

ADULT WHOLE-PLANT DORMANCY INDUCED BY STRESS IN LONG-LIVED ORCHIDS

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Abstract. Dormancy is a condition in which an herbaceous perennial does not sprout for one or more growing seasons. To test whether dormancy is an adaptive response to environmental stress, we defoliated and shaded individuals of two rare geophytic orchids, *Cypripedium calceolus* and *Cephalanthera longifolia*, in five Estonian populations early in the growing season in 2002 and 2003. We also censused plants at the same time, and conducted one more census in 2004. Mark-recapture models were used to estimate the probabilities of dormancy (d , the complement to resighting, p), and apparent survival (ϕ). Apparent survival varied little by treatment, with *Cypripedium* and *Cephalanthera* surviving at 0.986 ± 0.014 and 0.974 ± 0.021 (mean \pm SE), respectively. In contrast, treatment impacted dormancy dramatically. For both *Cephalanthera* and *Cypripedium*, defoliated (def.) plants were most dormant (0.320 ± 0.055 and 0.095 ± 0.036 , respectively). However, while both control (cont.) and shaded (sh.) plants were roughly equally least dormant in *Cypripedium* ($d_{\text{cont.}} = 0.048 \pm 0.020$ vs. $d_{\text{sh.}} = 0.045 \pm 0.021$), the least dormant *Cephalanthera* had been shaded (0.182 ± 0.040 vs. $d_{\text{cont.}} = 0.206 \pm 0.050$). We conclude that dormancy may allow the plant to buffer stress in the short term without increasing mortality risk.

Key words: *Cephalanthera longifolia*; clonal plants; *Cypripedium calceolus*; defoliation; mark-recapture; plant size; shading; survival.

INTRODUCTION

Adult whole-plant dormancy, hereafter “dormancy,” is a condition in which the rootstock of a perennial herbaceous plant fails to produce annual shoots during the growing season (Lesica and Steele 1994). A common phenomenon among geophytes, plants whose perennating structures occur belowground, it has been noted in the families Asclepiadaceae, Asteraceae, Liliaceae, Orchidaceae, Ophioglossaceae, and Ranunculaceae, among others (Epling and Lewis 1952, Wells 1981, Lesica and Ahlenslager 1996, Alexander et al. 1997, Morrow and Olfelt 2003, Miller et al. 2004). Unlike seed dormancy, its name derives not from an absolute lack of metabolism and growth, which may still occur, but from the lack of aboveground sprout development and hence lack of photosynthesis and sexual reproduction. Though potentially an extreme form of ramet dormancy (Kull 1995), adult dormancy consists of the lack of sprouting over the entire root stock.

Dormancy may be maintained for multiple years, provided that the metabolic needs of the plant are met in some way, though the mechanisms are unclear (Wells 1981, Kull 2002).

Speculation about dormancy is fueled by continuing attempts to understand this phenomenon through only observational studies of wild plant populations, usually orchids. Through this approach, dormancy probability has been observed to correlate negatively with plant size (Kull 1995), and increase with fruit-set (Primack and Stacy 1998). Dormancy probability correlates with climatic variables in at least some geophytes (Shefferson et al. 2001, Kéry et al. 2005), and may correlate across sites and species (Miller et al. 2004). In longitudinal studies, dormancy is often associated with a decline in survival (Hutchings 1987, Willems and Melser 1998, Shefferson et al. 2003), particularly in short-lived species (Kull 2002). All of these observations suggest that dormancy occurs more often in times of stress and may occur at a cost to survival (Shefferson et al. 2003).

However, elucidation of costs and trade-offs requires direct experimentation (Reznick 1985). Here we pre-

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sent the first study to directly address the nature of dormancy through experimentation. We hypothesized that dormancy is a response to environmental stress, and that it is adaptive, testing these hypotheses by imposing stress on wild orchid populations of two species and tracking their demographic responses over three years.

METHODS

Study species and sites

Cypripedium calceolus L. and *Cephalanthera longifolia* (L.) Fritsch., in the family Orchidaceae, are globally widespread, though locally rare, geophytes occurring primarily in Europe and Asia (Summerhayes 1968, Dafni and Ivri 1981). They typically occur in northern forests, both coniferous and deciduous, and pollination is by deceit of insect vectors. In *Cypripedium calceolus*, the perennating structure is a creeping rhizome, with annual increments of 0.5–1.1 cm (Curtis 1954, 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). The rootstock of *Cephalanthera longifolia* is generally long and erect, extending only 0.1 cm/yr (Summerhayes 1968, Kull and Tuulik 1994). The mycorrhizal partners of *Cypripedium calceolus* are fungi in the poorly understood family Tulasnellaceae (Shefferson et al. 2005) that includes some fungi known to form both ectomycorrhizae and orchidlike mycorrhizae (Bidartondo et al. 2003). Nothing is known of the mycorrhizal partners of *Cephalanthera longifolia*, although an achlorophyllous relative, *C. austiniiae*, associates with ectomycorrhizal members of the fungal family Thelephoraceae (Taylor and Bruns 1997).

We included *Cypripedium calceolus* individuals from two Estonian populations, referred to as Muhu and Varangu, and *Cephalanthera longifolia* individuals from three populations, referred to as Kolga, Laelatu, and Sarapiku. These sites represent a diverse assemblage of woodland communities in western and central Estonia. The Muhu population lies in an alvar pine forest on the western island of Muhu, while the Varangu population lies in a central Estonian drained peatland spruce forest close to a chalk quarry. Kolga is a pine forest on limestone bedrock, Laelatu is a species-rich wooded meadow, and Sarapiku is a former pasture replaced by a sparse pine forest and juniper bushes. Light penetration at ground level reached 18–24% at *Cypripedium* sites, and 30–40% at *Cephalanthera* sites.

Experimental methods

In late May and early June of 2002, we divided portions of each population for manipulation and system-

atically divided plants into two treatments, shading (sh.) or defoliation (def.), plus a control (cont.) group, in roughly equal proportions within each population. Sprouts were considered physiologically of the same plant when they occurred within 20 cm of each other (Shefferson et al. 2001). Among *Cypripedium* populations, 45 plants were chosen in Muhu while 61 plants were chosen in Varangu, and these samples represented <20% of their widely dispersed populations. Among *Cephalanthera* populations, 48, 45, and 49 plants were chosen in Kolga, Laelatu, and Sarapiku, respectively, and we attempted to include all individuals in each of these three rather small populations.

All manipulations were conducted in May and June of 2002 and 2003, just as plants began to sprout, so as to minimize the amount of experimentally unrestricted photosynthesis possible for the plant. We censused all plants immediately prior to treatment in 2002 and 2003, and in early spring of 2004 (census data are summarized in the Appendix), also recording plant size as the number of sprouts per plant. Plants were also monitored over the remainder of the growing season in case of late sprouting, though no late sprouting occurred. All study plants were marked with uniquely identified stakes. In the shading treatment, a tepee-style frame made of two or three wooden stakes was placed over and around each plant. Black or green shade cloth was then wrapped around the plant so as to reduce the amount of light entering by at least 75%. These shade devices were left standing for two years and periodically checked and maintained over that time, even over previously shaded plants that failed to sprout in 2003. In the defoliation treatment, we fully removed each plant's aboveground shoots at soil level prior to full leaf elongation each year. In 2003, previously defoliated plants that did not sprout were left undisturbed.

Analytical methods

We conducted an open population mark–recapture analysis in program MARK (White and Burnham 1999) to estimate (1) resighting (p), an estimator of the probability of recensusing an individual conditional upon its survival, and (2) apparent survival (ϕ), an estimator of the probability of survival corrected for dormancy (Lebreton et al. 1992, Shefferson et al. 2001). In animal studies, apparent survival is confounded with emigration, a phenomenon that does not occur in plants. In studies of dormant-prone plants, resighting may be thought of as the product of the probability of sprouting given that a plant is alive in the current year, and of the probability of detecting it given that it has sprouted (Shefferson et al. 2001). Since we assumed that we found all individuals that had sprouted, the probability of dormancy could be estimated as the complement to the probability of resighting (i.e., $d = 1 - p$).

To assess treatment-induced, population- and species-level variation in these probabilities, as well as potential variation by initial plant size (i.e., the number of sprouts per plant prior to treatment in 2002), a global model was developed in which apparent survival and resighting varied with an interaction between initial plant size, population, and treatment (model $\phi_{\text{size} \times \text{population} \times \text{treatment}}$, $P_{\text{size} \times \text{population} \times \text{treatment}}$, abbreviated as $\phi_{\text{sz} \times \text{pop} \times \text{trt}}$, $P_{\text{sz} \times \text{pop} \times \text{trt}}$), with three treatments each in two populations of *Cypripedium* and in three populations of *Cephalanthera*, for a total of 15 groups. In a three-year study, apparent survival and resighting are only estimable for the first transition and second year, respectively (Lebreton et al. 1992), so we did not model time effects. Because initial plant size was modeled as an individual covariate, no goodness-of-fit test of the global model was possible (White and Burnham 1999). Since none of the populations occurred sympatrically, species effects were modeled as nested within population effects. We modeled apparent survival first, trying the following parameterizations reduced from the global model: size \times species (spc) \times treatment, size + (population \times treatment), size + (species \times treatment), size + population + treatment, size + species + treatment, size \times population, size \times species, size \times treatment, size + population, size + species, size + treatment, population \times treatment, species \times treatment, population + treatment, species + treatment, size, population, species, treatment, and constancy (c). Using the best-fit model up to that point (i.e., the model with the lowest small sample-corrected Akaike's Information Criterion [AIC_c] value), we then modeled resighting in the same manner, and used the new best-fit parameterization of resighting to remodel apparent survival. A total of 61 models were developed. Maximum likelihood estimation proceeded through the logit-link function, and initial plant size was standardized automatically by program MARK (White and Burnham 1999).

Inference in the mark-recapture approach was made through three methods. First, we compared models through the calculation of AIC_c values, which, when compared with other models, evaluate a candidate model's relative level of information loss from the original data set (Burnham and Anderson 1998). Under this criterion, the best-fit model is the model with the lowest AIC_c value, and all models within 2.0 AIC_c units are equally parsimonious with it. Second, inference was made with Akaike weights (w), which are the probabilities that a given model is correct, given that all relevant models have been evaluated. Akaike weights are additive over models, and we calculated cumulative Akaike weights to test the strength of particular parameterizations within apparent survival, and also within resighting. Third, we tested parameterizations

through likelihood ratio tests of nested models, which assess whether a factor explains a significant proportion of the data.

Parameters were estimated via model averaging to reflect model-selection uncertainty (Burnham and Anderson 1998). All estimates are presented \pm SE.

RESULTS

Apparent survival.—The best-fit model suggested variation by initial plant size in survival, but no variation by treatment, population, or species (model 1, Table 1). However, a likelihood ratio test revealed that initial plant size was not quite significant (model 1 [ϕ_{sz} $P_{\text{sz+pop+trt}}$] vs. model 3 [ϕ_{c} $P_{\text{sz+pop+trt}}$]: $\chi^2_1 = 2.97$, $P = 0.085$; Table 1), and models positing constant survival were equally parsimonious with the best-fit model (models 3 and 4, Table 1). A likelihood ratio test of treatment effects in apparent survival was not significant (model 14 [$\phi_{\text{sz+trt}}$ $P_{\text{sz+pop+trt}}$] vs. model 1 [ϕ_{sz} $P_{\text{sz+pop+trt}}$]: $\chi^2_2 = 0.04$, $P = 0.981$; Table 1). Cumulative Akaike weights most supported constant survival, but also suggested some support for variation by initial plant size and additive variation between species and initial plant size (top five parameterizations: $w_{\text{cum(c)}} = 0.302$, $w_{\text{cum(sz)}} = 0.174$, $w_{\text{cum(sz+spc)}} = 0.117$, $w_{\text{cum(spc)}} = 0.051$, $w_{\text{cum(sz+spc+trt)}} = 0.051$).

Model-averaged overall apparent survival was 0.974 ± 0.021 per year for *Cephalanthera*, yielding an expected remaining lifespan of 37.6 years. Model-averaged overall apparent survival was 0.986 ± 0.014 for *Cypripedium*, yielding an expected remaining lifespan of 71.7 years. Averaged across populations, *Cypripedium* plants had approximately equal survival across treatments ($\phi_{\text{cont.}} = 0.986 \pm 0.022$, $\phi_{\text{def.}} = 0.986 \pm 0.025$, $\phi_{\text{sh.}} = 0.986 \pm 0.023$; Fig. 1). In contrast, shaded plants survived at the highest rate among *Cephalanthera* populations, while control plants survived least ($\phi_{\text{cont.}} = 0.969 \pm 0.041$, $\phi_{\text{def.}} = 0.973 \pm 0.035$, $\phi_{\text{sh.}} = 0.979 \pm 0.032$; Fig. 1).

Dormancy.—Dormancy responded significantly to treatment (model 3 [ϕ_{c} $P_{\text{sz+pop+trt}}$] vs. model 9 [ϕ_{c} $P_{\text{sz+pop}}$]: $\chi^2_2 = 6.10$, $P = 0.047$; Table 1; Fig. 2). Resighting probability was consistently an additive function of initial plant size, population, and treatment in the best-fit and two of the next three most parsimonious models (Table 1), suggesting strong, consistent responses to treatment in parallel across populations and plants of different sizes. The next strongest parameterization, consisting of an additive relationship between population and treatment, was supported only 11% as much (top five parameterizations: $w_{\text{cum(sz+pop+trt)}} = 0.817$, $w_{\text{cum(pop+trt)}} = 0.089$, $w_{\text{cum(sz+pop)}} = 0.042$, $w_{\text{cum(pop)}} = 0.020$, $w_{\text{cum(sz+(pop \times \text{trt}))}} = 0.019$), though initial plant size was not quite a significant factor (model 3 [ϕ_{c} $P_{\text{sz+pop+trt}}$]

TABLE 1. Best 15 models of relationships among apparent survival (ϕ) and resighting (p) for *Cephalanthera longifolia* and *Cypripedium calceolus* plants censused in Estonia over three years and growing in three and two populations, respectively.

Model	ϕ	p	No. parameters	Deviance	ΔAIC_c	w
1	sz	sz + pop + trt	10	431.01	0	0.173
2	sz + spc	sz + pop + trt	11	429.69	0.78	0.117
3	c	sz + pop + trt	9	433.98	0.88	0.112
4	c	pop + trt	8	436.53	1.35	0.089
5	sz + spc + trt	sz + pop + trt	13	427.10	2.43	0.051
6	spc	sz + pop + trt	10	433.45	2.44	0.051
7	pop	sz + pop + trt	13	427.43	2.76	0.044
8	pop + trt	sz + pop + trt	15	423.26	2.76	0.044
9	c	sz + pop	7	440.08	2.82	0.042
10	sz \times spc	sz + pop + trt	12	429.69	2.89	0.041
11	sz + (spc \times trt)	sz + pop + trt	15	423.37	2.97	0.039
12	sz + pop + trt	sz + pop + trt	16	421.30	3.05	0.038
13	sz + pop	sz + pop + trt	14	425.66	3.12	0.037
14	sz + trt	sz + pop + trt	12	430.97	4.18	0.022
15	c	pop	6	443.60	4.28	0.020

Notes: Open-population mark-recapture analysis in program MARK (White and Burnham 1999) was used to compare a total of 61 models. ΔAIC_c for the i th model is calculated as $AIC_{ci} - \min(AIC_c)$. Akaike weight (w) indicates the level of support for a model on a scale of 0 (no support) to 1.0 (full support). Abbreviations include: AIC_c , small sample-corrected Akaike's Information Criterion; sz, initial plant size; spc, species; pop, population; trt, treatment; and c, constancy. The best-fit and most parsimonious models ($AIC_c \leq 2.0$) are presented in boldface type.

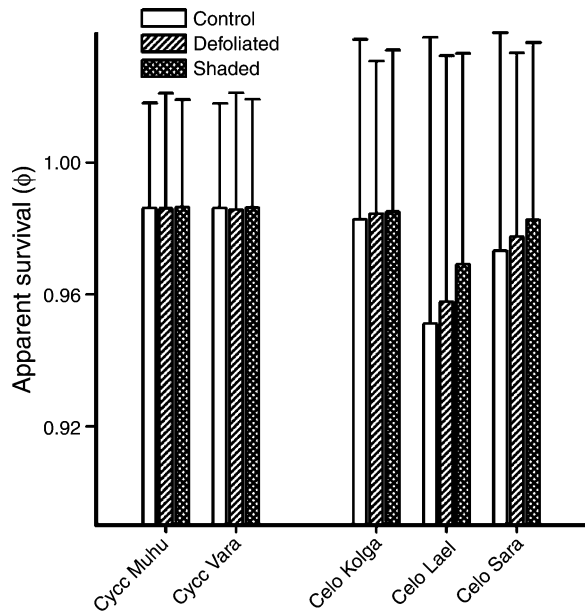


FIG. 1. Model-averaged apparent survival probability, ϕ , in response to shading and defoliation in 2002 and 2003 of *Cephalanthera longifolia* and *Cypripedium calceolus* plants growing in three and two populations, respectively, in Estonia. Abbreviations: Cycc, *Cypripedium calceolus*; Celo, *Cephalanthera longifolia*; Muhu, Muhu population; Vara, Varangu population; Kolga, Kolga population; Lael, Laelatu population; and Sara, Sarapiku population. Values are means + SE.

vs. model 4 ($\phi_c p_{pop+trt}$): $\chi^2_1 = 2.55$, $P = 0.110$; Table 1; Fig. 2).

Defoliation consistently resulted in increased dormancy. In *Cypripedium* populations, shaded plants were roughly as dormant as controls, but in *Cephalanthera* populations, shaded plants were noticeably least dormant (*Cephalanthera*: $d_{cont.} = 0.206 \pm 0.050$, $d_{def.} = 0.320 \pm 0.055$, $d_{sh.} = 0.182 \pm 0.040$; *Cypripedium*: $d_{cont.} = 0.048 \pm 0.020$, $d_{def.} = 0.095 \pm 0.036$, $d_{sh.} = 0.045 \pm 0.021$; Fig. 2). Overall, 0.236 ± 0.028 of *Cephalanthera* individuals per year experienced dormancy, as did 0.063 ± 0.015 of *Cypripedium* individuals.

DISCUSSION

Dormancy appears to be induced by stress and to buffer survival against it. This is a key condition to maintaining high fitness in long-lived organisms (Sæther and Bakke 2000). Cued by stress, dormancy may act as a "bet-hedge" against potentially catastrophic conditions, since clonal plants have developed life history strategies that may predict further environmental stress in order to "avoid" it (Sackville Hamilton et al. 1987). Though dormancy was associated with a survival cost in observational studies of other *Cypripedium* species (Hutchings 1987, Kull 2002, Sheffer et al. 2003), this does not appear due to a direct, immediate trade-off because survival did not consistently decrease and dormancy increase in response to treatment (Fig. 1). Thus dormancy does not seem to

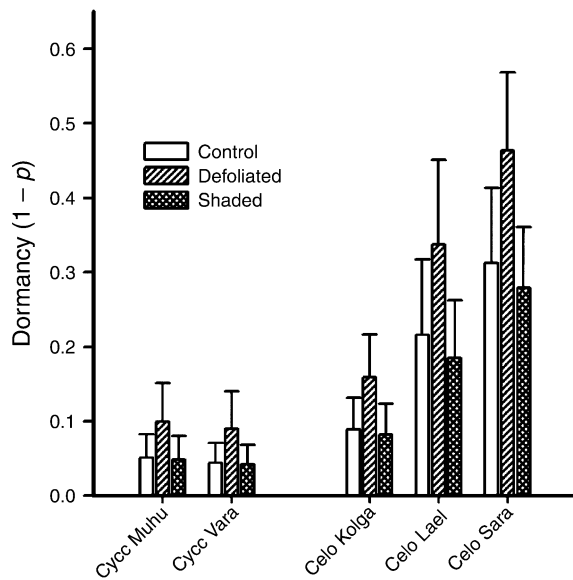


FIG. 2. Response of dormancy probability (d), estimated as the complement to model-averaged resighting (p), to shading and defoliation in 2002 and 2003 of *Cephalanthera longifolia* and *Cypripedium calceolus* plants growing in three and two populations, respectively, in Estonia. Abbreviations are as in Fig. 1. Values are means + SE.

correlate with mortality in the short term, but may do so in situations of consistent, long-term resource shortages.

Defoliation and shading led to unexpected differences among species. *Cypripedium calceolus* plants responded somewhat predictably, in that treated plants were as or more dormant than controls (Fig. 2). However, shaded *Cephalanthera longifolia* plants were generally less dormant than both controls and defoliated plants (Fig. 2), a result made even more striking, given that apparent survival was generally highest among these same shaded plants (Fig. 1). Though resource storage in previous growing seasons may be used for future sprouting and reproduction (Willems et al. 2001), stored resource use would need to differ markedly by species and treatment to result in the patterns we observed. Compensatory growth post-shading rather than post-defoliation suggests adaptation to poor light conditions, potentially including resource shifts toward aboveground tissue and away from root tissue and a stimulation of increased resource acquisition (Ryser and Eek 2000). However, acclimation to low light does not explain the unusual differences between shaded *Cephalanthera longifolia* and controls. The fact that initial plant size was a factor in the best-fit parameterizations for both apparent survival and resighting (model 1, Table 1) suggests that larger clonal plants may be more robust in dealing with environmental

stress than smaller plants (Caraco and Kelly 1991, Hutchings 1999), and that dormancy probability may decrease with increasing plant size.

In conclusion, our use of mark-recapture models allowed us to estimate the response to experimentally imposed environmental stress in two dormancy-prone plant species, and to separate this from effects on survival. These methods can accommodate a variety of life history conditions and other phenomena that create uncertainty in demographic parameter estimation, such as migration, dormancy, gender identification uncertainty, and observer error (Lebreton et al. 1992, Kéry et al. 2005, Nichols et al. 2004). Unfortunately, we could not legally maintain the experiment beyond the described end point due to conservation concerns. A longer study examining the mortality and dormancy effects of continued, year-after-year shading and defoliation may show increased mortality in shaded plants relative to controls over the long term, and would be a welcome contribution.

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APPENDIX

Responses of *Cypripedium calceolus* and *Cephalanthera longifolia* individuals among five Estonian populations to defoliation and shading in 2002 through 2004 can be found in ESA's Electronic Data Archive: *Ecological Archives* E086-170-A1.