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 ± 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 (dcont. = 0.048 ± 0.020 vs. dsh. = 0.045 ± 0.021), the least dormant Cephalanthera had been shaded (0.182 ± 0.040 vs. dcont. = 0.206 ± 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-
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 ectomycorrhizal and orchidlike mycorrhizae (Bidartondo et al. 2003). Nothing is known of the mycorrhizal partners of *Cephalanthera longifolia*, although an achlorophyllous relative, *C. austinae*, associates with ectomycorrhizal members of the fungal family Thelphoraceae (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-
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 $\phi_{sz\times pop\times trt}$ $P_{sz\times pop\times trt}$, abbreviated as $\phi_{sz\times pop\times trt}$ $P_{sz\times pop\times trt}$), 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 were 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, 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, parameters were estimated via model averaging to reflect model-selection uncertainty (Burnham and Anderson 1998). All estimates are presented ± 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 a significant factor (model 1 $\phi_{sz}$ $P_{sz\times pop\times trt}$ vs. model 3 $\phi_{sz}$ $P_{sz\times pop\times trt}$; $\chi^2 = 2.97$, $P = 0.085$; 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 $\phi_{sz\times trt}$ $P_{sz\times pop\times trt}$ vs. model 1 $\phi_{sz}$ $P_{sz\times pop\times trt}$; $\chi^2 = 0.04$, $P = 0.981$; 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: $w_{cum(sz)} = 0.302$, $w_{cum(sz) + spc} = 0.174$, $w_{cum(sz) + spc} = 0.117$, $w_{cum(spcl)} = 0.051$, $w_{cum(sz + spc + trt)} = 0.051$).

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 ($\phi_{cont} = 0.986 ± 0.022$, $\phi_{def} = 0.986 ± 0.025$, $\phi_{sh} = 0.986 ± 0.023$; Fig. 1). In contrast, shaded plants survived at the highest rate among Cephalanthera populations, while control plants survived least ($\phi_{cont} = 0.969 ± 0.041$, $\phi_{def} = 0.973 ± 0.035$, $\phi_{sh} = 0.979 ± 0.032$; Fig. 1).

**Dormancy.**—Dormancy responded significantly to treatment (model 3 $[\phi_{sz} P_{sz\times pop\times trt}]$ vs. model 9 $[\phi_{sz} P_{sz\times pop}]$: $\chi^2 = 6.10$, $P = 0.047$; 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: $w_{cum(sz + pop + trt)} = 0.817$, $w_{cum(pop + trt)} = 0.089$, $w_{cum(sz + pop)} = 0.042$, $w_{cum(pop)} = 0.020$, $w_{cum(sz + pop + trt)} = 0.019$), though initial plant size was not quite a significant factor (model 3 $[\phi_{sz} P_{sz\times pop\times trt}]$).
TABLE 1. Best 15 models of relationships among apparent survival (\(f\)) and resighting (\(p\)) for *Cephalanthera longifolia* and *Cypripedium calceolus* plants censused in Estonia over three years and growing in three and two populations, respectively.

<table>
<thead>
<tr>
<th>Model</th>
<th>(f)</th>
<th>(p)</th>
<th>No. parameters</th>
<th>Deviance</th>
<th>(\Delta AIC_c)</th>
<th>c</th>
<th>w</th>
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<tr>
<td>1</td>
<td>sz</td>
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<td>sz + pop + trt</td>
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<td>0.117</td>
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<td>c</td>
<td>pop + trt</td>
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<td>1.35</td>
<td>0.089</td>
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<td>sz + pop + trt</td>
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Notes: Open-population mark-recapture analysis in program MARK (White and Burnham 1999) was used to compare a total of 61 models. \(\Delta AIC_c\) for the \(i\)th model is calculated as \(2\min(AIC_c)\). Akaike weight (w) indicates the level of support for a model on a scale of \(AIC_c\) = 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.](image.png)

**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 (Søther 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-son 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
are as in Fig. 1. Values are means 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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**LITERATURE CITED**


**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.