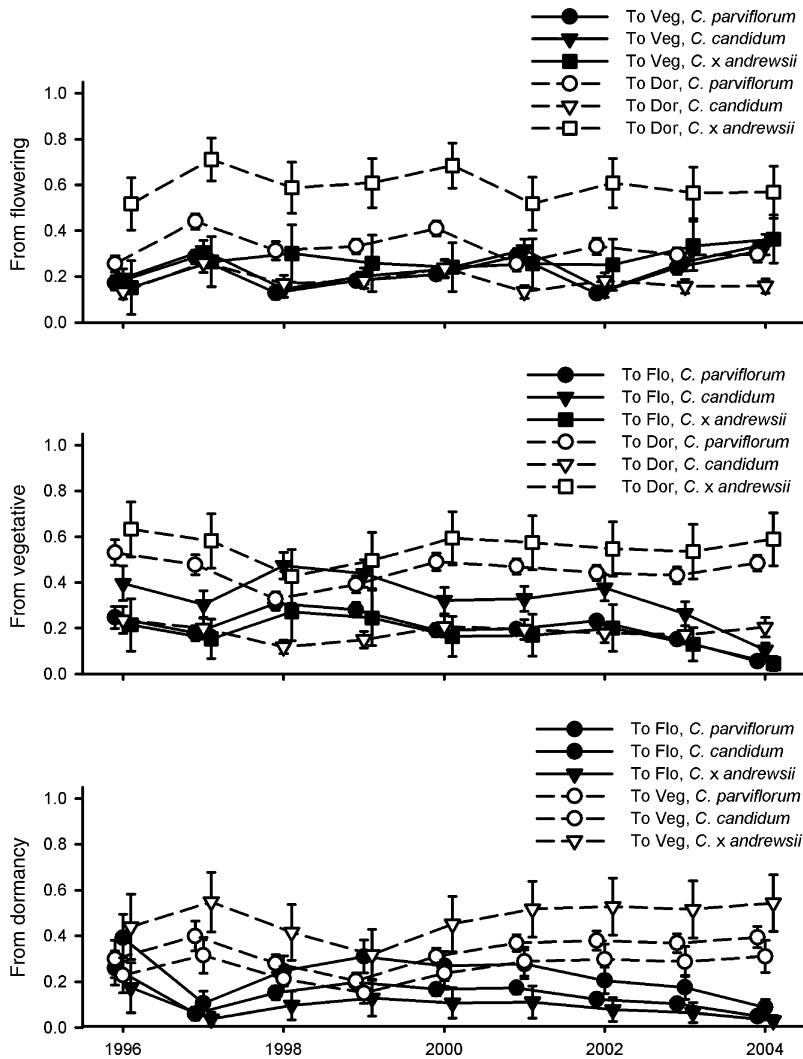


Fig. 3. Annual stratum-transition probabilities (Ψ) among flowering, vegetative sprouting, and dormant clonal fragments for *C. parviflorum*, *C. candidum*, and *C. x andrewsii* at Gavin Prairie, Illinois, USA, censused from 1994 to 2004. Abbreviations include: Flo for flowering, Veg for vegetative, and Dor for dormancy. Parameters from the best-fit model of a multi-strata mark-recapture analysis in program MARK (White and Burnham 1999; model 11, Table 2). Transitions for 1995 were inestimable.

Table 3. Estimates of annual stratum-transition probabilities among flowering, vegetative, and dormant stages of *Cypripedium parviflorum*, *C. candidum*, and *C. × andrewsii*, censused at Gavin Prairie, Illinois, USA, from 1994 to 2004. Stratum-transitions are similar to conventional stage-transitions but conditional upon survival, thus leading to estimates that sum to 1.00 across rows. Abbreviations include F for flowering, V for vegetative, and D for dormant. Estimates are from the best-fit model in multi-strata mark-recapture analysis (model 11, Table 2).

Stage	<i>C. parviflorum</i> transition to			<i>C. candidum</i> transition to			<i>C. × andrewsii</i> transition to		
	F	V	D	F	V	D	F	V	D
F	0.459 ± 0.031	0.199 ± 0.031	0.342 ± 0.039	0.580 ± 0.028	0.216 ± 0.033	0.205 ± 0.032	0.198 ± 0.030	0.191 ± 0.030	0.611 ± 0.034
V	0.192 ± 0.032	0.325 ± 0.042	0.483 ± 0.060	0.303 ± 0.047	0.432 ± 0.056	0.265 ± 0.082	0.162 ± 0.027	0.249 ± 0.033	0.589 ± 0.049
D	0.150 ± 0.023	0.354 ± 0.024	0.496 ± 0.018	0.223 ± 0.031	0.244 ± 0.019	0.533 ± 0.022	0.097 ± 0.016	0.491 ± 0.027	0.412 ± 0.020

growth, may provide one method of survival through these non-photosynthetic periods (Zimmerman and Whigham 1992). However, due to the extended length of time that plants can endure dormant periods – up to seven years in this study alone and up to 11 years in others (Kull 2002) – there may be other means of acquiring carbon. One hypothesis frequently mentioned as a possible means of carbon support for dormant plants is the orchid mycorrhiza (Gill 1989, Shefferson et al. 2001, Kull 2002). Orchids begin life as protocorms and seedlings without photosynthetic tissue and carbon reserves of their own, instead feeding from their mycorrhizal fungi (Leake 1994, Rasmussen 1995, Smith and Read 1997). Many orchid species, and even some liverworts, ericoids, and other plants, have evolved life histories in which they depend on this carbon throughout their lives, without ever photosynthesizing on their own (Taylor et al. 2002, Bidartondo et al. 2003). Although carbon transfer has never been demonstrated from a mycorrhizal fungus to a dormant plant, many photosynthetic orchids have nitrogen and carbon stable isotope signatures suggestive of carbon acquisition from ectomycorrhizal sources (Gebauer and Meyer 2003, Bidartondo et al. 2004). Furthermore, the primary mycorrhizal symbionts of both *Cypripedium candidum* and *C. parviflorum* are obscure fungi within the relatively unstudied basidiomycete family Tulasnellaceae (Shefferson et al. 2005b), a family known to include both saprobic and ectomycorrhizal fungi, which provide carbon to non-photosynthetic liverworts (Bidartondo et al. 2003). The terrestrial orchid *Goodyera pubescens* also associates with members of this family and is known to switch fungal host species during times of stress (McCormick et al. 2006), suggesting that the mycorrhiza is keenly important for plants as environmental stress increases. This may further suggest that smaller, more dormancy-prone plants are more likely rely on their mycorrhizal fungi in these times.

Survival was not lower for dormant plants, but instead was lower for smaller plants, with probability of dormancy decreasing with increasing number of sprouts in the year preceding dormancy (Fig. 2). Lower survival and higher dormancy in smaller plants suggest that smaller plants are more sensitive to their immediate environments than larger plants. Smaller plants may need to devote a greater proportion of their resources to survival and sprouting than larger plants, and likely have lower resource reserves than larger plants, giving the appearance of a cost where there may really be a lack of resources. Thus, they are more likely to suffer from the effects of both poor microsite conditions and environmental stochasticity than plants with more ramets (Wijesinghe and Hutchings 1997, Hutchings 1999, Whigham 2004). Size variation was previously noted in *Cypripedium acaule* (Primack and Stacy 1998), considered a relatively distant relative of the study taxa within

genus *Cypripedium* (Cribb 1997), suggesting that it may be a universal feature of the life history biology of dormancy in this genus. Thus, the costs of dormancy previously noted in *Cypripedium parviflorum* (Shefferson et al. 2003), and potentially those in *Ophrys sphegodes* (Hutchings 1987), and *Coeloglossum viride* (Willems and Melsner 1998), may in fact be artifacts of smaller plants being more dormant than larger plants, and smaller plants having higher mortality.

Smaller plants may be more dormancy-prone at least partially because of the likely positive relationship between age and size. In genus *Cypripedium*, vegetative growth and reproduction are often slow, with the youngest plants only having one ramet and acquiring more over many years (Curtis 1943, Kull 1999). The growth of new ramets allows the acquisition of not only more resources, but potentially a more complimentary mix of resources (Stuefer et al. 1996, Wijesinghe and Hutchings 1997). Age also brings increases in reserves. Plants often rely on resource reserves to buffer against times of stress (Magda et al. 1993, Pennings and Callaway 2000, Cheplick and Chui 2001). Younger plants should have both fewer ramets and less resource reserves than older plants, suggesting a negative correlation between dormancy and age. However, some fitness components vary with age but not necessarily size in perennial plants, as do some measures of competitive ability (Lamb and Cahill 2006), suggesting that age-based variation in dormancy will need to be further explored.

Pronounced parallelism among taxa in both the probability of dormancy and transitions to dormancy suggest that dormancy is a response to common climatic cues for the taxa in this study. Because the study taxa are closely related (Cox 1995, Cribb 1997), and because the proximity of the populations eliminates among-taxon variation in dormancy due to macroclimatic and geographic trends, the same or similar genetics likely underlies the expression of dormancy in these taxa. Correlation with a variety of weather variables suggests that much of this synchrony is climate-driven (Shefferson et al. 2001, Kéry et al. 2005). Furthermore, since dormancy appears to be common to many, if not all, *Cypripedium* species (Primack and Stacy 1998, Shefferson et al. 2001, Brzosko 2002, Kull 2002, Kéry et al. 2005), dormancy may have a common evolutionary origin in genus *Cypripedium*. The fact that the hybrid taxon, *C. × andrewsii*, does not exhibit intermediate dormancy probabilities relative to its parent taxa does not detract from this hypothesis, because hybrids across species often display non-intermediate phenotypes (McDade 1990, Rieseberg et al. 2003), and because the ages of the plants and populations are not known. I suggest that further research address whether this parallelism occurs for taxa throughout the plant kingdom, from close relatives, such as the study taxa, to

plants in distant families. Since dormancy may function differently in non-clonal plants than in clonal plants, further research on dormancy should give preference to non-clonal, dormancy-prone taxa, which have not been studied well. Lastly, I suggest an emphasis on research into the genetics of dormancy, in particular to understand the nature of any genetic variation in this trait and provide clearer support for any trade-offs than studies of phenotypic variation in demographic parameters allow (Reznick 1985).

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