

Timber harvest and *Cypripedium montanum*:  
Results of a long-term study on the  
Medford District BLM



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## Executive summary

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### Background

This report summarizes results from a long-term study of mountain lady's slipper (*Cypripedium montanum*) on the Medford District, Bureau of Land Management (BLM). This orchid is currently a Survey and Manage vascular plant species with the BLM and the U.S. Forest Service. Populations of this orchid were monitored from 1984 through 1998 in the Foothills Creek and Galls Creek watersheds of the Ashland Resource Area.

### Goals and Objectives

The overall goal of this project was to evaluate the effects of intensive forest management and document basic life-history traits of this poorly known species. Specific objectives included:

- # Compare populations of mountain lady's slipper with differing management histories for differences in characteristics such as number of stems, stem height, percentage of stems flowering, percentage of flowers setting fruit, and dormancy and mortality rates. Forest management included these four categories:
  - ▶ clearcut
  - ▶ shelterwood cut
  - ▶ second growth (1966 clearcut)
  - ▶ unmanaged forest (control)
  
- # Document and describe life-history process such as mortality, dormancy, and growth. Specific questions to address included, are plants more likely to go dormant if they flower or not? If they fruit or not? Are flowering plants likely to flower every year, or are they prone to becoming vegetative after blooming?

### Strengths and limitations

This is the first long-term study of mountain lady's slipper and represents the only carefully collected information on its response to forest management. It also represents the only demographic study of this rare orchid to date.

Results of this study must be interpreted carefully. Forest management treatments were not properly replicated for standard statistical tests, and the clearcut population was located 6 miles from the other populations. Therefore, the following conclusions are best stated as comparisons of populations rather than management actions.

### Conclusions

- # All measures of mountain lady's slipper abundance, size and reproduction varied substantially over the course of this long-term study. In fact, year to year variability was the most prominent pattern.

- # The population in the clearcut performed poorly compared to most of the other populations in most years. This population lost over 85% of its stems between 1985 and 1998, had relatively short stems, few flowers and low fruit set. Also, mortality was greatest in this population for the years 1991-94 (the period with demographic data), with 38% of the plants dying compared to about 10% in all other locations.
- # One of two control populations in an uncut forest stand also did not perform well, at least in some years. By 1998, it had lost 70% of its stems compared to 1985 and generally ranked low in stem height and percentage flowering.
- # The population in the shelterwood cuts, in contrast, out-paced the others in many regards. It generally increased or held steady its stem numbers, always was among the top two populations in terms of percentage of stems flowering, and ranked top in fruit set in several years and overall. The other populations generally were intermediate between these extremes.
- # Dormancy, the phenomenon of plants not appearing in some years, was the most notable life-history trait of mountain lady's slipper. Up to 30% of a population was observed to be dormant in any given year, suggesting that long-term studies of tagged individuals are necessary to document population trends in this species.

### **Summary**

The population of mountain lady's slipper in a clearcut declined dramatically and performed poorly compared to other populations in this study, especially seven years after forest harvest. One control population that was not harvested also declined. Plants in shelterwood habitat did well. Dormancy is a common state in this orchid species. The relatively poor growth, reproduction, and survival of *Cypripedium montanum* in a single clearcut does not provide conclusive evidence that forest harvest is detrimental to this species. Further studies will be necessary to resolve this with certainty. However, it may give land managers reason to be cautious and favor habitat protection or alternative forest harvest methods such as shelterwood cuts.

## Introduction

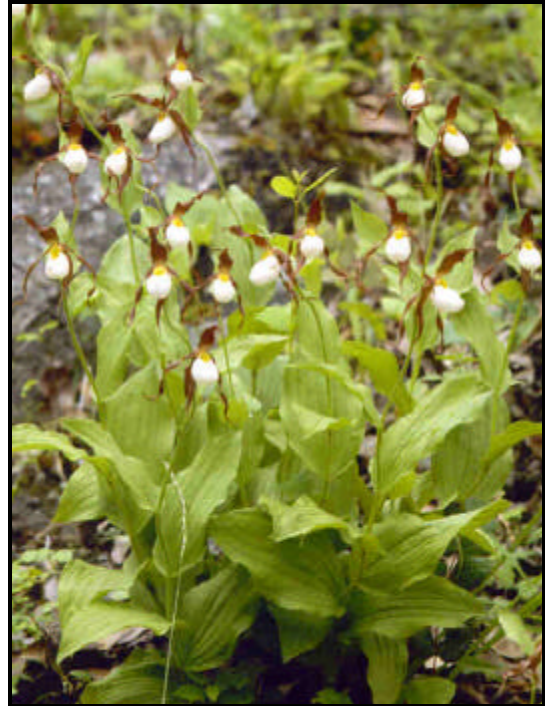
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### Background

*Cypripedium montanum*, mountain lady's slipper (Figure 1), is a rare plant of Oregon, California, Washington and Idaho. It occurs in coniferous forests on both sides of the Cascades Range. The species is currently a Survey and Manage species under the President's Forest Plan (USDA and USDI 1994). The Oregon Natural Heritage Program considers it a species of concern (List 4) (ONHP 1998). A study to evaluate the effects of intensive forest management and some aspects of the species life history was initiated in 1984 by the Medford District, Bureau of Land Management (BLM) in the Foothills Creek watershed. This report represents a summary of results from data collected over 15-years, from 1984 through 1998.

### Species biology

*Cypripedium montanum* has a relatively large geographic distribution. It is found in all northwestern states and Canadian provinces and can thrive in full sun or shade (Luer 1975). Most populations are small, with fewer than 10 plants each (Seevers and Lang 1999). In southwestern Oregon, the populations occur in forests with  $\geq 60\%$  canopy closure and dominated by *Pseudotsuga menziesii* (Douglas-fir), *Pinus ponderosa* (Ponderosa pine), and hardwood trees such as *Arbutus menziesii* (madrone) and/or *Lithocarpus densiflora* (canyon live oak). The species is able to occupy a wide variety of habitats and soil types, including serpentine and limestone (Seevers and Lang 1999). Plants are short-rhizomatous, can produce one to several flowering stems (each with 1-3 flowers), and reproduce by seed. Seeds of many orchid species germinate and grow only after contact with mycorrhizal fungi (e.g., *Rhizoctonia*) (Wells 1981, Sheviak 1990), and seedlings may exist in a subterranean, fungus-dependent state for several years prior to leaf emergence (Case 1987). Very little is known about the life history of *C. montanum* and its response to forest disturbance, including timber harvest and fire.



**Figure 1.** *Cypripedium montanum* (mountain lady's slipper) in the Foothills Creek watershed.

## **Goals and objectives**

The goals of this study are outlined in a monitoring plan for the species in the Foothills Creek Timber Sale (Seevers, 1982). The primary goal is to examine long-range effects of intensive forest management on *Cypripedium montanum* to aid in its management and status determination. A secondary goal is to document the species basic life-history.

Specific objectives targeted for this report include the following:

- Evaluate populations with differing management histories (e.g., clearcut, shelterwood cut, second growth, or unmanaged forest) for differences in characteristics such as number of *Cypripedium montanum* stems (ramets), stem height, percentage of stems flowering, and percentage of flowers setting fruit.
- Compare demographic traits of these populations to identify differences in the rates at which plants die or go dormant, and how often vegetative plants become reproductive.
- Document and describe life-history process such as mortality, dormancy, and growth. Specific questions to address include, are plants more likely to go dormant if they flower or not? If they fruit or not? Are flowering plants likely to flower every year, or are they prone to becoming vegetative after blooming?

## Methods

### Study sites

All of the sites included in this study were in the upper Right Fork Foothills Creek watershed, except one site in the nearby Galls Creek watershed (Table 1), south of Interstate 5 in mountainous country between Grants Pass and Jacksonville. Plots were staked in the field as transects along which permanent subplots were marked and resampled every year or several years. To compare populations with different forest histories, eight plots were established in 1984 in four habitat management types. These types included:

- ▶ clearcut
- ▶ shelterwood
- ▶ second growth (1966 clearcut)
- ▶ unmanaged (control)

Three plots (numbers 1-3) were located in neighboring shelterwood units. These partial forest stand cuts were harvested in May, 1983 and burned in early 1984 prior to placement of experimental plots. One of the plots also received a second partial harvest in 1994. Two plots (5 and 5A) were established in a second growth forest that had been clearcut in 1966 and replanted in 1970. One plot (no. 6) was placed in a recent clearcut that was harvested in early 1984 (again, prior to plot establishment) and never burned. Plots 4 and 7 were placed in uncut, unmanaged forests to serve as

**Table 1.** Summary of background information on *Cypripedium montanum* study populations. All populations are in the Right Fork Foothills Creek watershed, except #7 (control), which is about 6 miles away in the Galls Creek watershed.

population type	plot(s)	history	location	aspect	slope (range)	elevation (ft)	soil series
clearcut	6	clearcut Jan.-Mar., 1984 never burned planted Mar., 1986	T37S R3W S21 NE1/4 NE1/4	NE	31° (29°-32°)	3020- 3200	Caris- Offenbacher, gravelly loam
shelter- wood	1-3	1st entry Mar.-May 1983, slash burned & planted early 1984. 2 <sup>nd</sup> entry (plot 3 only) Jan. 1994	T37S R4W S27 S1/2 NW1/4	N to E	26° (16°-34°)	2340- 2720	" "
second growth	5 & 5A	clearcut July, 1966, planted 1970	T37S R4W S27 SW1/4 SW1/4	NE	25° (25°-25°)	3410- 3580	" "
control	4	uncut, unmanaged	T37S R4W S27 NE1/4 SW1/4	N	33° (27°-41°)	2560- 3000	" "
control	7	uncut, unmanaged	T37S R4W S21 NE1/4 SW1/4	E to ESE	28° (25°-32°)	2560- 2840	Vannoy, silt- loam

experimental controls. Plots 1 through 5, 5A, and 7 were located within one mile of each other in the Right Fork Foothills Creek watershed (T37S R4W Sec. 21 and 27), while plot 6, in the clearcut, was located about six miles to the east in the Galls Creek watershed. Plots 1-6 were on gravelly loam soils (Caris-Offenbacher series), but plot 7 was on a silty loam (Vannoy series). In addition, all plots were on east to northeast slopes, and plot 7 was partly on an east-southeast slope as well (Table 1).

### ***Plot sampling***

The following is a paraphrased description of the plot layout and sampling methodology from a 1984 report (Mumblo, Seevers, and Prusz 1984):

Permanent plots (transects) were located in each population area. The plots were set up by measuring baselines and placing a red-painted metal stake at each end of the line. The baseline tape was stretched between the metal stakes with the tape as close to the ground as possible. Subplots were established to mark the location of each plant or group of plants within the plot, and these subplots were marked with a metal peg and tag embossed with the subplot number. Subplot locations were recorded with the distance along the baseline, perpendicular distance from the baseline, and bearing of the subplot to the baseline.

Several variables were collected from each plot in each sampling year. In most years, the plots were visited twice, once in early summer to catch flower production, and once in late summer to measure fruit production. Variables measured in the early sample included slope, aspect, light (open, filtered, or shade), associated species, percentage cover of herbs, shrubs and trees, *Cypripedium montanum* stem height (measured to the top of leaves), phenology (flowering or vegetative), number of flowers, and vigor (poor, good, or excellent). During the second sample (not conducted in 1988), the number of fruits per stem were recorded. Some of these variables were too subjective to include in the analyses, and these are discussed below. Also, measurements of *C. montanum* for individual subplots were for stems, not individual plants. For this reason, much of the data reported are relevant to number, size, and reproduction of ramets, not individual plants (genets). However, an attempt to collect data on individual genets was initiated in 1990, and provided important information on basic demographic processes, especially from 1991-94. These data are evaluated separately.

### ***Data availability and evaluation***

Most data were originally entered into Aspen, a computer database. For this analysis, data were exported from Aspen in ASCII format and imported into QuattroPro, a spreadsheet software. The following variables were selected for statistical analysis:

- ▶ Percentage change in number of stems per plot from 1985. 1985 was selected as the baseline year for these measurements because many

plots were added after the 1984 season. This variable measures average population growth or decline.

- ▶ Average stem height, a measure of overall plant size.
- ▶ Percentage of stems flowering. This is a measure of the amount of the population that is reproductive.
- ▶ Flowers per stem.
- ▶ Demographic parameters, such as rates of mortality, dormancy, and growth.

The first four variables were selected to provide contrasts among populations related to population trends, plant size, population structure, and reproductive success.

Data available in Aspen included samples from 1984 through 1991. Data from later years were present as raw data sheets. Some data sheets from years that had not been entered had been lost (such as all data for plot 3, 1992). Because of this incomplete data entry and partial data loss, records from 1992 and 1993 were omitted from most analyses, with the exception of the demographic analyses. Also, data for some variables were not recorded in some subplots and some years, creating missing data for several variables. Some variables that were collected by field investigators were not analyzed in this report because the investigators themselves noted their subjectivity, lack of reliability, and tendency to differ among investigators. These variables included plant vigor, light reaching the plots, and percentage cover of associated species. I displayed percentage cover of herbs, shrubs and trees over time, but without any statistical analyses.

Starting in 1990, field investigators made efforts to record the location of stems and clusters of stems within the subplots by noting their distance and bearing from the subplot center stake. This location information made it possible for me to go back through the original data sheets and track individual plants through time. In order to make these records as complete as possible, I used all available data sheets. The most intensively collected demographic data were compiled annually from 1991 through 1994, and again in 1998. Some efforts to track individuals were either confusing or uncertain, and these individuals were omitted. Also, lost data from plot three in 1992 were considered missing and omitted from the analyses. Even with this partial data loss, a substantial number of individual plants were recorded for each population-type (see Table 5 for 1992-94). Each individual in each year was classified into one of the following categories:

- ▶ reproductive ( $\geq 1$  flower)
- ▶ vegetative (leaves only)
- ▶ dormant (not appearing above-ground in a given year, but present the year before and in any later year)
- ▶ dead (absent at least in 1994 and 1998, the last year of observation)

Note that this definition of dormancy requires plants to be observed above ground after dormancy. This definition ignores the possibility that some plants could go dormant and then die the following year. Therefore, estimates of dormancy used here are conservative, and ignore mortality of dormant plants. Also, plants that were missing in 1994 and again in 1998 were considered dead, but a small percentage of these might have been dormant in both years. Therefore, mortality rates may be slightly over-estimated.

For purposes of statistical tests, each plot was classified by forest management history and grouped accordingly. Specifically, plots 1-3 were considered one population because of their close proximity to one another, and similar and non-random treatment assignment. Plots 5 and 5A were considered one population because they were placed adjacent to one another in the same second growth stand. Plots 4 and 7, however, were not pooled even though they were both considered uncut controls because of the differences in habitats between them (e.g., different aspects, soil types, subwatersheds). See table 1 for a summary of plot assignment to population-type.

### **Statistical tests**

It is important to note here that the procedures described below test for differences between populations, not among the treatments per se, because the treatments themselves were not replicated (and where they were, they were not done so independently). Instead, a single treatment was applied and all plants within the population were included by sampling subplots. Therefore, the subplots represent pseudo-replicates (Hurlbert 1984) of the treatments, and these data should not be used to test for forest treatment effects. They can, however, be used to test for “population” effects by asking, “do all the populations behave the same?” Whether the populations differ due to natural variation or differences in management history is up to the reader to decide and cannot be answered here statistically.

### **Repeated measures**

Repeated measures Analysis of Variance (ANOVA) was used to evaluate differences among populations and years. This test was used to evaluate data on percentage change in number of stems per plot, stem height, percentage of stems flowering, and number of flowers per reproductive stem. Each variable was tested independently. Subplots were considered to be independent experimental units. The null hypothesis for each variable was that all populations and years were equal. Repeated measures ANOVA was selected for these variables because the same plots were sampled for several years, and differences in *Cypripedium montanum* population responses to the different forest treatments could take years to develop. These tests were performed in SAS (SAS 1986), a statistical computer software package. One response variable, percentage change in stems, had no missing values from 1986 through 1998, and was therefore suitable for SAS’s “proc glm.” However, the other three variables had missing

values and were tested with the “proc mixed” procedure, which can handle some omitted data. These variables met the test’s assumptions of equal variances and normal (or symmetrical) distributions, except for percentage change in number of stems, which was log-transformed prior to analysis. An unstructured model of covariance was assumed for these (proc mixed) repeated measures analyses after testing several covariance structures (including simple, toepel and autoregressive) to maximize Akaike’s information criterion.

### **Chi-square and binomial tests**

Some tests were performed by using individual plants or flowers rather than subplots as experimental units. Two types of tests were performed, tests to compare populations and tests which investigated basic demographic processes without regard to population or year.

Tests aimed at detecting population-level differences addressed the following specific questions:

- ▶ Does fruit-set (frequency of flowers forming fruits) vary from population to population, and does this effect vary from year to year?
- ▶ Does the frequency with which plants become dormant differ among populations?
- ▶ Do populations differ in the growth rate of vegetative plants to reproductive status?
- ▶ Does the clearcut population differ from the other in observed death rate?

Percentage flowers forming fruits was calculated by dividing the total number of fruits produced in a population by its total number of flowers. In this case, a chi-square ( $\chi^2$ ) test was performed for each year of data (1984, 85, 86, 90, 91, 94, and 98), and for all data pooled (equivalent to a weighted mean), to test the null hypothesis that the number of flowers forming fruits is independent of population. Population effects were also tested by  $\chi^2$  to examine the rate at which plants become dormant and the frequency with which vegetative plants become reproductive. Low sample sizes from the clearcut and shelterwood cut for the latter test forced me to compare only the second growth population with the two unmanaged populations. Also, mortality rates could not be tested by  $\chi^2$  because of a very low expected number of deaths in the clearcut population. Instead, mortality rates in this group were compared to those in the other populations combined by estimating the probability that the observed number of deaths in the clearcut would be expected given the death rate measured in the other groups under a binomial distribution. The last three tests described here used counts pooled across years, thus combining data from 1991-92, 1992-93, and 1993-94.

Tests of basic demographic processes were performed with  $\chi^2$  analyses to address these questions:

- ▶ Are plants more likely to go dormant after they are reproductive or vegetative?
- ▶ Compared to non-dormant plants, when dormant plants recover, are they more likely to be reproductive or vegetative?
- ▶ Are vegetative plants more likely than reproductive plants to reappear the following year as reproductive?
- ▶ Is death more likely after a year of being vegetative or flowering?
- ▶ Are reproductive plants that fruit more likely to die than non-fruiting plants?

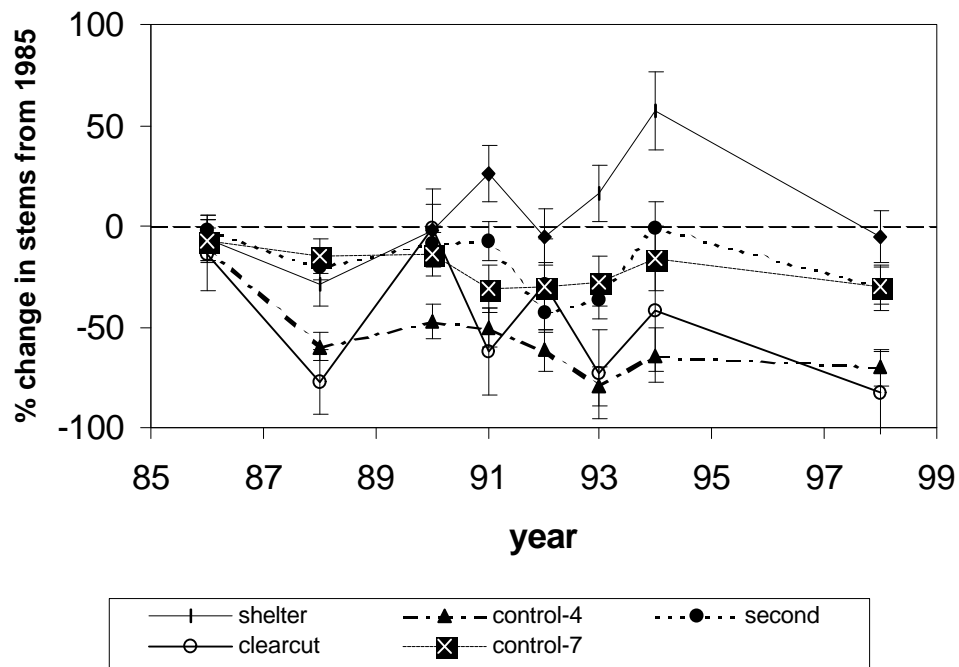
These tests were conducted after pooling counts across all treatments and years with reliable data (1991-94). Therefore, they do not compare populations or years, but treat the observations as coming from one large population.

## Results

### Population effects

#### Changes in number of stems

Percentage change in mean number of stems differed from population to population and year to year in a complex statistical interaction (Table 2). Put another way, the effect of population-type on stems depended on the year of observation. For example, there was no difference between populations in the percentage change in stems in 1986 (shortly after the clearcut and shelterwood disturbances), but there were significant differences in every year after that, except 1992 (Table 2). Most populations lost stems relative to their 1985 levels, except for the population in the shelterwood habitat, which had three years with relative gains. By 1998, however, it had about the



**Figure 2.** Percentage change in mean number of stems per subplot in five population-types over a 13 year period. Vertical lines represent 2 standard errors.

same number of stems as at the beginning of the study. The clearcut population posted the greatest overall losses, dropping 82% of its stems by 1998. The control population with plot 4 (control-4) declined in 1988 and stayed relatively low through 1998, when it had lost 70% of its original stems. The other populations had intermediate declines and did not differ from the shelterwood cut in 1998. In this

analysis, the losses in control-4 and the clearcut were significantly lower than the losses in the other populations, but not significantly different from each other.

**Table 2.** Repeated measures ANOVA of percentage change in number of stems per plot. Data were log-transformed prior to analysis. All measures (Wilks' lambda, Pillai's trace, Hotelling-Lawley trace, and Roy's greatest root) of population by treatment interactions were highly significant ( $P < 0.0001$ ), suggesting that differences between populations were not consistent among years. Wilks' lambda is shown below. Results are from SAS proc glm.

	F	Num DF	Den DF	Pr > F
Population	6.85	4	163	0.0001
Year	16.3634	7	157	0.0001
Year*population	3.3443	28	567	0.0001
Error			163	

One-way ANOVA for each year						
Year	DF	Type III SS	Mean Square	F Value	Pr > F	
86	4	0.25475951	0.06368988	0.33	0.8602	
88	4	6.13215583	1.53303896	7.72	0.0001	
90	4	3.69636457	0.92409114	3.63	0.0073	
91	4	5.51704820	1.37926205	4.80	0.0011	
92	4	2.15516426	0.53879106	1.76	0.1386	
93	4	8.35051362	2.08762841	7.78	0.0001	
94	4	9.14838809	2.28709702	7.52	0.0001	
98	4	6.95077092	1.73769273	6.64	0.0001	

### Stem height

Mean height of stems differed significantly among the populations, but this difference varied with year of observation. Repeated measures ANOVA detected a very strong interaction between population-type and year for stem height (year x population interaction  $P \leq 0.0001$ , Table 3). In 1984, the first year of the study, plants in the clearcut population were tallest and those in the second growth forest were shortest (Figure 3). By 1986, however, clearcut plants were shortest and plants in the control-7 population were tallest, with the other populations of intermediate height. Relative rankings of populations varied substantially after that, but control-7 plants tended to remain tallest, and clearcut plants were shortest, especially in 1991, 1994, and 1998.

### Percentage flowering

The percentage of stems with flowers also differed significantly among populations and years in a significant year x population interaction (repeated measures ANOVA,  $P = 0.0033$ , Table 3). In 1984 and 1985, the clearcut and shelterwood populations had higher proportions of reproductive stems (>60%) than the second growth and control populations (25–37%). But by 1998, all of the populations had between 21% and 31% flowering stems, showing that the clearcut and shelterwood populations either lost reproductive stems or gained vegetative stems, while the other populations maintained a more stable structure.

### Flowers per reproductive stem

The average number of flowers produced by individual reproductive stems varied substantially from year to year and site to site (year by population interaction  $P=0.0221$ , Table 3). In 1985, 1986, and 1990, plants in clearcuts produced the largest number of flowers (1.7–1.9 per stem), but after 1990 they produced the fewest or were tied with other populations (such as control-7 in 1998) for the poorest flower production (1.0 flowers per stem) (Figure 5). In 1991 and 1998, plants in the shelterwood population ranked highest in flower production, and nearly tied with clearcut plants in 1986 and 1988.

**Table 3.** Repeated measures ANOVAs for the effect of population and year on mean stem height, percentage of plants flowering, and number of flowers per reproductive stem. Results from SAS proc mixed. Note that there is a significant ( $\alpha \leq 0.05$ ) year x population interaction in each test. Numerator degrees of freedom (NDF) are the same for each test, but denominator degrees of freedom (DDF) differ due to missing data values.

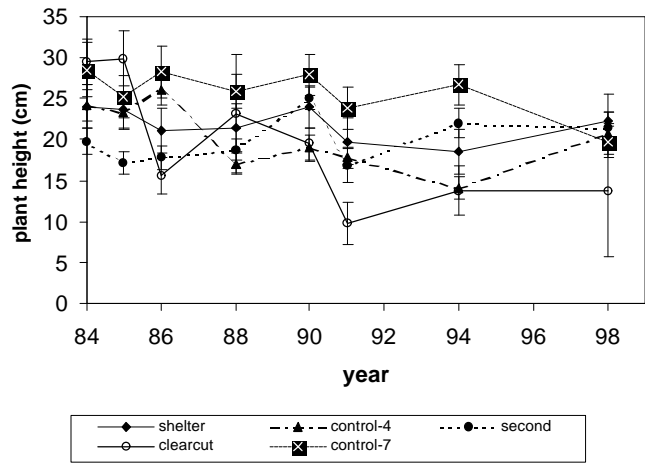
Effects	NDF	stem height			% flowering			flowers per reproductive stem		
		DDF	F	P	DDF	F	P	DDF	F	P
Population	4	168	3.11	0.0167	168	5.55	0.0003	132	2.22	0.0705
Year	7	168	3.97	0.0005	168	5.23	0.0001	132	6.71	0.0001
Year X pop'n	28	168	3.43	<b>0.0001</b>	168	2.03	<b>0.0033</b>	132	1.72	<b>0.0221</b>

### Fruit formation

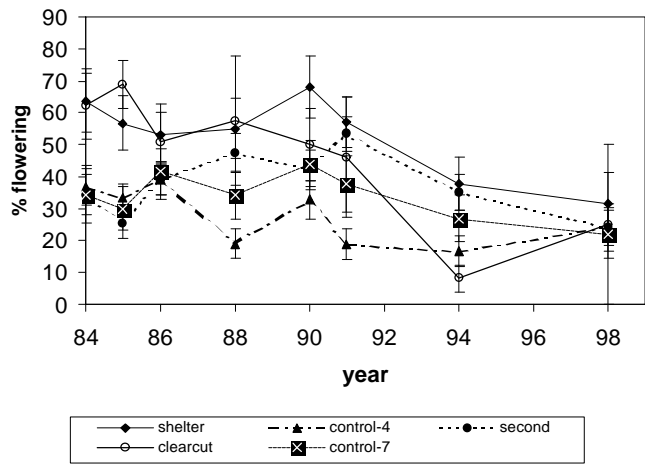
The percentage of flowers forming fruits differed significantly among populations in every year of this study in which statistical tests could be performed (data on fruit set were unavailable for 1988, and flower numbers were insufficient in the clearcut and control-7 for a  $\chi^2$  test in 1998). Flowers in clearcuts were frequently poor producers of fruit from 1985 on, especially in 1985, 1986, 1990, and 1998 (Figure 6a), and across all years pooled (Figure 6b). Fruit-set in this population was approximately 10% when flowers from all years were pooled. Fruit-set completely failed in the clearcut population in 1986 and 1998. Flowers in shelterwood cuts tended to have the highest fruit-set, especially in 1984, 1991, and 1994, and overall (49%, Figures 6a & b). Both of the control populations out-fruited the shelterwood population in 1988, and the highest fruit-set ever observed (>80%) occurred in control-7 in that year. The control-4 population produced no viable fruit in 1994, and the second growth population yielded intermediate fruit-set in most years (Figure 6a).

**Table 4.** Significance values for contingency table analyses ( $\chi^2$  tests) of fruit-set by population-type for several years and with data pooled across years.

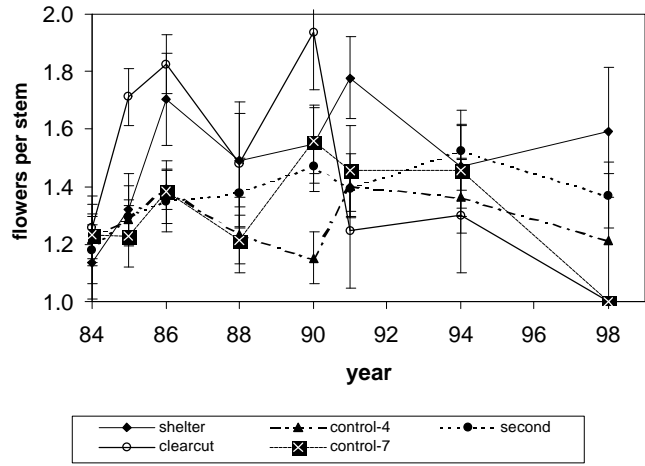
Year	P
1984	0.0011
1985	0.0001
1986	0.0001
1990	0.0001
1991	0.0001
1994	0.0001
pooled	0.0001



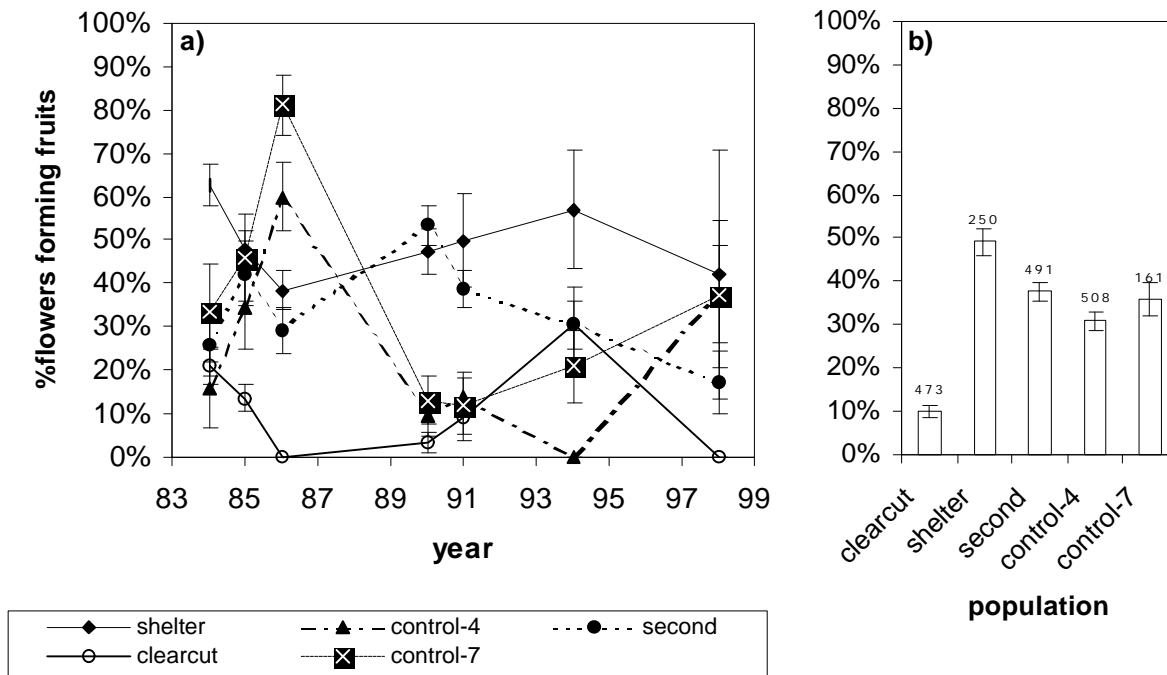
**Figure 3.** Average stem height of *Cypripedium montanum* as a function of year of observation and population-type.



**Figure 4.** Percentage of stems with flowers as a function of year of observation and population-type.



**Figure 5.** Number of flowers per reproductive stems as a function of year of observation and population-type.



**Figure 6.** Percentage of flowers forming fruits within five *Cypripedium montanum* populations in a) seven individual years, and b) all years pooled. Results of individual  $\chi^2$  tests for population effects were significant ( $P < 0.002$ ) for all years tested, as well as all years pooled (Table 4). The cumulative total number of flowers in each population are shown above bars in b). Vertical lines represent 2 standard errors.

### Mortality

Plant mortality was substantially higher in the clearcut population than the other populations. In the clearcut, the 1991-1994 mortality rate was 38%, while in the other populations mortality ranged from 9% to 10%, and averaged 9.4% (Figure 7). The probability that 6 (or more) of 16 plants in the clear cut would die given a prevailing mortality rate of 9.4% was very low ( $P = 0.0024$ ), suggesting that the clearcut population differed significantly from the others.

### Dormancy rates

Rates at which plants became dormant did not differ among the control populations and the second growth ( $P = 0.1132$ ). Note that the clearcut population was not included due to the small number of individuals there and the very low (<5) expected number of dormant plants. Dormancy rates ranged from 10% to 20% in these populations. In the clearcut, 1 out of 10 plants went dormant in the same time period.

## Growth rates

In a comparison ( $\chi^2$  test) of rates of growth from vegetative to reproductive states in second growth and control populations, no effect of population-type was detected ( $P=0.353$ ). Note that neither the clearcut nor the shelterwood populations were included in this analysis due to low numbers of vegetative plants. These annual rates of change from vegetative to reproductive stages ranged from 15% in the control-4 population to 23% in the second growth population.

## Demography and life-history

### Dormancy

One of the most prominent aspects of the life-history of *Cypripedium montanum* is the tendency of individuals to become dormant for one or more years. The years for which reasonably reliable estimates of dormancy can be obtained include 1992, 1993, and 1994. Estimates from each year and each population suggest that the percentage of plants dormant at any given time can vary from year to year and place to place. Dormancy ranged from a high of over 30% in the shelterwood population in 1993 to a low of 0% in the clearcut in 1994 (Table 5). Among the years, dormancy overall ranged from 7% to 21%. This pattern of dormancy suggests that in any given population and year, estimates of the number of plants present will habitually undercount the true population size by as much as 30%. Also, 23% of the dormant plants in a given year remained dormant the following year (Table 6).

**Table 5.** Estimated dormancy in *Cypripedium montanum* populations. Values are percentage of plants dormant in each year (followed by number of dormant individuals/total plants in each population).

<b>population-type</b>	<b>1992</b>	<b>1993</b>	<b>1994</b>
clearcut	11% (1/9)	9% (1/11)	0% (0/11)
shelterwood	7% (2/28)	30% (7/23)	9% (2/22)
second growth	26% (22/85)	24% (21/89)	6% (6/97)
uncut4 (plot 4)	13% (10/78)	21% (15/72)	11% (7/62)
uncut (plot 7)	9% (4/43)	14% (7/49)	4% (2/53)
<b>Pooled</b>	<b>16% (39/243)</b>	<b>21% (51/244)</b>	<b>7% (17/245)</b>

The frequency of dormant plants suggests important questions about the basic demography of *Cypripedium montanum*, centered on the role of dormancy in the species population dynamics. These questions were articulated in the Methods section (pages 7 & 8), and concern the rate at which vegetative and reproductive plants go

dormant, and recovery of dormant plants. All of these demographic tests used data presented in Table 6 grouped in specific ways, and, in some cases, with additional information on numbers of fruiting plants.

**Table 6.** Counts of individuals and percentages of individuals changing from one demographic state to another in one year, with all individuals pooled across population-types and years (1991-1994). Note that there are no estimates for dormant plants dying, since dormancy is defined by absence followed by presence.

		state at time <i>t</i>					
		contingency table (counts)			percentages		
		vegetative	reproductive	dormant	vegetative	reproductive	dormant
state at time <i>t</i> +1	vegetative	171	42	63	56%	19%	65%
	reproductive	51	127	12	17%	59%	12%
	dormant	46	33	22	15%	15%	23%
	dead	40	15	--	13%	7%	--
	sum	308	217	97			

**Are plants more likely to become dormant if they are vegetative or reproductive?**

The  $\chi^2$  statistic for this test was not significantly greater than expected ( $P=0.812$ ), suggesting that vegetative and reproductive plants reach dormancy at equal rates. Indeed, 15% of both types of plant became dormant (see Table 6).

**Are dormant plants less likely than non-dormant plants to come back reproductive?**

Dormant plants were much less likely than non-dormant plants to return the following year as reproductive plants ( $P<0.0001$ ). Overall, only 12% of dormant plants returned as reproductive plants, while 46% of non-dormant plant flowered the following year.

**Are reproductive plants more likely to go dormant if they fruit or not?**

This question addresses the notion that fruiting may be costly to a plant, forcing it to become dormant the following year. The test seems clear, however, that fruiting had no impact on the rate at which flowering plants went dormant. A total of 19% (19 of 101) of fruiting plants became dormant, and 13% (14 of 112) of non-fruiting (but flowering) plants went dormant, and these rates of dormancy do not differ statistically ( $P=0.204$ ).

Although the current state of a plant does not appear to be a good predictor of dormancy the following year, i.e., flowering or fruiting do not seem to cost the plants so many resources that they go dormant, it does appear that dormant plants are much more likely to be vegetative than reproductive plants when they recover. Other demographic questions include the following:

**Are reproductive plants more likely than vegetatives to return as reproductives?**

Reproductive plants are significantly more likely than vegetative plants to emerge the following year as flowering plants, and vice versa ( $P \leq 0.0001$ ). A total of 56% of vegetative plants remained vegetative the following year, while 59% of reproductives flowered again, suggesting a strong tendency for plants to re-emerge in the same state.

**Are plants more likely to die if they are vegetative or reproductive?**

Vegetative plants were far more likely to die the following year than reproductive plants ( $P \leq 0.0001$ ). A total of 39% of vegetative plants died while only 7% of reproductive plants failed to return.

## Discussion

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### **Summary of differences between populations**

All measures of *Cypripedium montanum* abundance, size and reproduction varied substantially over the course of this long-term study. In fact, year to year variability was the most prominent pattern. All tests suggested that differences between populations changed from year to year. Even so, some general differences between the populations were discernible. The population in the clearcut, in particular, performed poorly compared to most of the other populations. This population lost over 85% of its stems between 1985 and 1998, had relatively short stems and few flowers after the first seven years of the study, and went from a high percentage (>60%) of stems flowering at the beginning of the study to less than 30% in 1998 (and, in 1994, posted the lowest percentage flowering observed for all populations over the course of the study). This population also had dramatically lower overall fruit-set than the other populations, with 10% of the flowers forming fruits compared to 30-50% elsewhere. Finally, mortality was greatest in this population for the years 1991-94 (the period with demographic data), when 38% of the plants died compared to about 10% in all other locations. It should be emphasized here that although the clearcut population was in an area with slope, aspect, elevation, and soil type similar to the other sites, it was located six miles east in a different subwatershed. Incongruities between the clearcut population and the others could reflect differences in habitat not associated with timber harvest.

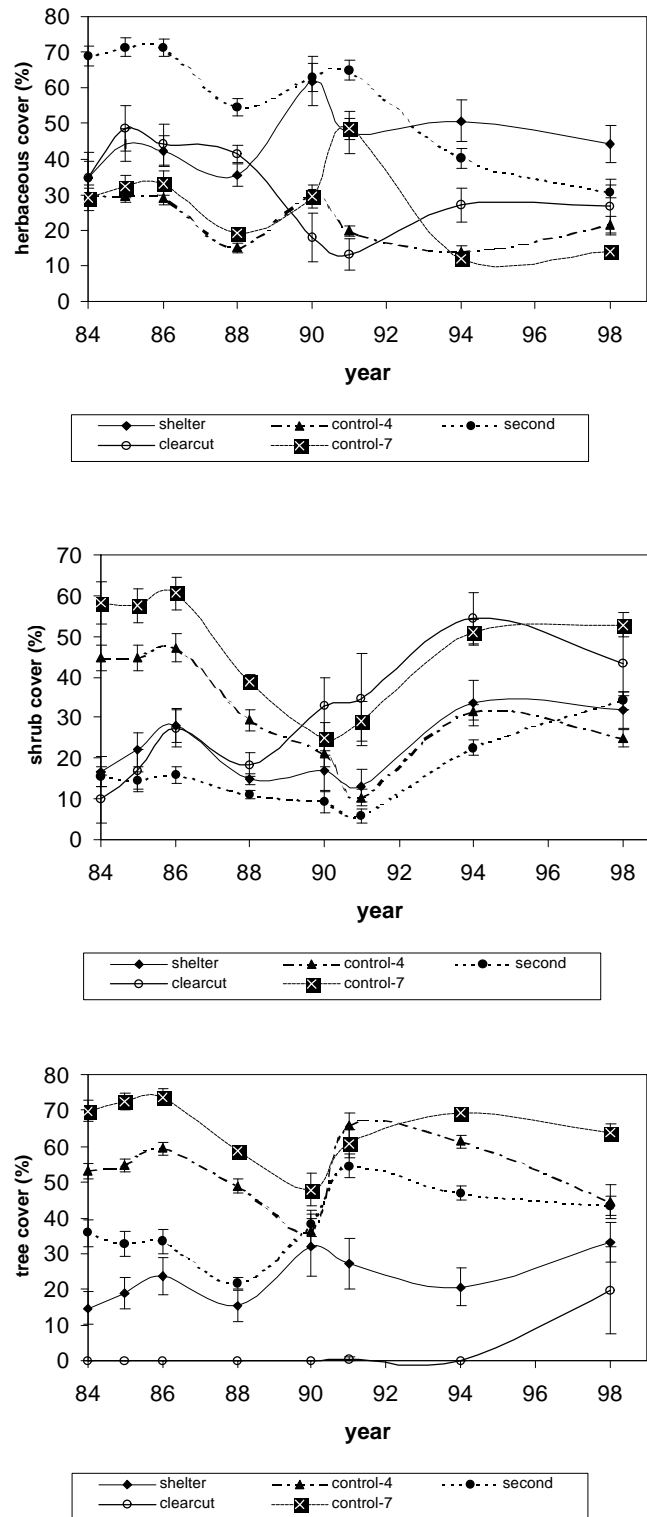
Although the clearcut population fared poorly, a control population (plot 4) in an uncut forest also did not perform well, at least in some years. By 1998, it had lost 70% of its stems compared to 1985 and generally ranked last or second to last in stem height and percentage flowering. In contrast, the population in the shelterwood cuts out-paced the others in many regards. It generally increased or held steady its stem numbers, always was among the top two populations in terms of percentage of stems flowering, and ranked top in fruit set in several years and overall. The other populations generally were intermediate between these extremes, with the exception of control-7, which had the tallest plants in five out of eight observation years.

### **Comparisons to other studies**

Very few published studies have evaluated the effects of disturbances on orchid species, but some are especially noteworthy here. In the Pacific Northwest, clearcut forest harvests resulted in local extinctions of four orchid species, *Corallorhiza maculata*, *C. mertensiana*, *Goodyera oblongifolia*, and *Listera cordata* (Halpern and Spies 1995). *G. oblongifolia*, in particular, appeared to be as sensitive to tree canopy removal as to fire, and the authors suggested some local extirpations were the result

poor re-colonization due to inadequate seed dispersal and inherently slow growth rates (Halpern and Spies 1995). Schoonmaker and McKee (1988) also reported local extirpation of *C. mertensiana* in their comparison of post-harvest stands and adjacent old-growth forests. Coleman (1995) reported that after forest harvest in northern California, a population of *Cypripedium montanum* dropped from several hundred widely scattered plants to just a few individuals at the edge of the clearcut. One study (Falb and Leopold 1993) of a related orchid, *C. candidum*, in a New York fen, compared plants in plots that had been cleared of shrubs with uncleared plots. No effects of shrub cutting on flowering success or plant size were detected, but flowering plants tended to occur in areas with higher solar radiation than vegetative plants. An earlier study of the same species (Curtis 1946) showed that mowing improves density and flowering of *C. candidum*. These studies suggest that, at least for some *Cypripedium* species, increased light and reduced competition may be beneficial. Other types of disturbance could have negative effects, however. Continuous grazing by cattle or sheep, for example, has been shown to depress fruit production and seedling recruitment in *Ophrys sphegodes* (Hutchings 1987a, 1989).

Fire may or may not have negative effects on *Cypripedium* species, depending on the site and fire intensity (e.g., Harrod et al. 1997). Activities that expose or damage the rhizome can kill plants (Harrod 1994 and Knecht 1996). In this study, *C. montanum* in the



**Figure 7.** Percentage cover of herbaceous plants (top), shrubs (center), and trees (bottom) in five population-types of *Cypripedium montanum* over a 15 year period. Vertical bars represent 2 standard errors.



**Figure 8-a.** The clearcut habitat in 1984, about three months after harvest.



**Figure 8-b.** The clearcut habitat in 1990, six years later.

shelterwood habitat outperformed most of the other populations, despite the fact the slash from timber harvest in this habitat was burned in 1984. Karl Urban noted the rapid reappearance of *C. montanum* after a wildfire on the Umatilla National Forest in eastern Oregon, an observation that suggested the original plants in the area were not killed by the burn (Seevers and Lang 1999). In contrast, S. Pappalardo and Julie Nelson noted that a 1981 population of 50 plants was reduced to three individuals after a 1987 fire (Seevers and Lang 1999), but it was not known if the population decline had occurred prior to the burn. These conflicting reports suggest that the response of this orchid to fire may vary with fire behavior and needs further study.

The behavior of *Cypripedium montanum* in the clearcut habitat suggests that there was a delayed reaction of the population to removal of the forest canopy. Some measures of plant health took seven years to show a decline. This could be related to gradual shrub and tree regrowth after the disturbance. Estimates of percentage cover of herbs, shrubs, and trees over time at the various populations were thought by various field-investigators associated with this study to be highly variable between observers. These values are presented in Figure 7. The rapid changes in estimated tree cover in unmanaged stands between 1990 and 1991, for example, forces the reader to question the reliability of these data. Despite these concerns, it seems likely that the relatively steady increase in shrub cover observed in the clearcut population may reflect an actual increase. Photographs of this habitat (Figure 8) available from 1984 (the year the trees were cut) and 1990 clearly show an increase in shrub and small tree cover. Also, the lack of tree cover reported from this population through 1994 (Figure 7) probably reflects a real lack of trees, although it seems likely from the photographs in Figure 8 that cover of small trees was lumped with shrubs during the early years of the study. It was not until 1998 that field investigators reported a substantial tree cover (18%) in this habitat. Therefore, one explanation for the poor growth, flowering, and fruit production of the clearcut population is that intense growth of woody plants caused heavy shading and competition to individual *C. montanum* plants, but only after several years of post-disturbance recovery of competing vegetation.

### ***Dormancy and other demographic patterns***

Dormancy is an important and frequent phenomenon in many orchids (Curtis 1954, Sheviak 1974, Wells 1981, Hutchings 1987a & 1989, Waite 1989, Falb and Leopold 1993), and *Cypripedium montanum* is no exception. In the populations and years for which data are available, dormancy ranged from 0% to 30%, and averaged 7%–21%. Hutchings (1987a) estimated that more than half of all *Ophrys sphegodes* were dormant during peak flowering in any given year. High rates of dormancy make estimates of total population size difficult because an unknown number of individuals may be alive but not apparent to the field investigator. Therefore, long-term studies that track individual plants through periods of dormancy are required for accurate population analyses for orchids like *C. montanum*.

Most dormant *Cypripedium montanum* plants re-emerged the following year, but a small but significant portion, 23%, remained dormant the following year. Only one plant was observed to be dormant for more than two years, a pattern also observed in other orchid species. *Ophrys sphegodes* (Hutchings 1976a), for example, very rarely remained dormant more than two years, and a three to four year limit seems the norm for many other orchids (Sheviak 1974, Mehrhoff 1989, Calvo 1990, Gregg 1991, Falb and Leopold 1993). If plants do not reappear after this period of time, they can reasonably be assumed dead.

The factors that lead to dormancy in orchids are difficult to identify. Damage like grazing or trampling has been implicated for some taxa (Case 1987, Sheviak 1990). Also, the amount of resources used by a plant has been shown to affect its subsequent growth. In *Cypripedium acaule*, fruiting lowers the probability of flowering the following year (Primack and Hall 1990), and repeated forced fruit formation reduces leaf area (Primack and Wilcock 1998). Fruit set also reduces subsequent leaf area in *Tipularia discolor* (Snow and Whigham 1989). On the other hand, *Ophrys apifera* plants with more leaves are more likely to flower the following year than smaller plants (Wells and Cox 1989). Hutchings (1987b) suspected fruiting or flowering might contribute to dormancy in *Ophrys sphegodes*, but found no evidence for this hypothesis. Instead, he concluded that dormancy was most likely to follow a vegetative state, and had little to do with whether or not a plant had flowered or fruited. For *C. montanum*, dormancy was not more likely after flowering or fruiting, and was equally likely to follow a vegetative or flowering state. As in other orchid species examined (e.g., Mehrhoff 1989), however, dormant *C. montanum* plants were far more likely to re-emerge as vegetative than flowering plants. Flowering plants were most likely to return as flowering plants and vegetative plants tended to remain so, as well.

Orchid species vary widely in their average life spans. *Cypripedium montanum* plants observed in this study appear to be fairly long-lived. Of the 80 plants documented in 1990 in this study, 71% remained in 1998. Long-term demographic studies by Tamm (1972), Williams (1982), Farrel (1985), Hutchings (1987a, 1987b, 1989), and Wells (1981) on several orchid species noted maximum recorded ages of 10 to 30 years, depending on the taxon.

A recent review by Neiland and Wilcock (1998) found that rare orchids are likely to be nectarless, and that nectarless orchids are likely to have very low fruit set (average for North American species=19%). *Cypripedium* species are nectarless and attract insect pollinators by deceit (they emit attractive fragrances without providing a nectar reward), and *C. montanum*, therefore, fits the generalization of a nectarless rare orchid. However, the notion that nectarless species have low fruit set is not confirmed in this study. *C. montanum* populations (outside of the clearcut) averaged about 30% to 50% fruit set, well within the range reported for nectariferous North American species. *C. montanum* appears to have rates of fruiting success above average for an orchid that attracts pollinators by nectar deceit. Despite high fruit production, observations of the

permanent plots monitored from 1984 to 1998 in five population-types failed to detect large numbers of newly recruited plants, suggesting that seedling establishment may be a rare phenomenon in *C. montanum*.

*Cypripedium montanum* varies tremendously from year to year in plant size, flower production, fruit set, percentage of stems reproductive, and other traits. It seems likely that climatic conditions are at least partly responsible for this variation. Temperatures and/or precipitation could influence these traits during a given year, or in the following year, by influencing bud formation and successful growth. Hutchings (1987a) attempted to correlate climatic variables with several plant measures for *Ophrys sphegodes*, and found that out of several tests conducted, only flower spike height was correlated with May to October precipitation. The data currently available for *C. montanum* should be tested for significant correlations with climatic variables.

The relatively poor growth, reproduction, and survival of *Cypripedium montanum* in a single clearcut does not provide conclusive evidence that forest harvest is detrimental to this species. Further studies will be necessary to resolve this with certainty. Combined with prior observations of poor orchid survival in managed forests, however, it may give land managers reason to be cautious and favor habitat protection or alternative forest harvest methods such as shelterwood cuts.

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