

## AN ABSTRACT OF THE THESIS OF

Nancy Ann Fredricks for the degree of Doctor of Philosophy in Botany and Plant Pathology presented on December 4, 1992. Title: Population Biology of Rare Mariposa Lilies (*Calochortus*: LILIACEAE) Endemic to Serpentine Soils in Southwestern Oregon.

Abstract approved: \_\_\_\_\_

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Kenton L. Chambers

Population dynamics, plant communities, and abiotic environments of three narrowly endemic, allopatric mariposa lilies (*Calochortus* Pursh) are described and compared. All were restricted to ultramafic soils in southwestern Oregon with high concentrations of nickel, zinc, and chromium, and low calcium to magnesium ratios. Soils inhabited by the three species differed significantly ( $p < 0.0001$ ) in pH and in concentrations of nickel, cadmium, manganese, magnesium, potassium, vanadium, molybdenum, strontium, and phosphorus.

During a nine-year demographic study of *Calochortus howellii* Watson, reproduction, recruitment, and mortality were evaluated, and possible limiting factors and causes of rarity were investigated. Reproduction fluctuates widely from year to year, with bud production correlated with spring (February to May) precipitation ( $r^2 = 0.80$ ,  $n = 9$ ,  $p = 0.01$ ). Recruitment and mortality were low and episodic, averaging 3.0% and 2.0%, respectively over 7 years. Capsule production averaged 3.8% during 1987 to 1991, declining from 17.8% the previous 4 years. Growth rates, particularly of seedlings, were extremely slow. Using size-classified transition matrices, changes in population structure and stability were assessed. Three methods of classifying data for transition matrix analysis yielded similar results in equilibrium population growth rates; based on all analyses, the study population was stable ( $\lambda = 1.0$ ).

Taxonomically very distinct, yet only recently discovered, *C. umpquaensis* Fredricks and *C. coxii* Godfrey & Callahan are serpentine endemics known from limited distributions. Despite its narrow edaphic restriction, *C. umpquaensis* occurs

locally within a wide range of habitats from meadows to forests. Based on a four-year study of *C. umpquaensis*, bud production was highest, plants were most dense, and on average were larger in the ecotone habitat. Equilibrium population growth rates were slightly lower in the meadow habitat. Low capsule production and seed-set, low recruitment, high mortality, and declining population trends ( $\lambda = 0.9$ ) indicate that *C. coxii* should be carefully monitored. The probability of local extinction of this taxon is high, if the years studied are typical.

**Population Biology  
of Rare Mariposa Lilies (*Calochortus*: LILIACEAE)  
Endemic to Serpentine Soils in Southwestern Oregon**

by

Nancy Ann Fredricks

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POPULATION BIOLOGY OF RARE  
MARIPOSA LILIES (*CALOCHORTUS*: LILIACEAE)  
ENDEMIC TO SERPENTINE SOILS IN SOUTHWESTERN OREGON

CHAPTER 1

INTRODUCTION

While searching for a suitable graduate research project in 1982, I encountered the following reference to Howell's mariposa lily: "*C. howellii*...belongs to a section with other uncommon species..and research exploring this group's systematic and ecological relationships may prove useful in deciphering the causes of specific rarity" (Meinke 1982). Over the next decade, this poorly known taxon became the focus of research specifically to examine its relationships with certain allied taxa and to evaluate various possible causes of its rarity.

In 1983, a long-term study was initiated within one of the largest known populations of *C. howellii* Watson. The goal was to monitor population trends of this species, which is a federal candidate for endangered species listing. Since this study began, closely related taxa have been discovered in southwestern Oregon (Fredricks 1989, Godfrey and Callahan 1988). Because of their limited distribution, restriction to serpentine-derived soils, and documented threats to population viability, these taxa were also considered for federal and state endangered species listing. In order to compare these newly described species, study population trends, and identify possible limiting factors contributing to rarity, long-term studies were initiated for *C. umpquaensis* Fredricks and *C. coxii* Godfrey and Callahan in 1989.

While the taxonomy and morphology of the genus have received attention since the turn of the century (Beal 1939, 1941, Beal and Ownbey 1943, Cave 1941, Hoover 1944, Ness 1989, Ownbey 1940, Painter 1911, Purdy 1901), until recently little has been published on the ecology of mariposa lilies. Although they make poor research subjects in the laboratory due to their slow growth and difficult propagation, their simple morphology, large entomophilous flowers and often

unique habitats make them highly suitable for ecological investigations *in situ*. Fiedler (1985a, 1985b, 1987) studied five species of *Calochortus*, including three serpentine endemics, with respect to their demography and accumulation of heavy metals. The reproductive ecology of *Calochortus* has been the subject of several graduate studies; eight Californian species were investigated by Jokerst (1981), while Holtsford (1985) focused on *C. leichlinii*.

The recent proliferation of literature in the area of conservation biology has emphasized both the need to protect unique habitats and to understand the autecology of rare species. Demographic studies of rare plants, essential in documenting population trends, are finally being undertaken. Some have involved the application of stage-classified transition matrix models (Fiedler 1987; Kuchenreuther 1990; Menges 1986, 1990), using approaches similar to analyses of rare animals including spotted owls and grizzly bears.

Because of the importance of documenting trends of rare species, transition matrix models are receiving attention by resource managers as well as scientists. They are being recognized and applied as a useful tool in predicting population trends, evaluating population stability, and identifying life history stages which may be limiting to rare taxa. Because information on many aspects of the life cycle are incorporated into these models, they provide effective frameworks for identifying bottlenecks to population growth. Analyses can be conducted which evaluate the sensitivity of various stages to changes in the environment. By incorporating stochasticity into these models, extinction probabilities under defined conditions can be calculated.

In Chapter 2, the ecology and environment of southwestern Oregon serpentine-inhabiting mariposa lilies will be described. Geology and soils, of crucial importance in defining their distribution, will be discussed and the relationships between precipitation and reproduction considered. The range and habitat of *C. howellii*, *C. umpquaensis*, and *C. coxii* are introduced in Chapter 2.

In Chapter 3, the nine-year studies of demography and reproduction in *C. howellii* are detailed, and the life history of this species described. The size-



classified transition matrix approach is applied to investigate population trends within five large plots, at a site referred to as Mariposa Meadow. By comparing several different size classifications and methods for calculating them, the robustness of the model is evaluated.

Chapter 4 compares the recently discovered *C. umpquaensis* and *C. coxii* to other mariposa lilies, including *C. howellii*. Because *C. umpquaensis* occurs along a continuum of habitats which differ in available resources, comparisons of reproduction, recruitment, growth, and mortality provide insights into factors limiting distribution. Analysis of demographic data using size-classified transition matrix models allow evaluation of population stability in forest, meadow, and ecotonal habitats. Two populations of *C. coxii*, a species primarily inhabiting ecotonal areas, are compared.

While the specific causes of rarity may continue to elude us, we now have a basic understanding of the life history of *C. howellii* and its recently discovered congeners. Yet the longer and more closely we study the interactions of co-existing members of the planet's biota, be they bottle-nosed dolphins, gray wolves, or rare mariposa lilies, the more we appreciate their complexity. This dissertation marks a preliminary step in our attempts at a scientific analysis of one such example.

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## CHAPTER 2

### THE ECOLOGY AND ENVIRONMENT OF THREE SERPENTINE-INHABITING MARIPOSA LILIES OF SOUTHWESTERN OREGON

#### ABSTRACT

The plant communities and abiotic environments of three narrowly endemic, allopatric mariposa lilies (*Calochortus* Pursh) are described and compared. Distribution patterns differ: *C. howellii* and *C. umpquaensis* are locally abundant, with restricted ranges, while *C. coxii* is not only restricted geographically but is locally sparse. Two species, *Ranunculus occidentalis* and *Danthonia californica*, showed high indices of association with all species in all habitats. *Calochortus umpquaensis* occurs over the widest range of habitats, from forest to meadow, while *C. coxii* inhabits transitional areas. *Calochortus howellii* is restricted to more heavily serpentinized soils, but soil analyses for all species confirmed their ultramafic derivation, including high concentrations of heavy metals (e.g. nickel, zinc, and chromium) and low calcium to magnesium ratios. Soils inhabited by the three species differed significantly ( $p > 0.0001$ ) in pH and in concentrations of nickel, cadmium, manganese, magnesium, potassium, vanadium, molybdenum, strontium, and phosphorus. Precipitation patterns varied within the range of the three species and among species. Precipitation was lowest where *C. howellii* populations are smallest. Correlations between February to May precipitation and bud and flower production supported casual observations of higher frequency of flowering during years when spring seasons were moist ( $r^2 = 0.80$  for *C. howellii* buds,  $n = 9$ ,  $p = 0.01$ ;  $r^2 = 0.99$  for *C. umpquaensis* flowers,  $n = 3$ ,  $p = 0.02$ ).

## INTRODUCTION

Of the approximately 60 currently recognized species in the western North American genus *Calochortus*, 17 taxa are currently candidates for federal listing under the Endangered Species Act (United States Department of Interior 1990). Many of these species are narrowly restricted edaphic endemics. At least 15 species inhabit ultramafic soils, with half of these restricted to them (Fiedler 1986). Recently, two new species endemic to ultramafic soils have been described (Fredricks 1989a, Godfrey and Callahan 1988). The relationship of these species, *C. umpquaensis* and *C. coxii*, plus an additional rare relative, *C. howellii*, to their environment was the subject of this investigation. These studies complement demographic research described in Chapters 3 and 4.

The goal of this study was two-fold. First, the plant communities inhabited by *C. howellii*, *C. umpquaensis*, and *C. coxii* are described and possible indicator plants, which have a high degree of association with these species, are identified. Second, abiotic factors, including soils and local precipitation are compared and correlations between these factors and distribution and reproduction are discussed. In sum, this investigation seeks to compare the biotic and abiotic environments of these rare mariposa lilies.

### Ecological investigations of serpentine plant communities of southwestern Oregon

The Siskiyou Mountains comprise the northern-most range of the Klamath Mountains, straddling the border between Oregon and California. Despite the diverse and fascinating flora of the Siskiyou Mountains, the region has been rather poorly studied botanically and no current floristic treatment is available for the Oregon Siskiyou. An estimated 25% of the Klamath flora is endemic (Denton 1979) and 281 taxa in 42 families are restricted to northwestern California and southwestern Oregon (Smith and Sawyer 1988).

Whittaker concluded in his classic studies of community ecology of the Siskiyou Mountains (1954, 1960, 1961) that the serpentine flora is climax, and that

trends in species diversity are based on substrate, with forb diversity higher on serpentine. Dramatic changes in vegetation occur along moisture gradients at low elevations on serpentine and diorite, and mesic broadleaf and sclerophyllous trees are absent on serpentine. Shrubs influence the distribution of herbaceous species in conifer woodlands occurring on serpentine-derived soils (Wilson 1988).

Many investigators have sought to define the soil-chemistry mechanisms responsible for the sharp vegetational gradients between serpentine and non-serpentine communities. Based on 36 transects intersecting this transition, heavy metals (including magnesium, chromium, and nickel) were found to contribute to serpentine soil infertility on 21 serpentine outcrops southern Oregon (White 1971). Legumes, in particular, were intolerant of these elements.

In some studies, descriptions of the serpentine communities have been incidental to larger landscape-scale investigations. Atzet (1979) described and classified the forests of the Illinois River drainage, and he has since expanded his preliminary classification to the Siskiyou National Forest (Atzet and Wheeler 1984). A classification for the central Siskiyous that is amenable to remote sensing analysis has been developed (Frenkel and Kiilsgaard 1984). Vegetation along the Illinois River has been classified and mapped (Emmingham 1973). Autecological studies, which include varying degrees of community analysis have been undertaken on the Klamath endemic *Chamaecyparis lawsoniana* (Hawk 1978, Zobel and Hawk 1980), and Siskiyou endemic *Phacelia capitata* (Shelly 1985, 1989).

While a paucity of recent literature exists on the plants of the Siskiyou Mountains, the flora of serpentine communities of the adjacent southern Oregon Cascade Range to the north is even more poorly documented. Ecological studies of serpentine areas in Douglas, Jackson, and northern Josephine County have not been published. One serpentine plant association was described for the southern Oregon Cascade Mountain province (Atzet and McCrimmon 1990) and a preliminary floristic survey of Douglas County was prepared by Hopkins and coworkers (1986). The juxtaposition of the Siskiyou and Cascade ranges, the eastern and western Cascade influences, and the ultramafic intrusions which characterize this area

contribute to high floristic diversity, which includes at least two endemic mariposa lilies and numerous disjunct taxa.

### Geology and soils

The word "serpentine" has been widely used to refer to rock, soil, and vegetation of ultramafic affinity. The common usage of this term as synonymous with ultramafic appears throughout the literature (Brooks 1987, Kruckeberg 1984) and is followed here, after the technical distinction is made.

In the strict sense, ultramafic refers to dark-colored, igneous rocks containing greater than 70% ferromagnesian minerals (typically olivine and orthopyroxene) with less than 45% silica (Brooks 1987). Alteration of olivine and orthopyroxene results in the formation of serpentine-group minerals ( $\text{Mg}_3\text{Si}_2\text{O}_5(\text{OH})_4$ ). These secondary minerals include chrysotile, antigorite, and lizardite. The conversion of olivine to serpentine (serpentinization) involves hydration and heat. The altered dark greenish rocks, containing serpentine-group minerals, are referred to as serpentinite and may contain varying degrees of olivine, pyroxene, hornblende, mica, garnet, and iron oxides. Peridotite is the ultramafic parent rock and includes harzburgite, dunite, (and pyroxenite) which differ in color and texture.

Ultramafics occur worldwide and are common in southwestern Oregon, where approximately 1200 square kilometers of serpentinitic ultramafic areas occur (Rai et al. 1970, Wagner and Ramp 1958, Walker and King 1969), typically in belts oriented along fault zones in metamorphic areas. Geologic maps delineating ultramafic areas in southwestern Oregon have been prepared by Beaulieu and Ramp (1972), Ramp (1986), Walker and King (1969), and Wells and Peck (1961).

These regions are noted for their unusual floras and high degree of endemism. Plants that inhabit ultramafic soils are often morphologically and physiologically specialized (Brooks 1987, Kruckeberg 1984). Morphological tendencies include shrubby growth form, stunting, greater development of root system, and increased glaucousness. A physiological feature includes the

accumulation of nickel and other metals within plant tissues and organs. In the extreme case of *Sebertia acuminata*, a tree native to New Caledonia, hyperaccumulation results in blue-colored sap containing up to 11.2% nickel in a nickel-citrate complex (Brooks 1987).

Nickel accumulation was also noted in serpentine-inhabiting *Calochortus howellii*, *C. tolmiei*, and *C. uniflorus* by Reeves and coworkers (1983). Fiedler (1985) reported high nickel and copper concentrations in *C. pulchellus*, *C. obispoensis*, *C. tiburonensis*, *C. albus*, and *C. striatus*. Concentrations of these elements are low for the soils inhabited by the latter two species, which are not serpentine-endemics.

Fiedler (1985) hypothesizes that heavy metal tolerance in *Calochortus* may be an exadaptation, which evolved early and has been repeatedly lost throughout the clade, rather than an evolutionary response by selected species to life on the ultramafic substrate. This suggestion seems plausible given the high degree of serpentine endemism and numbers of taxa occurring both on and off serpentine. Serpentine habitats clearly provide fertile ground for speciation within this genus, despite the actual infertility of their soils.

Physical and chemical properties of serpentine soils that may cause infertility include restricted rooting depth, stoniness, low levels of molybdenum, paucity of soil micro-organisms, low levels of available macronutrients (nitrogen, potassium, phosphorus and calcium), high levels of nickel, chromium, zinc, and magnesium, and low calcium to magnesium ratios (Rai et al. 1970). While some studies may seem to implicate a specific cause for the exclusion of many species on these specialized soils, a multiple-factor explanation, including physical, chemical, and biological causes is better supported (Kruckeberg 1987). Most research shows that in cultivation, serpentine endemics grow robustly on non-serpentine soil. Competition and the presence of pathogenic fungi not found on serpentine are most commonly suggested as factors limiting plants to serpentine soils.

Serpentine soils in southwestern Oregon fall into three soil orders: Inceptisols (embryonic soils with few diagnostic features), Alfisols (forest soils



with high base status), and Mollisols (grassland soils). A classification and description of soil series on which Oregon serpentine-inhabiting mariposa lilies occur is provided in Table II.1. As a result of the variation in degree of weathering among serpentine soils, there is wide range in the amount and kind of exchangeable cation and exchange capacity (Rai et al. 1970). They are typically reddish-brown, shallow, very stony or cobbly, fine textured, and well drained clay soils. Smectite (montmorillinite group) clays, which crack extensively, are typically formed when ultramafic rocks weather.

### Range and habitat

Intensive field surveys for these species have been conducted by the author and others between 1983 and 1992 (Fredricks 1986, 1988, 1989b, 1989c). Their distributions are allopatric (Figure II.1). *Calochortus howellii* is restricted to the Illinois River drainage of the Siskiyou Mountains of Josephine County, Oregon. *Calochortus umpquaensis* is known from disjunct populations spanning 80 km, from Ace Williams Mountain near the town of Glide, southwest to Sexton Mountain. *Calochortus coxii* populations occur within a narrow 50 km-long band of serpentinite running northeast to southwest of the town of Myrtle Creek. Known individual populations span 16 km.

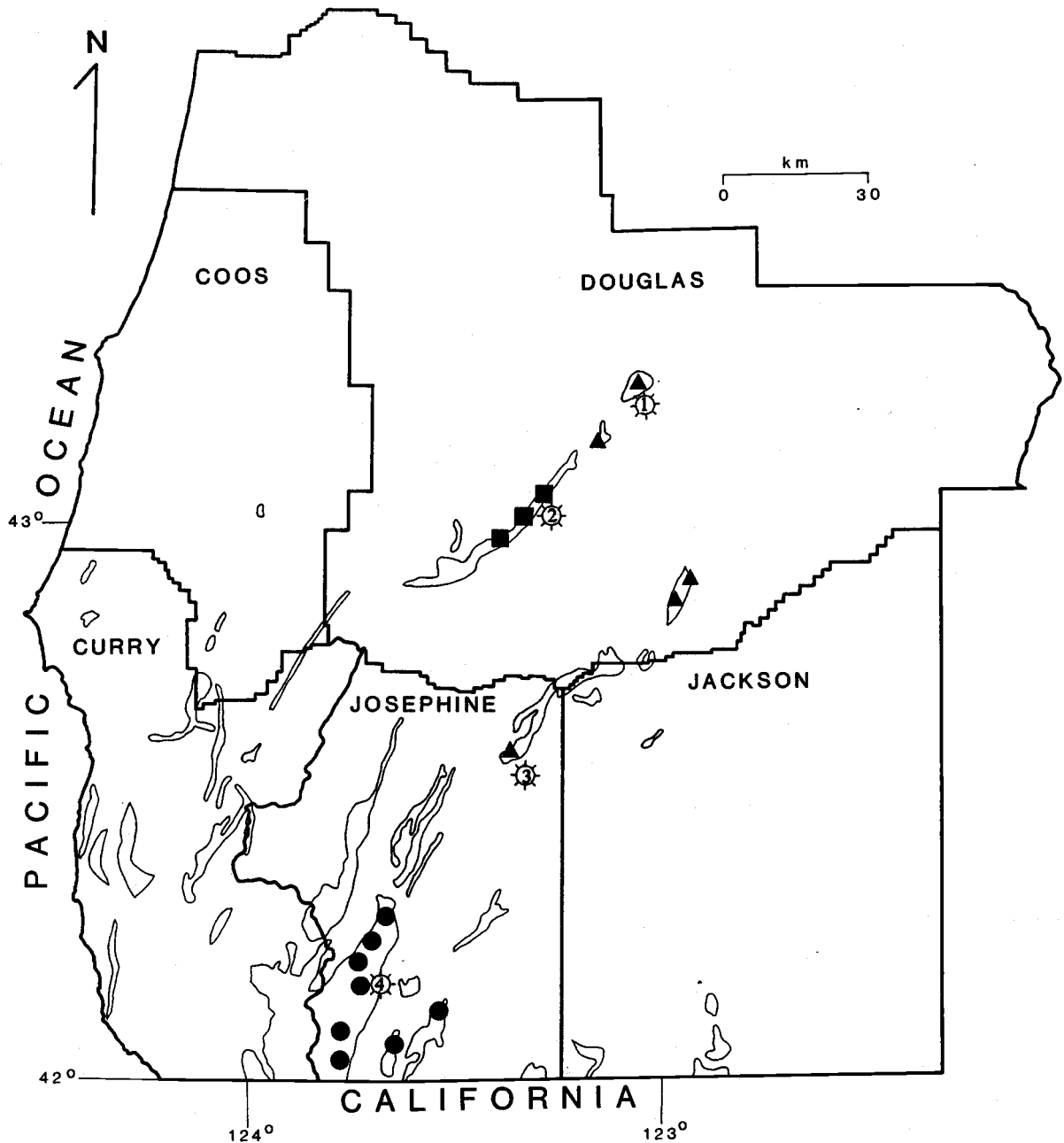
*Calochortus howellii* inhabits several community types (Fredricks 1986, 1988). The higher elevation sites are dominated by *Pinus jeffreyi*, *Lithocarpus densiflora*, *Quercus vaccinifolia*, and *Vaccinium occidentale*, with *Pinus lambertiana* and *Pseudotsuga menziesii* contributing to the sparse overstory. This corresponds best to Atzet and Wheeler's (1984) *Pinus jeffreyi*/*Pinus monticola* association. This community is well represented along Whiskey Creek/Wimer Road and the *C. howellii* population is large and vigorous at this site. In contrast, *C. howellii* populations are small at shrub-dominated sites near Waldo and Democrat Gulch. A third community-type is grass/forb-dominated savannah, with scattered *Pinus jeffreyi*, *Calocedrus decurrens*, and *Arctostaphylos*. Populations of

**Table II.1.** Classification and description of soil series on which *Calochortus howellii*, *C. coxii*, and *C. umpquaensis* occur (sources: Borine 1983, U.S.D.A. Soil Conservation Service 1975, and Wert et al. 1977).

Series	Cornutt	Dubakella	Eightlar
Great Group	mesic Ultic Haploxeralfs	mesic Mollic Haploxeralfs	mesic Typic Xerochrepts
Suborder	Xeralf	Xeralf	Ochrept
Order	Alfisol	Alfisol	Inceptisol
Depth	moderately deep	moderately deep	deep
Drainage	well drained	well drained	moderately well drained
Origin	alluvium and colluvium from ultramafics and altered sedimentary and extrusive igneous rocks	colluvium and residuum from serpentinite and peridotite	colluvium derived from serpentinite and peridotite
Location	mountainsides and alluvial fans	mountainsides and ridgetops	mountains
Surface Color (A1)	dark reddish brown gravelly clay loam	dark yellowish brown very cobbly clay loam	dark reddish brown and dark brown extremely stony clay
Surface Depth	2-6"	2"	10"
Subsoil Color (B1)	dark red	dark reddish brown	dark reddish brown and dark brown
Subsoil Texture	gravelly clay	very cobbly clay loam	extremely stony clay
Depth to Bedrock	40-60"	20 to 40"	60+ "
Elevation	800-5000'	1000-5000'	1350-4000'
<i>Calochortus</i>	<i>C. coxii</i> , <i>C. umpquaensis</i>	<i>C. howellii</i>	<i>C. howellii</i>

Series	Pearsoll	Peel
Great Group	mesic Lithic Xerochrepts	Vertic Haploxeralfs
Suborder	Ochrept	Xeralf
Order	Inceptisol	Alfisol
Depth	shallow to moderately deep	moderately deep
Drainage	well drained	moderately well drained
Origin	colluvium from serpentinite and peridotite	colluvium from serpentine
Location	mountainsides	hillslopes and footslopes
Surface Color (A1)	dark reddish brown extremely stony clay loam	very dark grayish brown clay loam
Surface Depth	5"	9"
Subsoil Color (B1)	dark reddish brown	dark brown, olive brown and olive gray
Subsoil Texture	extremely cobbly clay	gravelly silty clay and silty clay
Depth to Bedrock	14"	29"
Elevation	700-4000'	600-3500'
<i>Calochortus</i>	<i>C. howellii</i> , <i>C. umpquaensis</i> <i>C. coxii</i>	<i>C. umpquaensis</i>

**Figure II.1.** Distribution of *Calochortus howellii* (●), *C. umpquaensis* (▲), and *C. coxii* (■), with serpentine areas delineated (after Wells and Peck, 1961). Weather stations (⊛) numbered as follows: Little River 1, Myrtle Creek 2, Sexton Summit 3, and Cave Junction 4.



*C. howellii* are most extensive here, where an open understory is maintained. The study site, Mariposa Meadow, is representative of this community.

Despite its narrow edaphic restriction to serpentine-derived soils, *Calochortus umpquaensis* occurs within a rather broad continuum of habitats from closed canopy coniferous forest to open grass-forb meadow. In the transitional zone between the forest and meadow, referred to as the ecotone, the abiotic environment is moderated (e.g. light and temperature tend to be less extreme) and community elements of both forest and meadow overlap. In ecotonal and forested habitats, the overstory is composed of *Pinus jeffreyi*, *Pseudotsuga menziesii*, *Calocedrus decurrens*, and *Arbutus menziesii*. Meadows are species rich and dominated by grasses and herbaceous perennials. Vegetation cover may be patchy, with litter, bare soil, rock, and moss openings of varying size comprising the matrix.

*Calochortus coxii* occurs in ecotonal and grassland habitats similar to *C. umpquaensis*, with somewhat different understory species composition. The overstory is composed of *Pinus jeffreyi*, *Pseudotsuga menziesii*, *Calocedrus decurrens*, and *Arbutus menziesii*. Grasses commonly found in association with *C. coxii* include *Aira caryophylla*, *Danthonia californica*, *Festuca rubra*, *Koeleria cristata*, *Melica geyeri*, *Stipa lemmonii*, *Trisetum canescens*, *V. microstachys*, and *Vulpia octoflora*; typical forbs include *Achillea millefolium*, *Arenaria cismontana*, *Aspidotis densa*, *Brodiaea* spp., *Cerastium viscosum*, *Collinsia grandiflora*, *Cryptantha intermedia*, *Epilobium minutum*, *Githopsis specularioides*, *Lomatium nudicaule*, *Lotus micranthus*, *Luzula campestris*, *Madia madioides*, *M. elegans*, *Microsteris gracilis*, *Mimulus guttatus*, *Orthocarpus hispidus*, *Perideridia oregana*, *Phacelia capitata*, *Plectritis congesta*, *Ranunculus occidentalis*, *Sedum stenopetalum*, *Silene hookeri*, *Viola hallii*, and *Zigadenus venenosus*.

All three species inhabit a small subset of what appears to be suitable habitat. Intensive surveys of serpentine areas have failed to locate many additional populations (Fredricks 1988, 1989b, 1989c, Kagan 1992 pers. comm.). While the current distributions are the result of historical events which may remain unknown,

this study seeks to describe and characterize the occupied habitats in order to better understand the environment of these rare plants.

## METHODS

### Plant community data collection

At the onset of the study, only a few populations of *C. umpquaensis* were known, all within an area spanning 4 km. These populations range in size from 0.4 to 25 hectares. In 1988, preliminary sampling was conducted to compare plant communities and population structure and reproduction of *C. umpquaensis* at all known sites within the three habitats, forest, meadow, and ecotone. Sampling was conducted along belt transects which were subjectively located in areas of highest *Calochortus* density. The five sites known at the time were located within 3 km of Ace Williams Mountain (T26S R3W sec. 27). The largest known site was located near the summit of Ace Williams Mountain, where all three habitats were represented. The Watson Mountain site was forested and the Standley Road site was dominated by meadow vegetation. The transitional interface between the two habitats, or ecotone, was sampled at the Thunder Mountain Road and Little River Road sites. Both these sites are located near the base of Ace Williams Mountain. In each habitat, data were collected from 0.5-m<sup>2</sup> quadrants randomly selected within each meter along eight 10-m transects.

In 1989, permanent plots were established along belt transects for both *C. umpquaensis* and *C. coxii*. Two 5-m transects were selected for each habitat (forest, meadow, and ecotone) for *C. umpquaensis* at Ace Williams Mountain. Two 5-m transects were selected for each of two sites separated by approximately 2.2 km for *C. coxii*: the Smith site (T29S R5W sec. 3, SW<sub>1</sub>/<sub>4</sub> of SW<sub>1</sub>/<sub>4</sub>) and the Bilger Creek Road site (T28S R5W sec. 35, W<sub>1</sub>/<sub>2</sub> of SW<sub>1</sub>/<sub>4</sub>). One quadrant was randomly selected within each meter along each transect, for a total of 30 plots for *C. umpquaensis* and 20 for *C. coxii*. Data collected within each 1.0 m by 0.5 m plot included (1) cover value for each species present (plus percent cover of rock, litter,

moss/lichen and bare soil) and (2) leaf width and reproductive status for each individual. The analysis of the later is discussed in Chapter 4.

Floras used to identify associated species include Peck (1961), Munz (1959), and Hitchcock and Cronquist (1973). In general, the taxonomy follows Hitchcock and Cronquist, but includes more recently published nomenclatural changes.

### Plant community data analysis

To compare the three habitats for *C. umpquaensis* and the two sites for *C. coxii*, Margalef's ( $S/\sqrt{N}$ ) diversity indices were calculated (Ludwig and Reynolds 1988). Jaccard's index of community similarity was implemented as an index of species association (Muller-Dombois and Ellenberg 1974). The correlation in presence and absence of species between the sample plots was calculated using the following formula:  $IA_f = 100c/(a+b+c)$ , where  $c$  is the number of plots where the two species occur together;  $a$  and  $b$  are the number of plots in which each species occurs alone. This index was also recalculated substituting cover values of individual associated species and the number of *C. umpquaensis* individuals for frequency ( $IA_c = 100c/(a+b+c)$ , where  $a$  is total number of *C. umpquaensis* individuals in plots without the associated species,  $b$  is the total cover of the selected associated species in all plots without *C. umpquaensis*, and  $c$  is the total number of individuals of *C. umpquaensis* plus the total cover of the associated species in the plots with both species present.

### Soil sampling and analysis

In order to confirm the serpentine derivation of the soils and analyze their composition, surface and subsurface soils were sampled within *Calochortus* populations. Soils were sampled in July 1989 at three locations within the Mariposa Meadow study area, near permanent plots established to monitor *C. howellii*, and at two sites on nearby Eight Dollar Mountain. Samples were collected near each of the four permanent transects for *C. coxii* and the six permanent transects established to monitor *C. umpquaensis*. In addition, soils were

sampled at three other populations of *C. umpquaensis* and one of *C. coxii*, for comparison.

Using plastic trowels to avoid metal contamination, samples were collected from the surface (depth of 0-3 cm), where seed germination and seedling establishment may occur and from the subsurface (10-14 cm), where bulbs may establish. Soil samples (which were dry at the time of collection), were frozen to slow any microbial activity. Prior to processing, samples were thawed and screened with a 2 mm mesh soil sieve. Soil pH was measured with a glass electrode pH meter. Micronutrients were extracted from samples with diethylenetriamine pentaacetic acid (DTPA) and analyzed by Micro-Macro, International (Athens, Georgia) using an Thermo Jarrell Ash Model 9000 inductively coupled plasma emission spectrometer (ICP-AES). Dry color was determined using Standard Soil Color Charts (Oyama and Takehara 1967).

To determine if element concentrations differed with soil depth, the t-test procedure was applied to compare surface and subsurface means (SAS Institute Inc. 1988). Analysis of Variance, followed by the Tukey-Kramer test, which may be used with unequal sample sizes (Sokol and Rohlf 1981) was used to compare means of each element (surface and subsurface samples combined) for each species.

### Precipitation data

Precipitation data were available from the National Oceanic and Atmospheric Administration weather stations within the range of *C. howellii*, *C. umpquaensis*, and *C. coxii*. The Cave Junction weather station (elev. 390 m) is located 8.3 km southwest of the Mariposa Meadow site and within 3.6 km of the nearest population of *C. howellii*. The Little River station (elev. 369 m) is located 3.8 km southeast of the Ace Williams site and within 2.9 km of the nearest population of *C. umpquaensis*. Another population of this species is located 1.2 km west of the Sexton Mountain weather station (elev. 1169 m). The Riddle weather station (elev. 207 m) is located 3.1 km south of the nearest population of *C. coxii* and 20 to 22.6 km southwest of the two study sites.

In order to compare differences in precipitation among the sites, annual precipitation was graphed for the years available. Because seasonal precipitation may be more important to recruitment, reproduction, and mortality than total precipitation, pairs of months are illustrated for each of the four weather stations.

## RESULTS

### Community ecology of rare mariposa lilies

*Calochortus umpquaensis*. Data collected in 1988 from the five sites, within the three habitats, reveal differences in cover and frequency of associated understory species (Tables II.2-4, see Appendix II.1 for cross-reference to scientific names and codes; Appendices II.2-4 for raw data by plot). Based on 80 0.5 m<sup>2</sup> plots (20 m<sup>2</sup> total area) per habitat, these results are representative of densest *C. umpquaensis* populations throughout the northern portion of its range. Cover and frequency data collected in 1989 and 1990 from Ace Williams Mountain differed only slightly within the permanent plots; therefore only 1989 data are reported (Table II.5). Both study years contrast the three habitats, the 1988 data compare five different sites (Tables II.2-4); however, the 1989 data provide further comparison of the habitats within the Ace Williams site only (Table II.5). Results were similar for both years and are summarized below.

Due to the subjective placement of the plots within the densest populations of *C. umpquaensis*, frequency was high in all habitats, with 83, 89, and 75 percent of plots occupied in ecotone, meadow, and forest habitats, respectively in 1988 (Tables II.2-4). In 1989, at the Ace Williams Mountain site, *C. umpquaensis* occurred in 100% of plots within all habitats. Despite similar frequency values, density and bud production in *C. umpquaensis* differed significantly among habitats (Chapter 4).

In contrast to 1988, when average vegetation cover was highest in the



**Table II.2.** Mean cover (MEAN) and frequency (FREQ) for associated species of *Calochortus umpquaensis* (CAUM) based on 1988 transects in ecotone habitats. Frequencies greater than 50% are shaded. Species codes are defined in Appendix II.1; total vegetation (VEG), moss, rock, soil, and litter cover may be greater than 100%. CAUM% values are based on cover, CAUM # values are based on numbers of individuals. Species richness for Thunder Mt. Rd. = 31 (40 plots), Little River Rd. = 20 (20 plots), Ace Williams Mt. = 27 (20 plots), and all ecotone plots combined = 50 (80 plots).

Table II.2

Sitenames	Thunder Mt. Rd.			Little River Rd.			Ace Williams Mt.			All ecotone plots		
Species code	MEAN	N	FREQ	MEAN	N	FREQ	MEAN	N	FREQ	MEAN	N	FREQ
ACHMIL	0.43	6	0.15	0.85	9	0.45	1.15	8	0.40	0.71	23	0.29
AIRCAR	0.13	11	0.28				0.45	8	0.40	0.18	19	0.24
ASPDEN					1	0.05					1	0.01
BROELE							0.65	15	0.75	0.16	15	0.19
BROCAR	0.15	4	0.10							0.08	4	0.05
CALDEC	0.38	3	0.08				0.10	5	0.25	0.21	8	0.10
CALTOL							0.60	7	0.35	0.15	7	0.09
CERVIS		5	0.13	0.05	1	0.05	0.60	3	0.15	0.16	9	0.11
COLGRA							0.15	3	0.15	0.04	3	0.04
CRE							0.25	3	0.15	0.06	3	0.04
CRYINT	0.08	25	0.63					1	0.05	0.04	26	0.33
DACGLO	0.15	8	0.20	3.90	19	0.95	0.40	7	0.35	1.14	34	0.43
DANCAL	9.18	39	0.98	2.30	11	0.55	6.50	20	1.00	6.79	70	0.88
EPIMIN	0.08	7	0.18				0.05	1	0.05	0.05	8	0.10
ERILAN	4.20	28	0.70							2.10	28	0.35
ERYHEN	0.03	1	0.03							0.01	1	0.01
FESCAL							2.60	9	0.45	0.65	9	0.11
FESIDA							0.15	3	0.15	0.04	3	0.04
GALTRI		1	0.03								1	0.01
GITSPE							0.05	2	0.10	0.01	2	0.03
GOOBL		1	0.03								1	0.01
HYPPER		2	0.05								2	0.03
IRICHR				0.05	1	0.05				0.01	1	0.01
LATPOL				0.55	8	0.40				0.14	8	0.10
LOTMIC	0.38	35	0.88	0.35	13	0.65	0.05	7	0.35	0.29	55	0.69
LUZCAM	0.05	4	0.10				1.50	17	0.85	0.40	21	0.26
MADMAD	0.13	6	0.15	0.05	1	0.05				0.06	7	0.09
MICGRA		7	0.18								7	0.09
PANSCR				2.90	4	0.20				0.63	4	0.05
PERORE		9	0.23				0.15	2	0.10	0.04	11	0.14
PLECON	0.15	4	0.10					1	0.05	0.08	5	0.06
PSEMEN	0.13	2	0.05							0.06	2	0.03
RANOCC	2.43	39	0.98	1.20	16	0.80	4.80	20	1.00	2.70	75	0.94
SEDSTE							0.95	16	0.80	0.24	16	0.20
SIDVIR	1.90	21	0.53	5.95	16	0.80				2.44	37	0.46
SILHOO							0.75	15	0.75	0.19	15	0.19
SISBEL	0.03	1	0.03	9.10	20	1.00				2.04	21	0.26
SYNREN	0.03	1	0.03	0.10	1	0.05				0.04	2	0.03
THLMON	0.10	2	0.05				0.35	9	0.45	0.14	11	0.14
TRIDUB	1.63	21	0.53	0.70	4	0.20				0.98	25	0.31
TRITRI		1	0.03	0.60	6	0.30				0.15	7	0.09
TRIMAC				1.80	4	0.20				0.45	4	0.05
VERBLA				0.10	1	0.05				0.03	1	0.01
VICAME				0.70	8	0.40				0.18	8	0.10
VIDOOU							0.75	15	0.75	0.19	15	0.19
VIOHAL	0.08	7	0.18							0.04	7	0.09
VULMIC	11.00	33	0.83				0.05	1	0.05	5.51	34	0.43
unknown 1		3	0.08	4.20	18	0.90					3	0.04
unknown 2							4.75	15	0.75	1.19	15	0.19
unknown 3							0.45	5	0.25	0.11	5	0.06
CAUM%	0.93	28	0.70	4.20	18	0.90	4.45	20	1.00	2.56	66	0.83
	MEAN	N	FREQ	MEAN	N	FREQ	MEAN	N	FREQ	MEAN	N	FREQ
VEG	34	40	1.00	35	20	1.00	33	20	1.00	34	80	1.00
MOSS	34	21	0.53				6	9	0.45	19	30	0.38
ROCK	1	2	0.05							0	2	0.03
SOIL	20	28	0.70				3	6	0.30	10	34	0.43
LITTER	12	12	0.30	65	20	1.00	58	19	0.95	36	51	0.64
CAUM #	4.03	31	0.78	7.60	18	0.90	11.05	20	1.00	6.53	69	0.86

**Table II.3.** Mean cover (MEAN) and frequency (FREQ) for associated species of *Calochortus umpquaensis* (CAUM) based on 1988 transects in meadow habitats. Frequencies greater than 50% are shaded. Species codes are defined in Appendix II.1; total vegetation (VEG), moss, rock, soil, and litter cover may be greater than 100%. CAUM% values are based on cover, CAUM # values are based on numbers of individuals. Species richness for Standley Rd. = 30 (20 plots), and Ace Williams Mt. = 32 (60 plots) and all meadow plots combined = 41 (80 plots).

Table II.3

Sitenames	Standley Road			Ace Williams Mt.			All meadow plots		
Species code	MEAN	N	FREQ	MEAN	N	FREQ	MEAN	N	FREQ
ACHMIL				6.43	60	1.00	4.83	60	0.75
AIRCAR	0.15	7	0.35	2.10	44	0.73	1.61	51	0.64
ARECIS	2.15	12	0.60	0.27	12	0.20	0.74	24	0.30
AREDOU	3.05	5	0.25	0.18	4	0.07	0.90	9	0.11
ASPDEN	2.65	11	0.55	0.12	2	0.03	0.75	13	0.16
BROELE				0.30	33	0.55	0.23	33	0.41
CAMLEI				0.25	9	0.15	0.19	9	0.11
CENUMB	0.05	9	0.45				0.01	9	0.11
CERVIS		4	0.20	0.23	5	0.08	0.18	9	0.11
COLGRA		3	0.15	0.27	13	0.22	0.20	16	0.20
CRYINT		10	0.50	0.18	16	0.27	0.14	26	0.33
CYNECH					1	0.02		1	0.01
DANCAL	24.10	20	1.00	11.13	59	0.98	14.38	79	0.99
DODHEN		1	0.05					1	0.01
EPIMIN	0.05	17	0.85	0.40	44	0.73	0.31	61	0.76
ERINUD		1	0.05					1	0.01
FESIDA	0.20	8	0.40				0.05	8	0.10
GALAPA	0.05	1	0.05				0.01	1	0.01
GILCAP	0.10	3	0.15	0.02	5	0.08	0.04	8	0.10
GITSPE		10	0.50	0.13	35	0.58	0.10	45	0.56
LOLMUL	0.05	1	0.05				0.01	1	0.01
LOTMIC					2	0.03		2	0.03
LUZCAM		5	0.25	0.53	19	0.32	0.40	24	0.30
MADMAD		6	0.30	1.53	28	0.47	1.15	34	0.43
MIMGUT	1.90	13	0.65	0.07	7	0.12	0.53	20	0.25
ORTHIS					1	0.02		1	0.01
PERORE		5	0.25	0.05	2	0.03	0.04	7	0.09
PITTRI				0.03	9	0.15	0.03	9	0.11
PLECON	0.10	6	0.30	0.93	25	0.42	0.73	31	0.39
POA	0.20	1	0.05	3.87	16	0.27	2.95	17	0.21
RANOCC	4.95	20	1.00	3.57	51	0.85	3.91	71	0.89
SEDSTE				0.20	9	0.15	0.15	9	0.11
SIDVIR	0.20	1	0.05				0.05	1	0.01
SILHOO	0.10	3	0.15	0.97	44	0.73	0.75	47	0.59
SISBEL	0.95	7	0.35				0.24	7	0.09
THLMON				0.10	8	0.13	0.08	8	0.10
TRITRI		1	0.05					1	0.01
VIDOOU				0.75	41	0.68	0.56	41	0.51
VULMIC		1	0.05	1.32	34	0.57	0.99	35	0.44
ZIGVEN				0.40	11	0.18	0.30	11	0.14
unknown 4	1.05	3	0.15	0.25	4	0.07	0.45	7	0.09
CAUM%	0.80	20	1.00	1.63	51	0.85	1.43	71	0.89
	MEAN	N	FREQ	MEAN	N	FREQ	MEAN	N	FREQ
VEG	43	20	1.00	38	60	1.00	39	80	1.00
MOSS	7	3	0.15	41	59	0.98	33	62	0.78
ROCK	7	10	0.50	1	8	0.13	3	18	0.23
SOIL	39	16	0.80	9	24	0.40	16	40	0.50
LITTER	3	3	0.15	11	25	0.42	9	28	0.35
CAUM #	3.20	20	1.00	5.40	52	0.87	4.85	72	0.90

**Table II.4.** Mean cover (MEAN) and frequency (FREQ) for associated species of *Calochortus umpquaensis* (CAUM) based on 1988 transects in forest habitats. Frequencies greater than 50% are shaded. Species codes are defined in Appendix II.1; total vegetation (VEG), moss, rock, soil, and litter cover may be greater than 100%. CAUM% values are based on cover, CAUM # values are based on numbers of individuals. Species richness for Ace Williams Mt. = 23 (40 plots), and Watson Mt. = 28 (40 plots) and all forest plots combined = 35 (80 plots).

Table II.4

Sitenames	Ace Williams Mt.			Watson Mt.			All forest plots		
Species codes	MEAN	N	FREQ	MEAN	N	FREQ	MEAN	N	FREQ
ASPDEN	8.90	21	0.53	1.10	7	0.18	5.00	28	0.35
BROELE		6	0.15		2	0.05		8	0.10
CALDEC	0.03	3	0.08	0.03	5	0.13	0.03	8	0.10
CARINT		1	0.03					1	0.01
CERARV	0.05	3	0.08	0.05	2	0.05	0.05	5	0.06
CERVIS	0.15	3	0.08				0.08	3	0.04
CRE				0.43	7	0.18	0.21	7	0.09
CYNECH					1	0.03		1	0.01
CYSBUL		1	0.03					1	0.01
DANCAL	0.58	10	0.25	2.78	19	0.48	1.68	29	0.36
DELMEN				0.93	9	0.23	0.46	9	0.11
DODHEN				0.40	12	0.30	0.20	12	0.15
ERYHEN	0.05	9	0.23	0.03	1	0.03	0.04	10	0.13
FESIDA				0.05	2	0.05	0.03	2	0.03
GALAPA		1	0.03		2	0.05		3	0.04
GITSPE	0.10	3	0.08				0.05	3	0.04
GOOBL	0.23	7	0.18	0.05	1	0.03	0.14	8	0.10
HIEPAR	0.15	4	0.10				0.08	4	0.05
IRICHR				3.38	24	0.60	1.69	24	0.30
LUZCAM		5	0.13	0.58	20	0.50	0.29	25	0.31
PERORE					2	0.05		2	0.03
POA				0.10	2	0.05	0.05	2	0.03
POLMUN	0.08	3	0.08	0.60	4	0.10	0.34	7	0.09
PSEMEN		1	0.03	1.05	4	0.10	0.53	5	0.06
RANOCC	0.28	12	0.30	0.80	21	0.53	0.54	33	0.41
SEDSTE	0.03	1	0.03				0.01	1	0.01
SIDVIR				0.05	1	0.03	0.03	1	0.01
SILHOO	0.05	1	0.03	0.48	15	0.38	0.26	16	0.20
SISBEL				0.23	2	0.05	0.11	2	0.03
SYNREN	1.75	11	0.28	5.05	25	0.63	3.40	36	0.45
THLMON	0.93	11	0.28				0.46	11	0.14
THUPLI	0.23	20	0.50	0.23	9	0.23	0.23	29	0.36
VIDOOU				0.23	11	0.28	0.11	11	0.14
unknown 2				0.93	13	0.33	0.46	13	0.16
unknown 5	0.43	22	0.55	0.53	11	0.28	0.48	33	0.41
CAUM%	1.55	35	0.88	1.40	25	0.63	1.48	60	0.75
	MEAN	N	FREQ	MEAN	N	FREQ	MEAN	N	FREQ
VEG	16	40	1.00	21	40	1.00	18	80	1.00
MOSS	21	38	0.95	14	20	0.50	18	58	0.73
ROCK	1	1	0.03	1	2	0.05	1	3	0.04
SOIL	1	3	0.08	1	3	0.08	1	6	0.08
LITTER	62	40	1.00	63	37	0.93	62	77	0.96
CAUM#	5.63	36	0.90	4.15	25	0.63	4.89	61	0.76

**Table II.5.** Associated species of *Calochortus umpquaensis* within permanent plots established at Ace Williams Mt. in ecotone, forest, and meadow habitats, with mean cover (Mean) and frequency (Freq) summarized by habitat. Species codes are defined in Appendix II.1. Total vegetation (VEG), moss, rock, soil, and litter cover may be greater than 100%. Plot numbers are prefixed by habitat abbreviation; T = trace (< 1%). CAUM # indicates total number of *C. umpquaensis* individuals within plot. All data collected in 1989.

Table II.5

Habitat	ECOTONE												FOREST												MEADOW													
Species	E1	E2	E3	E4	E5	E6	E7	E8	E9	E10	Mean	Freq	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Mean	Freq	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	Mean	Freq		
ACHMIL	1			1	3	1		1			0.7	0.50															2		T	2	3	5	5	6	10	3.3	0.80	
AIRCAR	1	1	3	5	5			T			1.5	0.60																1		3	2			T			0.3	0.30
ARECIS																																						0.30
ASPDEN														1	7	3		2	10		8	3	17	5.1	0.80					T							0.10	
BROELE	T	1	1	T				1	T	T	0.3	0.80			T	T	T					T		0.50		T							1	1	T		0.2	0.50
CALDEC			T	T	T	T						0.50				1		T	1			T		0.2	0.40													
CARPUL																					T		T	0.20														
CERARV								1	T	2	0.3	0.40						T		1	1		0.2	0.40														
CERVIS								T				0.10																										
CYNECH	T	T	T	1	2						0.3	0.50																										
COLGRA																														T	T							0.20
CRYINT																															T							0.10
DACGLO																T								0.10			T											0.10
DANCAL	8	25	40	35	30	40	20	15	15	20	24.8	1.00		1	1	30		2		15	5	2	5.6	0.70	20	15	8	40	65	2						15	0.60	
DODHEN							7	2			0.9	0.20																										
EPIMIN																																						0.30
ERYHEN	T											0.10				T		T					0.20															
FESRUB	6		5	5	5			15			3.6	0.50																			1	T	T	1	1	0.3	0.50	
GITSPE																																						0.20
KOECRI		T					5	10	15	8	4.5	0.60														15	2	35	1	T							5.3	0.50
LOTMIC	T	2	2	1	2	1	T	T	1	1	1	1.00																										
LUZCAM	1	1		1		1		1	1	1	0.7	0.70					T			T		T	0.30		T		T	T		1	1	T	1	1	0.4	0.80		
MADELE																																						0.10
MADMAD																																1		2	1	0.4	0.30	
MELGEY																																T		1		0.1	0.20	
MICGRA							T	T				0.20																										
MIMGUT																																						0.1
PERORE																																						0.20
PLECON																																						0.2
POAPRA																																						0.10
RANOC	8	10	10	8	10	15	8	10	10	15	10.4	1.00	T			T	T	T	T	2	2	2	2	0.8	0.90	3	3	1	1	2	7	5	7	5	3	3.7	1.00	
SEDSTE	1						1	2		1	0.5	0.50					T		T					0.20		T	2	1	1	1		1				0.6	0.60	
SIDVIR							5	8	8		2.1	0.30																										
SILHOO		3	5	1	3	2	3		4	5	2.6	0.80		1								T		0.1	0.20				T	T	1	1	3	1	2	1	0.9	0.80
SYNREN																	10		4		1		1.5	0.30														
THLMON	T						T	T	1	1	0.2	0.60	1					T					0.1	0.20													0.40	
TRICAN							5				0.5	0.10											0.1	0.30													0.3	
TRIDUB							1		1		0.2	0.20																									0.1	
VIODOU		1	1				1		1	1	0.5	0.50																									0.4	
VULMIC	7										0.7	0.20																									0.1	
VEG	33	44	67	58	60	85	71	53	42	50	56.3		2	9	4	31	12	12	7	26	12	22	13.7		41	25	50	46	74	17	15	14	22	17	32.1			
LITTER	60	65	35	30	65	25	5	60	80	8	43.3		60	95	80	40	90	80	40	15	8	20	52.8		45	70	50	30	25							22.0		
MOSS	8	2	2			5	25			55	9.7		20		15	30	2	15	55	65	85	80	36.7		5	3	5	1		85	95	95	90	95	47.4			
ROCK																																						
SOIL				8	10		8	2			2.8					5			1				0.6			5	5	5		1			1			1.7		
CAUM#	42	42	29	34	17	8	10	9	29	18	23.8		15	12	7	7	1	9	10	14	12	38	12.5		6	3	3	3	5	28	25	31	30	5	13.9			



meadow habitats (39% for the meadow, versus 34% for the ecotone and 18% for the forest, Tables II.2-4), 1989 vegetation was densest in the ecotone, averaging 56% cover (32% in the meadow and 14% in the forest, Table II.5). In both years, litter covered over half the plots in the forest (62% for 1988 and 53% for 1989). Moss contributed up to 85% cover in some forest plots, but average cover was highest in the meadow (32.8% for 1988 and 47.4% for 1989).

In the ecotone permanent plots at Ace Williams Mountain, the species with highest frequency (greater than 50%, by decreasing frequency) were *Ranunculus occidentalis*, *Danthonia californica*, *Lotus micranthus*, *Brodiaea elegans*, *Silene hookeri*, *Luzula campestris*, *Thlaspi montanum* var. *siskiyouense*, *Aira caryophyllea*, and *Koeleria cristata* (Table II.5). Species unique to plots within the ecotone habitat were *Cerastium viscosum*, *Dodecatheon hendersonii*, *Sidalcea virgata*, *Lotus micranthus*, and *Cynosurus echinatus*. *Danthonia californica* contributed nearly 25% mean cover, followed by *Ranunculus occidentalis* with 10.4%. In 1988, cover in the ecotone plots was highest for *Vulpia microstachys* (dominant at one site only), *Danthonia californica*, and *Sidalcea virgata* (Table II.2).

Many species with high frequency in the ecotone habitat were also frequent in the meadow (Tables II.3, II.5). For example, *Achillea millefolium*, *Danthonia californica*, *Koeleria cristata*, and *Ranunculus occidentalis* were present in at least half the meadow plots in 1988 and 1989. Additional species with high frequency in the meadow included *Aira caryophyllea*, *Brodiaea elegans*, *Epilobium minutum*, *Githopsis specularioides*, *Luzula campestris*, *Plectritus congesta*, *Silene hookeri*, and *Viola hallii*. In 1989, *Arenaria cismontana*, *Collinsia grandiflora*, *Epilobium minutum*, *Githopsis specularioides*, *Melica geyeri*, *Mimulus guttatus*, *Poa pratensis*, and *Madia madioides* occurred only within the meadow plots and occupied few, if any, of the forest or ecotone plots in 1988. Cover was highest in the meadow for *Danthonia californica*, *Achillea millefolium*, *Koeleria cristata*, and *Ranunculus occidentalis*.

Understory vegetation in the forest is sparse. *Ranunculus occidentalis*, *Danthonia californica*, and *Aspidotis densa* occurred in more than 50% of the plots,

with the later two contributing 5.6% and 5.1% cover in 1989 to the mean 13.7% total vegetation cover within the forest habitat. In 1988, *Aspidotis densa* and *Synthyris reniformis* contributed most to cover. Species richness is lowest in the forested habitat, relative to the ecotone and meadow. The dominant herbs and grasses found in association with *Calochortus umpquaensis* in the 1988 forest plots were *Aspidotis densa*, *Danthonia californica*, and *Synthyris reniformis*. Additional species with high frequency included *Dodecatheon hendersonii*, *Erythronium hendersonii*, *Iris chrysophylla*, *Luzula campestris*, *Thlaspi montanum* var. *siskiyouense*, *Ranunculus occidentalis*, and *Viola hallii*. *Synthyris reniformis* and *Cardamine pulcherrima* were species unique to the forest plots.

Species with high indices of species association with *C. umpquaensis* across all habitats include *Ranunculus occidentalis* ( $IA_c = 0.98$  based on cover, 0.97 based on frequency) and *Danthonia californica* ( $IA_f = 0.88$  based on cover, 0.77 based on frequency).

Overall species richness (S) at Ace Williams Mountain was highest in the meadow and lowest in the forest, based on permanent plot data collected in 1989. Because of the differences in plot number due to sampling limitations at several of the *C. umpquaensis* sites, overall species richness by habitat cannot be compared directly for 1988. Number of species per plot, however, was highest in the meadow for 1988, with averages of 9.8 and 10.0 species per plot for the Standley Road and Ace Williams Mountain sites, respectively (overall average was 9.9 species). In 1989, the Ace Williams meadow transects averaged 10.2 species per plot. The forest plots averaged 4.0 and 5.9 species for Ace Williams and Watson Mountain in 1988 (overall average 4.9), with 5.7 species at the former site in 1989. The intermediate ecotone habitat, which averaged 8.5 species overall, had 8.4, 7.2, and 10.0 species at the Thunder Mountain Road, Little River Road, and Ace Williams Mountain sites, respectively. In 1989, the average number of species in the ecotone habitat at the Ace Williams site was 10.9, slightly higher than the meadow habitat.

Margalef's diversity index, which incorporates plot number (N), was applied

to the habitats of *C. umpquaensis*. Diversity was lowest in the forest, based on data collected in 1988 and 1989 (Table II.6). When data for all sites were combined, ecotone diversity was highest in 1988. In 1989, the meadow habitat was highest in species diversity.

*Calchortus coxii*. *Ranunculus occidentalis* was the only species present in more than half of the plots at both the Smith and Bilger Creek Road sites (Table II.7). *Festuca rubra*, noteworthy in its high cover and presence in all plots at the Bilger Creek site, was not found within the plots at the Smith site. Species richness, diversity, and average number of species per plot were lowest for the Bilger Road site, where *C. coxii* populations are being heavily grazed by deer (Table II.6). Average number of species per plot was 7.5, with 8.3 species for the Smith site and 6.7 species for the Bilger Road site.

#### Correlations between soils and distribution

*Calochortus howellii*. Geological maps, prepared at a scale of 1:24,000 for a large portion of the range of *C. howellii* (Ramp 1986) were used to investigate the species' fidelity to specific geological formations and rock types. *Calchortus howellii* occurs on Josephine harzburgite tectonite and serpentinite (greater than 50% serpentinization) from the mid to lower Jurassic and nearby Pleistocene terrace gravel.

Josephine County soils maps at 1:20,000 scale (Borine 1983) were used to determine the soil series on which the species occurs. Six serpentinitic soil series have been identified in the county. Soil series on which *C. howellii* occurs (Table II.1) include Eightlar, Dubakella, and Pearsoll, which all originate from colluvium or residuum derived from serpentinite and peridotite. They are extremely stony clay loams or clays located on mountainsides with dark reddish brown subsoil. Other serpentinitic soils on which *C. howellii* did not occur include Brockman, Cornutt, Copsey, and Takilma variant. Cornutt soils which are deep and well-

**Table II.6.** Margalef diversity indices for habitats of *Calochortus umpquaensis* and *C. coxii*.

Habitat/Sitename	N	S	Margalef
<b><i>Calochortus umpquaensis</i>: 1988</b>			
ECOTONE			
Thunder Mt. Rd.	40	31	4.90
Little River Rd.	20	20	4.47
Ace Williams Mt.	20	37	8.27
All ecotone plots	80	50	5.59
MEADOW			
Standley Rd.	20	30	6.71
Ace Williams Mt.	60	32	4.13
All meadow plots	80	41	4.58
FOREST			
Ace Williams Mt.	40	23	3.64
Watson Mt.	40	28	4.43
All forest plots	80	35	3.91
<b><i>Calochortus umpquaensis</i>: 1989</b>			
Ace Williams Mt.			
ECOTONE	10	24	7.59
MEADOW	10	30	9.49
FOREST	10	15	4.74
<b><i>Calochortus coxii</i>: 1989</b>			
Smith	10	27	8.54
Bilger Creek Rd.	10	18	5.69

**Table II.7.** Associated species of *Calochortus coxii* within permanent plots established at two sites, Smith and Bilger Creek Rd., with mean cover (Mean) and frequency (Freq) summarized by site. Species codes are defined in Appendix II.1. Total vegetation (VEG), moss, rock, soil, and litter cover may be greater than 100%. Plot numbers are prefixed by habitat abbreviation, T = trace (< 1%). CACO # indicates total number of *C. coxii* individuals within plot. All data collected in 1989.

Table II.7

Sitename	Smith site plots													Bilger Creek Rd. site plots												
Species Code	1	2	3	4	5	6	7	8	9	10	Mean	N	Freq	11	12	13	14	15	16	17	18	19	20	Mean	N	Freq
ACHMIL							1				0.1	1	0.10			1			1		8	4	2	1.6	5	0.50
AIRCAR	T					T	2				0.2	3	0.30													
ASPDEN	15			20	5		7			4	5.1	5	0.50		T										1	0.10
CALDEC										10	1	1	0.10	20	3			20	7	7			2	5.9	6	0.60
CERARV	T											1	0.10						1		4		1	0.6	3	0.30
CYNECH	5	4	2			5	2	2	10		3	7	0.70													
CRYINT		1	1	T	1						0.3	4	0.40				T								1	0.10
CYNECH	T	2	3	1	1		1	2	4	2	1.6	9	0.90													
CYP						1					0.1	1	0.10													
DANCAL																							3	0.3	1	0.10
EPIMIN					T	T						2	0.20	T	T			T				1	T	0.1	5	0.50
ERYHEN	T	T							T			3	0.30													
FESRUB														7	15	55	15	7	4	15	15	25	30	18.8	10	1.00
IRI														2										0.2	1	0.10
GAL	T	T	1	T	T	T		T		T	0.1	8	0.80													
LOMMAC		T								T		2	0.20								4	4		0.8	2	0.20
LOMNUD				1		2					0.3	2	0.20			3				5				0.8	2	0.20
LUZCAM						1	1			T	0.2	3	0.30	2	2	2	1	T	2		2	2	1	1.4	9	0.90
MADELE																										
MADMAD		T			T	1	T				0.1	4	0.40													
MELGEY														1			1		3	4	4	3		1.6	6	0.60
PINJEF						1		1	T	1	0.3	4	0.40										15	1.5	1	0.10
PLECON	1				T	1	T				0.2	4	0.40													
RANOCC						2	2	1	1	T	0.6	5	0.50	2	1	2	2	2	3	7		1	1	2.1	9	0.90
RHUDIV																				T				1	0.10	
SEDSTE	1					1		1	1	1	0.5	5	0.50													
SILHOO		1			1					T	0.2	3	0.30	1		1								0.2	2	0.20
VULMIC						T						1	0.10													
ZIGVEN																				T				1	0.10	
Unknown	3				3			5	1	2	1.4	5	0.50	1										0.1	1	0.10
VEG	20	4	2	20	5	5	12	2	10	14	9.4	10	1.8	20	3	1		20	9	7	12	4	5	8.1	15	1.5
LITTER	60	80	90	90	70	70	5		35	85	58.5	9	0.90	70	80	40	80	80	80	70	50	40	30	62	10	1.00
MOSS	7					30	85	90	45	2	25.9	6	0.60	8	2						8	5	5	2.8	5	0.50
ROCK	10		7		20			3	10	10	6	6	0.60				1	1			5			0.7	3	0.30
LOG		20									2	1	0.10													
SOIL					5						0.5	1	0.10						4			8	5	1.7	3	0.30
CACO	5	4	8	13	4	13	45	21	41	46	20	10	1.00	8	30	19	3	8	21	9	21	12	12	14.3	10	1.00

drained, formed from colluvium, while Brockman, Copsey, and the Takilma variant are alluvial soils.

Three sites were mapped as Dubakella-Pearsoll complex (35 to 75% slopes), four included Eightlar extremely stony clay (5 to 35% slopes), four were Eightlar-Dubakella complex (35 to 65% slopes), and four were Pearsoll-rock outcrop complex (20 to 90% slopes).

*Calochortus umpquaensis* and *C. coxii*. *Calochortus umpquaensis* occurs on three soil series, Cornutt, Pearsoll, and Peel, and their complexes, while *C. coxii* is known from the Cornutt and Pearsoll series. A soil survey of Douglas county is in preparation by the Soil Conservation Service. Soils have been mapped for portions of the range of *C. umpquaensis* and *C. coxii* by the Bureau of Land Management (B.L.M.) (Wert et al. 1977).

The portions of the range of *C. umpquaensis* which are managed by the B.L.M. and most of the *C. coxii* sites fall within two mapping units of the Pearsoll gravelly clay loam-Cornutt gravelly clay loam association. Pearsoll and Cornutt soils co-occur in a random fashion, with Pearsoll more prevalent on steeper slopes (Wert et al. 1977). Inclusions of deep black, sometimes poorly drained, unnamed serpentinitic soils comprise approximately 10% of both mapping units.

### Soil analysis

While clear correlations exist between the distribution of serpentine soil series and the species considered, site specific soil analyses further confirm the ultramafic derivation of the soils inhabited by these species. Low macronutrient levels (potassium and phosphorus), low calcium/magnesium ratio, and above average concentrations of nickel, chromium, cobalt, and zinc were noted (Table II.8).

Surface soil ranged from dull reddish brown to brownish black (typically brownish black) for *C. howellii* and tended to have lower chromas and values than for the other two species (Table II.9). Soil were typically brown but ranged from

**Table II.8.** Elemental analyses for soils inhabited by *Calochortus howellii*, *C. coxii*, and *C. umpquaensis*, ranked by species, sample depth, and location. Subsurface samples were collected between 10 and 14 cm, surface samples within the top 3 cm. Numbers following sitenames refer to permanent plots (F=forest, E=ecotone, M=meadow). See text for explanation. Means for each species, with subsurface and surface sampled pooled, are shaded.

Sitenames and Plot #	pH	Ag	Al	B	Ba	Ca	Cd	Co	Cr	Cu	Fe	K	Mg	Mn	Mo	Na	Ni	P	Pb	Si	Sr	V	Zn	Ca/Mg
<b>SUBSURFACE SAMPLES</b>																								
<i>Calochortus howellii</i>																								
Mariposa Meadow #2	7.0	0.00	0.15	0.01	0.01	19.12	0.01	0.17	0.09	0.16	1.37	4.20	66.94	2.83	0.03	1.32	14.27	0.18	0.03	2.04	0.01	0.03	0.18	0.29
Mariposa Meadow #3	7.1	0.00	0.31	0.02	0.00	38.91	0.04	0.14	0.21	0.98	2.88	5.95	511.04	1.73	0.11	5.46	24.91	0.87	0.26	7.25	0.01	0.13	0.31	0.08
Mariposa Meadow #4/5	7.7	0.01	0.14	0.02	0.40	94.15	0.04	0.24	0.24	0.95	2.93	8.94	329.07	3.77	0.04	5.10	24.49	0.94	0.26	7.84	0.22	0.14	0.35	0.29
Eight Dollar Mt.	7.1	0.00	2.49	0.03	0.09	77.13	0.06	0.97	0.43	1.03	14.88	11.17	207.67	14.18	0.04	7.37	38.68	0.86	0.21	18.65	0.08	0.11	0.39	0.37
Eight Dollar Mt.	7.1	0.00	0.19	0.03	0.50	54.41	0.05	0.34	0.24	0.91	1.99	10.90	513.86	4.87	0.10	5.93	32.78	1.20	0.32	4.27	0.23	0.10	0.38	0.11
Mean (n=5)	7.2	0.00	0.66	0.02	0.20	56.75	0.04	0.37	0.24	0.81	4.81	8.23	325.72	5.48	0.06	5.04	27.03	0.81	0.22	8.01	0.11	0.10	0.32	0.23
S.D.	0.3	0.00	1.03	0.01	0.23	29.81	0.02	0.34	0.12	0.36	5.66	3.07	194.07	5.00	0.04	2.25	9.25	0.38	0.11	6.39	0.11	0.05	0.09	0.13
<b>SURFACE SAMPLES</b>																								
Mariposa Meadow #2	7.2	0.01	0.24	0.03	0.02	50.40	0.06	0.38	0.19	1.08	2.29	13.93	393.51	5.70	0.08	4.94	51.37	1.18	0.33	4.88	0.02	0.09	0.61	0.13
Mariposa Meadow #3	7.3	0.00	16.50	0.01	0.24	85.85	0.09	0.31	2.33	0.96	82.72	8.26	380.41	5.09	0.11	5.95	31.03	1.27	0.36	80.39	0.19	0.21	0.41	0.23
Mariposa Meadow #4/5	7.4	0.01	0.21	0.03	0.34	85.71	0.08	0.23	0.28	0.92	2.08	8.92	699.34	3.16	0.11	6.40	23.12	1.21	0.33	8.98	0.19	0.17	0.41	0.12
Eight Dollar Mt.	7.1	0.00	0.09	0.01	0.00	70.99	0.05	0.24	0.18	1.18	4.31	12.87	125.47	6.07	0.04	4.07	38.42	0.84	0.17	4.61	0.01	0.08	0.38	0.57
Eight Dollar Mt.	7.4	0.01	0.09	0.01	0.01	101.24	0.03	0.14	0.11	0.85	1.70	15.53	77.27	3.34	0.02	4.03	32.17	0.80	0.19	5.33	0.01	0.07	0.35	1.31
Mean (n=5)	7.3	0.00	3.43	0.02	0.12	78.84	0.06	0.26	0.62	1.00	18.62	11.90	335.20	4.67	0.07	5.08	35.22	1.06	0.28	20.84	0.08	0.12	0.43	0.47
S.D.	0.1	0.00	7.31	0.01	0.16	19.16	0.02	0.09	0.96	0.13	35.85	3.18	249.28	1.35	0.04	1.08	10.54	0.22	0.09	33.34	0.10	0.06	0.10	0.50
Mean (n=10)	7.2	0.00	2.04	0.02	0.16	67.79	0.05	0.32	0.43	0.90	11.71	10.07	330.46	5.08	0.07	5.06	31.13	0.93	0.25	14.43	0.10	0.11	0.38	0.35
S.D.	0.2	0.00	5.13	0.01	0.19	26.34	0.02	0.24	0.68	0.28	25.26	3.52	210.67	3.48	0.04	1.66	10.30	0.32	0.10	23.62	0.10	0.05	0.11	0.37
CV	2.8	79.44	251.46	61.96	118.86	38.85	40.66	77.10	156.91	30.60	215.66	35.01	63.75	68.53	56.07	32.86	33.09	34.30	40.32	163.73	102.17	46.51	28.46	106.23
<i>Calochortus coxii</i>																								
Smith site # 1	7.1	0.01	0.22	0.02	0.17	52.50	0.07	0.17	0.43	1.11	14.00	17.72	114.70	6.72	0.03	8.50	49.57	2.05	0.31	2.52	0.31	0.05	0.61	0.46
Smith site # 10	6.9	0.01	0.31	0.04	0.23	64.15	0.07	0.53	0.47	1.23	24.18	14.83	89.37	6.77	0.03	8.13	61.67	2.71	0.28	1.50	0.36	0.05	0.58	0.72
Bliger Cr. Rd. #15	7.0	0.00	0.08	0.02	0.32	90.19	0.06	0.69	0.41	0.86	15.60	16.38	85.36	8.88	0.03	5.34	57.72	2.47	0.28	4.28	0.46	0.03	0.68	1.38
Bliger Cr. Rd. #16	6.9	0.01	0.21	0.02	0.28	101.85	0.08	1.11	0.39	0.95	14.44	27.99	52.56	13.08	0.03	6.58	87.17	3.07	0.47	1.94	0.33	0.04	0.88	1.94
Mean (n=4)	7.0	0.01	0.21	0.02	0.25	77.17	0.07	0.62	0.42	1.04	17.06	19.23	80.50	8.86	0.03	7.14	64.03	2.58	0.34	2.56	0.36	0.04	0.69	1.12
S.D.	0.1	0.01	0.09	0.01	0.06	22.78	0.01	0.39	0.03	0.16	4.80	5.96	27.43	2.99	0.00	1.46	16.23	0.43	0.09	1.22	0.07	0.01	0.13	0.67
<b>SURFACE SAMPLES</b>																								
Smith site # 1	6.7	0.00	0.72	0.01	0.10	90.11	0.08	0.96	0.25	0.89	16.99	44.42	50.78	14.41	0.02	7.66	70.50	3.90	1.18	2.72	0.34	0.04	1.18	1.77
Smith site # 10	7.0	0.00	0.26	0.02	0.00	48.25	0.05	0.31	0.30	0.73	23.57	28.20	198.42	4.84	0.05	4.46	44.96	2.01	0.48	0.92	0.01	0.05	0.44	0.24
Bliger Cr. Rd. #15	6.8	0.01	0.20	0.02	0.06	102.45	0.07	0.85	0.41	0.69	22.74	30.52	70.11	11.29	0.03	4.81	60.56	3.20	0.54	2.70	0.28	0.04	0.75	1.46
Bliger Cr. Rd. #16	6.8	0.00	0.16	0.02	0.05	83.74	0.08	1.72	0.36	0.72	14.44	40.02	73.86	20.72	0.02	8.11	80.02	5.79	0.75	2.65	0.22	0.03	0.98	1.13
Mean (n=4)	6.8	0.00	0.34	0.02	0.05	81.14	0.07	0.96	0.33	0.76	19.44	35.79	98.29	12.82	0.03	6.26	64.01	3.73	0.74	2.25	0.21	0.04	0.84	0.95
S.D.	0.1	0.00	0.26	0.01	0.04	23.26	0.01	0.58	0.07	0.09	4.43	7.70	67.51	6.61	0.01	1.89	14.98	1.58	0.32	0.89	0.15	0.01	0.32	0.73
Mean (n=8)	6.9	0.01	0.26	0.02	0.15	74.31	0.08	0.91	0.35	0.89	16.40	33.17	107.22	12.92	0.03	6.43	73.50	3.12	0.54	2.77	0.29	0.04	0.78	1.14
S.D.	0.1	0.01	0.18	0.01	0.11	24.75	0.02	0.57	0.09	0.18	6.93	19.80	70.21	7.92	0.01	1.73	31.49	1.16	0.29	1.45	0.12	0.01	0.23	0.62
CV	1.9	99.21	70.86	33.61	75.72	33.30	30.15	63.19	26.14	20.51	42.22	59.70	65.49	61.28	24.94	26.86	42.85	37.27	52.54	52.31	42.91	21.92	29.55	54.03



Table II.8 (continued)

Sitename and Plot #	pH	Ag	Al	B	Ba	Ca	Cd	Co	Cr	Cu	Fe	K	Mg	Mn	Mo	Na	Ni	P	Pb	Si	Sr	V	Zn	Ca/Mg
<b>SUBSURFACE SAMPLES</b>																								
<i>Calochortus umpquaensis</i>																								
Tiller	6.8	0.14	0.48	0.02	0.09	83.46	0.10	0.59	0.10	0.96	13.92	20.70	57.24	10.83	0.03	9.22	95.48	2.35	0.42	1.72	0.28	0.03	0.89	1.46
Tiller	6.9	1.30	0.23	0.01	0.14	78.66	0.11	0.54	0.10	1.01	6.71	18.61	42.30	8.28	0.03	5.47	120.72	2.43	0.44	1.63	0.46	0.03	0.81	1.86
Watson Mt.	7.1	0.01	0.26	0.02	0.07	119.19	0.06	0.51	0.29	2.14	8.56	41.55	70.62	8.21	0.02	5.27	54.77	2.96	0.30	1.45	0.23	0.08	0.91	1.69
Ace Williams Mt. #1F	6.8	0.00	0.30	0.03	0.07	90.73	0.10	1.32	0.21	0.79	5.21	35.69	34.84	17.70	0.02	24.31	113.62	3.66	0.62	3.72	0.19	0.04	1.37	2.60
Ace Williams Mt. #10F	6.9	0.00	0.19	0.00	0.42	46.62	0.12	1.14	0.68	1.74	28.29	23.49	116.48	14.80	0.03	11.03	137.20	3.09	0.38	3.17	0.29	0.04	0.86	0.40
Ace Williams Mt. #11M	7.2	0.00	0.22	0.00	0.42	89.68	0.07	0.44	0.45	2.03	14.09	21.45	115.23	7.71	0.03	11.23	91.27	2.84	0.24	3.80	0.36	0.05	0.88	0.78
Ace Williams Mt. #6M	7.0	0.00	0.20	0.01	0.47	81.34	0.11	0.85	0.54	1.76	17.94	23.34	101.15	12.71	0.04	8.21	135.84	2.98	0.43	3.12	0.34	0.05	0.91	0.80
Ace Williams Mt. #1E	7.2	0.00	0.17	0.00	0.57	107.51	0.13	1.11	0.45	1.73	10.73	43.87	61.91	14.25	0.03	7.51	167.57	3.54	0.48	3.65	0.45	0.06	1.03	1.74
Ace Williams Mt. #10E	6.8	0.00	2.04	0.02	0.58	54.41	0.15	1.02	0.49	2.68	30.82	30.64	100.26	16.70	0.04	13.97	158.81	3.88	0.39	6.33	0.36	0.03	1.05	0.54
sw of Lane Mt.	6.4	0.00	0.95	0.03	0.20	80.94	0.13	2.10	0.22	2.04	33.44	36.41	149.90	27.54	0.04	12.82	134.98	4.86	0.59	0.76	0.29	0.03	1.17	0.54
s of Lane Mt.	6.7	0.00	0.42	0.02	0.25	41.34	0.13	1.30	0.33	1.04	35.02	30.85	97.43	15.83	0.04	9.26	147.43	4.48	0.49	1.38	0.27	0.02	0.90	0.42
Mean (n=11)	6.9	0.13	0.50	0.02	0.30	79.44	0.11	0.99	0.35	1.63	18.61	29.69	86.12	14.05	0.03	10.76	123.43	3.37	0.43	2.80	0.32	0.04	0.98	1.17
S.D.	0.2	0.39	0.56	0.01	0.20	24.04	0.03	0.49	0.19	0.60	11.22	8.81	35.50	5.71	0.01	5.27	32.99	0.80	0.11	1.61	0.08	0.02	0.17	0.74
<b>SURFACE SAMPLES</b>																								
Tiller	6.6	0.02	0.95	0.03	0.01	75.83	0.10	1.40	0.11	0.91	8.50	45.38	83.63	30.22	0.04	11.80	110.91	4.08	0.56	1.49	0.44	0.04	1.30	0.91
Tiller	6.8	0.01	0.77	0.04	0.09	62.18	0.11	1.42	0.11	0.97	12.94	30.97	109.81	27.32	0.04	7.73	108.07	3.31	1.00	2.52	0.40	0.03	13.15	0.57
Watson Mt.	6.8	0.01	0.32	0.02	0.00	105.90	0.06	0.54	0.25	1.74	7.51	47.79	60.56	10.14	0.03	4.65	44.98	3.07	0.26	1.33	0.06	0.08	0.91	1.75
Ace Williams Mt. #1F	6.9																							
Ace Williams Mt. #10F	6.7	0.00	0.41	0.00	0.29	85.40	0.10	1.95	0.32	0.78	18.35	55.30	71.35	22.72	0.03	15.62	128.04	4.89	1.04	1.36	0.43	0.00	1.14	1.20
Ace Williams Mt. #11M	7.4																							
Ace Williams Mt. #6M	6.7	0.00	0.61	0.00	0.15	126.71	0.13	0.76	0.31	1.84	24.23	49.00	93.67	13.24	0.04	11.98	135.87	4.62	0.66	1.01	0.40	0.03	1.46	1.35
Ace Williams Mt. #1E	6.8	0.00	0.30	0.01	0.10	103.60	0.10	0.99	0.44	1.22	18.46	67.82	105.58	16.99	0.04	6.20	114.39	5.04	0.60	2.23	0.35	0.05	1.17	0.98
Ace Williams Mt. #10E	6.9	0.00	0.65	0.00	0.34	105.10	0.13	1.16	0.42	2.25	28.29	58.42	91.58	22.33	0.04	8.42	165.76	6.29	0.66	0.08	0.45	0.04	1.62	1.15
sw of Lane Mt.	6.5	0.00	0.70	0.02	0.00	90.78	0.11	1.48	0.21	1.72	28.04	43.24	169.15	23.71	0.04	5.01	113.15	6.17	0.85	1.08	0.03	0.03	1.21	0.54
s of Lane Mt.	6.6	0.00	0.42	0.01	0.07	93.73	0.10	1.91	0.22	0.80	17.70	35.43	47.83	25.67	0.03	5.90	123.66	5.18	0.81	1.56	0.33	0.01	1.14	1.98
Mean (n=11)	6.8	0.00	0.57	0.01	0.12	94.36	0.10	1.29	0.27	1.36	18.00	48.15	92.57	21.37	0.04	8.59	116.09	4.74	0.72	1.41	0.32	0.04	2.57	1.16
S.D.	0.2	0.01	0.22	0.01	0.12	18.88	0.02	0.48	0.12	0.54	7.37	11.36	35.16	6.63	0.01	3.76	32.05	1.12	0.24	0.71	0.16	0.02	3.97	0.48
Mean (n=22)	6.8	0.07	0.53	0.02	0.22	86.16	0.11	1.13	0.31	1.51	18.34	38.00	89.03	17.34	0.03	9.78	120.13	3.98	0.56	2.17	0.32	0.04	1.70	1.16
S.D.	0.2	0.29	0.43	0.01	0.19	22.63	0.02	0.50	0.16	0.57	9.45	13.56	34.56	7.05	0.01	4.67	31.93	1.16	0.23	1.44	0.12	0.02	2.71	0.62
CV	3.5	388.07	81.69	73.49	87.65	26.27	22.01	43.96	51.92	38.12	51.52	35.70	38.82	40.62	19.75	47.75	26.58	29.19	40.42	66.33	37.84	50.74	159.54	53.34

**Table II.9.** Soil colors for samples collected near *Calochortus howellii* (CAHO), *C. umpquaensis* (CAUM), and *C. coxii*. Odd numbers were samples from surface (0-3 cm), even numbers were from depths 10-14 cm. V/C = value/chroma.

Species	Site number and name	Hue	V/C	Standard Soil Color Name
CAHO	1 Mariposa Meadow	7.5YR	2/2	brownish black
	2 Mariposa Meadow	7.5YR	3/2	brownish black
	3 Mariposa Meadow	7.5YR	3/3	dark brown
	4 Mariposa Meadow	7.5YR	4/4	dull reddish brown
	5 Mariposa Meadow	7.5YR	3/2	brownish black
	6 Mariposa Meadow	5YR	4/3	dull reddish brown
	7 Mariposa Meadow	7.5YR	3/2	brownish black
	8 Mariposa Meadow	7.5YR	3/2	brownish black
	9 Eight Dollar Mt.	7.5YR	2/2	brownish black
	10 Eight Dollar Mt.	7.5YR	2/2	brownish black
CACO	11 Smith site	7.5YR	4/4	brown
	12 Smith site	7.5YR	4/4	brown
	13 Smith site	7.5YR	5/4	dull brown
	14 Smith site	7.5YR	5/4	dull brown
	15 Bilger Cr. Rd.	7.5YR	5/4	dull brown
	16 Bilger Cr. Rd.	7.5YR	5/4	dull brown
	17 Bilger Cr. Rd.	7.5YR	4/3	brown
	18 Bilger Cr. Rd.	7.5YR	5/4	dull brown
	19 w of Myrtle Cr. Beacon	5YR	3/6	dark reddish brown
CAUM	21 Grate Cr., Tiller	5YR	4/4	dull reddish brown
	22 Grate Cr., Tiller	5YR	4/4	dull reddish brown
	23 Grate Cr., Tiller	7.5YR	2/2	brownish black
	24 Grate Cr., Tiller	7.5YR	4/4	dull reddish brown
	25 Watson Mt.	7.5YR	4/3	brown
	26 Watson Mt.	7.5YR	4/3	brown
	27 Ace Williams Mt., Forest	7.5YR	2/1	black
	28 Ace Williams Mt., Forest	7.5YR	3/4	dark brown
	29 Ace Williams Mt., Meadow	7.5YR	3/4	dark brown
	30 Ace Williams Mt., Meadow	7.5YR	4/3	brown
	32 Ace Williams Mt., Forest	7.5YR	4/3	brown
	33 Ace Williams Mt., Meadow	7.5YR	5/4	dull brown
	34 Ace Williams Mt., Meadow	5YR	4/4	dull reddish brown
	35 Ace Williams Mt., Meadow	7.5YR	5/4	dull brown
	36 Ace Williams Mt., Ecotone	7.5YR	5/4	dull brown
	37 Ace Williams Mt., Ecotone	7.5YR	5/4	dull brown
	38 Ace Williams Mt., Ecotone	5YR	4/4	dull reddish brown
	39 sw of Lane Mt.	7.5YR	5/4	dull brown
	40 sw of Lane Mt.	7.5YR	5/4	dull brown
	41 s of Lane Mt.	7.5YR	5/4	dull brown
	42 s of Lane Mt.	7.5YR	5/4	dull brown

dull reddish brown to black soils for *C. umpquaensis* and dark reddish brown to brown (typically brown) for *C. coxii*.

Soils inhabited by *Calochortus howellii* differed significantly in pH from those inhabited by the other two species ( $p = 0.0001$ ), with a mean of 7.2 (Table II.8). On average, soils were more acidic in the vicinity of *C. umpquaensis* (6.9) and *C. coxii* (6.8), where density of conifers was higher and more organic matter was present. On Ace Williams Mountain, subsurface soil pH was lowest in the forest and highest in the meadow, but sample sizes were inadequate to be statistically valid.

### Heavy metals and macronutrients

Analysis of 22 elements from soils inhabited by the three species revealed high variance (coefficient of variation values in Table II.8). Because variation was typically greater within subsurface and surface samples than between them (see Appendix II.5 for results of t-tests), results were pooled for subsequent statistical analyses.

Analysis of Variance and multiple comparison tests revealed significant differences in soil element concentrations among soils of sites inhabited by different *Calochortus* species (Appendix II.6). Concentrations of nickel, cadmium, manganese, magnesium, potassium, vanadium, molybdenum, strontium, and phosphorus differed at the 0.0001 level. Cobalt and copper also differed significantly at the 0.0002 and 0.001 levels, respectively.

Nickel concentrations for soils inhabited by *C. umpquaensis* were the highest for all species, averaging 120.1 ppm (Table II.8). Averages for *C. coxii* and *C. howellii* were 73.5 ppm and 31.1 ppm, respectively. Based on Tukey-Kramer tests, nickel concentrations differed significantly among all species, while cadmium, manganese, potassium, and copper differed for *C. umpquaensis*, and molybdenum, strontium, magnesium, vanadium, potassium, and cobalt differed for *C. howellii*.

Although average zinc concentration for soils inhabited by *C. umpquaensis* was 1.7 ppm, as compared with 0.4 and 0.8 ppm for those of *C. howellii* and *C.*

*coxii*, respectively, zinc values were not significantly different. Manganese concentrations, however, differed at the 0.0001 level, with averages highest for *C. umpquaensis* (17.3 ppm) and lowest for *C. howellii* (5.1 ppm). The samples from Ace Williams Mountain were lowest in manganese and phosphorus in the meadow, but larger sample sizes are necessary to determine if differences among habitats are statistically significant.

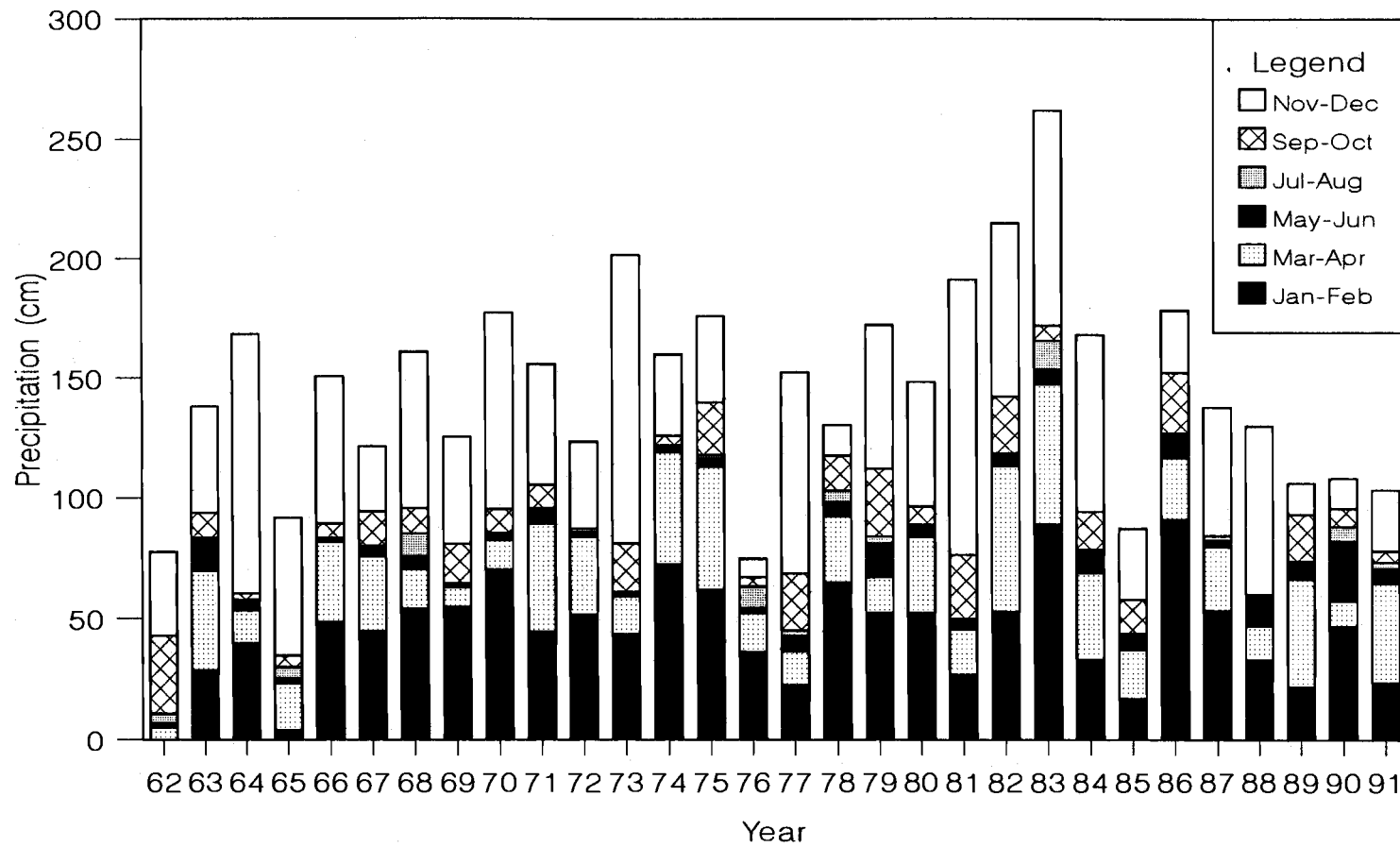
The calcium to magnesium ratios were significantly different between *C. howellii* and the other species ( $p = 0.002$ ). Means for potassium were 10.1 ppm, 33.2 ppm, and 38.0 ppm for *C. howellii*, *C. coxii*, and *C. umpquaensis*, respectively. Potassium, lead, and barium were the only elements which differed in concentration with soil depth when all species were pooled ( $p = 0.01$ , 0.005, and 0.003, respectively). Phosphorus was significantly lower ( $p = 0.0001$ ) at *C. howellii* sites (0.9 ppm versus 3.1 and 4.0 for *C. coxii* and *C. umpquaensis*).

### Precipitation

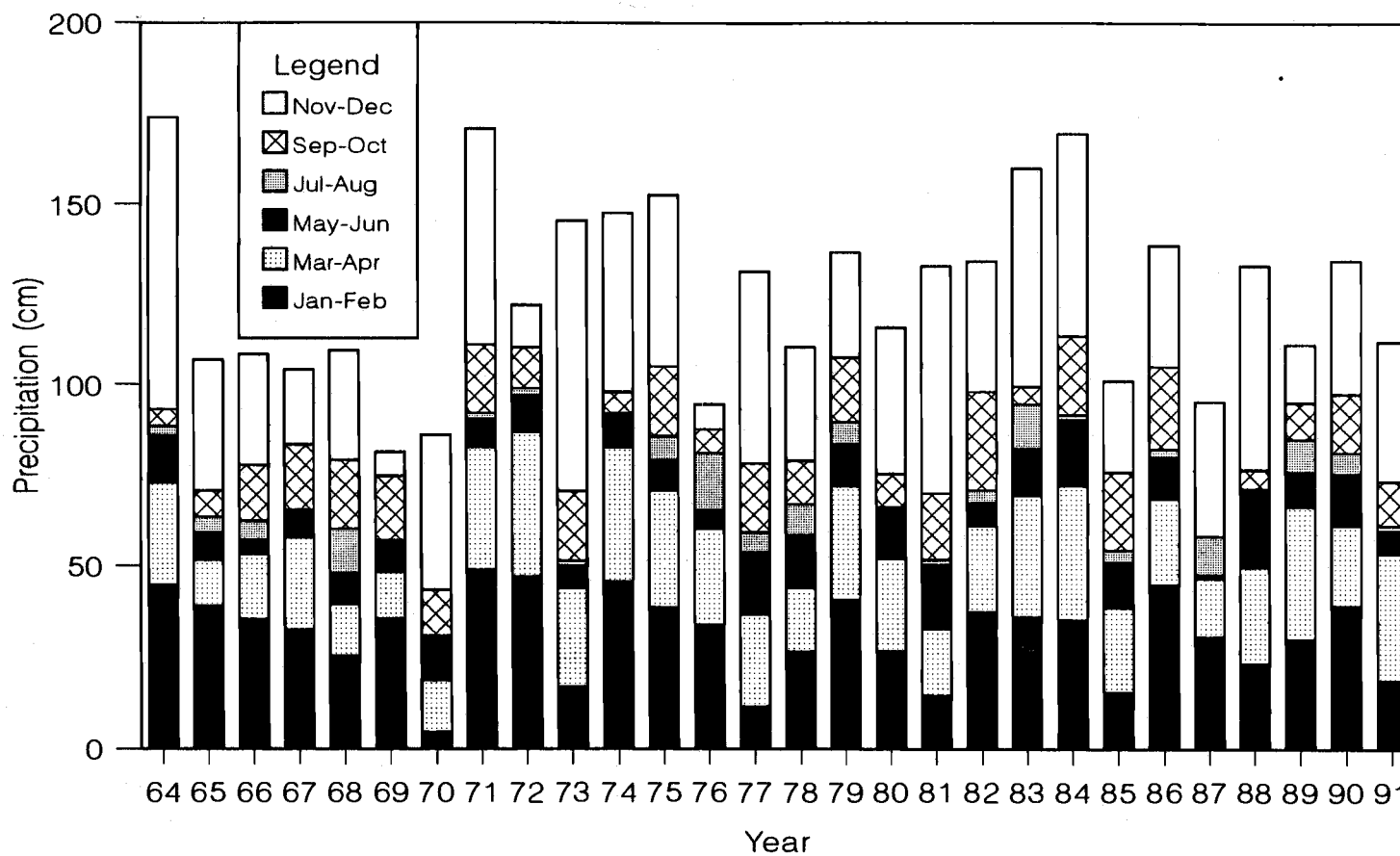
Precipitation patterns varied among the four southwestern Oregon weather stations selected for their proximity to *Calochortus* populations (Figures II.2-5, Appendices II.7-10; see Figure II.1 for locations). In 1983, the highest annual precipitation in the history of the Cave Junction (Figure II.2, Appendix II.7) and Riddle (Figure II.4, Appendix II.9) stations was recorded. High precipitation was also received at Little River (Figure II.3, Appendix II.8) and Sexton Summit (Figure II.5, Appendix II.10) for 1983, but higher totals were reported at Little River in 1984, 1971, and 1964 and numerous years were wetter at Sexton Summit. Little River station totals show less variation. Cave Junction receives less rainfall in summer but higher precipitation during the other seasons, based on recent ten year average monthly precipitation (Figure II.6).

During the years of the monitoring studies for *C. howellii* at Mariposa Meadow (1983 to 1991), two precipitation extremes occurred. While 1983 was the wettest in the history of the nearby Cave Junction weather station (data only post-1961), total precipitation was exceptionally low in 1985. Only 1976 was drier.

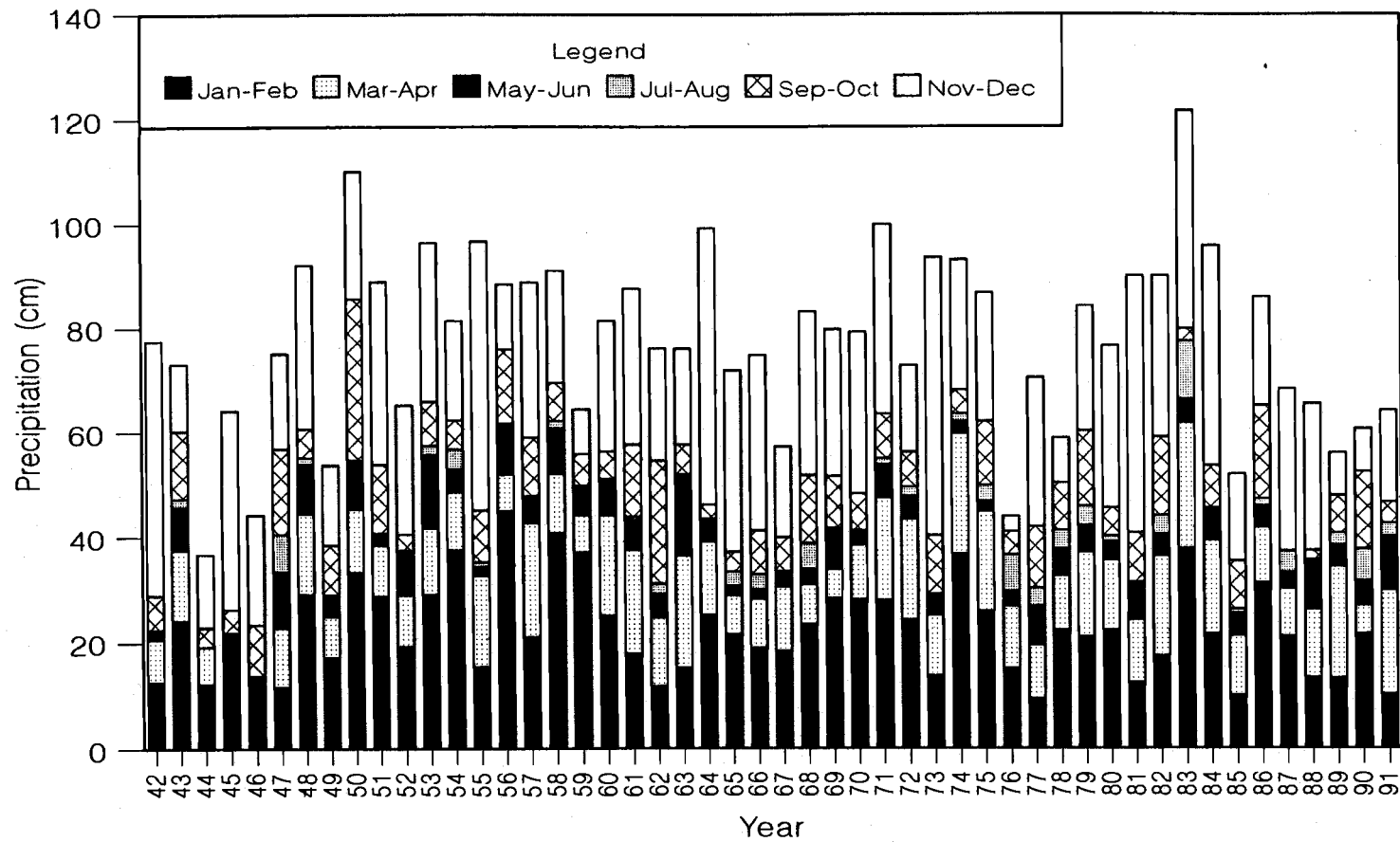
**Figure II.2.** Annual precipitation at Cave Junction weather station for 1962 to 1991.



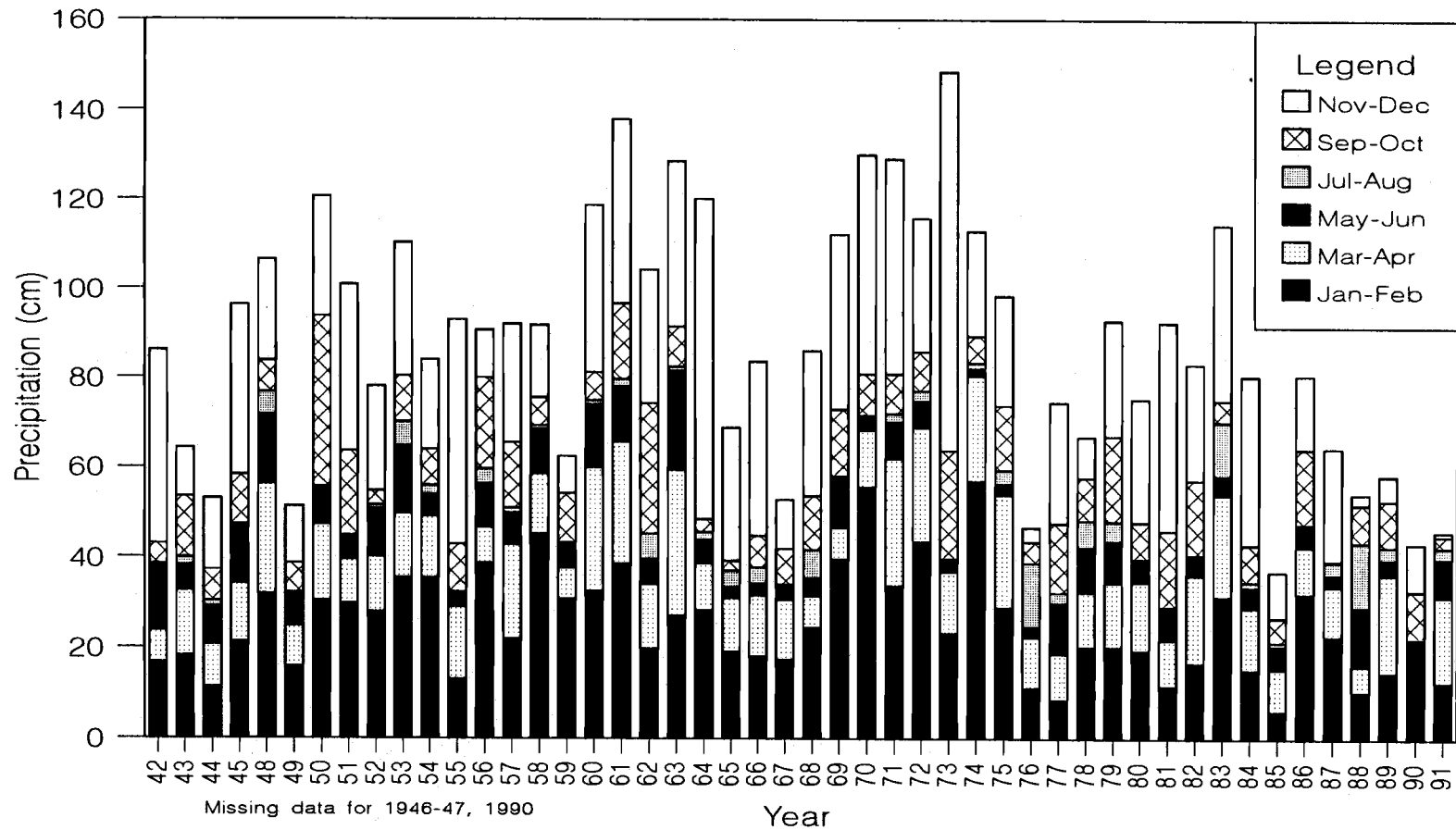
**Figure II.3.** Annual precipitation at Little River weather station for 1964 to 1991.



**Figure II.4.** Annual precipitation at Riddle weather station for 1942 to 1991.

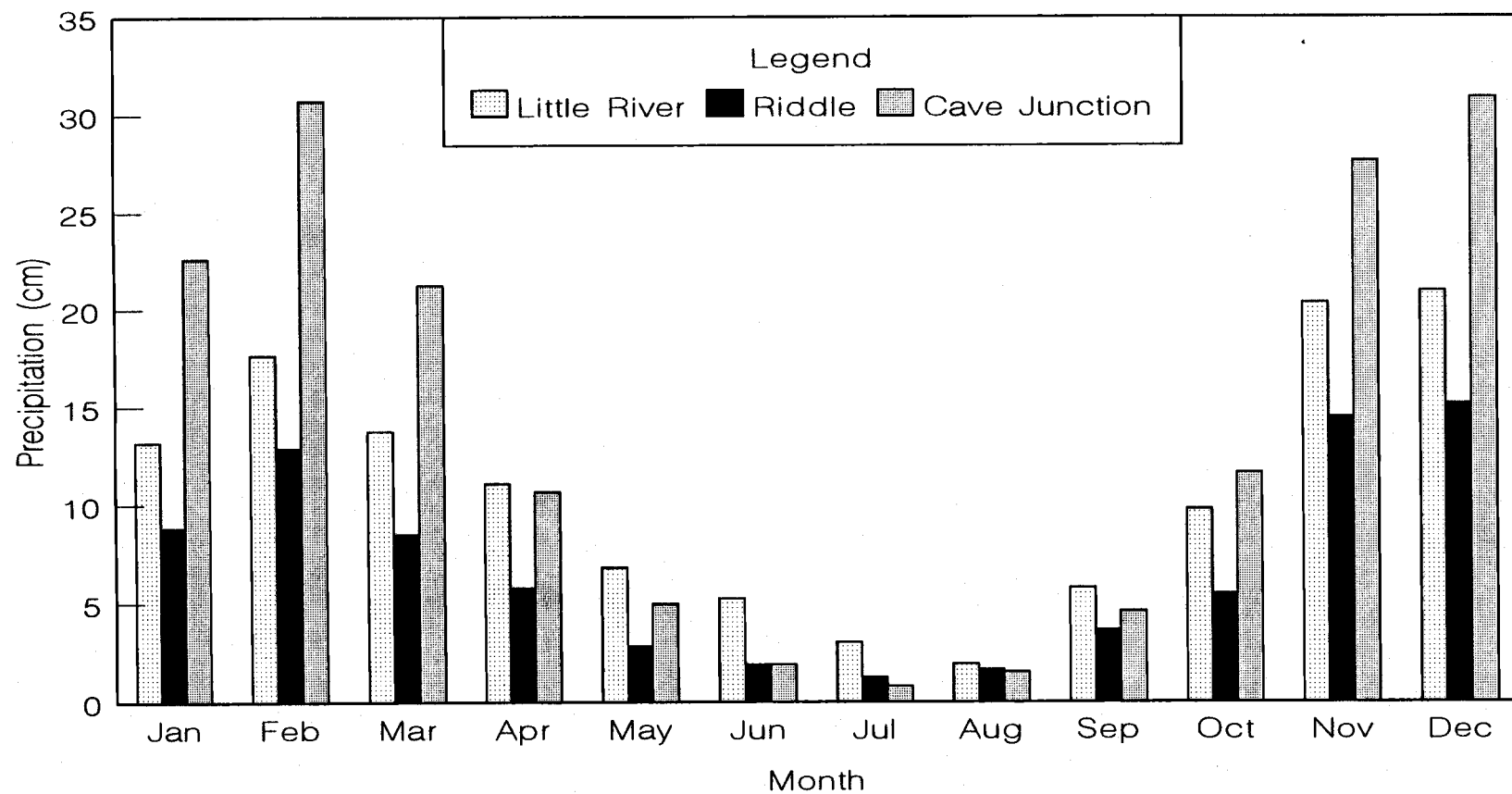


**Figure II.5.** Annual precipitation at Sexton Summit weather station for 1942 to 1991.





**Figure II.6.** Average monthly precipitation (1978-1991) for Cave Junction, Riddle, and Little River weather stations.

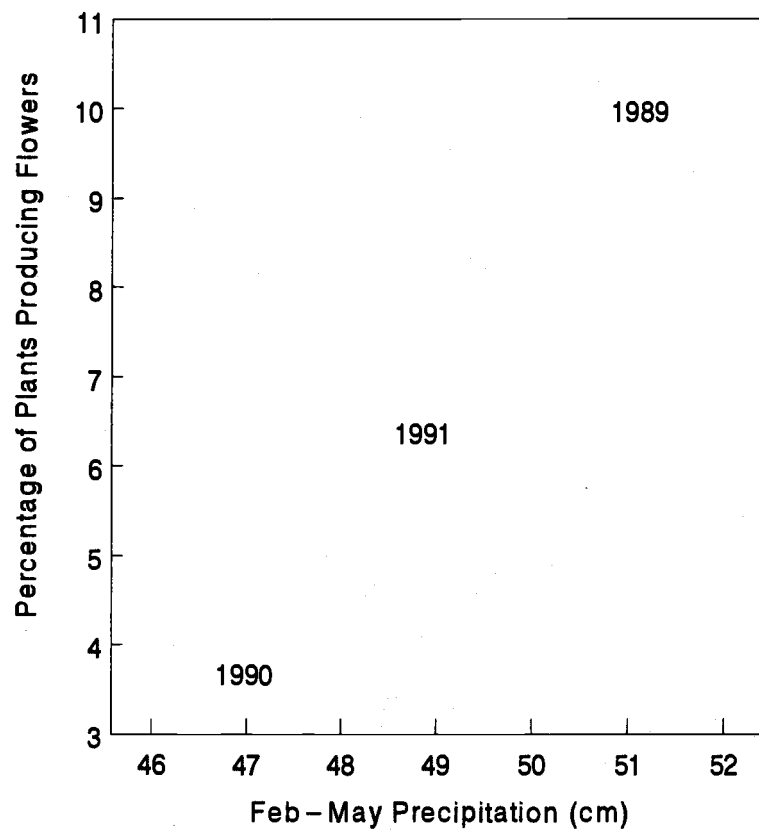


**Precipitation and *Calochortus howellii*.** Precipitation within the range of *C. howellii* varies widely (Froehlich et al. 1982). Average annual precipitation for the southwestern-most population, on the West Fork of the Illinois River, approached 254 cm. Density of *C. howellii* is highest at this site. The eastern-most Democrat Gulch and Waldo sites, where the populations appear to be dwindling, receive approximately 120 cm and 140 cm annually. Precipitation for other populations range from around 150 to 210 cm.

Seasonal precipitation follows a similar pattern (McNabb et al. 1982); for example, dry season (May to September) rainfall is lowest at the Democrat Gulch site (around 10 cm) and highest along the West Fork of the Illinois River (around 23 cm). Seasonal precipitation may reveal more meaningful correlations to population trends than monthly precipitation, and previous season precipitation may affect carbohydrate storage and formation of subsequent years' floral primordia. Analysis of correlations between precipitation and recruitment, mortality, and bud, flower, and capsule production (Chapter 3) reveal that late winter to spring precipitation (especially February to May) may be important to bud production ( $r^2 = 0.80$ ,  $n = 9$ ,  $p = 0.01$ ), and precipitation may affect mortality and recruitment indirectly.

**Precipitation and *Calochortus umpquaensis* and *C. coxii*.** Although only three years of data are available for *C. umpquaensis* and *C. coxii*, correlations between February through May precipitation and flower production are evident for *C. umpquaensis* ( $r^2 = 0.99$ ,  $n = 3$ ,  $p = 0.02$ ; Figure II.7). Additional years of data will be necessary to test the prediction value of this variable, as well as to determine if correlations exist between precipitation and recruitment and mortality.

**Figure II.7.** Precipitation (Feb-May) at Little River weather station versus flowering for *Calochortus umpquaensis* ( $r^2 = 0.99$ ,  $n = 3$ ,  $p = 0.01$ ).



## DISCUSSION

### Similarities and differences in community structure among the three species

Distribution patterns differ among the three rare mariposas; *C. howellii* and *C. umpquaensis* are locally abundant, with restricted ranges, while *C. coxii* is not only restricted geographically but is locally sparse. *Calochortus coxii* also occupies a narrower habitat range, occurring most frequently in ecotonal areas. Community structure varies most for *C. umpquaensis*, which ranges from forested habitats with low vegetation cover and closed conifer canopy, through ecotonal areas with high vegetation cover, to grass-dominated meadows and more sparsely vegetated serpentine barrens. However, this species is most abundant in partially shaded ecotones. In forested habitats, *C. umpquaensis* is less vigorous. *Calochortus howellii* inhabits open Jeffrey pine savannah and is most sparse where shrub competition, particularly *Ceanothus*, is greatest.

One theory proposed to explain rare species is that they are poor competitors (Stebbins 1942, Griggs 1940). This hypothesis may have merit for *C. howellii*; limited light or moisture may reduce vigor, increase mortality, or limit recruitment, causing populations to dwindle where *Ceanothus* and other shrubs invade. The effect of competition on *C. umpquaensis* and *C. coxii*, however, is less obvious.

In 1989, the number of individuals of *C. umpquaensis* was highest in the ecotone, where vegetation cover was also highest. In the forest, where cover was lowest, *C. umpquaensis* was most sparse. For *C. coxii*, cover did not vary significantly between sites. Regressions of number of individuals and cover by plot for both species failed to reveal correlations. Although competition for space does not directly limit distributions of *C. coxii* or *C. umpquaensis*, reduced light within the forest habitat and decreased moisture within the meadow may be indirectly limiting.

Most known populations of *C. howellii*, *C. umpquaensis*, and *C. coxii* occur within relatively intact, undisturbed plant communities which are dominated by

native species. Some communities that historically have been grazed by cattle were lower in diversity. Serpentine communities may be somewhat more resilient to grazing pressure, due to the toxicity of their soils to many non-native invasive species (Rollé 1992, pers. comm.). The specific effect of grazing on *Calochortus*, however, is to reduce vigor (Fredricks, unpublished data) and, by lowering seed set, to reduce recruitment. Cattle grazing did not occur at the study sites during the years reported, but historic factors must be considered when assessing local rarity and distribution patterns. Prior to the establishment of the permanent plots, the *C. howellii* population was within a Forest Service grazing allotment (McLennan 1992, pers. comm.). During 1975 to 1982 the area was grazed from around April 15 to June 15. It was also frequently grazed by cattle and horses prior to 1975.

Mining may have contributed to the local extirpation of populations of *C. howellii*, which inhabit areas heavily mined for gold since the 1850s. In addition, bulbs of this species were collected by Purdy during the late 1800's. At his self-proclaimed collection rate of 4,000 bulbs a day (Purdy 1976), the impact on an extremely slow-growing, geographically limited species is apparent. While the two other species are newly described and obviously not referenced in Purdy's brochures, it is possible that their bulbs were collected, as well.

### **The abiotic environment and its relation to the distribution and reproduction of southwestern Oregon mariposa lilies**

Intensive field surveys both on and off serpentine have failed to locate any populations of *C. howellii*, *C. umpquaensis*, or *C. coxii* on non-serpentine soils. This study also confirmed the close association of these three species to serpentine soils based on soil and geological maps and elemental analysis. The high nickel concentrations (especially for *C. umpquaensis* and *C. coxii*) and the low calcium to magnesium ratios (especially for *C. howellii*) were the most obvious serpentine factors exhibited in these soils.

Soil color, pH, heavy metal and macronutrient concentrations differed among the serpentine-derived soils inhabited by the three species. Soil

concentrations of nine elements differed significantly at the 0.0001 level.

*Calochortus howellii* soils were most distinctive, but *C. umpquaensis* soils were characterized by highest nickel, cadmium, manganese, and potassium concentrations. The average pH for soils inhabited by *C. umpquaensis* (6.8) and *C. coxii* (6.9) were comparable to the mean pH of 6.8 for serpentine soils worldwide (Brooks 1987).

None of the species appeared to be restricted to narrow precipitation or elevational isolines, based on range maps overlaid on precipitation (Froehlich et al. 1982, McNabb et al. 1982) and topographic maps. Microsite and microclimate analyses are clearly necessary to study the potential relationships between distribution and soil moisture relations. However, correlations between local precipitation and recruitment, mortality, and reproduction seem to indicate that climate may affect the distribution of these species. However, because of the difficulty in propagating these species in the laboratory, and the undesirability of manipulative research on federal candidate species, long-term demographic studies of population trends and life history characteristics have proven to be a more fruitful method of investigating rarity in these species than environmental analysis. The next two chapters describe the results of this approach.

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### CHAPTER 3

#### A NINE-YEAR STUDY OF DEMOGRAPHY AND REPRODUCTION IN *CALOCHORTUS HOWELLII*, A RARE SERPENTINE LILY

##### ABSTRACT

A long-term, continuing demographic study of the narrow serpentine endemic *Calochortus howellii* was initiated in 1983 to evaluate reproduction, recruitment, and mortality and to investigate possible limiting factors and causes of rarity. Using size-classified transition matrices, changes in population structure and stability are assessed. Three methods of classifying data for transition matrix analysis were compared. Theoretically derived categories, using Moloney's algorithm, yielded slightly higher average lambda values, but differences in results among methods were probably not biologically significant. Reproduction fluctuates widely from year to year, with bud production correlated with spring (February to May) precipitation ( $r^2 = 0.80$ ,  $n = 9$ ,  $p = 0.01$ ). While seed germination is high in the laboratory, heavy capsule predation limits seedling recruitment, which averaged 3.0% over 7 years. Low mortality (mean 2.0%) contributes to stable population structure and equilibrium population growth rates. Natural disturbance, which has resulted in a dramatic increase in total mortality due to localized activities of valley pocket gopher (*Thomomys bottae*), provides opportunity to study population recovery of this extremely slow-growing, long-lived lily.

## INTRODUCTION

Until recently, the importance of long-term ecological research has not been fully recognized. The reorganization of the National Science Foundation Biology Directorate to incorporate the Long-term Projects in Environmental Biology section, and the establishment of the Long-term Ecological Research Network and the Long-term Study Section of the Ecological Society of America represent noteworthy advances toward recognition of the vital importance of extended studies. Thus far, however, intensive demographic studies of plants have rarely spanned more than three years, yet they are the only way to answer basic life history questions: how long do plants live and when do they become reproductive, are there large fluctuations in recruitment and mortality, and if so, to what environmental parameters are they correlated, and are the populations stable over time. These questions are particularly important in the evaluation of rare species, in the event that intervention is deemed necessary to prevent species extinction.

A nine-year study was undertaken to investigate population trends of a federal candidate for endangered species listing, *Calochortus howellii*. This long-lived lily inhabits serpentine-derived soils in Jeffrey-pine savannah of southwestern Oregon. Recruitment, growth, reproduction, and mortality were investigated within one of the most vigorous populations of this species, and size-classified transition matrix models were applied to evaluate population stability.

Transition matrix analysis yields several statistics useful in the evaluation of population stability. Lambda ( $\lambda$ ) refers to the equilibrium population growth rate and is calculated as the dominant eigenvalue of the matrix (Lefkovich 1965). A population that is stable has a rate of 1.0, while those with  $\lambda$  values greater or less than 1.0 are increasing or declining. A population with a  $\lambda$  of 2.0, for example, will double in size over the time period indicated, while one with a  $\lambda$  of 0.5 will be reduced by half, assuming age, stage, or size distribution is stable. Estimates of time to extinction may be extrapolated for populations on the decline, but long-term projections are clearly misleading.

The equilibrium stage structure is derived from the dominant right eigenvector

and is useful in comparing the current population structure. Populations are considered unstable if they deviate significantly from the projected stable structure at equilibrium. The relative importance of each stage to population growth is indicated by the reproductive values, which is calculated as the dominant left eigenvector of the matrix.

Sensitivity and elasticity values are perhaps the most useful parameters to management, since they aid in predicting population response to hypothetical changes in growth, reproduction, and survival of individual life-history classes. The contribution to lambda of each matrix value is evaluated, and therefore the importance to population growth of various stages and functions can be determined. Sensitivities are proportional to the product of the reproductive value of stage 1 and the abundance of stage 2 in the stable stage distribution (Caswell 1978, 1989). They are calculated for each value in the matrix as  $\Delta\lambda/\Delta a_{ij}$ , where  $a_{ij}$  is the transition rate between i and j. Small increases in elements with large sensitivity values result in proportionally greater increases in lambda. Sensitivity values may be difficult to compare because they have no common scale: they may vary by several orders of magnitude and may be negative if reproductive values decline during the transition.

Elasticity values provide valuable information regarding the extent to which population growth depends on survival, growth, and reproduction at different stages in the life cycle (Caswell 1989). They are calculated as

$$e_{ij} = \frac{\frac{\Delta\lambda}{\lambda}}{\frac{\Delta a_{ij}}{a_{ij}}} \quad \text{where } a_{ij} = \text{parameter (e.g. transition rate between i and j, calculated for each value in matrix).}$$

Elasticities are proportional sensitivities which sum to 1. Because they are relative and have a common scale, they are more readily interpretable than sensitivities.

### **Range and habitat of *C. howellii***

*Calochortus howellii* is restricted to the Illinois River drainage of the Siskiyou Mountains of Josephine County, Oregon (Figure II.1, Fredricks 1986, 1988). All

populations fall within the boundaries of ultramafic formations mapped by Wells and Peck (1961) and all known populations occur on serpentine-derived soils (Chapter 2). The majority of populations occur within a narrow band extending from Eight Dollar Mountain south to near Oregon Mountain, just north of the California border; the total range of the species spans approximately 30 km. Elevations range from 390 to 610 m.

The sites on which *C. howellii* occurs are typically rocky slopes with sparse vegetation. These serpentine "barrens" are characterized by scattered Jeffrey-pine and incense cedar, sclerophyllous shrubs including species of *Arctostaphylos* and *Ceanothus*, bunchgrasses, and a high diversity of perennial herbs, including many endemic species (Fredricks 1986).

#### Description of the study site

The study site, Mariposa Meadow, is located on land managed by the United States Department of Agriculture Forest Service approximately 3.6 km southwest of the summit of Eight Dollar Mountain (T38S R8W, nw 1/4 of sec. 30). It is located near the northern extent of the range of the species. Due to the rocky terrain and sparse vegetation, plants at this study site could be easily monitored with minimal impact. Specifically, this site was selected for its high density of *C. howellii* (the population is one of the largest and most vigorous), level topography, ease of access, and relative lack of disturbance. Although the site was previously grazed, there is no obvious evidence of ground disturbing activity in the immediate area. However, other populations of the species have been impacted by mining, which has occurred throughout the area since the summer of 1850. Gold was first discovered in Oregon within 1 km of the study site near the confluence of the Illinois River and Josephine Creek (Brooks and Ramp 1968), and the area has been subsequently dredged repeatedly.

Plots were located within a Jeffrey-pine savannah opening, situated on a bench above Josephine Creek, which is 0.5 km to the east. The gently sloping topography ranges from 440 m to 465 m in elevation. The Cave Junction weather station is

located within 8 km of the study site, and provides the best available estimate of precipitation.

Based on the high total herb cover, the study site falls within the *Pinus jeffreyi/Ceanothus pumilus* plant association of Atzet and Wheeler (1984), and the corresponding *Pinus jeffreyi/Festuca rubra* association of Frenkel and Kiilsgaard (1984). Sparse *Pinus jeffreyi* and *Calocedrus decurrens* comprise the overstory. The shrub layer is limited to widely scattered *Arctostaphylos viscida*, and herbs and grasses dominate the community. Species with high frequency within the plots include *Ranunculus occidentalis*, *Camassia leichtlinii*, *Ceanothus pumilus*, *Horkelia sericata*, *Allium falcifolium*, *Senecio hesperius*, and *Viola cuneata*. All but the first two species are considered serpentine endemics (Brooks 1987, Kruckeberg 1984, White 1971). Other endemics inhabiting this area are *Arabis aculeolata*, *Balsamorhiza sericea*, *Microseris howellii*, *Hastingsia alba*, *Lewisia oppositifolia* and *Viola hallii*. Bunchgrasses, including *Deschampsia cespitosa*, *Festuca rubra*, *Melica geyeri*, and *Stipa lemmonii* contribute to the high species diversity (Fredricks 1986).

## METHODS

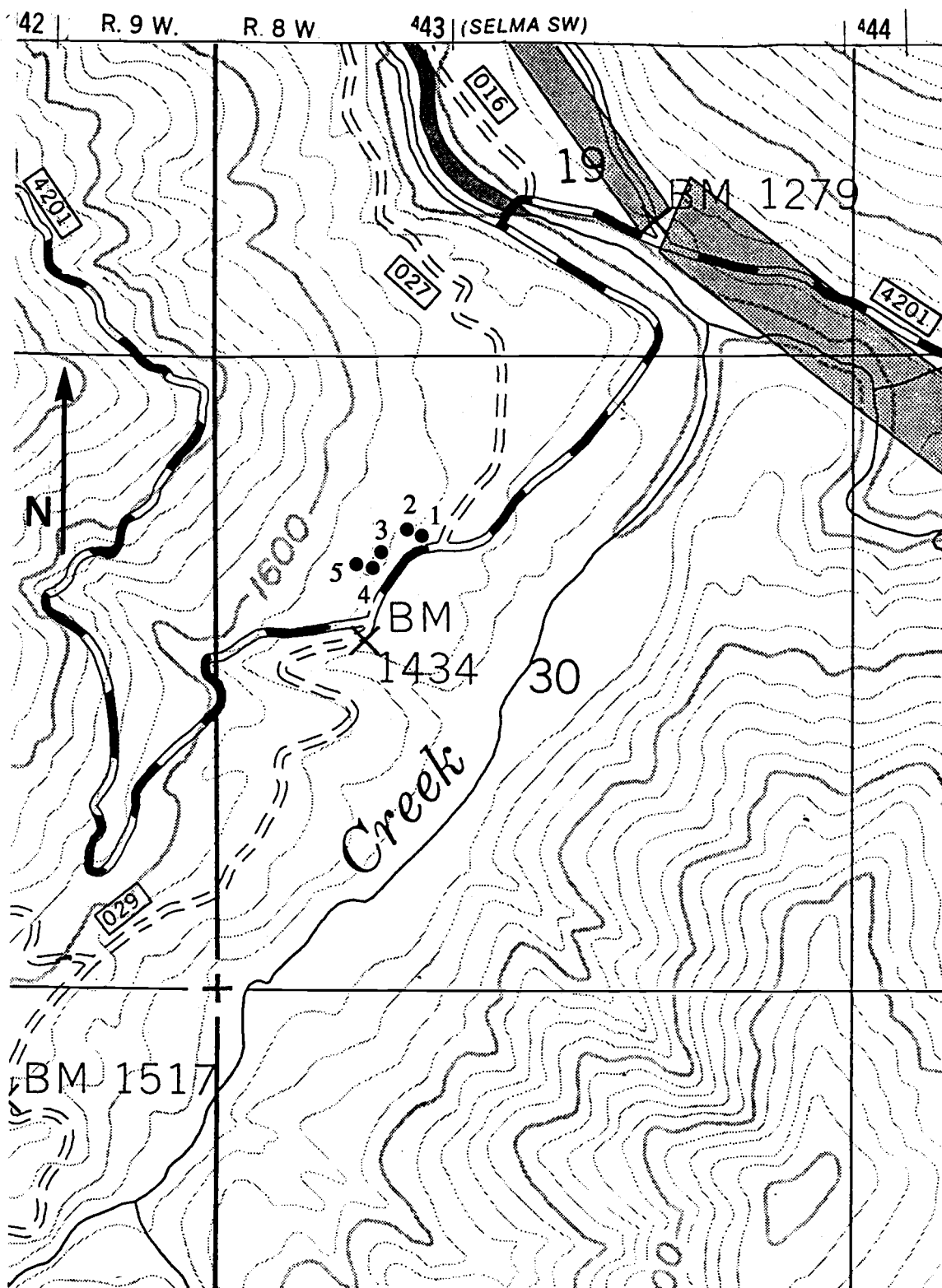
### Monitoring methods

In 1983, five 5-m<sup>2</sup> plots were established within an area 400 by 200 meters. Approximate locations of permanent plots are identified in Figure III.1. The five plots incorporate the narrow range of microhabitats occupied by this species at this site, with soil moisture highest in plots 2 and 3, due to seasonal subsurface flow.

Beginning in 1983, each individual within the plots was assigned a number, tagged and mapped. Small aluminum tags with embossed numbers were attached to plastic coated wire stakes. These tags were inserted within 3 cm of each individual; they were found to be durable and inconspicuous, and were believed to pose minimal risk to the individuals and environment. To aid in relocation and interpretation of recruitment patterns (relative to seed production), each plant was mapped on graph paper. Coordinates were later entered into a computer, so that



**Figure III.1.** Locations of permanent plots in Mariposa Meadow study area, Josephine Co., Oregon (T38S R8W, nw 1/4 of sec. 30).



maps could be easily updated and graphics could be prepared illustrating patterns of mortality, recruitment and seed set.

A minimum of four visits were made to the study area each year, with specific timing of visits determined by plant phenology. During the first visit in mid to late April, presence/absence was determined for all previously tagged individuals, and new recruits were tagged and mapped. In mid to late May, morphological data were collected (leaf length from 1983-1985; leaf width from 1985-1991), and potentially reproductive individuals were identified by the presence of developing inflorescences. Leaf widths were measured to the nearest millimeter and ranged from 1 to 18 mm. In late June to early July, numbers of flowers produced per plant were recorded; and in mid to late July, capsules were counted and measured within the plots. At this time, capsules were also collected, as described below, for seed-set analysis.

Direct observations of predation on *Calochortus* were limited to insects, although herbivorous mammals were observed in the study areas grazing on vegetation outside of the plots. The height of vegetation removal, dentation patterns, knowledge of feeding habitats, and observations were used to evaluate predation on *Calochortus* within the study area. Removal of tissue by insects and mammals were in most cases easily distinguished.

### Data analysis

Data were entered into a relational database for calculation of matrices and preparation for statistical analysis. Year of recruitment, year of mortality, and annual measurements for leaf width, bud, flower, and capsule production were recorded for each individual. The database also facilitated conversions of various leaf-width ranges to predetermined categories, generating size-classified matrices and enabling queries on growth rates, recruitment, and mortality per year by leaf width, transect, habitat, or site.

Inflorescences of *Calochortus howellii* begin to emerge in late April at the study site. By May, buds are well formed and are susceptible to grazing by deer

and jackrabbits. While bud production is a poor predictor of final seed set, the reproductive effort of bud production was investigated. The question asked was if the production of buds during one year influences the probability of bud production the subsequent year. The numbers and proportions of plants producing buds which had not initiated inflorescences the previous year were compared to those which produced buds, flowers, and capsules the previous year. In addition, plants producing buds three consecutive years and only alternate years are compared.

Transition matrices, incorporating information on recruitment, growth (change in leaf width between two consecutive years), and mortality were analyzed using the APL program DEMOG (Wilson 1992). Size-classified matrices were generated using three methods. First, categories were empirically selected based on evaluation of the life history of the species. The second approach involved theoretical derivation of categories, based on an algorithm developed by Vandermeer (1978) and improved by Moloney (1986) which minimizes the errors of estimation and errors of distribution resulting from inappropriate size classification. In the third approach, the raw leaf width data, which was recorded to the nearest millimeter, was not further classified into categories. This approach allowed sampling error to be quantified and the robustness of the model evaluated. The large data set (nine years and nearly 700 plants) provides a unique opportunity to compare different methods of selecting categories with minimal sampling error.

For the empirical classification analysis, three categories were selected which best represented life history stages of the species: seedlings, juveniles, and adults. The first category, seedlings, consists of plants with maximum leaf widths no greater than 3 mm. These individuals may remain in this category for many years.

An individual did not typically become reproductive until its leaf attained a minimum width of 6 mm. Plants with leaf widths greater than 3 mm and less than or equal to 6 mm were considered juveniles and comprised category 2. Plants above this threshold were classified as adults, category 3, whether or not they actually were reproductive.

Reproduction in the transition matrix is calculated as the number of new plants

appearing in the plots the second year divided by the total number of plants in that category the first year. These numbers appear in the first row of the matrix and are typically largest for the adults (category 3). Occasionally, juvenile plants produce capsules (e.g. plot 3), therefore total seedling recruitment is represented by the second and third columns of the first row of the transition matrix. Capsule data were used to determine proportion of reproductive plants in each category. For example, if 10% of the capsule-producing plants within the plots were in the juvenile category, 10% of the seedling recruitment the subsequent year was attributed to category 3.

A small number of new juvenile and adult plants have appeared in the plots each year since the onset of the study. For the present analysis, these plants were ignored. *Calochortus howellii* does not typically spread clonally and although plants may occasionally produce offsets, this method of vegetative reproduction is far more common in other taxa (e.g. *C. uniflorus*, *C. longebarbatus*). Other possible explanations for the appearance of previously undetected juvenile and adult plants are discussed later.

In order to evaluate the impact of localized episodes of mortality and recruitment, data were analyzed separately by plot. This approach also allows standard deviations for lambda to be calculated. Standard deviation of the lambda values was also determined for the summarized data over time.

The software package RAMAS Stage (Ferson 1990) was used to calculate sensitivity and elasticity values, discussed below. CATSIZE, a computer program implementation of Moloney's generalized algorithm for determining category size, developed by Millstein (1992), was used to generate the size classification for the theoretically derived categories.

### **Capsule and seed collection and analysis**

In order to estimate average numbers of seeds produced per plant for the demographic analysis, inflorescences were collected at the time of capsule maturity and prior to seed dissemination, at a location approximately 1.1 km from the study

plots. The number of capsules collected each year depended upon yearly variation in capsule production and predation and ranged from 20 to 75. Capsules were measured, dissected, and seeds and ovules were counted. If more than one capsule was produced, their positions on the inflorescence were recorded in order to compare reproductive allocation among terminal and axillary fruits. To determine if capsule length was a good predictor of seed number or seed set, linear regressions were performed for capsule length versus seed number, seed set, and total number of ovules produced.

A subset of seeds collected were germinated in the laboratory using methods described in Fredricks (1986). Seedlings development was observed over two years, with some bulbs excavated and observed after the first growing season. Seeds not used in germination trials were deposited at the Berry Botanic Garden in Portland, Oregon, or returned to the site.

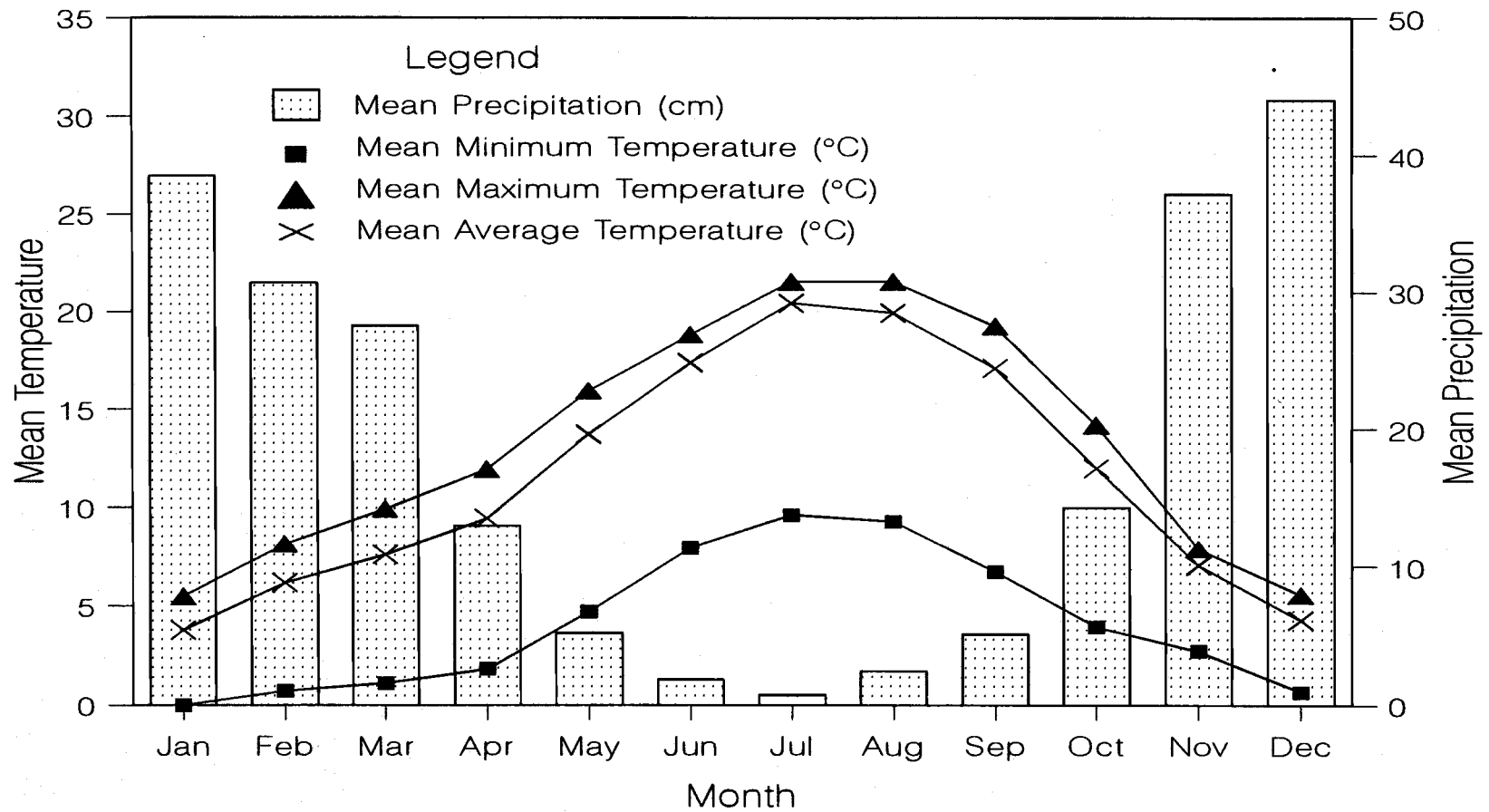
## RESULTS AND DISCUSSION

### Life history of *C. howellii*

**Germination.** Seeds require approximately 8 weeks at 5° C. for germination (Fredricks 1986). Temperatures at the Cave Junction weather station, near the study site average 5° C or less during December and January (Figure III.2). In the laboratory, nearly 100% germination was achieved (Fredricks 1986). Small bulbs develop during the first season, and seedling leaves tend to wither as soil moisture decreases, typically by the end of May.

**Recruitment of seedlings.** Seedling recruitment is patchy and episodic (Table III.1), with new individuals typically arising within a short distance (less than 1 meter) of a plant which dispersed seed the previous year. In most cases, seedlings establish north and east of a seed-producing parent. This is likely explained by the prevailing southwesterly winds at the study area during late July when seeds are

**Figure III.2.** Climate diagram illustrating mean precipitation and temperature for Cave Junction weather station, based on data for 1963-1987.



**Table III.1a.** Permanent plot data for *Calochortus howellii*, summarized by plot for 1985 through 1991. Vegetative plants did not initiate inflorescence. Plants which produced buds, flowers, and capsules are tallied separately, by plot. Morts are defined as those individuals which failed to appear two consecutive years and are considered dead. Plants with leaves no wider than 3 mm appearing for the first time are new seedlings; larger plants new to the plots are referred to as new juveniles or adults, based on leaf width.

1983						
Plot Number	1	2	3	4	5	All Plots
Vegetative	0	3	6	33	6	48
Buds	22	13	26	36	65	162
Flowers	22	11	23	31	60	147
Capsules	5	7	10	10	31	63
All plants	22	16	32	69	71	210
1984						
Plot Number	1	2	3	4	5	All Plots
Vegetative	32	23	20	40	37	152
Buds	15	15	18	31	28	107
Flowers	8	13	15	29	24	89
Capsules	5	10	10	11	16	52
Morts	0	0	0	0	0	0
All plants	47	38	38	71	65	259
1985						
Plot Number	1	2	3	4	5	All Plots
Vegetative	39	36	22	65	58	220
Buds	8	9	21	42	39	119
Flowers	7	8	18	39	34	106
Capsules	4	1	12	12	0	29
Morts	0	0	3	3	0	6
New seedlings	0	0	0	0	0	0
New juveniles/adults	0	7	8	39	32	86
All plants	47	45	43	107	97	339
1986						
Plot Number	1	2	3	4	5	All Plots
Vegetative	52	19	29	62	48	210
Buds	37	26	26	66	66	221
Flowers	30	19	17	17	40	123
Capsules	23	1	5	9	16	54
Morts	2	1	2	0	2	7
New seedlings	1	0	1	0	1	3
New juveniles/adults	41	1	13	19	18	92
All plants	89	45	55	128	114	431
1987						
Plot Number	1	2	3	4	5	All Plots
Vegetative	86	42	68	120	100	416
Buds	9	9	14	16	20	68
Flowers	1	3	2	3	8	17
Capsules	0	1	1	1	6	9
Morts	0	1	0	1	3	5
New seedlings	0	4	22	2	3	31
New juveniles/adults	6	3	5	7	6	27
All plants	95	51	82	136	120	484
1988						
Plot Number	1	2	3	4	5	All Plots
Vegetative	80	38	55	86	96	355
Buds	24	25	36	58	37	180
Flowers	10	19	33	51	32	145
Capsules	2	13	7	9	11	42
Morts	0	1	3	0	2	6
New seedlings	2	12	8	2	12	36
New juveniles/adults	7	1	4	6	3	21
All plants	104	63	91	144	133	535
1989						
Plot Number	1	2	3	4	5	All Plots
Vegetative	46	32	81	67	78	304
Buds	58	30	25	81	75	269
Flowers	22	21	12	34	38	127
Capsules	5	0	2	0	1	8
Morts	2	10	2	2	3	19
New seedlings	1	6	13	1	21	42
New juveniles/adults	2	4	4	5	2	17
All plants	104	62	106	148	153	573
1990						
Plot Number	1	2	3	4	5	All Plots
Vegetative	69	21	79	70	98	337
Buds	33	19	34	73	61	220
Flowers	6	1	9	5	10	31
Capsules	1	0	3	3	1	8
Morts	3	21	7	9	0	40
New seedlings	1	0	8	1	5	15
New juveniles/adults	2	0	9	4	1	16
Total	102	40	113	143	159	557
1991						
Plot Number	1	2	3	4	5	All Plots
Vegetative	82	9	82	72	87	432
Buds	20	8	37	74	76	115
Flowers	11	8	22	23	36	64
Capsules	5	7	5	3	16	36
Morts	0	25	0	5	1	31
New seedlings	0	1	5	7	4	17
New juveniles/adults	0	3	1	1	1	6
All plants	102	17	119	146	163	547

**Table III.1b.** Permanent plot data for *Calochortus howellii*, summarized by plot for 1985 through 1991. All numbers are percentages. Vegetative plants did not initiate inflorescence. Plants which produced buds, flowers, and capsules are tallied separately, by plot. Morts are defined as those individuals which failed to appear two consecutive years and are considered dead. Recruits are plants appearing in the plots for the first time, regardless of size.

1983						
Plot	1	2	3	4	5	All plots
Vegetative	0.0	18.8	18.8	47.8	8.5	22.9
Buds	100.0	81.3	81.3	52.2	91.5	77.1
Flowers	100.0	68.8	71.9	44.9	84.5	70.0
Capsules	22.7	43.8	31.3	14.5	43.7	30.0
1984						
Plot	1	2	3	4	5	All plots
Vegetative	68.1	60.5	52.6	56.3	56.9	58.7
Buds	31.9	39.5	47.4	43.7	43.1	41.3
Flowers	17.0	34.2	39.5	40.8	36.9	34.4
Capsules	10.6	26.3	26.3	15.5	24.6	20.1
Morts	0.0	0.0	0.0	0.0	0.0	0.0
1985						
Plot	1	2	3	4	5	All plots
Vegetative	83.0	80.0	51.2	60.7	59.8	64.9
Buds	17.0	20.0	48.8	39.3	40.2	35.1
Flowers	14.9	17.8	41.9	36.4	35.1	31.3
Capsules	8.5	2.2	27.9	11.2	0.0	8.6
Morts	0.0	0.0	7.9	4.2	0.0	2.3
Recruits	0.0	15.6	18.6	36.4	33.0	25.4
1986						
Plot	1	2	3	4	5	All plots
Vegetative	58.4	42.2	52.7	48.4	42.1	48.7
Buds	41.6	57.8	47.3	51.6	57.9	51.3
Flowers	33.7	42.2	30.9	13.3	35.1	28.5
Capsules	25.8	2.2	9.1	7.0	14.0	12.5
Morts	4.3	2.2	4.7	0.0	2.1	2.1
Recruits	49.4	2.2	25.5	14.8	16.7	22.5
1987						
Plot	1	2	3	4	5	All plots
Vegetative	90.5	82.4	82.9	88.2	83.3	86.0
Buds	9.5	17.6	17.1	11.8	16.7	14.0
Flowers	1.1	5.9	2.4	2.2	6.7	3.5
Capsules	0.0	2.0	1.2	0.7	5.0	1.9
Morts	0.0	2.2	0.0	0.8	2.6	1.2
Recruits	6.3	13.7	32.9	6.6	7.5	12.0
1988						
Plot	1	2	3	4	5	All plots
Vegetative	76.9	60.3	60.4	59.7	72.2	66.4
Buds	23.1	39.7	39.6	40.3	27.8	33.6
Flowers	9.6	30.2	36.3	35.4	24.1	27.1
Capsules	1.9	20.6	7.7	6.3	8.3	7.9
Morts	0.0	2.0	3.7	0.0	1.7	1.2
Recruits	8.7	20.6	13.2	5.6	11.3	10.7
1989						
Plot	1	2	3	4	5	All plots
Vegetative	44.2	51.6	76.4	45.3	51.0	53.1
Buds	55.8	48.4	23.6	54.7	49.0	46.9
Flowers	21.2	33.9	11.3	23.0	24.8	22.2
Capsules	4.8	0.0	1.9	0.0	0.7	1.4
Morts	2.9	17.5	2.2	1.4	2.3	3.9
Recruits	2.9	16.1	16.0	4.1	15.0	10.3
1990						
Plot	1	2	3	4	5	All plots
Vegetative	67.6	52.5	69.9	49.0	61.6	60.5
Buds	32.4	47.5	30.1	51.0	38.4	39.5
Flowers	5.9	2.5	8.0	3.5	6.3	5.6
Capsules	1.0	0.0	2.7	2.1	0.6	1.4
Morts	4.8	35.5	9.4	6.8	0.0	8.2
Recruits	2.9	0.0	15.0	3.5	3.8	5.7
1991						
Plot	1	2	3	4	5	All plots
Vegetative	80.4	52.9	68.9	49.3	53.4	79.0
Buds	19.6	47.1	31.1	50.7	46.6	21.0
Flowers	10.8	47.1	18.5	15.8	22.1	11.7
Capsules	4.9	41.2	4.2	2.1	9.8	6.6
Morts	0.0	67.5	0.0	3.5	1.3	6.1
Recruits	0.0	23.5	5.0	5.5	3.1	4.2



disseminating. Capsule morphology facilitates wind dispersal; like other liliaceous genera including *Camassia* and *Zigadenus*, the elongated dried stem vibrates, shaking the capsule contents until the seeds are shed. Animals may aid in dispersal by further agitating the dried stems.

New seedlings contributed an average of 3.0% to the population from 1986 to 1991 (Table III.2). Seedling recruitment was highest during 1987 through 1989, then dropped sharply in 1990. A modest correlation ( $r^2 = 0.56$ ,  $n = 7$ ,  $p = 0.19$ ) between recruitment and February precipitation may indicate a need for adequate moisture during late winter, but precipitation in other months is negatively correlated with recruitment. Recruitment was modestly correlated to numbers of capsules produced during previous year ( $r^2 = 0.58$ ,  $n = 7$ ,  $p = 0.16$ ).

An increasing trend in the number of small *C. howellii* seedlings (1 to 2 mm leaf width) is evident between 1986 and 1989 (Figures III.3-5). Capsule production during previous years (1986, 1988) is correspondingly high (Tables III.1 and III.2). Reduced capsule production during 1989 and 1990 corresponds with reduced recruitment during the following two years (Table III.1).

Mortality of first year seedlings is high relative to established plants; 39, 48, and 44% of seedlings 1 mm or less recruited in 1987, 1988, and 1989, respectively, had died by 1991 (Table III.3a). Seedlings may vary in size depending on resource availability and may not increase in width for many years. For example, 82% of individuals which were 1 mm or less in 1987 which had not died by 1991, had not grown (Table III.3a). Growth rates accelerate somewhat later in life; only 15 and 29% of those individuals with widths of 4 mm and 5 mm respectively in 1987 were the same size in 1991 (Table III.3b). Often, decreases or failure to increase were due to partial or total leaf herbivory during previous years.

Growth of seedlings, as previously noted, can be extremely slow. Typically, there is a long period of little or no increase in leaf width, while resources are allocated for underground development of the bulbs. During this time, contractile roots effectively lower seedling bulbs through the soil profile. Once plants are well

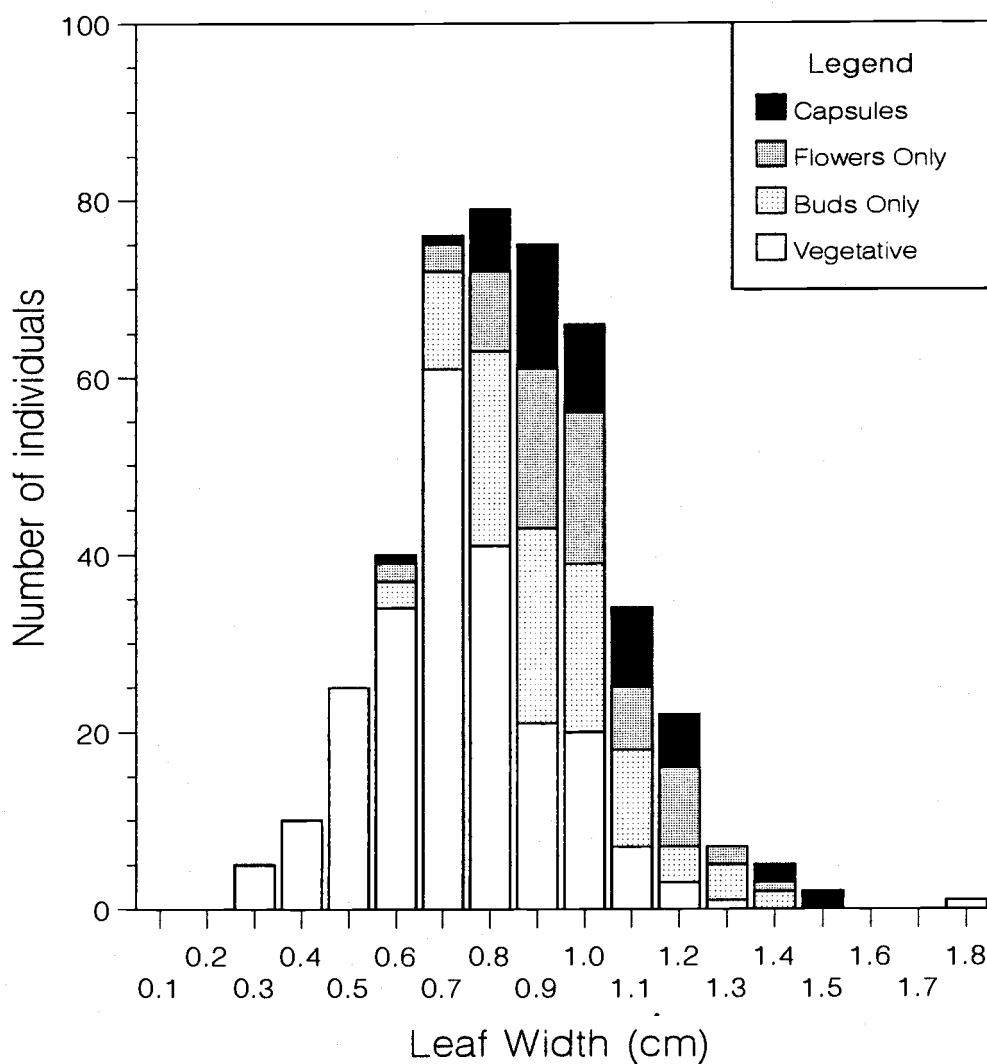
**Table III.2a.** Summary of data collected within all five plots at Mariposa Meadow for *Calochortus howellii* between 1983 and 1991, including number of plants producing buds, flowers, and capsules, recruitment, and mortality. Seedlings are defined as individuals with leaves no wider than 3 mm, juveniles with leaves between 3.5 mm and 6 mm, adults with widths greater 6 mm.

Year	1983	1984	1985	1986	1987	1988	1989	1990	1991
<b>Reproduction</b>									
Buds	162	107	119	221	68	180	269	220	215
Flowers	147	89	106	123	17	145	127	31	100
Capsules	63	52	29	54	9	42	8	8	36
Total	210	259	339	431	484	535	573	557	547
<b>Recruitment</b>									
Seedling	----	----	4	2	31	36	42	15	17
Juvenile	----	----	27	32	20	16	6	13	5
Adult	----	----	55	63	7	5	6	3	1
Total	----	----	86	97	58	57	54	31	23
<b>Mortality</b>									
Seedling	----	----	0	0	0	5	7	13	5
Juvenile	----	----	0	1	0	0	1	5	2
Adult	----	----	0	6	5	1	12	20	27
Total	----	----	0	7	5	6	20	38	34

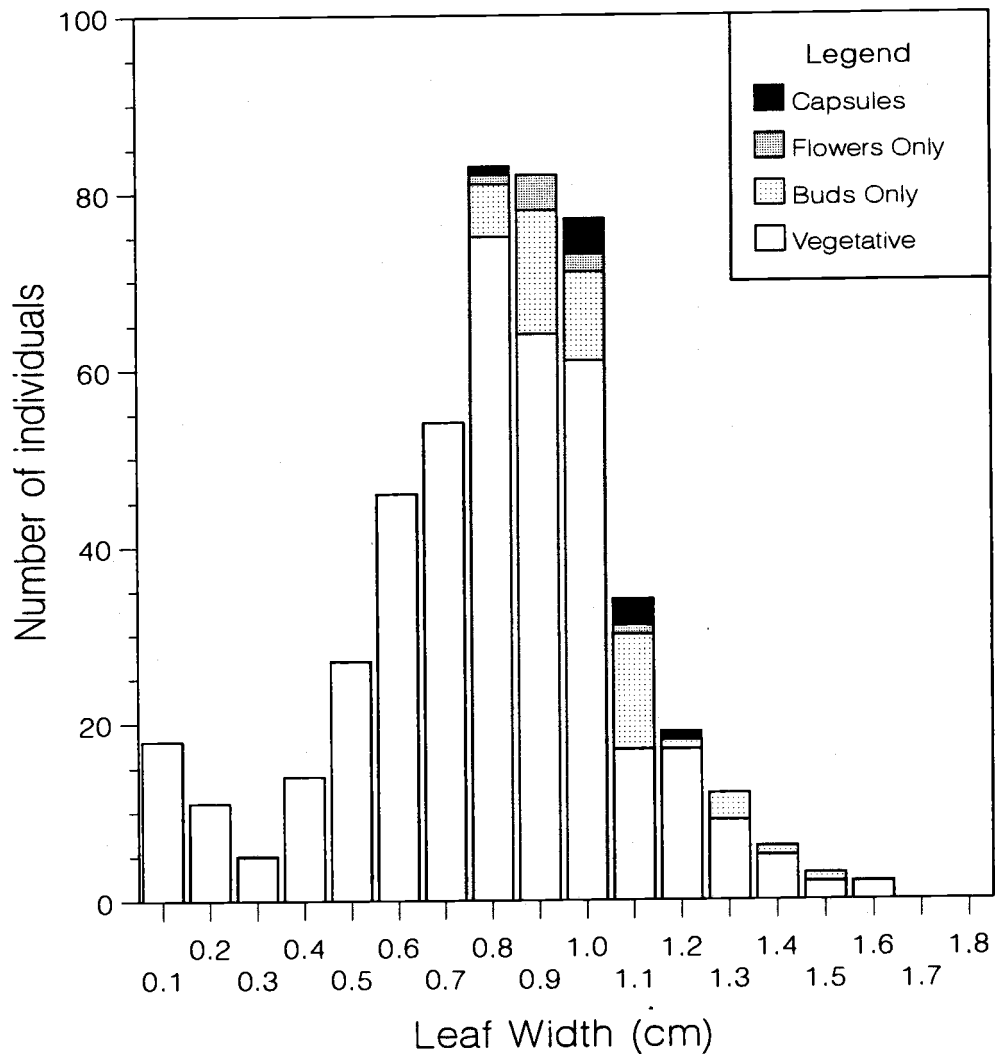
**Table III.2b.** Summary of data collected within all five plots at Mariposa Meadow for *Calochortus howellii* between 1983 and 1991, including percentage of plants producing buds, flowers, and capsules, recruitment, and mortality. Seedlings are defined as individuals with leaves no wider than 3 mm, juveniles with leaves between 3.5 mm and 6 mm, adults with widths greater than 6 mm.

Year	1983	1984	1985	1986	1987	1988	1989	1990	1991	Mean
<b>Reproduction</b>										
Buds	77.1	41.3	35.1	51.3	14.0	33.6	46.9	39.5	39.3	37.8
Flowers	70.0	34.4	31.3	28.5	3.5	27.1	22.2	5.6	18.3	24.1
Capsules	30.0	20.1	8.6	12.5	1.9	7.9	1.4	1.4	6.6	9.0
<b>Recruitment</b>										
Seedling	----	----	1.2	0.5	6.4	6.7	7.3	2.7	3.1	2.8
Juvenile	----	----	8.0	7.4	4.1	3.0	1.0	2.3	0.9	2.7
Adult	----	----	16.2	14.6	1.4	0.9	1.0	0.5	0.2	3.5
Total	----	----	25.4	22.5	12.0	10.7	9.4	5.6	4.2	9.0
<b>Mortality</b>										
Seedling	----	----	0.0	0.0	0.0	0.9	1.2	2.3	0.9	0.5
Juvenile	----	----	0.0	0.2	0.0	0.0	0.2	0.9	0.4	0.2
Adult	----	----	0.0	1.4	1.0	0.2	2.1	3.6	4.9	1.3
Total	----	----	0.0	1.6	1.0	1.1	3.5	6.8	6.2	2.0

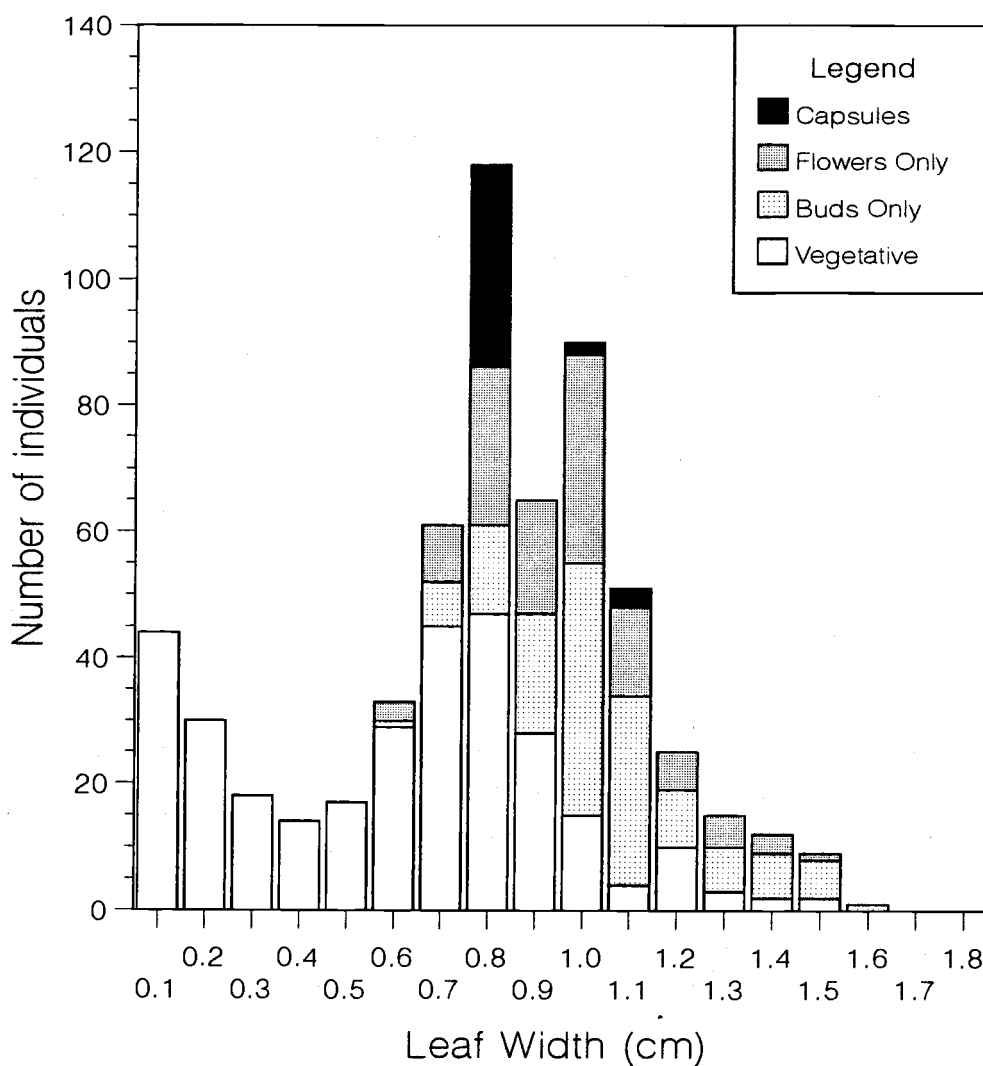
**Figure III.3.** Frequency distribution and reproductive stages attained by *Calochortus howellii* based on leaf width for 1986. The sum of the three upper bar segments are the total number of buds produced; upper two segments total for flowers. Most buds which failed to develop flowers or capsules were removed through grazing.



**Figure III.4.** Frequency distribution and reproductive stages attained by *Calochortus howellii* based on leaf width for 1987. The sum of the three upper bar segments are the total number of buds produced; upper two segments total for flowers. Most buds which failed to develop flowers or capsules were removed through grazing.



**Figure III.5.** Frequency distribution and reproductive stages attained by *Calochortus howellii* based on leaf width for 1989. The sum of the three upper bar segments are the total number of buds produced; upper two segments total for flowers. Most buds which failed to develop flowers or capsules were removed through grazing. Note recruitment of small plants.



**Table III.3a.** Fate of 1 mm wide *Calochortus howellii* seedlings in width recruited in 1987, 1988, and 1989 after 2 to 4 years, including actual numbers and percent which died, remained 1 mm, and grew. Percent mortality based on total; percent in remaining categories based on those alive that year.

Fate in 1991		Dead		1 mm		2 mm		3 mm		4 mm	
Recruit year	Total	N	Percent	N	Percent	N	Percent	N	Percent	N	Percent
1987	18	7	38.9	9	81.8	2	18.2	0	0.0	0	0.0
1988	25	12	48.0	7	53.8	4	30.8	1	7.7	1	7.7
1989	23	11	47.8	8	66.7	4	33.3	0	0.0	0	0.0

**Table III.3b.** Fate of *Calochortus howellii* plants which had leaf widths of 4 mm and 5 mm in 1985, 1986, or 1987 and their change in size in 1991. Percent increases based on numbers present in 1991 (i.e. excluding missing plants).

Fate in 1991		Missing		= or <		1 mm increase		2 mm increase		3 mm increase		4+ mm increase	
0.4 cm	Total	N	Percent	N	Percent	N	Percent	N	Percent	N	Percent	N	Percent
1985	8	2	25.0	1	16.7	0	0.0	1	16.7	2	33.3	2	33.3
1986	9	0	0.0	2	22.2	5	55.6	0	0.0	1	11.1	1	11.1
1987	13	1	7.7	2	16.7	4	33.3	3	25.0	4	33.3	0	0.0
0.5 cm													
1985	19	3	15.8	0	0.0	3	18.8	1	6.3	6	37.5	6	37.5
1986	25	3	12.0	3	13.6	4	18.2	4	18.2	2	9.1	9	40.9
1987	21	6	28.6	6	40.0	3	20.0	5	33.3	3	20.0	4	26.7

established, accelerated above-ground growth has been observed, and occasionally seedlings may show leaf-width increases of several millimeters in successive years. However, growth is typically slow, and many additional years of study may be necessary to determine the average period of time necessary for seedlings to reach reproductive maturity. No seedlings recruited during the study have yet advanced beyond the seedling or juvenile stage.

**Juveniles.** Juveniles (leaves between 3.5 mm and 6 mm in width) do not make up a large proportion of the population, but they differ from the smaller seedlings in their reduced mortality rate. Average mortality for this stage over a six year period was 1.7%.

Once established, juveniles grow slowly until reproductive maturity is reached. Of the plants that were scored as juveniles in 1985, 1986, and 1987, the following percentages, respectively, had failed to increase in size when observed in 1991: 4.5, 16.1, and 29.6 (Table III.3b). In these juvenile cohorts of 1985, 1986, and 1987, a large increase in growth (4 mm or more in leaf width) was observed in only 3.6, 3.2, and 1.5%, respectively (Table III.3b.).

**Accounting for new juveniles and adults.** The high incidence of new adult individuals appearing in the plots during the earlier years of the study was thought to be explained by the poorly documented phenomenon of vegetative dormancy (Fredricks 1986). However, continued study has led to the conclusion that these adult individuals were not new to the population, but instead they were previously grazed at ground level shortly after emergence and therefore were unobserved. Once it became evident that herbivores could remove all aboveground organs, closer examination in the vicinity of apparently missing individuals often revealed stems present immediately below the surface (pers. obs.). Because the recruits in Table III.1 include all plants newly observed in the plots, these numbers overestimate actual recruitment. The true dynamics of the population are better illustrated by transition matrix analyses which incorporate only seedling recruitment



and the leaf width frequency diagrams (Figures III.4 and III.5). In addition, the appearance of a small number of new juveniles might reflect the difficulty in locating the tiny seedlings and their tendency to wither early in the season.

**Reproduction.** Bud, flower, and capsule production by leaf width is illustrated for three years: a good reproductive year for *C. howellii*, 1986, a poor reproductive year, 1987; and the year with the highest bud production and heavy predation, 1989 (Figures III.3-5). The increasing percentage of reproductive individuals as leaf width increases is particularly evident for 1986 and 1989. Most individuals which failed to produce flowers or capsules after initiating buds had been grazed.

On average, plants were more likely to produce buds if they had not initiated buds the previous year (Table III.4). However, large numbers of plants produced buds three consecutive years, suggesting that bud production does not drain carbohydrate reserves sufficiently to preclude repeated reproductive effort.

Reproductive effort in *C. howellii* is closely correlated to size: individuals rarely produce buds until leaf widths are 6 mm or greater. As leaf widths increase, the proportion of vegetative individuals decreases, and nearly all larger individuals are reproductive. Larger individuals are also more likely to produce two or more buds per inflorescence.

For many nonannual plants (monocarpic and polycarpic perennials), size is a good predictor of onset of flowering (Lacey 1986). As lifespan lengthens, the age at first reproduction is delayed for both plants (Harper and White 1974) and animals (Stearns 1976). In addition, the observation that larger individuals produce larger inflorescences and greater seed-set is not unexpected; Lacey (1986) provides numerous references that in many monocarps and polycarps, fecundity rises and mortality declines with increasing size.

Average seed-set varied from 29 to 58% for the six years sampled Table III.5a. A modest correlation ( $r^2$  from 0.49 to 0.52,  $n = 37$  to 75) exists between capsule length and seed number for 1989 to 1991 (Table III.6). In Figure III.6, capsule length versus the number of seed produced per capsule are plotted for three years.

**Table III.4.** Flower-bud formation in *Calochortus howellii* in relation to previous years' reproductive fate.

**Actual data**

Years	1983-84	1984-85	1985-86	1986-87	1987-88	1988-89	1989-90	1990-91
Buds following no reproduction	50	85	147	34	146	176	86	85
Buds 2 consecutive years	57	34	74	34	34	93	137	130
Buds following flowers	51	27	66	17	7	73	57	14
Buds following capsules	17	12	19	5	3	20	2	1
Years	1983-85	1984-86	1985-87	1986-88	1987-89	1988-90	1989-91	
Buds 3 consecutive years	23	11	24	85	19	49	85	
Buds alternate years	65	64	21	101	39	82	124	

**Percentage based on total numbers of individuals producing buds for latest year.**

Years	1983-84	1984-85	1985-86	1986-87	1987-88	1988-89	1989-90	1990-91	Average
Buds following no reproduction	46.7	71.4	66.5	50.0	81.1	65.4	39.1	39.5	57.5
Buds 2 consecutive years	53.3	28.6	33.5	50.0	18.9	34.6	62.3	60.5	42.7
Buds following flowers	47.7	22.7	29.9	25.0	3.9	27.1	25.9	6.5	23.6
Buds following capsules	15.9	10.1	8.6	7.4	1.7	7.4	0.9	0.5	6.5
Years	1983-85	1984-86	1985-87	1986-88	1987-89	1988-90	1989-91		
Buds 3 consecutive years	19.3	5.0	35.3	47.2	7.1	22.3	39.5		25.1
Buds alternate years	54.6	29.0	30.9	56.1	14.5	37.3	57.7		40.0

**Table III.5a.** Seed and capsule analysis for *Calochortus howellii* based on capsules collected outside of permanent plots. Totals for each year are sums of average seed number and undeveloped ovule number per capsule. Note high seed set and large capsules for 1987.

Year	N	Capsule Length (cm)		Seeds		Undeveloped ovules		Total Seeds + ovules		Seed Set (%)	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
1991	75	1.69	0.24	14.49	7.89	34.69	9.34	49.19	8.54	0.29	0.15
1990	37	1.93	0.26	14.29	7.48	23.50	7.95	37.79	14.96	0.35	0.07
1989	54	1.92	0.30	17.78	9.19	32.39	9.41	50.17	11.42	0.35	0.16
1988	59	2.00	0.33	21.88	10.09	34.17	10.24	56.05	10.97	0.39	0.16
1987	20	2.06	0.24	25.90	7.83	22.30	13.49	48.20	14.43	0.58	0.19
1984	24	---	---	31.88	13.54	32.38	11.09	64.25	8.36	0.49	0.17
Mean	S.E.	1.92	0.06	21.04	2.59	29.91	2.06	50.94	3.28	0.41	0.04

**Table III.5b.** Analysis of effect of capsule position on length and seed production for *Calochortus howellii*, 1991 and 1989. Numbers 1, 2, and 3 refer to position of capsule on inflorescence and correspond developmentally and chronologically, with 1 produced first in the terminal position, 2 subumbellate to 1, and 3 being axillary. Not all individuals produce more than one bud. Statistically significant effect of position denoted by \*\* ( $p < 0.001$ ) or \*\*\* ( $p < 0.0001$ ), based on Kruskal-Wallis test.

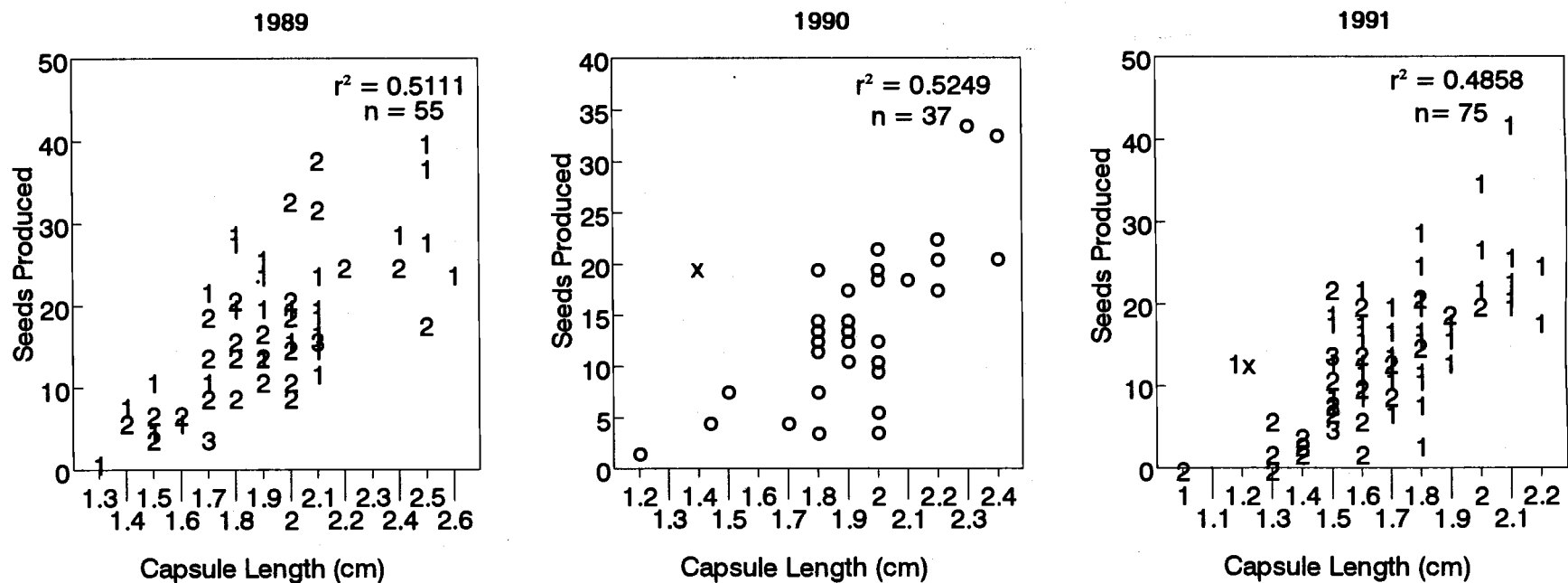
1991 Position	N	Capsule Length (cm)		Seeds		Undeveloped ovules		Total		Seed Set (%)	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
All	75	1.69	0.24 **	14.49	7.89 ***	34.69	9.34	49.19	8.54 ***	0.29	0.15
1's	49	1.76	0.21	16.92	7.24	35.35	9.62	52.27	7.57	0.33	0.14
2's & 3's	26	1.55	0.22	9.92	7.09	33.46	8.83	43.38	7.24	0.23	0.16

1989 Position	N	Capsule Length (cm)		Seeds		Undeveloped ovules		Total		Seed Set (%)	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
All	54	1.92	0.30	17.78	9.19	32.39	9.41	50.17	11.42	0.35	0.16
1's	28	1.94	0.36	19.00	9.57	30.57	8.37	49.57	12.04	0.37	0.15
2's & 3's	26	1.91	0.24	16.46	8.76	34.35	10.22	50.81	10.91	0.32	0.16

**Table III.6.** Pearson correlation coefficients for *Calochortus howellii* seed number and seed set versus capsule length. For 1989  $n = 55$ , 1990  $n = 37$ , and 1991  $n = 75$ . Values were recalculated after one outlier for each year was deleted (cf. Figure III.7).

	Year	Capsule Length	
		All data	w/o outlier
Seeds	1989	0.51	
	1990	0.40	0.52
	1991	0.47	0.49
Seed set	1989	0.02	
	1990	0.07	0.24
	1991	0.32	0.49
Total	1989	0.49	
	1990	0.50	0.60
	1991	0.21	0.27

**Figure III.6.** Capsule length versus seeds produced per capsule for *Calochortus howellii*, 1987 through 1991. Correlation coefficients were calculated after outliers (denoted by x) were eliminated. See Table III.6 for additional analysis. For 1989 and 1991, numbers 1, 2, and 3 refer to position of capsule on inflorescence and correspond developmentally and chronologically, with 1 produced first in the terminal position, 2 subumbellate to 1, and 3 being axillary. Note that capsules produced later tend to be smaller. For 1990, position was not recorded.



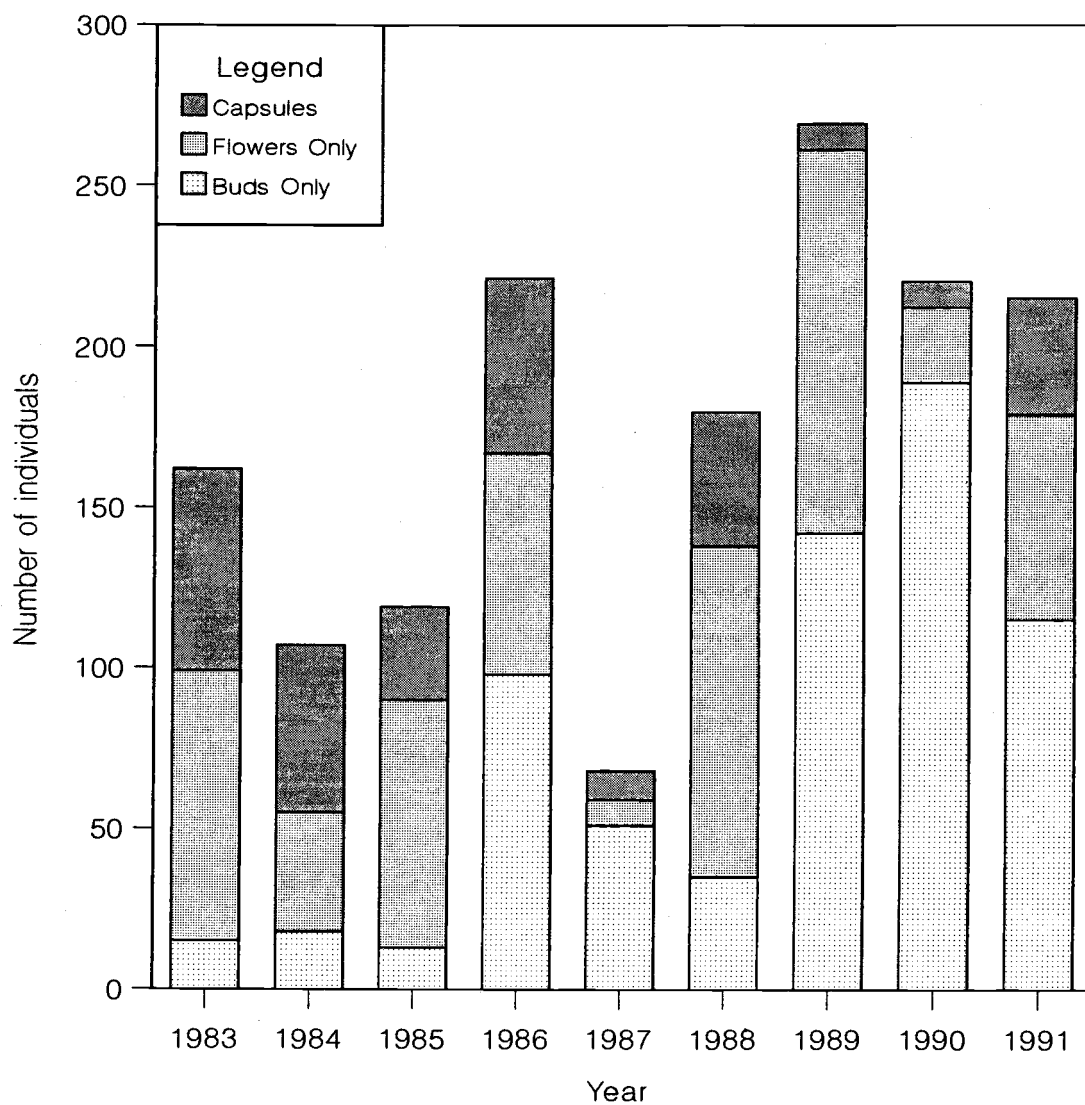
For 1989 and 1991, the effect of position of the capsule is compared. In 1991, those capsules which develop first were significantly larger ( $p = 0.0002$ ), produced more ovules ( $p = 0.00003$ ), and set more seed ( $p = 0.00005$ ) than those produced later, based on Kruskal-Wallis analysis (Table III.5b). Precipitation was over three times higher during June and July in 1991 than in 1989 (Appendix II.7). Average seed set was higher for 1989, but far fewer capsules were produced within the plots during the drier summer (8 capsules in 1989 versus 36 in 1991, Table III.1).

In 1987, 1989, and 1990 reproductive success was extremely low, with only 1.9, 1.4, and 1.4% of the plants producing capsules, compared to the average of 14.3% for the six other years (Table III.2; Figure III.7). An average of 21.5% of individuals producing buds produced capsules (S.D. = 15.0,  $n = 7$ ) and 34.4% of flowering individuals produced capsules (S.D. = 16.7,  $n = 7$ ) over all years studied. Holtsford (1985) reported that *C. leichtlinii* individuals typically produce two flowers, but mature only one fruit. In his experiments, second flowers produced seed when the first flowers were damaged or when soil moisture was supplemented. Watering also increased seed set. In *C. howellii*, precipitation was correlated with numbers of capsules produced within the plots ( $r^2 = 0.72$  for February-May,  $n = 9$ ,  $p = 0.03$ ), but was not correlated with seed set or numbers of seeds per capsule, based on data from capsules collected outside of plots.

Based on the consistent height of vegetation removed and dentation patterns on remaining inflorescences, herbivory accounted for most of the reduction in capsule production. Herbivores observed in the study area included blacktail deer (*Odocoileus hemionus*), blacktail jackrabbits (*Lepus californicus*), weevils (*Carpocoris sulcatus*: Pentatomidae) and mealy bugs. A small percentage of fruits failed to mature; this typically occurred on plants producing more than one capsule. Only three capsules aborted early in their development in 1991 and six were less than 1.5 cm at the time of dispersal. Ten were partially or totally eaten by insects.

If resources are not limiting, individuals of *C. howellii* might be expected to flower repeatedly during consecutive years. The large fluctuations in bud, flower, and capsule production (Table III.2, Figure III.7) suggest that extrinsic factors are

**Figure III.7.** Reproductive stages attained by *Calochortus howellii* for 1983 through 1991. The sum of the three bar segments are the total number of buds produced; upper two segments total for flowers. Most buds which failed to develop flowers or capsules were removed through grazing.





involved. The correlations between flowering and precipitation are discussed below.

### **Correlations between precipitation and reproduction**

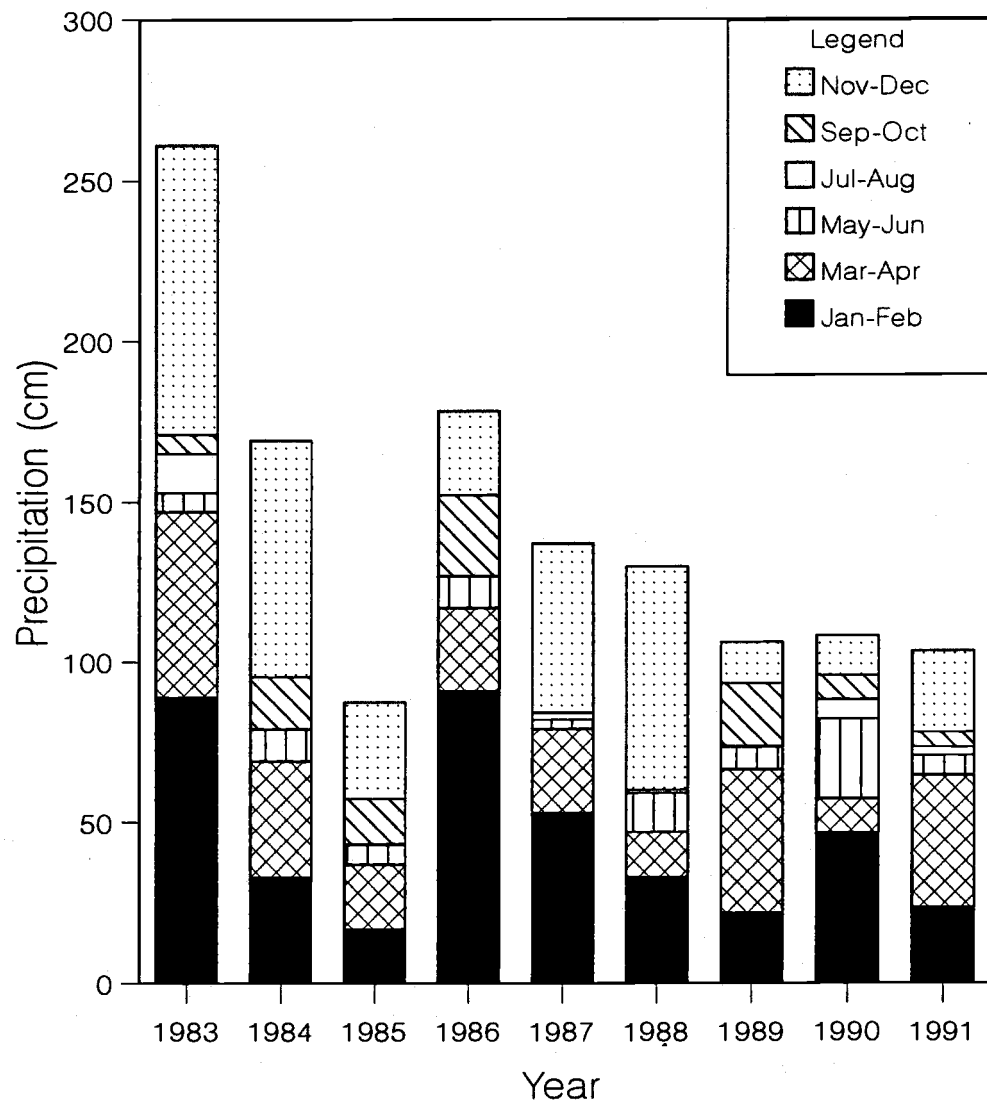
During the study period, annual precipitation varied from 87 cm to 262 cm for the Cave Junction weather station (Appendix 2). Precipitation over the 28-year period from 1963 to 1991 averaged 148 cm, with a maximum of 262 cm received in 1983 and minimum in 1976 of 75 cm. Average monthly precipitation peaks in December and gradually declines until July (Figure III.2). June, July, and August precipitation is typically very low with 28 year averages of less than 2 cm per month. Precipitation patterns are highly idiosyncratic, varying greatly from year to year (Figure III.8).

While annual precipitation varies widely both spatially throughout the species' range and temporally, precipitation still appears to play a role in annual reproduction and recruitment of *C. howellii*.

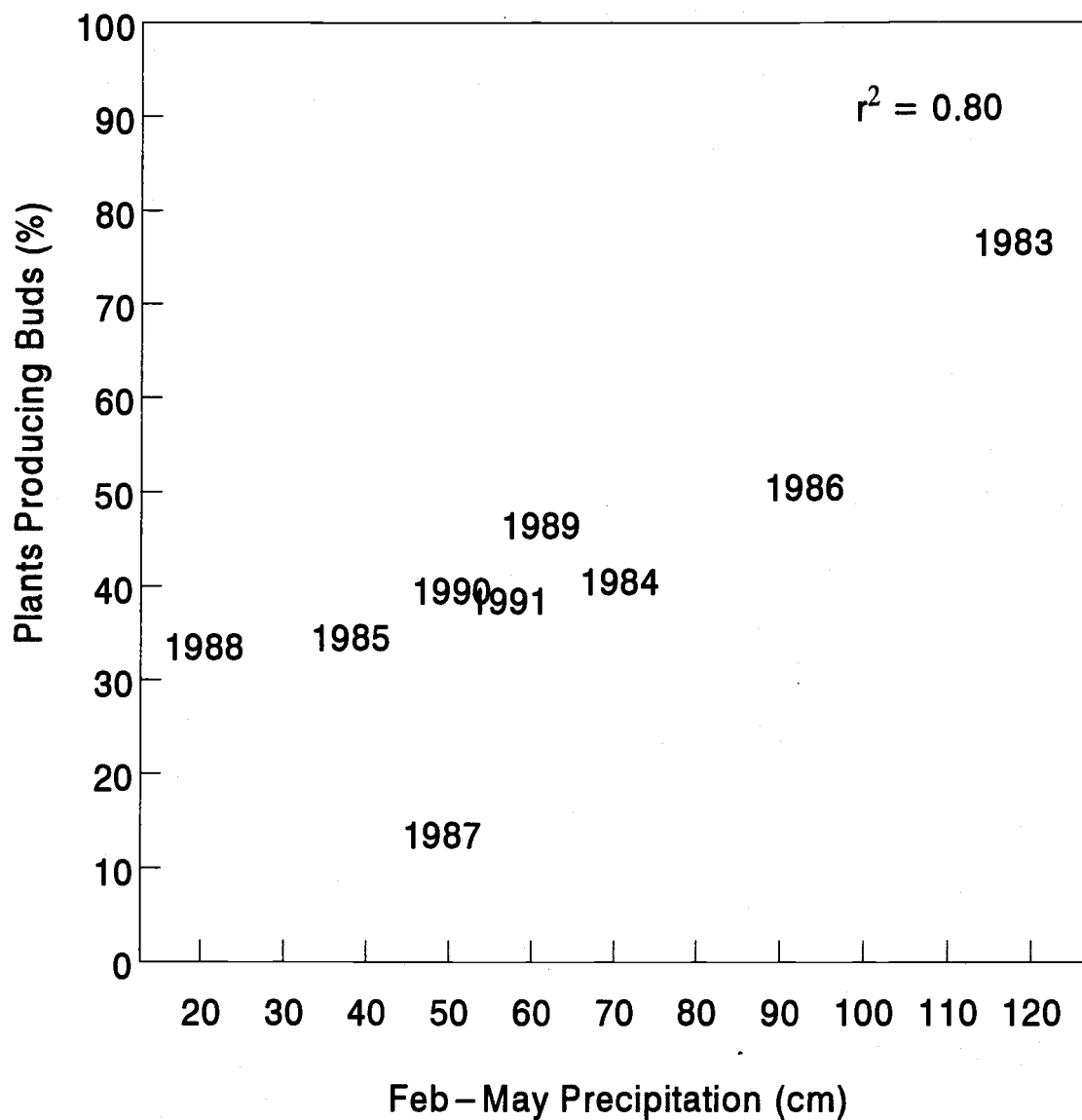
Bud production was highly correlated with February through May precipitation (Table III.7;  $r^2 = 0.80$ ,  $n = 9$ ,  $p = 0.01$ ). An outlying year, 1987, (Figure III.9) may be explained by the extremely low precipitation in April and May of that year, which corresponds to the lowest bud production during the entire study period. In addition, reproduction was exceptionally high during 1986. The previous year's reproductive effort, confounded by negligible precipitation during the time buds are being produced, may have acted synergistically to reduce dramatically the initiation of inflorescences in 1987. Correlations between flower production and precipitation are lower, but are similar to those of bud production (Table III.7).

Capsule production is more strongly correlated with late winter to spring precipitation (February through May  $r^2 = 0.72$ ,  $n = 9$ ,  $p = 0.03$ ) than with rainfall during the period of capsule development in June and July. This suggests that June and July moisture is not the most limiting factor to seed set. Observations also support the premise that the degree of flower and capsule herbivory may be the most limiting factor in *C. howellii* seed production. However, capsule production

**Figure III.8.** Annual bimonthly precipitation at Cave Junction weather station for 1981-1991.



**Figure III.9.** Spring precipitation (February-May) at Cave Junction weather station versus bud production for *Calochortus howellii* for 1983-1991.



**Table III.7.** Pearson correlation coefficients for monthly and seasonal precipitation versus bud, flower, and capsule production, mortality, and recruitment of *Calochortus howellii*. Statistically significant correlations denoted by \* ( $p < 0.10$ ), \*\* ( $p < 0.05$ ), and \*\*\* ( $p < 0.01$ ).

Precipitation	Jan	Feb	Mar	Apr	May	Feb–May	Jun	Jul	Previous Year Mar–June
Buds	0.16	0.64	0.61	0.39	0.11	0.80 ***	–0.17	0.40	0.40
Flowers	0.04	0.59 *	0.60 *	0.43	–0.32	0.67 **	0.13	0.39	0.51
Capsules	0.08	0.70 **	0.53	0.42	–0.26	0.72 **	0.08	0.41	0.66 *
Mortality	–0.15	–0.15	0.04	0.14	0.70 *	0.15	–0.25	0.38	0.51
Recruitment	–0.15	0.56	–0.06	–0.51	–0.32	0.23	0.10	–0.53	–0.09

remains well correlated with both bud and flower production ( $r^2 = 0.73$  and  $0.92$ ,  $n = 9$ ,  $p = .03$ ,  $0.0004$ ), indicating that herbivory does not overshadow initial reproductive effort in determining seed set for a given year. In other words, herbivores eat a fairly constant percentage of available inflorescences/infrutescences.

**Mortality.** Because of the possibility that plants may not emerge every year or may be grazed shortly after emergence, before they can be measured, plants were not counted as dead until they failed to appear for at least two consecutive years. Mortality is calculated as the proportion of the previous years' plants which failed to emerge after two or more years during the study. From 1985 through 1988 mortality was very low, averaging 1.5% per year (Table III.2). In 1989, the dramatic increase in total mortality (3.9%) reflects an increase in valley pocket gopher (*Thomomys bottae*) activity within plot 2 (17.4% mortality). Mortality continued to increase within plot 2 in 1990 (35.4%) and is estimated at 67.5% for 1991 (Table III.1). It is suspected that in addition to burrowing and displacing large amounts of soil within this plot, the gophers are also feeding on the *Calochortus* bulbs. The highest mortality within the other plots occurred in 1990, which corresponded to the lowest combined precipitation for March and April and highest May precipitation during the study period.

Mortality due to pocket gophers may be indirectly correlated with precipitation. Pocket gopher activity is highest where soil is moist and more easily worked (Burt and Grossenheider 1976). Higher than average precipitation could conceivably result in pocket gopher activity in areas otherwise inaccessible, increasing *Calochortus* mortality. Lowest total precipitation for February through April occurred during 1988 (Appendix II.7); mortality during this season was negligible. In addition to the potential indirect effects of precipitation on predation, pollinator activity may be affected by rainfall during May and June.

Correlations between precipitation and mortality may warrant further study. Total mortality was modestly correlated with previous years spring (February to

May) precipitation ( $r^2 = 0.51$ ,  $n = 7$ ,  $p = 0.24$ ) and current years May precipitation ( $r^2 = 0.70$ ,  $n = 7$ ,  $p = 0.08$ ). As noted earlier, seedling mortality increased dramatically in 1990 when May precipitation was exceptionally high. Based on greenhouse propagation, seedlings are known to be susceptible to rotting, which may cause mortality in the field, as well. Fiedler (1987) noted that seedlings of *Calochortus* often succumbed to common rots, such as *Botrytis cinerea*.

Seedling recruitment also appears to be affected by precipitation. Recruitment is negatively correlated with April precipitation ( $r^2 = -0.51$ ,  $n = 7$ ,  $p = 0.24$ ), which also suggests that saturated soils may inhibit seedling establishment (i.e. seeds may germinate, but seedlings do not survive).

Distribution of *C. howellii* also suggests a relationship to soil moisture. Within plots 2 and 3, fed by subsurface water flow, the wettest portions of the plots were unoccupied or sparsely occupied by *C. howellii* (Appendix 1). *Calochortus uniflorus*, a species of moist meadows both on and off serpentine, occurred within the moister areas of these two plots.

### **Transition matrix modeling of *C. howellii*: A seven-year study**

**The model and its limitations.** Transition matrix models, developed for assessing population stability, are reviewed elsewhere (Caswell and Werner 1978, Bierzychudek 1982, Menges et al. 1986, Caswell 1989). They require specific information on mortality, recruitment, growth, and reproduction, and are therefore useful tools for identifying demographic bottlenecks. They provide a useful framework for organizing life-history information on a given population or species.

Using size-classified matrices rather than age-classified matrices is easily justified for long-lived herbaceous perennials. The time of first flowering becomes increasingly size-dependent and less age-dependent as the vegetative lifespan increases (Lacey 1986). The variability in growth and mortality during the early vegetative phases, discussed earlier supports the separation of categories of seedling, juvenile, and adult, rather than simply non-reproductive and reproductive.

While transition matrix models provide forecasting capabilities, the results are only accurate to the extent that the years studied are typical. The potential for misuse of the results is reduced if there is a clear understanding of the limitations of the model. Environmental stochasticity is not directly addressed here, nor is density dependence. Assumptions of transition matrix models are summarized well by Lefkovitch (1965), Bierzychudek (1982), and Caswell (1989).

**Comparison of different size-classifications.** The importance of selecting an appropriate size-classification is discussed by several authors (Vandermeer 1978, Moloney 1986, Ferson 1990). Some investigators use life-history stages, precluding the need for delineating categories within a size continuum. Vandermeer's algorithm, which aids selection of categories that minimize errors of distribution and estimation, was used by Bierzychudek (1982) and Fiedler (1987). Moloney (1986) provides an example using categories derived from a modification of Vandermeer's method. Comparisons of results using different classifications are reported here as an evaluation of the robustness of the model, and to aid others in decisions regarding the design of similar studies.

Knowledge of life history parameters permits a defensible classification without requiring the time-consuming step of applying the Vandermeer/Moloney algorithms. Comparisons provided by the present study may be useful to those using life-history stages alone for analyses or deliberating whether theoretical classification is warranted.

**Analysis using empirically derived categories.** The average lambda value over the seven year period was 0.99, based on all plants classified using the three life history categories: seedlings, juveniles, and adults (S.D. 0.034, Table III.8). Separate analyses reveal differences among plots (Tables III.9-10, Figure III.10). Plot 2, due to the high mortality as a result of pocket gopher activity, contributed the greatest variance; beginning in 1989 the lambda values plummeted sharply.

**Table III.8.** Comparison of lambda values for analysis of *Calochortus howellii* data from Mariposa Meadow by plot (1985-1991). Note declining values for plot 2 in later years.

Years	All plants	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Mean	S.D.
1985-1986	0.986	1.046	1.021	0.972	0.963	0.962	0.993	0.038
1986-1987	1.046	1.000	0.984	0.975	0.991	1.000	0.990	0.011
1987-1988	1.021	1.000	1.000	1.000	1.016	1.040	1.011	0.018
1988-1989	0.972	0.989	0.930	1.051	0.996	0.933	0.980	0.050
1989-1990	0.963	0.972	0.714	1.046	0.937	1.031	0.940	0.134
1990-1991	0.962	1.000	0.500	0.994	1.000	1.000	0.899	0.223
Mean	0.992	1.001	0.858	1.006	0.984	0.994		
S.D.	0.034	0.025	0.208	0.034	0.029	0.041		



**Table III.9.** Comparison of lambda values for analysis of *Calochortus howellii* data from Mariposa Meadow (1985-1991) using various approaches to size-category selection. See text for explanations of analyses.

Transition Years	Raw Data	Empirical	Theoretical
1985-1986	1.000	0.986	0.993
1986-1987	0.989	1.046	1.066
1987-1988	1.002	1.021	0.987
1988-1989	1.004	0.972	1.025
1989-1990	0.994	0.963	0.974
1990-1991	0.947	0.962	0.963
Mean	0.989	0.992	1.001
S.D.	0.022	0.034	0.038

**Table III.10a.** Size-classified transition matrices for 1985-86 by plot, based on analysis using three empirically-selected categories. Category 1 = seedlings with leaf widths no greater than 3 mm, 2 = juveniles with leaf widths between 3.5 and 6 mm, 3 = adults with leaf widths greater than 6 mm. Each number in the matrix is the proportion of plants which transfer from the column category (1985) to the row category (1986). Reproduction is incorporated into first row, as the percent of seedlings produced per individual in each reproductive category. Mortality is the percent of plants in each category which died during the transition. Initial category distributions (%) are based on the numbers of plants in each category in 1985 (Init85); stable distributions (%) and lambda values were calculated using DEMOG. See text for further explanation.

All plots		lambda = 0.986		
Category		1	2	3
1		0.500	0.000	0.007
2		0.500	0.439	0.046
3		0.000	0.544	0.932
Morts		0.000	0.018	0.021
Init85		4	57	281
Category Distribution				
Initial		1.2	16.7	82.2
Stable		1.3	8.0	89.9

Plot 3		lambda = 0.963		
Category		1	2	3
1		0.000	0.000	0.000
2		0.000	0.357	0.067
3		0.000	0.571	0.900
Morts		0.000	0.000	0.067
Init85		0	14	30
Category Distribution				
Initial		0.0	31.8	68.2
Stable		0.0	9.9	90.1

Plot 1		lambda = 0.960		
Category		1	2	3
1		0.000	0.000	0.000
2		0.000	0.667	0.028
3		0.000	0.167	0.944
Morts		0.000	0.000	0.056
Init85		0	6	36
Category Distribution				
Initial		0.0	14.3	85.7
Stable		0.0	8.7	91.3

Plot 4		lambda = 1.000		
Category		1	2	3
1		0.000	0.000	0.000
2		1.000	0.429	0.034
3		0.000	0.571	0.966
Morts		0.000	0.000	0.000
Init85		1	21	87
Category Distribution				
Initial		0.9	19.3	79.8
Stable		0.0	5.7	94.3

Plot 2		lambda = 1.000		
Category		1	2	3
1		1.000	0.000	0.000
2		0.000	0.273	0.067
3		0.000	0.727	0.900
Morts		0.000	0.000	0.033
Init85		2	11	30
Category Distribution				
Initial		4.7	25.6	69.8
Stable		100.0	0.0	0.0

Plot 5		lambda = 1.000		
Category		1	2	3
1		0.000	0.000	0.011
2		1.000	0.400	0.034
3		0.000	0.600	0.954
Morts		0.000	0.000	0.011
Init85		1	15	87
Category Distribution				
Initial		1.0	14.6	84.5
Stable		1.1	70.0	91.9

**Table III.10b.** Size-classified transition matrices for 1986-87, by plot, based on analysis using three empirically-selected categories. Category 1 = seedlings with leaf widths no greater than 3 mm, 2 = juveniles with leaf widths between 3.5 and 6 mm, 3 = adults with leaf widths greater than 6 mm. Each number in the matrix is the proportion of plants which transfer from the column category (1986) to the row category (1987). Reproduction is incorporated into first row, as the percent of seedlings produced per individual in each reproductive category. Mortality is the percent of plants in each category which died during the transition. Initial category distributions (%) are based on the numbers of plants in each category in 1986 (Init86); stable distributions (%) and lambda values were calculated using DEMOG. See text for further explanation.

All plots		lambda = 1.046		
Category	1	2	3	
1	0.750	0.000	0.087	
2	0.250	0.575	0.061	
3	0.000	0.425	0.925	
Mort87	0.000	0.000	0.014	
Init86	4	73	358	
Category Distribution				
Initial	0.9	16.8	82.3	
Stable	18.5	18.1	63.4	

Plot 3		lambda = 0.975		
Category	1	2	3	
1	0.000	0.000	0.579	
2	0.000	0.611	0.026	
3	0.000	0.389	0.947	
Mort87	0.000	0.000	0.000	
Init86	0	18	38	
Category Distribution				
Initial	0.0	32.1	67.9	
Stable	35.6	4.3	60.0	

Plot 1		lambda = 1.000		
Category	1	2	3	
1	0.000	0.000	0.000	
2	1.000	0.538	0.059	
3	0.000	0.462	0.941	
Mort87	0.000	0.000	0.000	
Init86	1	13	68	
Category Distribution				
Initial	1.2	15.9	82.9	
Stable	0.0	11.3	88.7	

Plot 4		lambda = 0.991		
Category	1	2	3	
1	0.000	0.000	0.019	
2	0.000	0.542	0.048	
3	0.000	0.458	0.943	
Mort87	0.000	0.000	0.010	
Init86	0	24	105	
Category Distribution				
Initial	0.0	18.6	81.4	
Stable	1.7	9.4	88.9	

Plot 2		lambda = 0.984		
Category	1	2	3	
1	1.000	0.000	0.000	
2	0.000	0.667	0.077	
3	0.000	0.333	0.897	
Mort87	0.000	0.000	0.026	
Init86	2	6	39	
Category Distribution				
Initial	4.3	12.8	83.0	
Stable	74.3	5.1	20.7	

Plot 5		lambda = 1.000		
Category	1	2	3	
1	1.000	0.000	0.035	
2	0.000	0.400	0.024	
3	0.000	0.571	0.953	
Mort87	0.000	0.000	0.024	
Init86	1	35	85	
Category Distribution				
Initial	0.8	28.9	70.2	
Stable	99.2	0.0	0.8	

**Table III.10c.** Size-classified transition matrices for 1987-88, by plot, based on analysis using three empirically-selected categories. Category 1 = seedlings with leaf widths no greater than 3 mm, 2 = juveniles with leaf widths between 3.5 and 6 mm, 3 = adults with leaf widths greater than 6 mm. Each number in the matrix is the proportion of plants which transfer from the column category (1987) to the row category (1988). Reproduction is incorporated into first row, as the percent of seedlings produced per individual in each reproductive category. Mortality is the percent of plants in each category which died during the transition. Initial category distributions (%) are based on the numbers of plants in each category in 1987 (Init87); stable distributions (%) and lambda values were calculated using DEMOG. See text for further explanation.

All plots		lambda = 1.021		
Category		1	2	3
1		0.794	0.011	0.097
2		0.059	0.425	0.008
3		0.000	0.563	0.989
Mort88		0.147	0.000	0.003
Init87		34	87	372
Category Distribution				
Initial		6.9	17.6	75.5
Stable		28.9	3.8	67.3

Plot 3		lambda = 1.000		
Category		1	2	3
1		0.864	0.053	0.182
2		0.000	0.474	0.000
3		0.000	0.474	1.000
Mort88		0.136	0.000	0.000
Init87		22	19	44
Category Distribution				
Initial		25.9	22.4	51.8
Stable		57.1	0.0	42.9

Plot 1		lambda = 1.000		
Category		1	2	3
1		0.000	0.000	0.027
2		0.000	0.471	0.027
3		0.000	0.529	0.973
Mort88		0.000	0.000	0.000
Init87		0	17	73
Category Distribution				
Initial		0.0	18.9	81.1
Stable		2.5	4.8	92.7

Plot 4		lambda = 1.016		
Category		1	2	3
1		0.500	0.000	0.018
2		0.500	0.476	0.000
3		0.000	0.524	1.000
Morts88		0.000	0.000	0.000
Init87		2	21	114
Category Distribution				
Initial		1.5	15.3	83.2
Stable		3.2	2.9	93.9

Plot 2		lambda = 1.000		
Category		1	2	3
1		0.833	0.000	0.324
2		0.000	0.300	0.000
3		0.000	0.700	1.000
Mort88		0.167	0.000	0.000
Init87		6	10	37
Category Distribution				
Initial		11.3	18.9	69.8
Stable		66.0	0.0	34.0

Plot 5		lambda = 1.040		
Category		1	2	3
1		0.500	0.000	0.115
2		0.250	0.350	0.010
3		0.000	0.650	0.981
Mort88		0.250	0.000	0.010
Init87		4	20	104
Category Distribution				
Initial		3.1	15.6	81.3
Stable		16.4	7.0	76.6

**Table III.10d.** Size-classified transition matrices for 1988-89, by plot, based on analysis using three empirically-selected categories. Category 1 = seedlings with leaf widths no greater than 3 mm, 2 = juveniles with leaf widths between 3.5 and 6 mm, 3 = adults with leaf widths greater than 6 mm. Each number in the matrix is the proportion of plants which transfer from the column category (1988) to the row category (1989). Reproduction is incorporated into first row, as the percent of seedlings produced per individual in each reproductive category. Mortality is the percent of plants in each category which died during the transition. Initial category distributions (%) are based on the numbers of plants in each category in 1988 (Init88); stable distributions (%) and lambda values were calculated using DEMOG. See text for further explanation.

All plots		lambda = 0.972		
Category	1	2	3	
1	0.766	0.018	0.100	
2	0.125	0.052	0.050	
3	0.000	0.439	0.919	
Mort89	0.109	0.018	0.031	
Init88	64	57	419	
Category Distribution				
Initial	11.9	10.6	77.6	
Stable	30.6	7.5	61.8	

Plot 3		lambda 1.051		
Category	1	2	3	
1	0.926	0.083	0.236	
2	0.074	0.750	0.073	
3	0.000	0.167	0.909	
Mort89	0.000	0.000	0.018	
Init88	27	12	55	
Category Distribution				
Initial	28.7	12.8	58.5	
Stable	57.1	19.7	23.2	

Plot 1		lambda = 0.989		
Category	1	2	3	
1	0.000	0.000	0.012	
2	0.500	0.533	0.037	
3	0.000	0.400	0.951	
Mort89	0.500	0.067	0.012	
Init88	2	15	82	
Category Distribution				
Initial	2.0	15.2	82.8	
Stable	1.1	8.5	90.4	

Plot 4		lambda 0.996		
Category	1	2	3	
1	0.333	0.000	0.008	
2	0.333	0.429	0.024	
3	0.000	0.571	0.969	
Mort89	0.333	0.000	0.008	
Init88	3	14	127	
Category Distribution				
Initial	2.1	9.7	88.2	
Stable	1.1	4.6	94.3	

Plot 2		lambda = 0.930		
Category	1	2	3	
1	0.765	0.000	0.182	
2	0.118	0.250	0.061	
3	0.000	0.750	0.848	
Mort89	0.118	0.000	0.273	
Init88	17	4	33	
Category Distribution				
Initial	31.5	7.4	61.1	
Stable	9.0	8.9	82.1	

Plot 5		lambda 0.933		
Category	1	2	3	
1	0.667	0.000	0.181	
2	0.133	0.500	0.078	
3	0.000	0.500	0.914	
Mort89	0.200	0.000	0.009	
Init88	15	12	116	
Category Distribution				
Initial	10.5	8.4	81.1	
Stable	32.9	18.8	48.4	

**Table III.10e.** Size-classified transition matrices for 1989-90, by plot, based on analysis using three empirically-selected categories. Category 1 = seedlings with leaf widths no greater than 3 mm, 2 = juveniles with leaf widths between 3.5 and 6 mm, 3 = adults with leaf widths greater than 6 mm. Each number in the matrix is the proportion of plants which transfer from the column category (1989) to the row category (1990). Reproduction is incorporated into first row, as the percent of seedlings produced per individual in each reproductive category. Mortality is the percent of plants in each category which died during the transition. Initial category distributions (%) are based on the numbers of plants in each category in 1989 (Init89); stable distributions (%) and lambda values were calculated using DEMOG. See text for further explanation.

All plots		lambda = 0.965		
Category	1	2	3	
1	0.667	0.000	0.041	
2	0.111	0.481	0.035	
3	0.016	0.426	0.918	
Mort90	0.206	0.093	0.046	
Init89	63	54	368	
Category Distribution				
Initial	13.0	11.1	75.9	
Stable	11.0	8.4	80.6	

Plot 3		lambda = 1.046		
Category	1	2	3	
1	0.700	0.000	0.163	
2	0.133	0.529	0.020	
3	0.000	0.412	0.980	
Mort90	0.167	0.059	0.000	
Init89	30	17	49	
Category Distribution				
Initial	31.3	17.7	51.0	
Stable	28.9	9.9	61.2	

Plot 1		lambda = 0.972		
Category	1	2	3	
1	0.000	0.000	0.018	
2	0.000	0.333	0.091	
3	0.000	0.444	0.909	
Mort90	0.000	0.222	0.000	
Init89	0	9	55	
Category Distribution				
Initial	0.0	14.1	85.9	
Stable	1.6	12.3	86.1	

Plot 4		lambda = 0.937		
Category	1	2	3	
1	0.000	0.000	0.008	
2	0.000	0.556	0.008	
3	0.000	0.444	0.927	
Mort90	1.000	0.000	0.065	
Init89	1	9	124	
Category Distribution				
Initial	0.7	6.7	92.5	
Stable	0.8	2.1	97.1	

Plot 2		lambda = 0.714		
Category	1	2	3	
1	0.400	0.000	0.000	
2	0.133	0.333	0.000	
3	0.000	0.167	0.714	
Mort90	0.467	0.500	0.286	
Init89	15	6	28	
Category Distribution				
Initial	30.6	12.2	57.1	
Stable	0.0	0.0	100.0	

Plot 5		lambda = 1.031		
Category	1	2	3	
1	0.882	0.000	0.045	
2	0.059	0.500	0.054	
3	0.059	0.500	0.946	
Mort90	0.000	0.000	0.000	
Init89	17	14	111	
Category Distribution				
Initial	12.0	9.9	78.2	
Stable	21.0	9.4	69.6	

**Table III.10f.** Size-classified transition matrices for 1990-91, by plot, based on analysis using three empirically-selected categories. Category 1 = seedlings with leaf widths no greater than 3 mm, 2 = juveniles with leaf widths between 3.5 and 6 mm, 3 = adults with leaf widths greater than 6 mm. Each number in the matrix is the proportion of plants which transfer from the column category (1990) to the row category (1991). Reproduction is incorporated into first row, as the percent of seedlings produced per individual in each reproductive category. Mortality is the percent of plants in each category which died during the transition. Initial category distributions (%) are based on the numbers of plants in each category in 1990 (Init90); stable distributions (%) and lambda values were calculated using DEMOG. See text for further explanation.

All plots		lambda = 0.962		
Category	1	2	3	
1	0.842	0.113	0.046	
2	0.070	0.645	0.101	
3	0.000	0.210	0.855	
Mort91	0.088	0.032	0.044	
Init90	57	62	366	
Category Distribution				
Initial	11.8	12.8	75.5	
Stable	36.4	21.5	42.1	

Plot 3		lambda = 0.994		
Category	1	2	3	
1	0.931	0.217	0.089	
2	0.069	0.696	0.089	
3	0.000	0.087	0.732	
Mort91	0.000	0.000	0.000	
Init90	29	23	56	
Category Distribution				
Initial	26.9	21.3	51.9	
Stable	74.5	19.1	63.0	

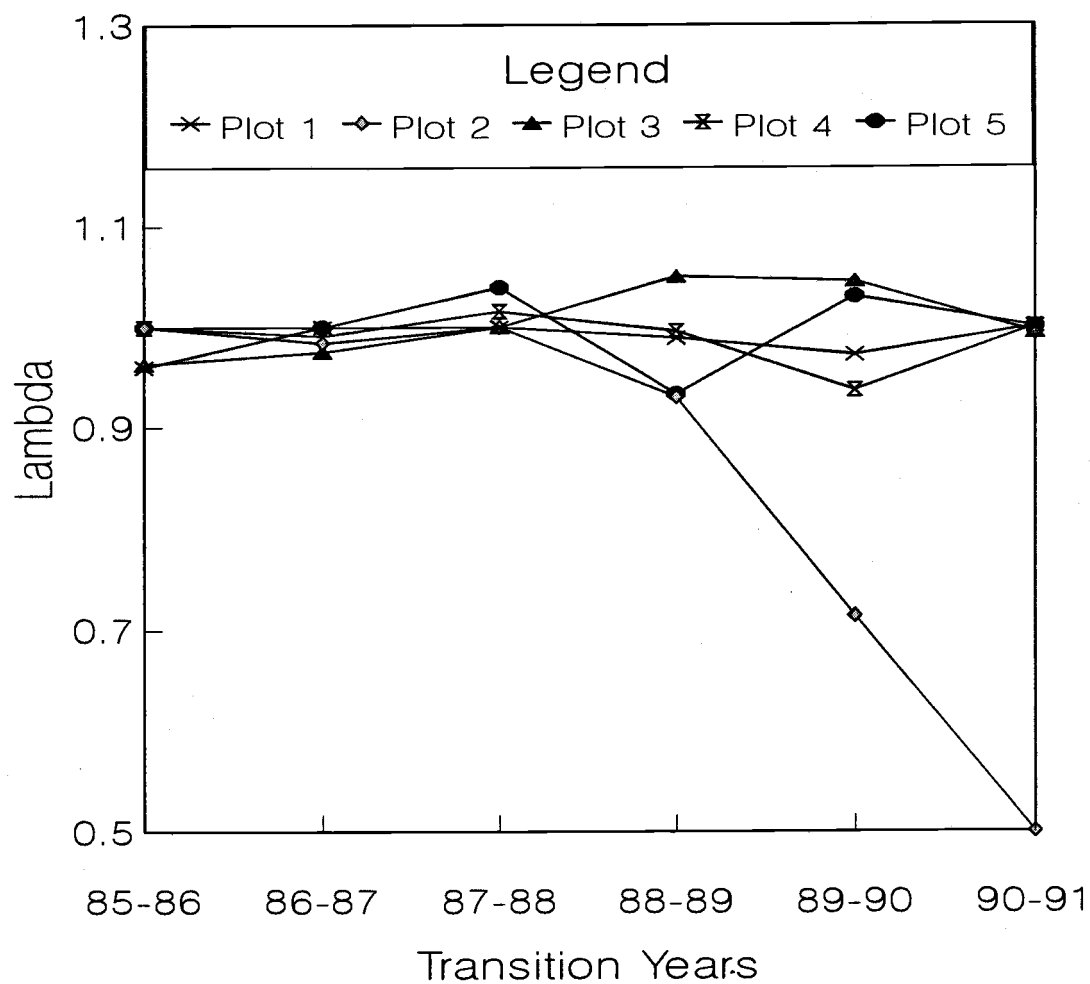
Plot 1		lambda = 1.000		
Category	1	2	3	
1	0.000	0.000	0.000	
2	1.000	0.500	0.145	
3	0.000	0.500	0.855	
Mort91	0.000	0.000	0.000	
Init90	1	10	55	
Category Distribution				
Initial	1.5	15.2	83.3	
Stable	0.0	22.5	77.5	

Plot 4		lambda = 1.000		
Category	1	2	3	
1	1.000	0.100	0.059	
2	0.000	0.800	0.085	
3	0.000	0.100	0.881	
Mort91	0.000	0.000	0.034	
Init90	1	10	118	
Category Distribution				
Initial	0.8	7.8	91.5	
Stable	100	0.0	0.0	

Plot 2		lambda = 0.500		
Category	1	2	3	
1	0.000	0.000	0.045	
2	0.167	0.333	0.000	
3	0.000	0.000	0.500	
Mort91	0.833	0.667	0.500	
Init90	6	3	22	
Category Distribution				
Initial	19.4	9.7	71.0	
Stable	7.7	77.0	84.6	

Plot 5		lambda = 1.000		
Category	1	2	3	
1	1.000	0.063	0.035	
2	0.000	0.625	0.124	
3	0.000	0.313	0.867	
Mort91	0.000	0.000	0.009	
Init90	20	16	113	
Category Distribution				
Initial	13.4	10.7	75.8	
Stable	99.5	0.1	0.4	

**Figure III.10.** Comparison of lambda values among five plots established to monitor trends of *Calochortus howellii* at Mariposa Meadow.





During the last transition (1990-1991), all plots except number 2 converged to a stable growth rate (Figure III.10).

The difference between the initial population structure (based on actual data) and the predicted stable population structure provides an additional measure of population stability (Keyfitz 1977). The index of dissimilarity is calculated as the sum of the differences for all categories. The transition year 1990-1991 (33.4) yielded the highest value, while the lowest value was for the previous transition, 1989-1990 (4.7). The remaining indices were 7.7 for 1985-1986, 18.9 for 1986-1987, 22.0 for 1987-1988, and 18.7 for 1988-1989.

**Analysis using the raw data.** The lambda values for the raw data analysis were on average slightly lower than for the empirical analysis, but were not consistently lower when transition years were compared individually (Tables III.8, III.11, Figure III.11). Standard deviation was also lowest for this analysis. For the 1986 to 1987 transition, lambda is considerably lower for raw data analysis. Simulating increased reproduction and recruitment did not appreciably increase lambda for this transition. The errors of estimation, which would be expected to skew a finely delineated classification, may have been offset somewhat by the large sample size. However, the results from this analysis were reported for comparison only; because this is the most tedious and least accurate method of calculating lambda, it is not recommended. Analysis by plot, though not performed here, would undoubtedly reveal larger sampling error due to smaller sample sizes.

**Analysis using theoretically derived categories.** A computerized implementation of Moloney's generalized algorithm for determining category sizes (Millstein 1992), which minimizes errors of estimation and distribution, was applied to the *C. howellii* dataset. Because the program will not handle missing data points, small individuals are highly under-represented over the entire study year period. By using only the last four years of data, a greater proportion of small plants was included. When the algorithm was run on the subset of plants that had data for

**Table III.11.** Transition matrices for 1985-86, 1986-87, 1987-88, 1988-89, 1989-90, and 1990-91, based on actual leaf widths (to nearest 0.1 cm). Each number in the matrix is the proportion of plants which transfer from the column category (year 1) to the row category (year 2). Reproduction is incorporated into first row, as the percent of seedlings produced per individual for each leaf-width category. Mortality is the percent of plants in each category which died during the transition. Vector of initial numbers of plants for each leaf-width category (e.g. Init85) was multiplied by matrix to determine lambda.

1985-1986																	lambda = 1.000
Leaf width	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7
0.1								0.029									
0.2																	
0.3		1.000															
0.4			0.500	0.125													
0.5			0.500	0.750	0.158	0.133	0.014			0.023							
0.6				0.125	0.316	0.133	0.114	0.015	0.033								
0.7					0.368	0.500	0.271	0.162	0.017								
0.8					0.105	0.200	0.271	0.382	0.133	0.047							
0.9							0.243	0.221	0.333	0.186	0.087						
1.0							0.057	0.162	0.350	0.326	0.130	0.125					
1.1				0.053				0.029	0.050	0.256	0.304	0.375	0.167				1.000
1.2								0.015	0.050	0.083	0.261	0.375	0.333				
1.3										0.023	0.174	0.125					
1.4											0.043		0.333	1.000			
1.5										0.023					1.000		
1.6														0.167			
Mortality						0.033	0.029	0.015	0.033	0.023							
Init85		2	2	8	19	30	70	66	60	43	23	8	6	1	1		1

1986-1987																	lambda = 0.989
Leaf width	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7
0.1						0.013	0.007	0.051	0.125	0.123	0.206	0.238	0.500	1.500			
0.2		0.500															
0.3			0.250														
0.4			0.250	0.200	0.042												
0.5				0.500	0.375	0.077	0.041	0.026			0.029						
0.6				0.300	0.417	0.231	0.135	0.051	0.014	0.015							
0.7					0.125	0.231	0.176	0.154	0.194	0.015	0.029						
0.8						0.333	0.324	0.308	0.153	0.046	0.059	0.048					
0.9					0.042	0.077	0.216	0.244	0.319	0.262	0.059	0.048	0.143				
1.0						0.051	0.054	0.167	0.208	0.385	0.294	0.286					
1.1							0.027	0.038	0.069	0.185	0.176	0.190					
1.2								0.013	0.028	0.046	0.176	0.143	0.286	0.250			
1.3										0.031	0.088	0.143	0.143	0.500	0.500		
1.4										0.015	0.059	0.095		0.250			
1.5													0.429				
1.6															0.500	1.000	
Mortality							0.027		0.014		0.029	0.048					
Init86		4	10	24	39	74	76	72	65	34	21	7	4	2	1		

1987-1988																	lambda = 1.002
Leaf width	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7
0.1	0.667						0.055		0.047	0.079	0.031						
0.2	0.111	0.818															
0.3		0.091	0.600	0.071													
0.4			0.400	0.071													
0.5				0.643	0.321			0.012									
0.6					0.429	0.133	0.018		0.012								
0.7					0.214	0.143	0.578	0.273	0.146	0.058	0.026	0.031					
0.8						0.071	0.133	0.400	0.232	0.163	0.066	0.031	0.056				
0.9							0.089	0.164	0.341	0.256	0.079	0.094					
1.0								0.127	0.244	0.349	0.408	0.375	0.167	0.083	0.333		
1.1								0.044	0.018	0.012	0.093	0.263	0.156	0.056			0.500
1.2								0.036	0.022		0.012	0.070	0.079	0.156	0.389	0.333	0.333
1.3												0.053	0.156	0.222	0.083	0.167	
1.4													0.056	0.417		0.333	
1.5											0.013		0.056	0.083	0.167	0.333	0.500
1.6																	
Mortality	0.222	0.091								0.013							
Init87	18	11	5	14	28	45	55	82	86	76	32	18	12	6	3		2

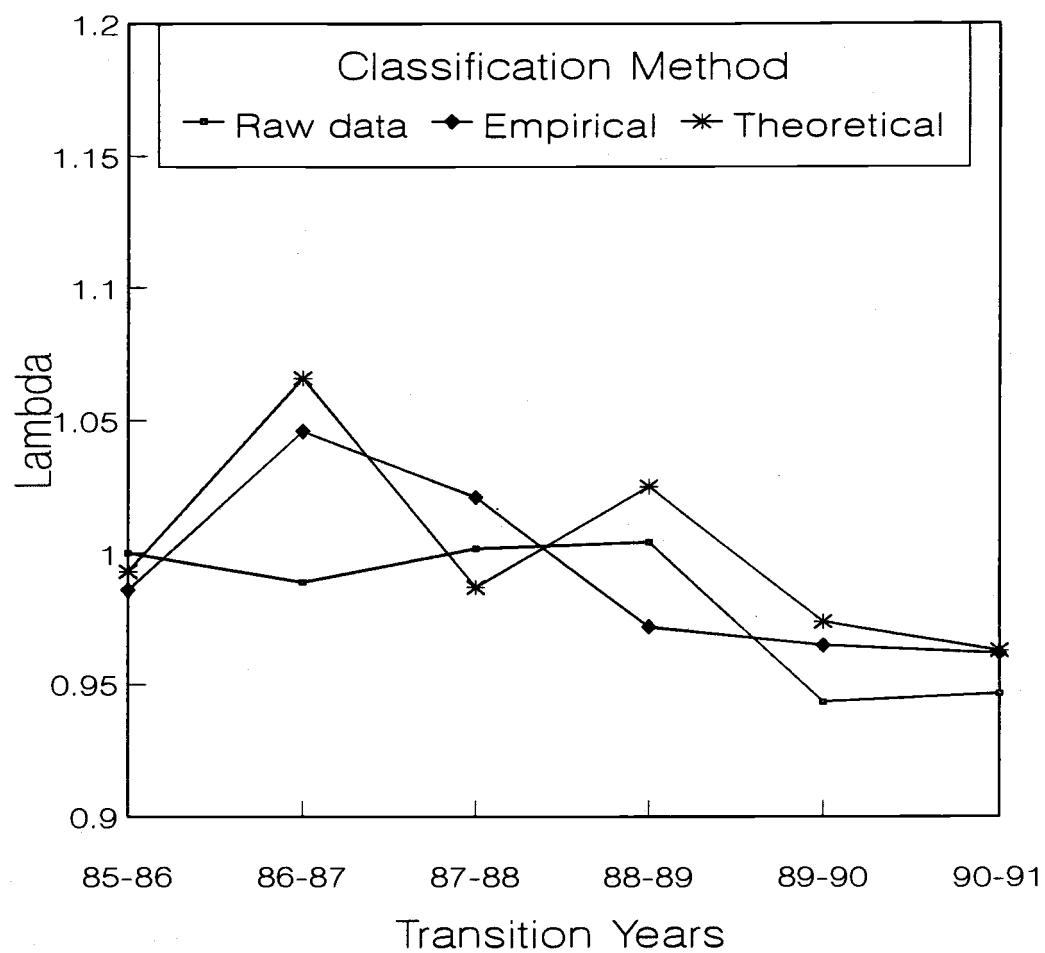
Table III.11 (continued)

1988-1989															
lambda = 1.004															
Leaf width	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5
0.1	0.583						0.041	0.114	0.137	0.144	0.081	0.057		0.143	
0.2	0.250	0.444	0.100	0.111											
0.3		0.444	0.200												
0.4		0.056	0.500	0.667	0.043		0.027								
0.5			0.200	0.222	0.174	0.080	0.041	0.014							
0.6					0.478	0.180	0.082	0.029	0.088	0.019					
0.7					0.067	0.480	0.233	0.229	0.096	0.038	0.027				
0.8					0.130	0.160	0.370	0.271	0.219	0.106	0.081	0.029	0.071	0.143	
0.9					0.043	0.040	0.096	0.229	0.205	0.183	0.027	0.057		0.143	
1.0						0.040	0.096	0.171	0.233	0.346	0.189	0.171	0.143		0.167
1.1									0.137	0.212	0.189	0.286		0.143	0.167
1.2							0.014	0.014	0.014	0.058	0.216	0.114	0.214		0.167
1.3						0.040			0.014	0.019	0.027	0.200		0.429	
1.4							0.014				0.135	0.057	0.286	0.143	0.500
1.5											0.027	0.057	0.143		
1.6													0.071		
Mortality	0.167	0.056			0.043		0.027	0.043	0.014	0.019	0.081	0.029	0.071		
Init88	36	18	10	9	23	25	73	70	73	104	37	35	14	7	6

1989-1990															
lambda = 0.943															
Leaf width	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5
0.1	0.533							0.085		0.060	0.122				
0.2	0.167	0.500													
0.3		0.250	0.482												
0.4	0.033		0.385	0.083	0.083										
0.5			0.077	0.333	0.167	0.067		0.013			0.024				
0.6				0.417	0.167	0.300	0.088	0.039		0.024					0.125
0.7					0.417	0.267	0.246	0.169	0.085	0.036	0.024			0.100	
0.8		0.050			0.083	0.100	0.333	0.286	0.153	0.071	0.024	0.050	0.100	0.100	
0.9					0.083	0.067	0.246	0.221	0.254	0.190	0.073				
1.0					0.083	0.067	0.053	0.195	0.271	0.202	0.195	0.200	0.300	0.100	
1.1							0.035	0.039	0.085	0.250	0.220	0.050	0.100		
1.2									0.068	0.095	0.244	0.300	0.100	0.125	
1.3									0.017	0.071	0.073	0.100	0.100		
1.4											0.073	0.150	0.300	0.100	0.375
1.5														0.400	1.000
1.6															0.250
1.7														0.100	
1.8														0.100	
Mortality	0.267	0.200	0.077	0.083		0.133		0.039	0.068	0.060	0.049	0.150			
Init89	30	20	13	12	12	30	57	77	59	84	41	20	10	10	8

1990-1991															
lambda = 0.947															
Leaf width	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5
0.1	0.773	0.316				0.063		0.094	0.029	0.086	0.067				
0.2	0.136	0.474	0.438	0.063											
0.3	0.045	0.053	0.250	0.375											
0.4		0.053	0.188	0.313	0.357	0.094									
0.5				0.188	0.214	0.125	0.077		0.029						
0.6				0.063	0.143	0.438	0.269	0.156	0.071	0.014	0.023				
0.7					0.143	0.156	0.385	0.391	0.157	0.129	0.045	0.033	0.077		
0.8						0.094	0.192	0.203	0.286	0.229	0.205	0.133	0.077		
0.9						0.071	0.063	0.019	0.156	0.271	0.200	0.136	0.100	0.154	0.077
1.0									0.031	0.129	0.271	0.364	0.233	0.154	
1.1										0.014	0.100	0.091	0.267	0.231	0.154
1.2											0.014	0.068	0.200	0.154	0.077
1.3							0.016					0.033		0.385	
1.4													0.077	0.154	
1.5														0.154	0.167
1.6															1.000
1.7															0.167
1.8															
Mortality	0.045	0.105	0.125		0.071	0.031	0.058	0.047	0.043	0.043	0.068		0.077		
Init90	22	19	16	16	14	32	52	64	70	70	44	30	13	13	6

**Figure III.11.** Comparison of lambda values for analysis of *Calochortus howellii* plot data from Mariposa Meadow using three different size-classifications.



1988 through 1991, a classification resulted with the following leaf width categories:

- 1  $\leq 6$  mm
- 2  $> 6$  and  $\leq 7$  mm
- 3  $> 7$  and  $\leq 10$  mm
- 4  $> 10$  and  $\leq 13$  mm
- 5  $> 13$  mm.

Lambda values were then recalculated using this new five-category classification (Table III.8, III.12). As above, reproduction was incorporated into the matrix by estimating the proportion of seedlings produced per category during the transition period. These values were based on the proportion of plants producing capsules in each category the previous year. The number of new recruits per category was divided by the total number of plants which were in that category the previous year.

On average, the lambda values generated using the theoretically derived categories were slightly higher than those for other methods (Figure III.11, Table III.8). Standard deviation among years was also slightly higher for this classification method. The average index of dissimilarity (14.1) was lower than for the empirical analysis (17.6). The transition years 1985-1986 and 1990-1991 had the highest dissimilarity values; 40.2 and 43.8, respectively. The remaining transitions averaged 11.2, with values of 8.0 for 1986-1987, 14.0 for 1987-1988, 12.5 for 1988-1989, and 10.1 for 1989-1990.

**Sensitivity analysis.** A sensitivity analysis allows an evaluation of the importance to lambda of each value in the matrix. One approach is to modify selected values in the matrix to determine the impact on population parameters. This approach has been used by other investigators to evaluate the significance of seed-set. Fiedler (1987) found that substituting the maximum number of seeds per capsule for an average would have little effect on the population growth rate for three rare species of *Calochortus*, but would increase the growth rate by 29 to 31% in the common species. Using sensitivity analyses, Bierzychudek (1982) discovered that the

**Table III.12.** Size-classified transition matrices for 1985-86, 1986-87, 1987-88, 1988-89, 1989-90, and 1990-91 based on theoretically determined leaf-width categories, calculated using Moloney's algorithm (category 1  $\leq 6$  mm; category 2  $> 6$  mm and  $\leq 7$  mm; category 3  $> 7$  mm and  $\leq 10$  mm; category 4  $> 10$  mm and  $\leq 13$  mm; and category 5  $> 13$  mm). Each number in the matrix is the proportion of plants which transfer from the column category (year 1) to the row category (year 2). Reproduction is incorporated into first row, as the percent of seedlings produced per individual in each reproductive category. Mortality is the percent of plants in each category which died during the transition. Initial category distributions (%) are based on the numbers of plants in each category in 1990 (e.g. Init85); stable distributions (%) and lambda values were calculated using DEMOG. See text for further explanation.

1985-1986					
Category	1	2	3	4	5
1	0.475	0.129	0.035	0.000	0.000
2	0.361	0.271	0.070	0.000	0.000
3	0.131	0.571	0.731	0.162	0.000
4	0.016	0.000	0.146	0.730	0.333
5	0.000	0.000	0.006	0.108	0.667
Mortality	0.016	0.029	0.023	0.000	0.000
Init85	61	70	171	37	3
Category Distribution					
Actual	17.8	20.5	50.0	10.8	0.9
Stable	4.0	5.7	38.3	38.5	13.4

1988-1989					
Category	1	2	3	4	5
1	0.727	0.192	0.186	0.058	0.008
2	0.116	0.233	0.109	0.012	0.000
3	0.083	0.562	0.652	0.267	0.231
4	0.008	0.014	0.174	0.465	0.462
5	0.000	0.014	0.000	0.198	0.308
Mortality	0.066	0.027	0.024	0.058	0.000
Init88	121	73	247	86	13
Category Distribution					
Actual	22.4	13.5	45.7	15.9	2.4
Stable	32.7	10.1	36.7	15.9	4.6

1986-1987					
Category	1	2	3	4	5
1	0.597	0.176	0.112	0.113	1.000
2	0.156	0.176	0.126	0.016	0.000
3	0.247	0.595	0.698	0.371	0.000
4	0.000	0.027	0.130	0.452	0.571
5	0.000	0.000	0.005	0.113	0.429
Mortality	0.000	0.027	0.005	0.032	0.000
Init86	77	74	215	62	7
Category Distribution					
Actual	17.7	17.0	49.4	14.3	1.6
Stable	24.6	11.3	48.1	13.2	2.7

1989-1990					
Category	1	2	3	4	5
1	0.641	0.087	0.146	0.056	0.052
2	0.111	0.245	0.095	0.014	0.052
3	0.094	0.631	0.604	0.295	0.105
4	0	0.035	0.218	0.478	0.052
5	0	0	0	0.126	0.736
Mortality	0.153	0	0.054	0.070	0
Init89	117	57	220	71	19
Category Distribution					
Actual	24.2	11.8	45.5	14.7	3.9
Stable	24.0	8.6	38.7	18.7	10.0

1987-1988					
Category	1	2	3	4	5
1	0.554	0.036	0.135	0.048	0.091
2	0.273	0.273	0.078	0.016	0.000
3	0.099	0.691	0.717	0.339	0.182
4	0.033	0.018	0.189	0.516	0.455
5	0.000	0.000	0.004	0.129	0.364
Mortality	0.041	0.000	0.004	0.000	0.000
Init87	121	55	244	62	11
Category Distribution					
Actual	24.5	11.2	49.5	12.6	2.2
Stable	17.8	11.4	42.2	23.5	5.1

1990-1991					
Category	1	2	3	4	5
1	0.832	0.346	0.157	0.013	0.000
2	0.059	0.385	0.221	0.046	0.000
3	0.050	0.212	0.598	0.575	0.043
4	0.000	0.000	0.049	0.310	0.565
5	0.000	0.000	0.000	0.011	0.391
Mortality	0.058	0.044	0.046	0.000	0.000
Init90	119	52	204	87	23
Category Distribution					
Actual	24.5	10.7	42.1	17.9	4.7
Stable	64.9	14.1	19.5	1.5	0.0

greatest depression in population growth rate occurred when the condition of limited pollination was simulated.

Caswell (1978) has provided a more analytical approach, using a formula for calculation of sensitivity values which correspond to each element in the matrix. Sensitivities are defined as the partial derivative of the eigenvalue with respect to the value of the element; they measure the impact of small changes in the matrix elements on the asymptotic behavior of the population (Ferson 1990). These values, in conjunction with selective manipulation of matrix elements, provide a comprehensive analysis of population response to changes in life history events. Assumptions include linearity and time-invariance; density effects and temporal fluctuations in the environment are not considered. Sensitivity values for *C. howellii* are provided by year, with means and standard deviations provided for each element over the six transition years (Table III.13).

As Caswell and Werner reported for *Dipsacus* (1978), sensitivities for *C. howellii* tend to increase down rows of the matrix, with increasing size or stage. Elements with highest sensitivity to change are found in the lower right corner of the matrix, corresponding to adult plants (Table III.13).

**Elasticities.** Elasticity values provide a measure of the contribution of each element in a constant projection matrix to the magnitude of the equilibrium population growth rate of the matrix (Ferson 1990). Because elasticity values are proportional (i.e. sum to 1), they are more intuitively interpretable than sensitivities, which may increase asymptotically. Elasticities for the *C. howellii* matrices are consistently highest for the element representing the adult to adult transition (Table III.14), which contributes an average of 73% to lambda. The next most important element was the seedling to seedling transition, with an average elasticity value of 8.5%. Seedlings remaining in category 1 were particularly important in 1990-1991.

Recruitment of new seedlings was relatively unimportant based on this analysis; higher recruitment in 1987, 1988, and 1989 did not markedly increase elasticities.

**Table III.13.** Sensitivity values for *Calochortus howellii* population at Mariposa Meadow, based on size-classified transition matrix analysis using three empirically selected categories. Category 1 = seedlings with leaf widths less than 3 mm, 2 = juveniles with leaf widths between 3.5 and 6 mm, 3 = adults with leaf widths greater than 6.5 mm. Mean and standard deviation are calculated for each element over the six matrices. See text for explanation.

1985 – 1986			
Category	1	2	3
1	0.013	0.090	0.920
2	0.013	0.088	0.894
3	0.013	0.088	0.899

1988 – 1989			
Category	1	2	3
1	0.120	0.030	0.242
2	0.198	0.049	0.401
3	0.412	0.101	0.831

1986 – 1987			
Category	1	2	3
1	0.151	0.147	0.514
2	0.178	0.174	0.609
3	0.198	0.193	0.675

1989 – 1990			
Category	1	2	3
1	0.046	0.035	0.333
2	0.105	0.080	0.770
3	0.120	0.091	0.874

1987 – 1988			
Category	1	2	3
1	0.091	0.012	0.213
2	0.353	0.046	0.820
3	0.371	0.484	0.863

1990 – 1991			
Category	1	2	3
1	0.229	0.135	0.264
2	0.391	0.231	0.452
3	0.469	0.276	0.541

Means of Sensitivities			
Category	1	2	3
1	0.108	0.075	0.414
2	0.206	0.111	0.658
3	0.264	0.206	0.781

Standard Deviations of Sensitivities			
Category	1	2	3
1	0.077	0.058	0.270
2	0.144	0.075	0.203
3	0.181	0.155	0.142



**Table III.14.** Elasticity values for *Calochortus howellii* population at Mariposa Meadow, based on size-classified transition matrix analysis using three empirically selected categories. Category 1 = seedlings with leaf widths less than 3 mm, 2 = juveniles with leaf widths between 3.5 and 6 mm, 3 = adults with leaf widths greater than 6.5 mm. Values in each matrix sum to 1. Mean and standard deviation are calculated for each element over the six matrices. See text for explanation.

1985 – 1986			
Category	1	2	3
1	0.007	0.000	0.007
2	0.007	0.039	0.042
3	0.000	0.049	0.850

1988 – 1989			
Category	1	2	3
1	0.095	0.001	0.025
2	0.026	0.003	0.021
3	0.000	0.046	0.786

1986 – 1987			
Category	1	2	3
1	0.108	0.000	0.043
2	0.043	0.096	0.036
3	0.000	0.078	0.597

1989 – 1990			
Category	1	2	3
1	0.031	0.000	0.014
2	0.012	0.040	0.028
3	0.002	0.040	0.832

1987 – 1988			
Category	1	2	3
1	0.071	0.000	0.020
2	0.020	0.019	0.007
3	0.000	0.027	0.836

1990 – 1991			
Category	1	2	3
1	0.200	0.016	0.013
2	0.029	0.155	0.047
3	0.000	0.060	0.481

Means of Elasticities			
Category	1	2	3
1	0.085	0.003	0.020
2	0.023	0.059	0.030
3	0.000	0.050	0.730

Standard Deviations of Elasticities			
Category	1	2	3
1	0.068	0.006	0.013
2	0.013	0.057	0.015
3	0.001	0.018	0.154

These results suggest that the low capsule production and seedling recruitment is not limiting to this population at present. This differs from results of a sensitivity analysis on the rare species *Calochortus tiburonensis* and *C. pulchellus*, where reduced seed number resulted in a great decrease in  $\lambda$  (Fiedler 1987).

Of the limited number of studies which apply transition matrix models, few report elasticity values. Opportunities for comparisons among populations and species are awaited, since this may be a more useful value than the more standard  $\lambda$ .

### **Practical application of the model, conclusions, and recommendations.**

By tagging and tracking individuals of *C. howellii* over nine years we learned that this species is extremely long-lived and slow growing, has overall low mortality and recruitment, and currently has a stable population structure. No seedlings recruited during the study have yet advanced beyond the seedling or juvenile stage. For example, 82% of the individuals which were 1 mm or less in 1987 still had not grown by 1991. Despite nearly a decade of monitoring, the length of time required for plants of this species to reach reproductive maturity remains unknown. The harsh environment may contribute to this slow growth rate.

While few studies of this nature have been conducted on rare plants, Fiedler (1987) performed nearly identical investigations of three rare and one common species of *Calochortus* over a three year period in California. In addition, studies of two rare close relatives of *C. howellii* initiated in 1989 are discussed in the next chapter. Fiedler concluded that the four different *Calochortus* species she studied were idiosyncratic in their demographic properties, allowing few generalizations across taxa. Predation of bulbs and disturbance by pocket gophers, rotting of seedlings, and herbivory by black-tailed jackrabbits, blacktailed and mule deer, and various insects were phenomena noted both in the present study of *C. howellii* and in Fiedler's study of the three rare California taxa. She also reported that episodic flushes of reproduction punctuating long periods of low reproductive output may

characterize certain rare species and ensure their persistence. Reproduction in *C. howellii* also appears to be episodic in this way.

Fiedler (1987) cautions against extrapolating the population data to the species as a whole. While I believe that the data for *C. howellii* reflect the dynamics of the population sampled, further generalizations would be misleading, since Mariposa Meadow was selected because it was among the most vigorous and densest known populations.

Results from transition matrix analysis indicate that the monitored population of *C. howellii* has been stable, but has been recently declining. A marked increase in mortality in one plot with high levels of pocket gopher disturbance, contributed most to the overall decrease in lambda values. Separate analysis by plot supports this conclusion. Localized mortality from natural causes reveals the vulnerability of the population to catastrophic loss; the slow growth and recruitment rates lead to slow recovery of populations following disturbance. Episodic mortality could serve to limit expansion of *C. howellii*, just as periodic bursts of recruitment may maintain population stability.

The difference in lambda values generated by the three approaches to category selection for transition matrix analysis (Figure III.11, Table III.8) are probably not biologically significant. This indicates a high degree of robustness of the model when using large data sets and supports tracking larger numbers of individuals, even if some precision in measurement must be sacrificed. The selection of biologically meaningful categories has merit and is defensible here, since the theoretically derived classification failed to produce significantly different results.

Results from this study also indicated that grazing by native herbivores plays an important role in suppressing seed production by removing buds, flowers, and capsules prior to seed-set. An average of 9% of the plants that initiated inflorescences produced capsules during the study period; and during three years, less than 2% of the plants successfully produced seed. Given that an average of 31% of individuals initiate inflorescences each year, the percentage of successfully reproducing plants is small. While this observation may not be unusual for long-

lived perennials, it serves to highlight the importance of the few capsules that survive predation in a given year and their potential contribution to the gene pool. It is worth noting that the sporadic and patchy recruitment also results from a limited number of capsule-producing plants.

This study did not specifically address management of habitat for *C. howellii*, but nonetheless it provides a valuable baseline for comparison with effects of prescribed treatments, such as fire or herbivore exclusion. While this long-lived species does not apparently require high recruitment to maintain stable populations, the small amount of seed which survives herbivory is undoubtedly important to the long-term stability of the population, particularly where episodic mortality is high. Removal of leaf tissue also reduces average leaf width of the grazed plants the subsequent year (unpublished data), suggesting that carbohydrate reserves may be depleted by herbivory. This observation, and the relatively small amount of seed which survives native herbivores, support the conclusion that the current practice of excluding livestock in *C. howellii* habitat should be continued.

The Jeffrey-pine communities inhabited by *C. howellii* historically experienced frequent ground fires at one to twenty year intervals (United States Department of Agriculture Forest Service 1991) and the Forest Service has indicated that it plans to reintroduce fire to the Jeffrey-pine savannah ecosystems within the northern portion of the species' range (United States Department of Agriculture Forest Service 1991). The limited fuel and sparse canopy preclude stand-replacement fires in this ecosystem, but fire suppression has increased stand density and fuels, creating greater potential for catastrophic fire in some areas. The impact of these intense fires during the growing season on *C. howellii* is unknown; controlled burns during the dormant season would clearly pose less risk. More subtle changes can occur through fire suppression; increasing stand density could influence understory species by altering hydrology (e.g. reducing available soil moisture), increasing shading, and enhancing competition from bunchgrasses. Within some populations, understory competition and the relative sparseness of *C. howellii* suggest that fire may have been important in maintaining habitat for this species, but fire could

alternatively serve to stimulate germination of *Ceanothus cuneatus*, a species which appears to be outcompeting *C. howellii* at the Democrat Gulch site. Investigating the response of populations to prescribed fire would provide an important followup to the present study, and it is recommended that several of the established plots will be burned, so that the response of this species to fire can be scientifically documented. An opportunity exists also to study the effect of fire on other species within the established plots and perhaps begin to investigate the role of competition in limiting populations of *C. howellii*.

A rare species like *C. howellii*, having a limited distribution, requiring more than a decade to reach reproductive maturity, successfully producing very few seeds, and having low seedling recruitment, may require many decades of study. Investigating the species' response to fire may be key to successful management and may explain its absence or decline at other sites. The correlations between precipitation and reproduction, recruitment, and mortality suggest that climatic changes may influence distribution of this species. A slow-growing, local species with low fecundity may be slow to respond to environmental change. However, the responses of these plants to change may provide clues to specific causes of rarity that have heretofore eluded us. It is through baseline studies such as the one presented here that we can begin to evaluate scientifically the effects of factors such as climatic change and fire suppression, in order to manage better for biological diversity and perhaps unlock some of the mysteries of certain rare species.

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## CHAPTER 4

COMPARATIVE DEMOGRAPHY OF RARE MARIPOSA LILIES  
(*CALOCHORTUS*: LILIACEAE) ENDEMIC TO SERPENTINE SOILS  
IN SOUTHWESTERN OREGON

## ABSTRACT

Population dynamics of two rare *Calochortus* species from southwestern Oregon are analyzed using size-classified transition matrices, and the results are compared with those of similar studies on related taxa. Taxonomically very distinct, yet only recently discovered, *C. umpquaensis* and *C. coxii* are serpentine endemics known from limited distributions. Despite its narrow edaphic restriction, *C. umpquaensis* occurs locally within a wide range of habitats from meadows to forests. Preliminary studies in 1988 indicated differences in reproduction and recruitment in forest, meadow, and transitional ecotone habitats. During the following three years, permanent plots were monitored within these three habitats for *C. umpquaensis* and at two sites for *C. coxii*. Bud production was highest, plants were most dense, and on average were larger in the ecotone habitat. Mortality was significantly higher in 1991 than in 1990 for both species. Individual growth rates were higher on average in *C. umpquaensis*, and its tendency to be less habitat-specific suggests an ability to colonize. However, equilibrium population growth rates indicate that the population is stable rather than increasing. Low reproductive success, due to predation and low recruitment, and declining population trends indicate that *C. coxii* should be carefully monitored. The probability of local extinction this taxon is high, if the years studied are typical.

## INTRODUCTION

*Calochortus umpquaensis* and *C. coxii* are recently discovered rare lilies occurring on serpentine-derived soils of southwestern Oregon (Fredricks 1989a; Godfrey and Callahan 1989). Both are highly localized and threatened by activities including logging, grazing, and bulb digging. In 1990, *Calochortus umpquaensis* was listed in Oregon as an endangered species under ORS 564.100-564.135 and is a Federal Category 2 species under consideration for listing under the Endangered Species Act by the U.S. Fish and Wildlife Service. *Calochortus coxii* is also under consideration for both state and federal listing. While these two species are not sympatric, they share similar habitats (Chapter 2). Both are restricted to serpentine soils derived from ultramafic parent material, which contain low macronutrient levels (potassium and phosphorus), low calcium/magnesium ratio, and above average concentrations of nickel, chromium, cobalt, and zinc (Table II.9). All known populations fall within intrusive serpentinite and minor peridotite geologic formations (Wells and Peck 1961, Beaulieu and Ramp 1972). *Calochortus umpquaensis* is known from disjunct populations spanning 80 km, from Ace Williams Mountain near the town of Glide, southwest to Sexton Mountain (Figure II.1). *Calochortus coxii* populations occur within a narrow 50 km-long band of serpentinite running northeast to southwest of the town of Myrtle Creek. Known individual populations span 16 km.

In Chapter 3, the results of a long-term monitoring study on another southwestern Oregon serpentine endemic, *C. howellii*, were reported. Similar methods and analysis allow comparisons among these taxa. Fiedler's (1987) study of three rare (including two serpentine-endemic) and one common *Calochortus* species provide additional congeneric comparisons. The remarkably high incidence of rarity in the genus has lead to a search for shared features or constraints, which might explain the disproportionate number of highly local endemics.

The perennial habit, simple growth form, lack of significant vegetative reproduction, and prolonged blooming period of *C. howellii*, *C. umpquaensis*, and *C. coxii* make them amenable to a long-term demographic study. Distinctive

pubescence on the undersurface of the solitary leaf aids in distinguishing vegetative adults and seedlings of these three species from other relatives.

Despite the narrow edaphic restriction to serpentine-derived soils, *C. umpquaensis* occurs within a rather broad continuum of habitats from closed canopy coniferous forest to open grass-forb meadow. In the narrow transition between the forest and meadow, referred to as the ecotone, the abiotic environment is moderated (e.g. light, temperature tend to be less extreme) and community elements of both forest and meadow overlap. In ecotonal and forested habitats, the overstory is composed of *Pinus jeffreyi*, *Pseudotsuga menziesii*, *Calocedrus decurrens*, and *Arbutus menziesii*. Grasses including *Koeleria cristata*, *Festuca rubra*, and *Danthonia californica* dominate the meadow and ecotonal understory, and species diversity is high (Chapter 2). By selecting plots within each habitat type, differences which may influence seedling establishment, reproductive success and mortality may be identified.

*Calochortus coxii* occurs in narrow ecotones between mixed coniferous forests and grass-forb meadows. As with *C. umpquaensis*, native grasses dominate the understory, and while composition differs somewhat, species diversity is also high. Sites inhabited by *C. coxii* are typically intact, relatively undisturbed plant communities.

Because of the legal protection and endangered status of these rare lilies and their vulnerability to human threats, it is important to begin collection of demographic data to document population trends. Changes in the number of populations and individuals are useful statistics; however, more sophisticated analyses are necessary to evaluate population stability, calculate extinction probability, and identify life history stages or events that may be critically sensitive to environmental changes or habitat modifications.

The objective of this study was to investigate the life history of rare southwestern Oregon mariposas, in an attempt to identify shared features that could account for their limited distribution. Recruitment, growth, reproduction, and mortality rates are compared. Limiting resources may determine distribution within

serpentine habitat. While narrow habitat specificity typifies *C. coxii* (ecotone) and *C. howellii* (meadow), *C. umpquaensis* occurs across a wide range of habitats, offering a unique opportunity to compare reproductive success, recruitment, and survival in habitats with different resources. Forest, ecotone, and meadow habitats differ in availability of light, moisture, pollen vectors, and nutrients. These potentially limiting factors are indirectly considered for *C. umpquaensis*. Finally, an evaluation of population trends was undertaken to determine if management intervention is warranted to maintain viable populations of *C. umpquaensis* and *C. coxii*.

## METHODS

At the onset of the study, only four populations of *C. umpquaensis* were known, all within an area spanning 4 km. These populations range in size from 0.4 to 25 hectares. At one site, Ace Williams Mountain, *C. umpquaensis* occurs in forest, meadow, and ecotone habitats, but at other sites, its distribution was more limited. In 1988, preliminary sampling was conducted along belt transects to compare population structure and reproduction of *C. umpquaensis* at all known sites within the three habitats. At each one meter interval along 10-m transects, a plot frame (0.5-m<sup>2</sup>) was placed in a randomly selected quadrant. Data collected within each plot included (1) leaf width and reproductive status (including number of buds, flowers, or capsules) for each *Calochortus* individual and (2) cover value for each species present (plus cover of rock, litter, moss/lichen and bare soil). Results from the analysis of the cover data were discussed in Chapter 2.

The 1988 data were analyzed using Analysis of Variance procedures (SAS 1988) to determine if significant differences among habitats exist for numbers of individuals or for flower production. For each variable, the data were analyzed using the summary data (means for each of the transects), the Ace Williams data alone (the site with all three habitat types represented), and the unclassified data. Fisher's Protected Least Significant Difference separation of means tests were performed when results of ANOVA indicated statistically significant differences

among the habitat types. Data for transects, sites, and habitats were summarized, and leaf width frequency distributions for each site and habitat, and flowering by leaf width and habitat were graphed. Maximum leaf widths were measured to the nearest millimeter and ranged from 1 to 15 mm. To further compare differences in flowering among habitats, the number of individuals initiating inflorescences per meter was summed over all sites. The fate of buds was tallied by these categories: grazed, aborted, and number of successfully produced flowers.

In 1989, permanent plots were established to begin monitoring trends within a population of *C. umpquaensis* located on Ace Williams Mountain (T26S R3W sec. 27) under management by the Bureau of Land Management (B.L.M.). Because of the high seedling density and shallow bulb depth, it was considered undesirable to risk microsite disturbance and damage to the plants by tagging, so a method was employed to investigate population trends which minimized impact. Within each of the three habitat types, two five meter transects were subjectively selected within dense patches of *Calochortus*, avoiding steep slopes and deer trails. A permanent aluminum marker, with the plot numbers and the direction (relative to magnetic north) and distance to the transect was attached to a nearby tree in the vicinity of each transect. Each meter along the transect was divided into 4 quadrats and one of the four quadrats randomly selected for monitoring. Ten 0.5 x 1.0 m plots for each habitat (15 m<sup>2</sup> total area) were sampled for this species. In each of the four plot corners, 6" x 3/4" PVC pipe pieces were sunk into the ground, level with the soil surface. A mapping table, with telescoping legs (1/2" base diameter), and a plexiglas surface was used to record the location of each individual on clear plastic sheets. The table was designed to fit into the sunken PVC pipe pieces, which allowed accurate repositioning and relocating of individuals throughout the season. As a backup to this method, all individuals were marked with a colored toothpick, which also facilitated mapping. This essentially tagless method was chosen to reduce impact on the site, allowing individuals to be mapped and relocated without disturbing them. The total numbers of plants mapped within the permanent plots on

Ace Williams Mountain were 286 in the ecotone, 149 in the meadow, and 236 in the forest habitat.

Twenty 1.0 m by 0.5 m permanent plots were established in 1989 to compare trends of *C. coxii*. Two sites were selected on federal land under management by the B.L.M., referred to as the Smith site (T29S R5W sec. 3, SW $\frac{1}{4}$  of SW $\frac{1}{4}$ ) and the Bilger Creek Road site (T28S R5W sec. 35, W $\frac{1}{2}$  of SW $\frac{1}{4}$ ). At each of these two sites, separated by approximately 2.2 km, two five-meter transects were subjectively selected within dense *Calochortus* patches. Methods for plot establishment and data collection were identical to those for *C. umpquaensis*, with the exception that transects were not selected within specified habitat types, because *C. coxii* occurs primarily in ecotonal areas. A total of 374 plants were mapped for this species, with 215 and 159 at the Smith and Bilger localities, respectively.

Data collected annually on each individual of both species for 1989 through 1991 included maximum leaf width, number of buds per plant, number of flowers per plant, number and lengths of capsules per plant. Analysis of both maximum width and length of *C. howellii* leaves indicated that width provides the best long-term measure of growth; environmental factors (primarily precipitation) confound leaf length, and the high incidence of grazing further reduces the usefulness of this parameter (pers. obs.). Fiedler (1985) also used maximum leaf width in her analyses after demonstrating a modest but significant correlation between bulb wet weight and maximum basal leaf width.

When recording each individual for the first time, the microhabitat (moss, litter, bare soil, rock, or vegetation) was recorded. In addition, cover for each associated species was estimated in 1989 (analysis of these results are presented in Chapter 2). In general, plants were mapped and leaf widths measured in early May, once maximum width was attained, but before leaf width could be reduced by desiccation or increasing levels of herbivory. Flowering was monitored at its peak (mid-June), and capsules counted and measured near time of dehiscence (early August). Estimates of cover values for associated species within the plots were made in late May and early July. Associated species vouchers were deposited at

the Oregon State University Herbarium. Capsules of both *C. umpquaensis* and *C. coxii* were collected outside the plots in 1991. In the laboratory, each capsule was measured, and seeds and ovules were counted.

Direct observations of predation on *Calochortus* were limited to insects, although herbivorous mammals were observed in the study areas grazing on vegetation outside of the plots. The height of vegetation removal, dentation patterns, knowledge of feeding habitats, and demographic information from Oregon Department of Wildlife were used to evaluate predation on *Calochortus* within the study area. Evidence of tissue removal by insects and mammals was in most cases easily distinguished.

Size-classified transition matrices, incorporating information on recruitment, growth (change in leaf width between two consecutive years), and survival were analyzed using the APL program DEMOG (Wilson 1992). Three categories were used based on maximum leaf width: (1) seedlings with leaves 1 to 3 mm wide, (2) small adults with leaves larger than 3 mm, but no larger than 6 mm, (3) and large adults with widths greater than 6 mm. Occasionally, plants with widths as small as 3 mm produced buds, but most bud production occurred in larger plants. The matrices were constructed by calculating the proportion of plants in each category which remained that category, changed category, or died the subsequent year. Reproduction in the transition matrix is calculated as the number of new plants appearing in the plots the second year divided by the total number of plants in that category the first year. These numbers appear in the first row of the matrix. Total seedling recruitment is represented by the second and third columns of the first row of the transition matrix. Capsule data was used to determine proportion of reproductive plants in each category. For example, if 40% of the capsule-producing plants within the plots were in category 2, 40% of the seedling recruitment the subsequent year was attributed to that category.

Several statistics were calculated for each matrix. The equilibrium population growth rate or lambda ( $\lambda$ ) is calculated as the dominant eigenvalue of the matrix. A population that is stable has a rate of 1.0, while those with  $\lambda$  values greater or

less than 1.0 are increasing or declining, respectively. The equilibrium size structure is derived from the dominant right eigenvector and is useful in comparing the current population structure. Populations are considered unstable if they deviate significantly from the projected stable structure at equilibrium. The difference between the actual category distribution and the stable distributions, referred to as an index of dissimilarity (Keyfitz 1977), provides an additional measure of population stability.

## RESULTS

### *Calochortus umpquaensis* field studies: testing the initial hypothesis

**Differences in reproduction in 1988.** Differences in flower production among habitats were highly significant for 1988 ( $p = 0.0001$ ), with the ecotone and meadow, and ecotone and forest habitats differing at the 0.05 level using Fisher's Protected Least Significant Difference multiple comparison test. These results supported the hypothesis that differences exist in flower production among habitats (Table IV.1, Figure IV.1). Initiation of inflorescences and successful flowering was most frequent in the ecotone habitat and least common in the forest. Only the ecotone habitat produced individuals which bore more than two flowers per inflorescence (Figure IV.1). Losses of flowers to herbivory were nearly 50% for all habitat types. Capsule abortion was proportionately greatest in the forest.

When data from the Ace Williams site were analyzed separately, differences in flowering among habitats were less significant ( $p = 0.03$ ). Only the forest differed from the other habitats at the 0.05 level.

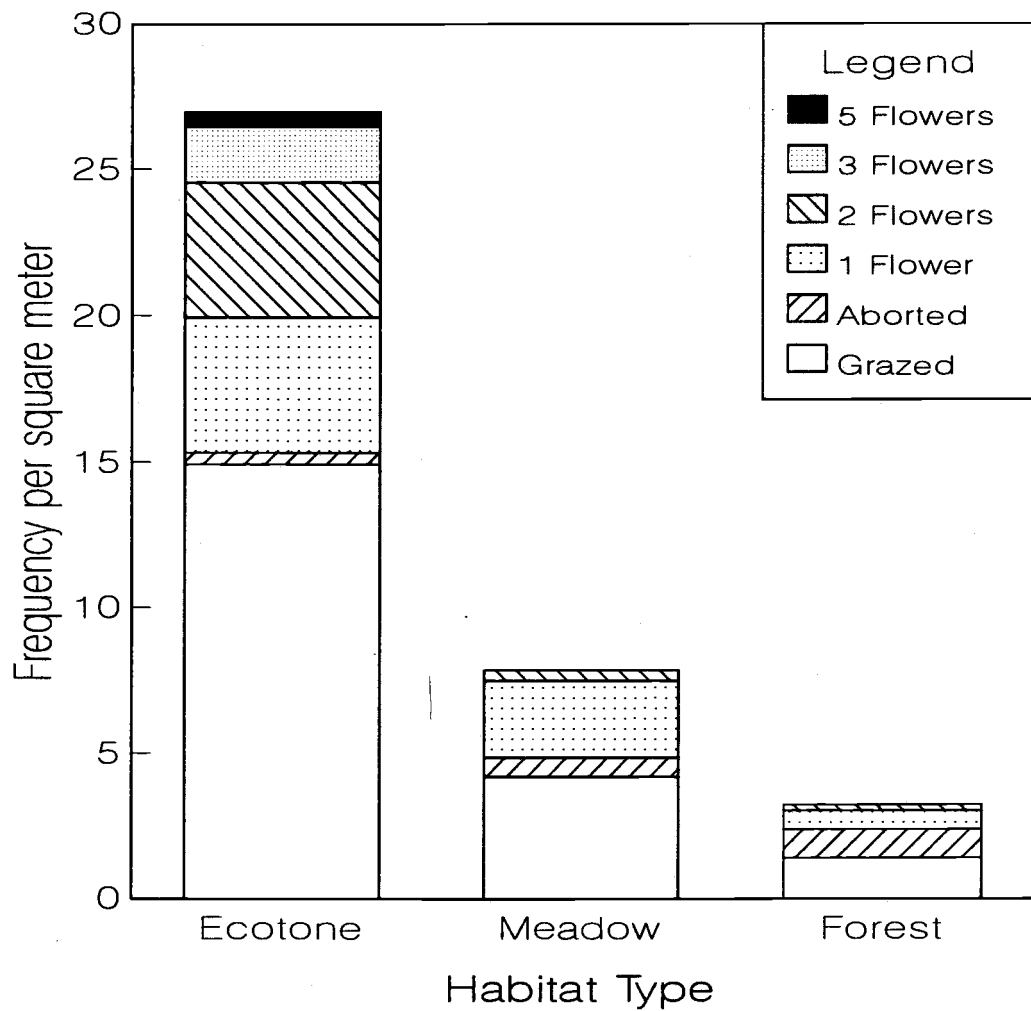
**Population structure in 1988.** Differences in density and population structure among the three habitats for 1988 were less distinct. Mean numbers of plants per meter were 26.8, 19.4, and 23.4 for the ecotone, meadow, and forest habitats,



**Table IV.1.** Summary data for 1988 study of *Calochortus umpquaensis* by site, habitat, and transect. Flowering was not determined at the Thunder Mt. Rd. site, due to the high incidence of grazing. Summaries for flowering are based only on the Little River Rd. and Ace Williams sites for the ecotone habitat.

Habitat	Site name	Number of Plots	N	Density (/m <sup>2</sup> )	Leaf-width (mm.)		Flowering	
					Mean	S.D.	N	Percent
Ecotone	Thunder Mt. Rd.	40	163	16.3	3.9	2.20	--	--
	Little River Rd.	20	152	30.4	8.7	2.30	83	55
	Ace Williams Mt.	20	221	44.2	4.2	1.60	28	13
Meadow	Standley Rd.	20	64	12.8	4.6	2.30	11	17
	Ace Williams Mt.	20	105	21	4.5	1.80	31	30
	Ace Williams Mt.	40	219	21.9	4.2	2.00	24	11
Forest	Ace Williams Mt.	40	225	22.5	3.9	2.20	8	4
	Watson Mt.	40	242	24.2	4.7	1.70	11	5
Ecotone	Summary	80	536	26.8	5.4	1.6	111	30
Meadow	by	80	388	19.4	4.3	2.0	42	11
Forest	Habitat	80	467	23.4	4.3	2.0	19	4
Total		240	1391	23.2	4.7	2.4	350	25

**Figure IV.1.** Flowering by habitat type for *Calochortus umpquaensis* in 1988, including tallies for inflorescences grazed or aborted before flowering.



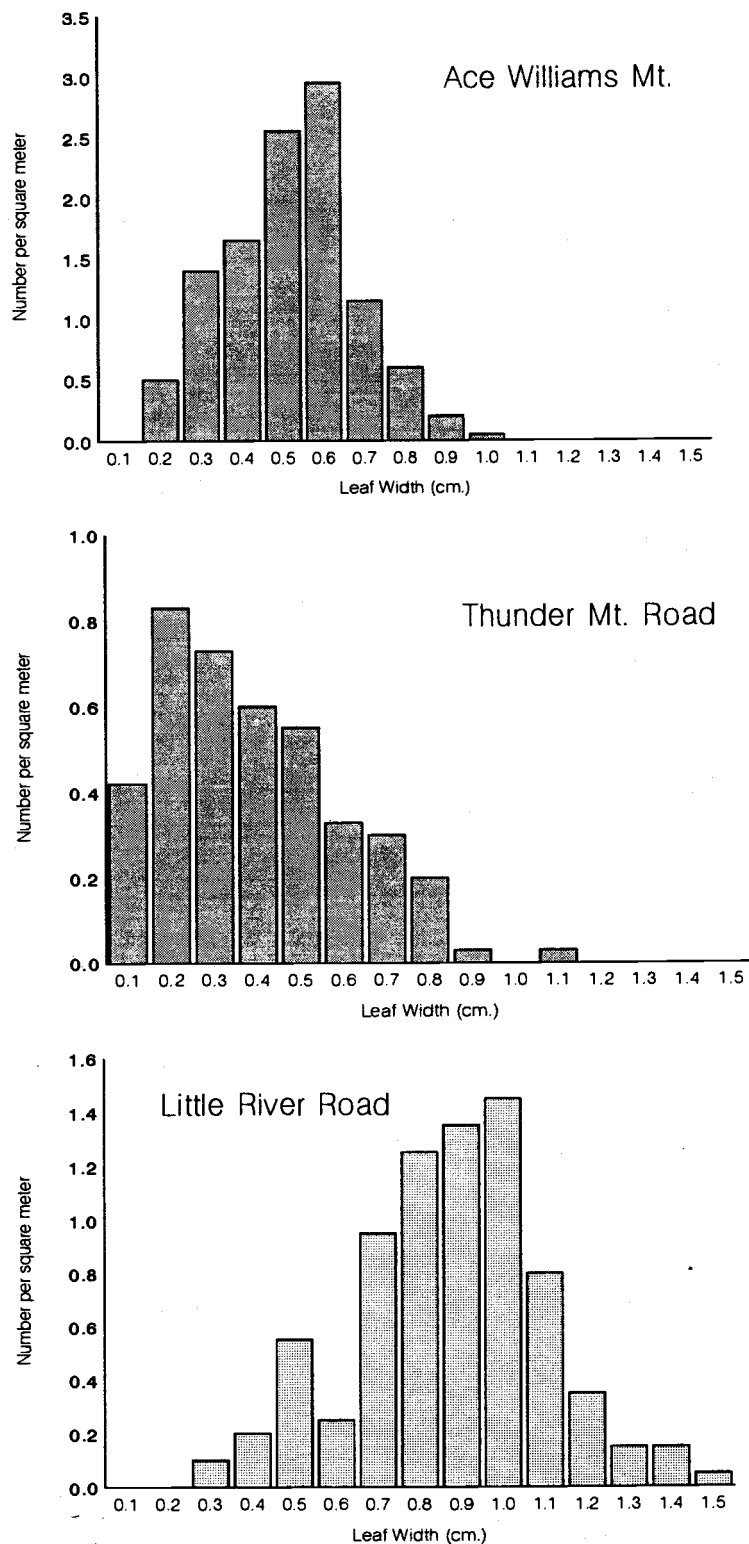
respectively (Table IV.1). Only the ecotone and meadow means differed significantly at the 0.05 level.

Population structure, based on leaf width, varied greatly from site to site, but not consistently within a habitat type (Figures IV.2-5). The leaf width frequency histograms suggest that the distributions at each site probably represent unique patterns of recruitment, growth, and mortality. The Thunder Mountain Road ecotone site (Figure IV.2), for example, may reflect a high level of recruitment, while the proportion of larger individuals decreases with increased leaf width. Population structure is skewed toward the smaller individuals, with the mean leaf width 3.9 mm ( $n = 161$ ). In contrast, at the Little River Road site, mean leaf width was 8.7 mm ( $n = 152$ ), with no individuals smaller than 3.0 mm. This lack of seedlings is noteworthy, in light of the fact that this site produced the largest number of flowers and abundant capsules, suggesting an adequate seed supply. In addition, 39% of the individuals had widths greater than 9.0 mm, as contrasted with the two other ecotone sites, with 1.2% and zero. The overall distributions for both the Little River Road and Ace Williams Mountain ecotone sites are bell-shaped, with the Ace Williams site shifted toward the smaller leaf widths.

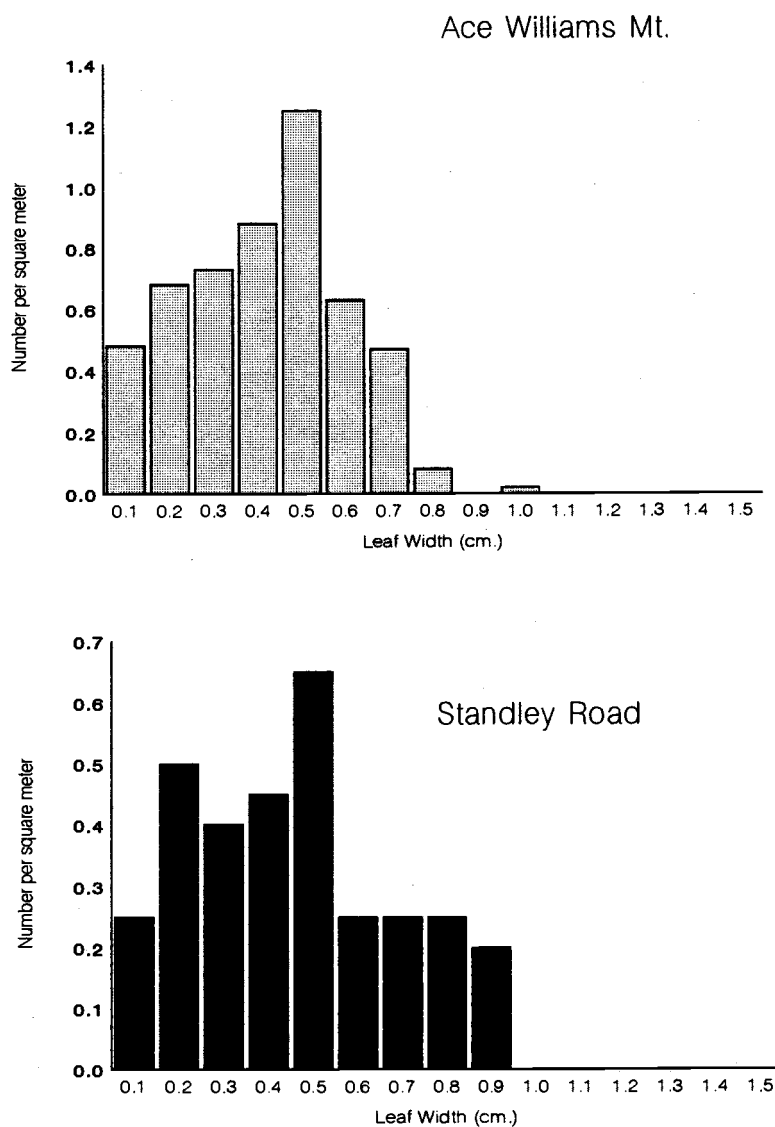
Of the two sites sampled for the meadow habitat, density was lowest at the Standley Road site, averaging 12.8 plants per square meter (Table IV.1, Figure IV.3). The forested site on Ace Williams Mountain was similar to the Thunder Mountain Road ecotone site in being skewed toward the smaller age classes, reflecting higher recruitment or slower growth rate (Figure IV.4). The mean leaf width was 3.9 mm ( $n = 225$ ), as contrasted with 4.7 mm ( $n = 231$ ) for Watson Mountain, which exhibits a more bell-shaped distribution.

When all sites are summarized, the frequency distributions were bell-shaped for all habitats (Figure IV.5), despite variations among sites. The proportion of flowering plants is higher for all size classes in the ecotone and meadow habitats. While the proportion of non-reproductive plants tend to decrease with increasing leaf width in all habitats, the proportion of flowering individuals was by far the lowest in the forested habitat for all sites. The frequency histograms (Figure IV.5)

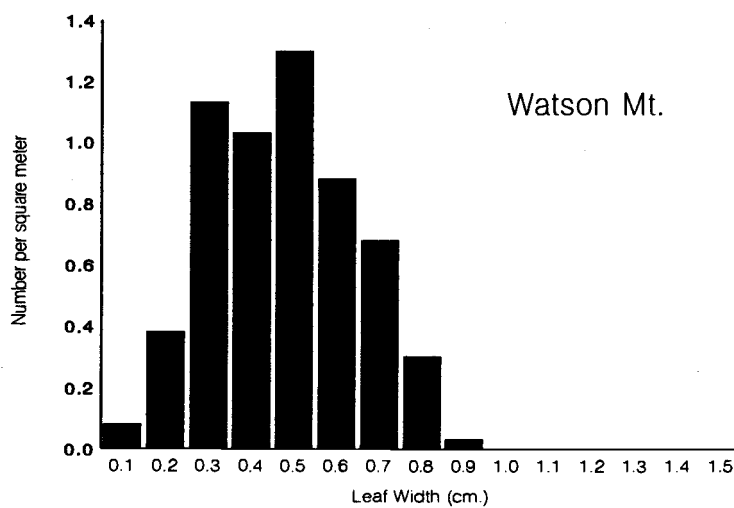
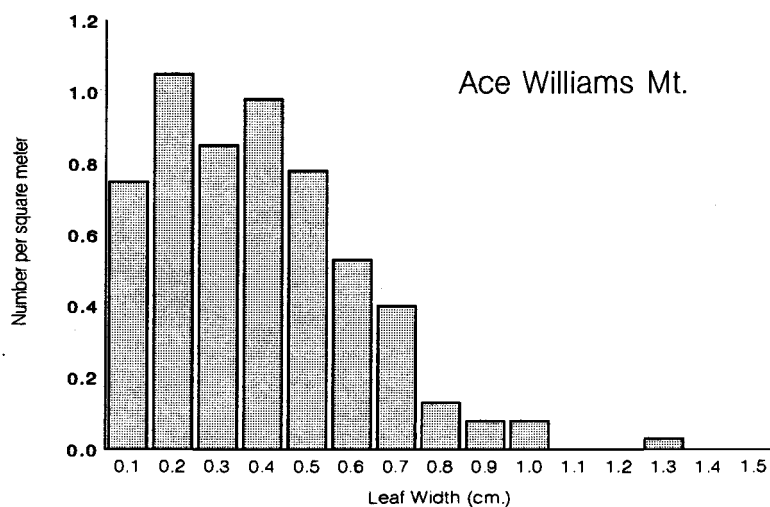
**Figure IV.2.** Leaf width frequency distributions for *Calochortus umpquaensis* in ecotone habitat at Ace Williams Mountain, Thunder Mountain Road, and Little River Road sites based on data collected in 1988.



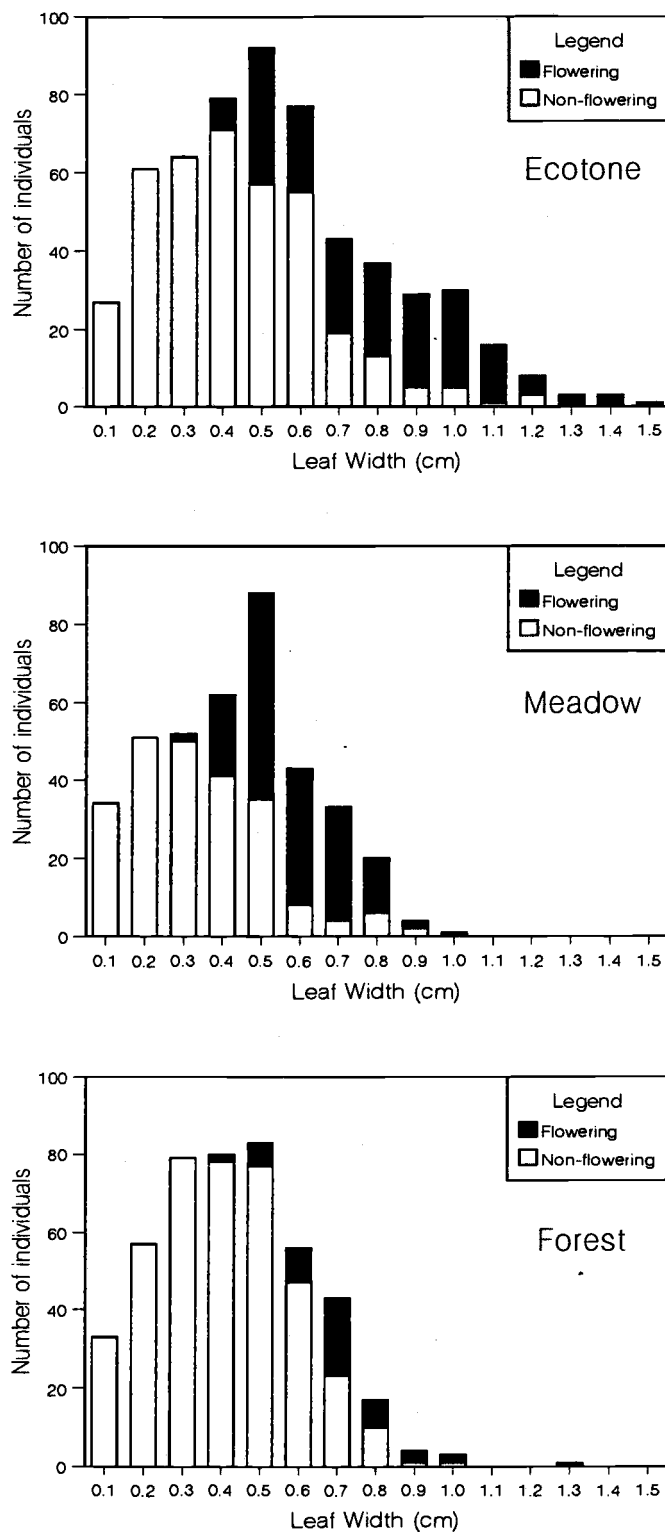
**Figure IV.3.** Leaf width frequency distributions for *Calochortus umpquaensis* in meadow habitat for Ace Williams Mountain and Standley Road sites based on data collected in 1988.



**Figure IV.4.** Leaf width frequency distributions for *Calochortus umpquaensis* in forest habitat for Ace Williams Mountain and Watson Mountain sites based on data collected in 1988.



**Figure IV.5.** Leaf width frequency distributions for *Calochortus umpquaensis* by habitat illustrating flowering status, based on data collected in 1988. Note greater proportion of non-flowering plants in forest relative to other habitats, despite similar size distributions.



confirm that the differences in reproduction are not due to difference in population structure. In order to further investigate and quantify these differences, permanent plots were established in 1989.

### **Preliminary results from long-term trend study**

**Reproductive biology of *C. umpquaensis*.** The pattern of reproductive success of *C. umpquaensis* within the plots during 1989, 1990, and 1991 (Figure IV.6, Table IV.2a) is similar to that observed in 1988 (Figure IV.1, Table IV.1). In all years, the total numbers of individuals and the percentage of reproductive plants are greatest for the ecotone habitat, and lowest for the forest.

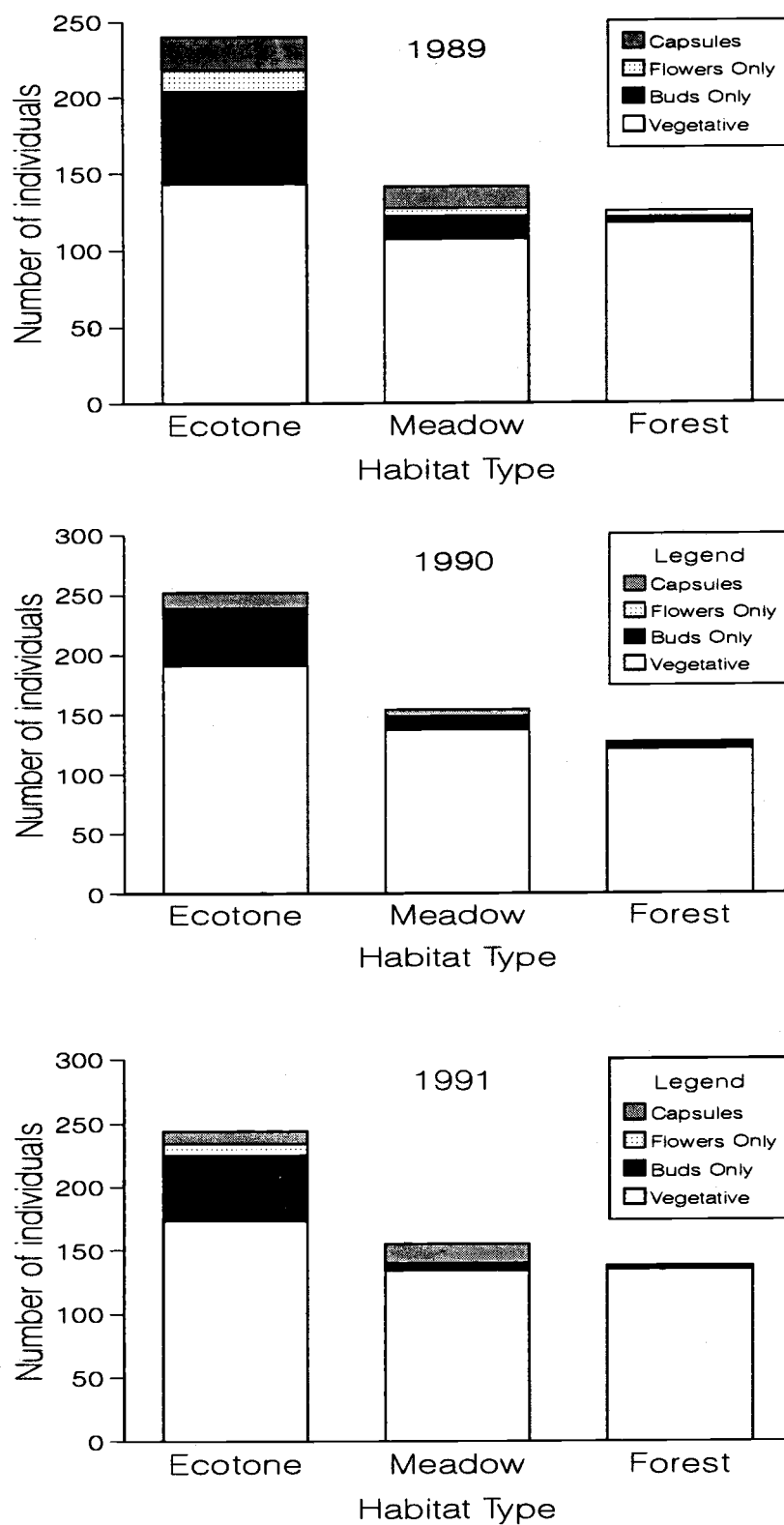
Within the permanent plots, the proportion of reproductive individuals was highest for all habitats in 1989, corresponding to the year of highest spring precipitation, then declined sharply in the following years (Table IV.2a). Bud production was higher in the ecotone (40.4%) than meadow (26.2%) in 1989, but resulting capsule production that year was nearly the same for both habitats. A similar pattern emerged in 1990. In 1991, although nearly twice as many buds were produced in the ecotone, heavy predation resulted in greatly reduced capsule production. Average capsule production over the three years was similar for the ecotone and meadow habitats, despite consistently lower bud production in the meadow. Predation, probably mostly by deer based on observations, was responsible for 99% of the loss of buds, flowers, and capsules in the ecotone and meadow in all years, with the remaining 1% aborting.

No capsules were produced in the forest habitat plots for 1989 or 1990, and only one capsule was produced in 1991. Flowering in the forest habitat was uncommon and those individuals which did flower rarely produced seed. Typically, after the flowers in the forest habitat lost their petals, the pistils remained erect. This was in contrast to those in the meadow and ecotone, which often became pendent before the petals dropped.

The average seed set for capsules collected at the study site, outside of the



**Figure IV.6.** Reproductive stages attained by *Calochortus umpquaensis* by habitat type for 1989 through 1991. Compare data for 1988, illustrated in Figure IV.1.



**Table IV.2a.** Summary of permanent plot data from Ace Williams Mountain for *Calochortus umpquaensis* and *C. coxii* plots for 1989 through 1991. Recruits are individuals appearing in the plots for the first time, regardless of size. Morts for 1990 also failed to appear in 1991, morts for 1991 may overestimate actual mortality.

Actual number of plants								Percent of total					
Year	Total	Vegetative	Buds	Flowers	Capsules	Recruits	Morts	Vegetative	Buds	Flowers	Capsules	Recruits	Morts
Ecotone													
1989	235	140	95	28	22			59.6	40.4	11.9	9.4		
1990	267	206	61	15	13	39	7	77.2	22.8	5.6	4.9	14.6	2.6
1991	255	184	71	19	10	12	24	72.2	27.8	7.5	3.9	4.7	9.4
Forest													
1989	125	117	8	4	0			93.6	6.4	3.2	0.0		
1990	142	136	6	1	0	21	4	95.8	4.2	0.7	0.0	14.8	2.8
1991	138	135	3	1	1	3	7	97.8	2.2	0.7	0.7	2.2	5.1
Meadow													
1989	141	104	37	18	15			0.0	26.2	12.8	10.6		
1990	185	168	17	6	5	67	23	90.8	9.2	3.2	2.7	36.2	12.4
1991	173	152	21	16	15	28	40	87.9	12.1	9.2	8.7	16.2	23.1
All habitats													
1989	501	361	140	50	37			72.1	27.9	10.0	7.4		
1990	594	510	84	22	18	127	34	85.9	14.1	3.7	3.0	21.4	5.7
1991	566	471	95	36	26	43	71	83.2	16.8	6.4	4.6	7.6	12.5

**Table IV.2b.** Summary of permanent plot data from Smith and Bilger Creek Road sites collected in 1989-1991.

Actual number of plants								Percent of total					
Year	Total	Vegetative	Buds	Flowers	Capsules	Recruits	Morts	Vegetative	Buds	Flowers	Capsules	Recruits	Morts
Smith site													
1989	196	111	85	61	12			56.6	43.4	31.1	6.1		
1990	202	115	87	27	3	12	6	56.9	43.1	13.4	1.5	5.9	3.0
1991	196	129	67	24	5	7	13	65.8	34.2	12.2	2.6	3.6	6.6
Bilger Cr. Rd. site													
1989	145	104	41	4	0			71.7	28.3	2.8	0.0		
1990	142	87	55	0	0	4	7	61.3	38.7	0.0	0.0	2.8	4.9
1991	136	73	63	4	1	10	16	53.7	46.3	2.9	0.7	7.4	11.8
Both sites													
1989	341	215	126	65	12			63.0	37.0	19.1	3.5		
1990	344	202	142	27	3	16	13	58.7	41.3	7.8	0.9	4.7	3.8
1991	332	202	130	28	6	17	29	60.8	39.2	8.4	1.8	5.1	8.7

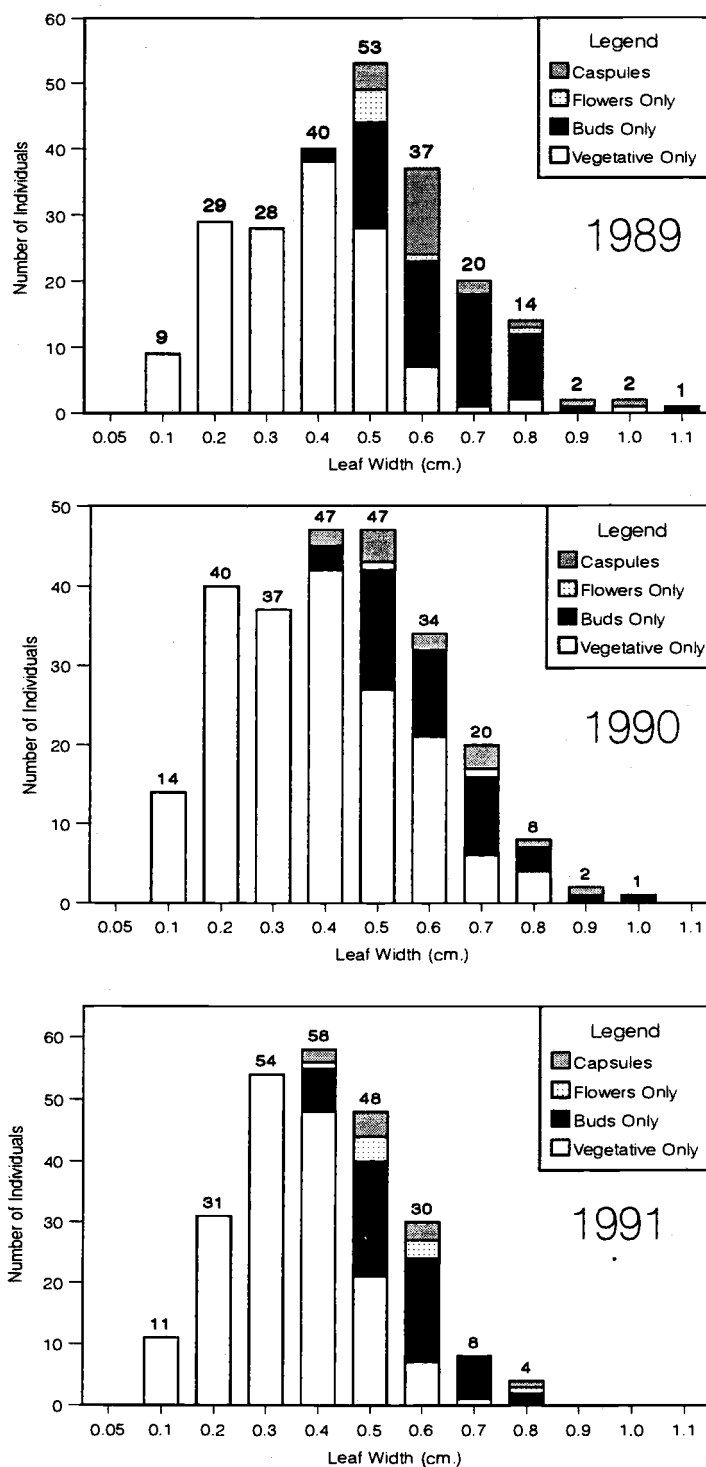
plots, in 1991 was 50.1% ( $n = 24$ ). Seed number averaged 38.6 per capsule and mean capsule length was 2.7 cm. A modest correlation was found between capsule length and number of seeds produced ( $r^2 = 0.51$ ). Mean capsule lengths within plots were similar for all three years: 2.7 cm for meadow and 2.5 cm for ecotone in 1989, 3.7 for meadow, 2.8 for ecotone in 1990, and 2.5 cm for meadow, and 2.3 cm for ecotone in 1991.

**Population biology of *C. umpquaensis*.** While some annual variation in population structure within each site is evident (Figures IV.7-9), overall patterns are similar, as expected for a long-lived perennial. A noteworthy increase in the 1 mm individuals in the meadow habitat in 1991 (Figure IV.8) represents a pulse of recruitment. A similar pulse is shown in 1989 in the forest habitat (Figure IV.9). Because of the slow growth rate of plants in this habitat, the actual year of recruitment of these individuals probably preceded 1989.

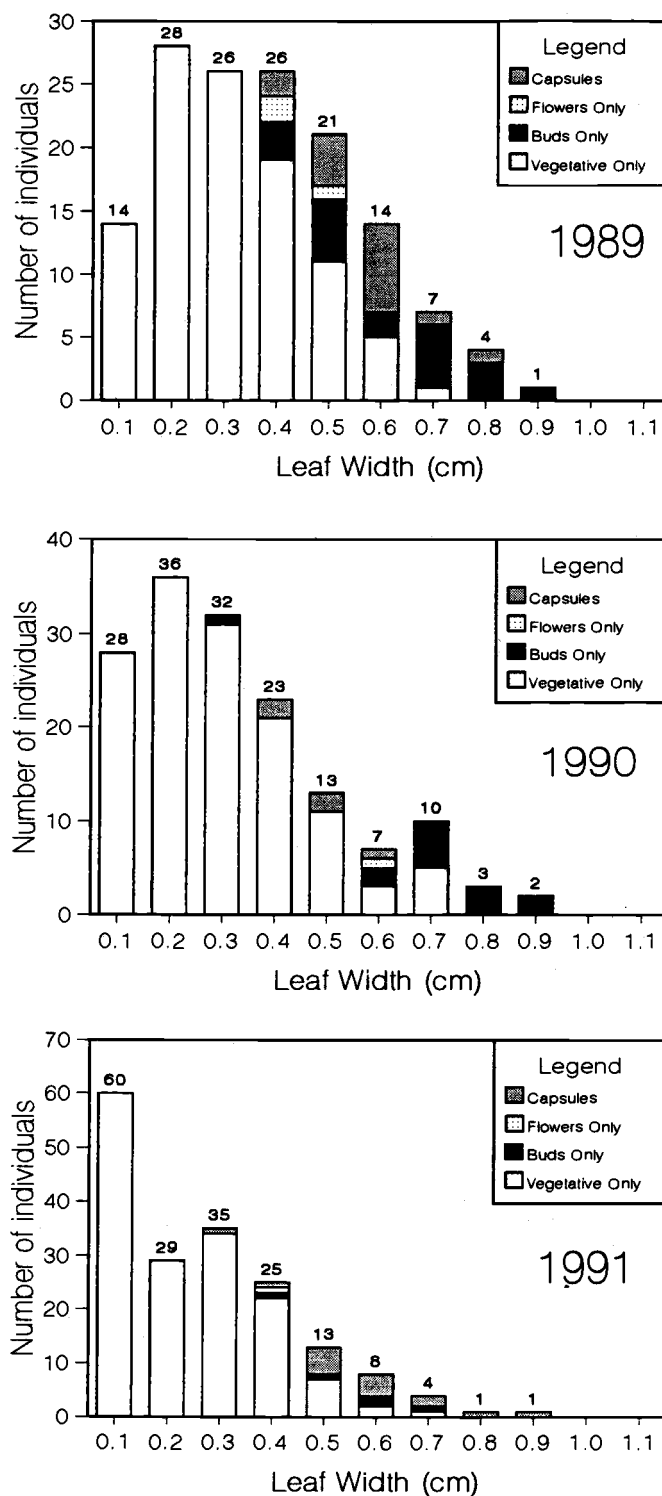
The fate of these smaller individuals (i.e. what proportion survive, decline, or grow) over a three year interval differs among habitats (Table IV.3). The majority of plants increased in size in the meadow and ecotone, but remained the same or decreased in the forest. The growth rate for small meadow- and ecotone-inhabiting individuals contrasts with *C. howellii* seedlings, which often remain the same size for many years. For example, 81.8% of the plants with leaves 1 mm wide in 1987 which were still alive in 1991, had not increased in size (Chapter 3).

While the leaf width frequency distributions are similar among habitats (Figure IV.7-9), subtle differences may be significant. The forest and meadow habitat distributions are skewed toward the smaller size classes, with the mean 1989 leaf widths 3.2 mm and 3.4 mm, respectively. In contrast, the mean leaf width for the ecotone in 1989 was 4.7 mm, with the distribution skewed towards the larger classes. A downward shift in the mode (4 mm) and mean (4.0 mm) widths may reflect reduced spring precipitation in 1991. As in 1988, the density in the ecotone habitat was highest, and differs notably from both the forest and meadow (Table III.2).

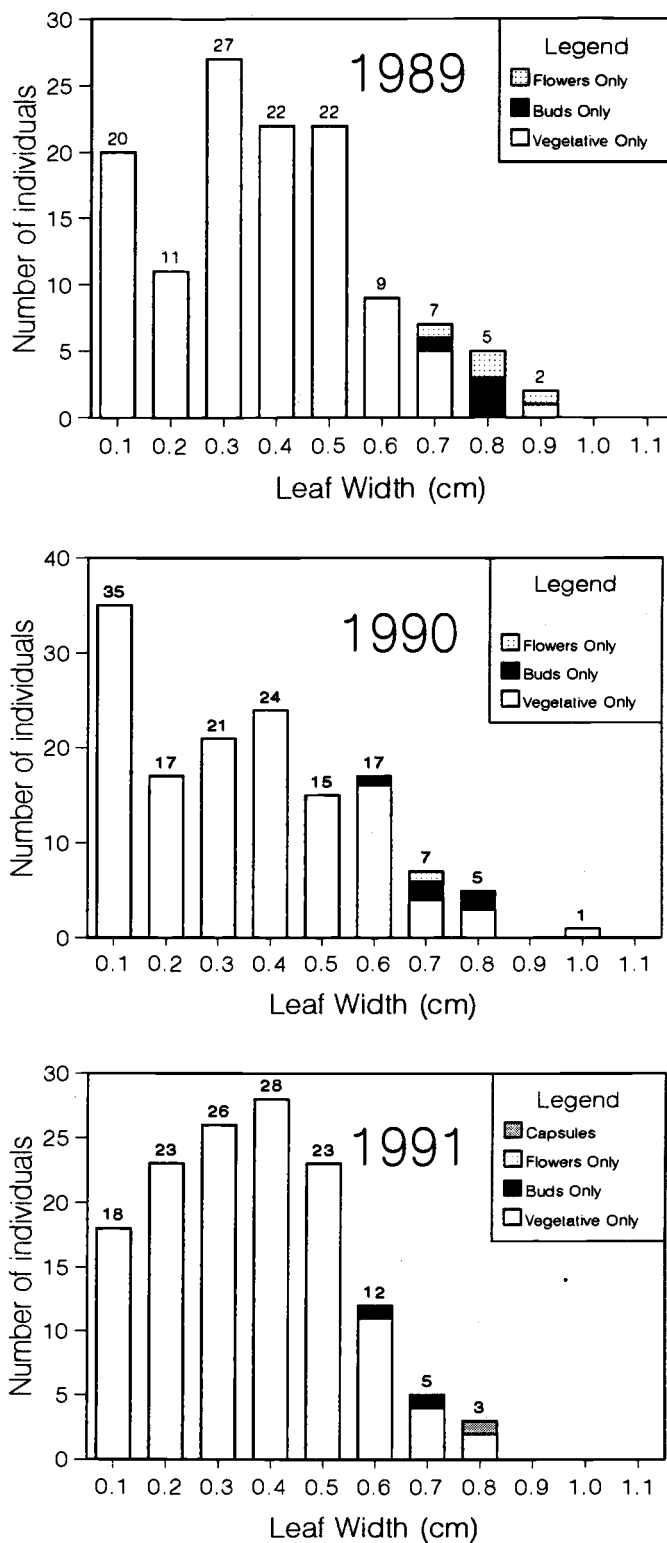
**Figure IV.7.** Reproductive stages attained by *Calochortus umpquaensis* in ecotone habitat for 1989 through 1991, by leaf width. Number of individuals are provided above each bar.



**Figure IV.8.** Reproductive stages attained by *Calochortus umpquaensis* in meadow habitat for 1989 through 1991, by leaf width. Number of individuals are provided above each bar.



**Figure IV.9.** Reproductive stages attained by *Calochortus umpquaensis* in forest habitat for 1989 through 1991, by leaf width. Number of individuals are provided above each bar.



**Table IV.3.** Change in leaf width after two years for small plants of *Calochortus umpquaensis* by habitat and *C. coxii*, in percent of total number of plants of that width. Calculations exclude plants which died between 1989 and 1991.

<i>Calochortus umpquaensis</i>						
Forest						
1991						
1	Leaf width	0.1 cm	0.2 cm	0.3 cm	0.4 cm	0.5 cm
9	0.1 cm	68.8	18.8	12.5	0.0	0.0
8	0.2 cm	11.1	66.7	22.2	0.0	0.0
9	0.3 cm	0.0	16.0	44.0	20.0	20.0

Meadow								
1991								
1	Leaf width	0.1 cm	0.2 cm	0.3 cm	0.4 cm	0.5 cm	0.6 cm	0.8 cm
9	0.1 cm	15.4	38.5	46.2	0.0	0.0	0.0	0.0
8	0.2 cm	6.7	40.0	26.7	20.0	6.7	0.0	0.0
9	0.3 cm	5.0	15.0	25.0	30.0	10.0	10.0	5.0

Ecotone							
1991							
1	Leaf width	0.1 cm	0.2 cm	0.3 cm	0.4 cm	0.5 cm	0.6 cm
9	0.1 cm	0.0	66.7	16.7	16.7	0.0	0.0
8	0.2 cm	8.3	25.0	50.0	16.7	0.0	0.0
9	0.3 cm	3.8	11.5	19.2	26.9	26.9	11.5

<i>Calochortus coxii</i>							
1991							
1	Leaf width	0.1 cm	0.2 cm	0.3 cm	0.4 cm	0.5 cm	0.6 cm
9	0.1 cm	0.0	0.0	0.0	0.0	0.0	0.0
8	0.2 cm	9.1	81.8	0.0	0.0	9.1	0.0
9	0.3 cm	0.0	17.1	37.1	37.1	5.7	2.9

Summary of changes in leaf width from 1989–1991 for plants 1–3 mm in 1989

Species	<i>C. umpquaensis</i>			<i>C. coxii</i>
Status in 1991	Forest	Meadow	Ecotone	
No change	56.0	27.1	19.6	47.8
Decreased	10.0	10.4	10.7	13.0
Increased	34.0	62.5	69.6	39.1

Microhabitats strongly influence seedling establishment. The average percent cover of litter, moss, soil, and vegetation within the plots were compared with the percent of seedlings and older plants established in those microsites (Table IV.4). In all habitats, plants rarely established in close proximity to other vegetation. In the forest habitat, distribution of plants corresponded closely to the availability of microsites (e.g. ca. 50% of seedlings occurred on litter, which comprised 47.8% of the ground cover). In the meadow, where desiccation may pose a greater threat to young seedlings, plants were more likely to occur on mossy microsites. Litter, on the other hand, was the most common substrate for plants established in the ecotone.

Mortality is highest in the meadow habitat both in 1990 and 1991, but recruitment is also higher there (Table IV.2a). Exposure to desiccation could also play a role in increased mortality, particularly in dry years. Mortality for plants recruited in 1989 was 18.0% (7/39) and 16.4% (11/67) in the ecotone and meadow habitats, while only 4.8% in the forest (1/21).

#### **Population and reproductive biology of *Calochortus coxii*.**

Bud production of *C. coxii* differed significantly between the two sites (Table IV.2b, Figure IV.10), with plants at the Bilger site producing only 48% and 63% as many buds as those at the Smith site in 1989 and 1990. However, bud production in 1991 was similar at both sites. Flower and capsule production was highly reduced at the Bilger site during all three years. Only four plants produced flowers in 1989 and 1991 and none flowered in 1990. Predation was primarily responsible for the low percentage of capsules produced at both sites; only 14.1% of plants which produced buds, or 6.1% ( $n = 12$ ) of the individuals tagged produced capsules at the Smith site in the best year, 1989. The high rate of predation at the Bilger site, resulting in the production of only one capsule within the plots over three years, has not resulted in significantly lower recruitment, and mortality did not differ between the two sites (Table IV.2b). Frequency distributions based on leaf widths (Figure IV.11), however reveal larger numbers of



**Table IV.4.** Microhabitat analysis for *Calochortus umpquaensis* by habitat and *C. coxii* based on data collected from permanent plots. Figures are percentages of total number of plants in each size-category that established in litter, moss, soil, and vegetation. Actual cover values for these categories are based on 1990 plot data.

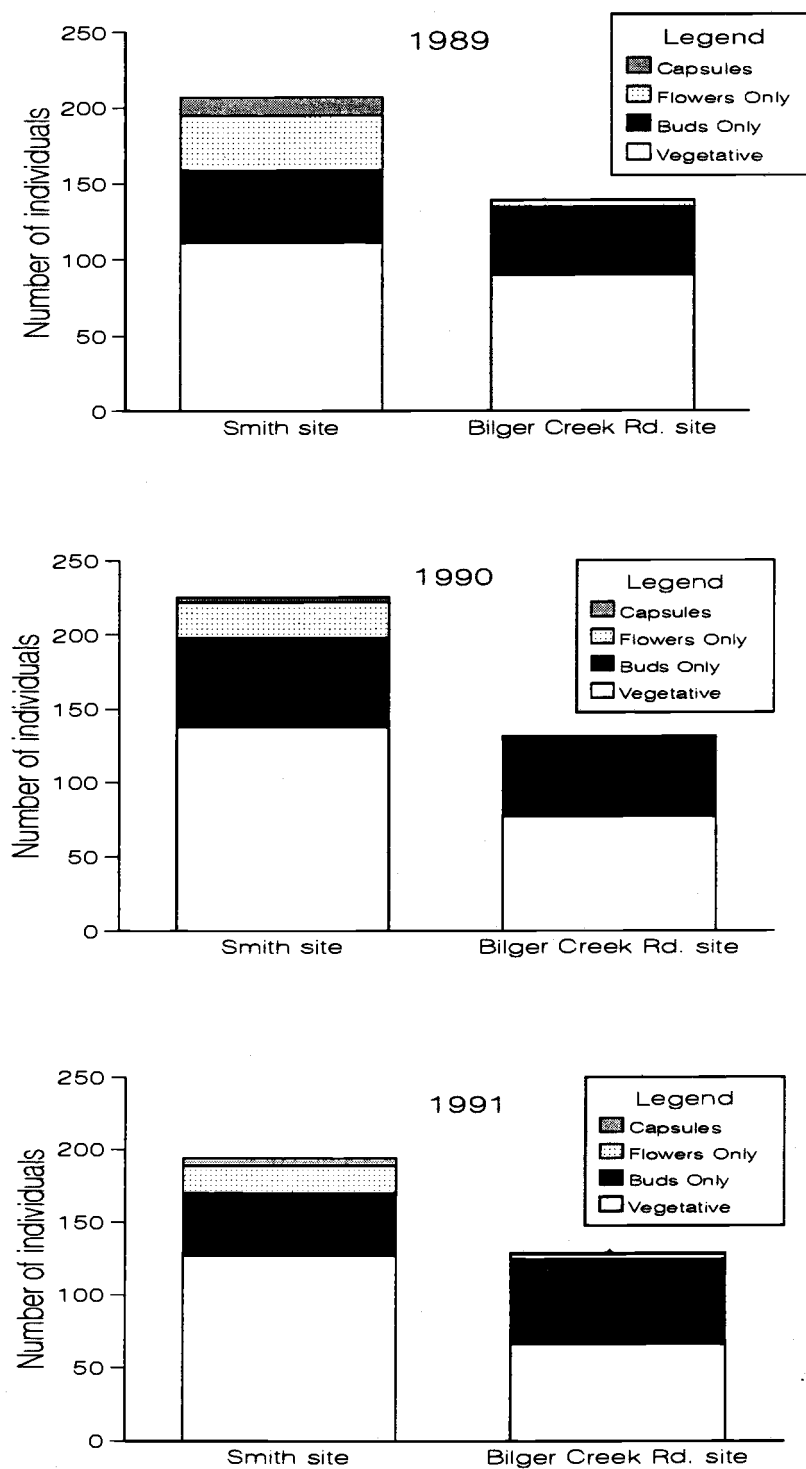
*Calochortus umpquaensis*

Microhabitat	Litter	Moss	Soil	Vegetation
<b>FOREST</b>				
Cover	47.8	39.4	1.0	12.8
Leaf widths $\leq 3$ mm	54.9	37.3	7.8	0.0
Leaf widths $> 3$ mm	70.4	28.1	1.6	0.0
<b>MEADOW</b>				
Cover	16.5	48.4	2.8	40.4
Leaf widths $\leq 3$ mm	11.0	85.7	0.0	3.3
Leaf widths $> 3$ mm	17.0	74.5	4.3	4.3
<b>ECOTONE</b>				
Cover	34.5	18.8	1.0	51.5
Leaf widths $\leq 3$ mm	77.0	9.2	0.0	13.8
Leaf widths $> 3$ mm	68.5	12.1	2.0	17.5

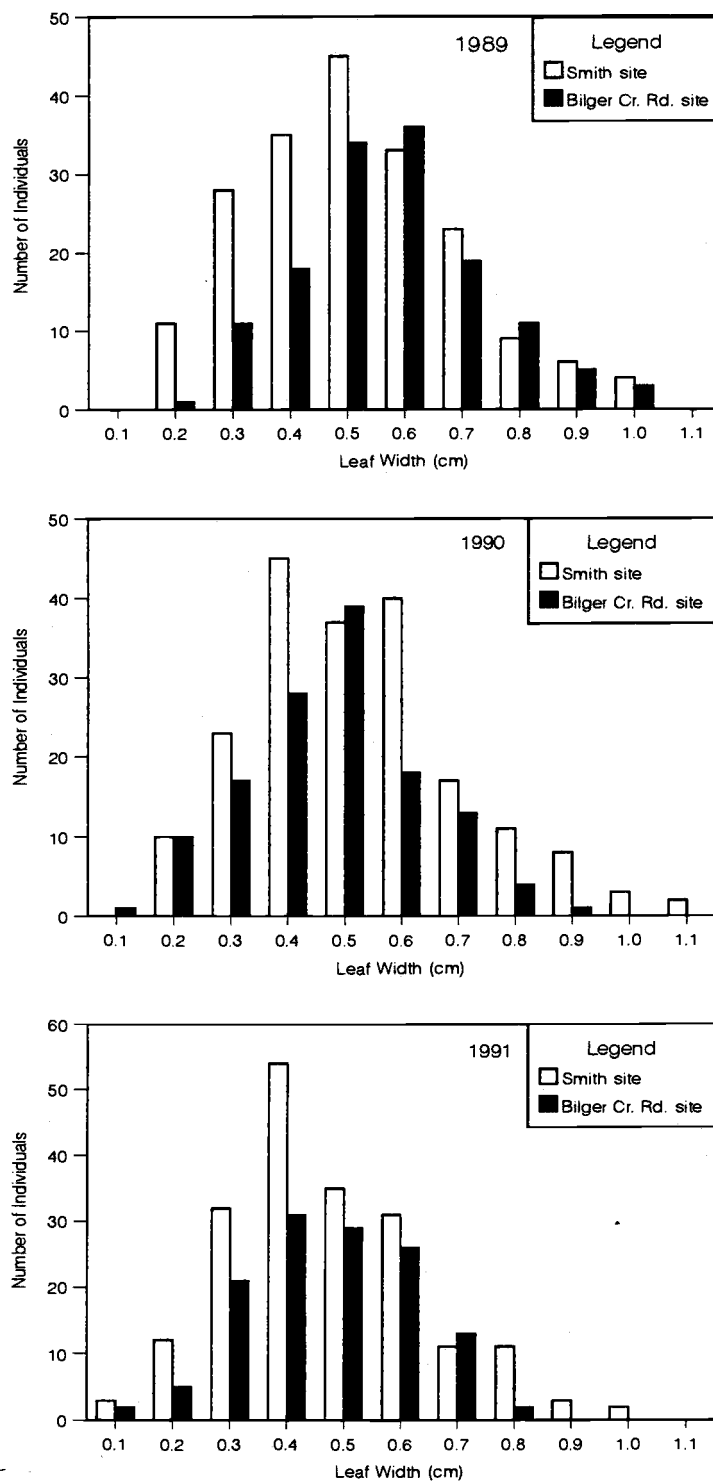
*Calochortus coxii*

Microhabitat	Litter	Moss	Soil	Vegetation
Cover	59.8	14.4	1.1	28.4
Leaf widths $\leq 3$ mm	67.2	27.9	0.0	4.9
Leaf widths $> 3$ mm	61.0	31.3	0.4	7.3

**Figure IV.10.** Reproductive stages attained by *Calochortus coxii* by site for 1989 through 1991.



**Figure IV.11.** Leaf width frequency distributions *Calochortus coxii* by site for 1989 through 1991. Note lower numbers of small plants at the Bilger Creek Road site.



smaller individuals at the Smith site. Individuals with leaf widths less than 4 mm are under-represented at the Bilger site, perhaps indicative of a longer term limitation of seedling recruitment.

As leaf widths increase, the proportion of plants producing buds increases (Figure IV.12). Plants with leaf widths as small as 3 mm occasionally produced buds.

The low production of capsules at the study sites made it difficult to collect them for seed-set analysis. Based on nine capsules collected, the mean seed set was 52.5% (S.D. = 31.4), with an average of 34.4 seeds produced per capsule. Capsule length, which averaged 2.6 cm, was correlated with seeds produced ( $r^2 = 0.73$ ).

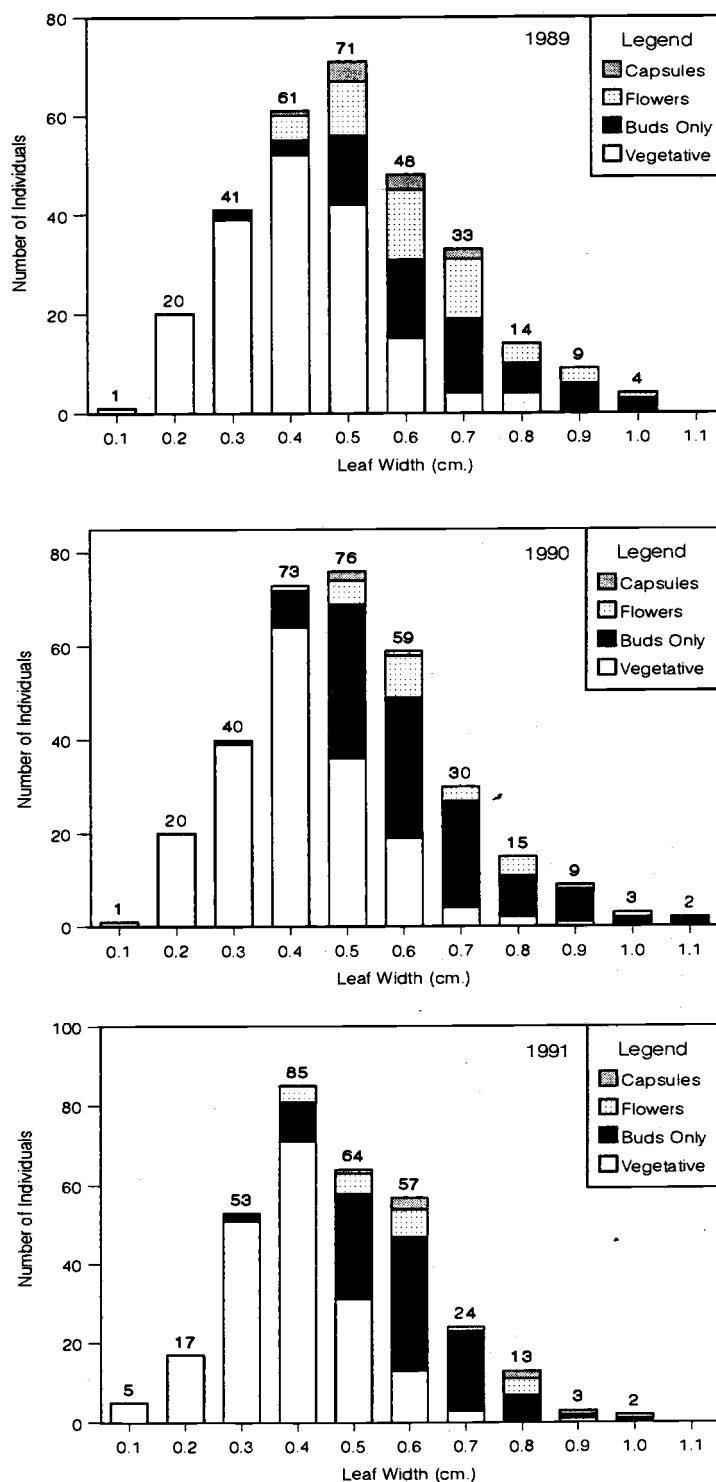
Growth rates of small plants of *C. coxii* appear slower than those of *C. umpquaensis*, especially when comparing across the same habitat, the ecotone (Table IV.3). Ninety-one percent of those plants with leaves 2 mm wide or less in 1989 had not grown by 1991. Because removal of photosynthetic surface area tends to result in reduced width in subsequent years (unpubl. data), it is not clear if the apparently slow growth rate of small plants is genetically or environmentally induced.

Microhabitats commonly occupied by *C. coxii* included both litter and moss (Table IV.4). Litter comprised the greatest cover within the plots, with a corresponding high occupation of both seedlings and larger plants within this microsite. While the transects were located in partially shaded habitats, approximately 30% of all plants established on the more desiccation-resistant moss layer, which comprised 14% of the ground cover.

### Transition matrix analysis for *C. umpquaensis* and *C. coxii*

In Chapter 3, several approaches to determining size categories for transition matrix analysis were evaluated. Categories for *C. howellii* were calculated using Moloney's algorithm (Moloney 1986) which minimizes the errors of estimation and errors of distribution resulting from inappropriate size classification. Because the

**Figure IV.12.** Reproductive stages attained by *Calochortus coxii* for 1989 through 1991, by leaf width. Data for the two sites are combined. Number of individuals are provided above each bar.



sample size was large, and thus the errors of distribution minimized, the unclassified data were also analyzed to compare the results of this extremely finely delineated classification. Finally, the data were classified using life history information, which resulted in three categories: seedlings, juveniles, and adults, based on leaf widths. The results using theoretically optimal categories were similar to those using categories based on life history information, so Moloney's algorithm was not applied here to determine the size categories for *C. umpquaensis* and *C. coxii*.

While vegetative reproduction occurs in many other members of the genus, it is rare in the three species studied here. In addition, vegetative dormancy (i.e. bulbs which fail to produce leaves every year) has not been confirmed. A small number of large new plants were noted in the plots in 1990 and 1991. These plants were not incorporated into the analysis. These individuals may actually represent plants that were grazed in previous years before the plots were visited.

Transition matrices were compiled and compared for the years 1989-1990 and 1990-1991 using three size categories based on leaf width: seedlings, small adults, and larger adults for *C. umpquaensis* (Table IV.5) and *C. coxii* (Table IV.6). Matrices were calculated by habitat for *C. umpquaensis* and by site for *C. coxii* (Table IV.7). Average lambda values were highest for the ecotone and lowest for the meadow for *C. umpquaensis* and were highest consistently across habitats for the 1989-1990 transition. The Bilger Creek Road site had the lowest lambda values for *C. coxii*. This species also exhibited lower growth rates during the 1990-1991 transition.

Indices of dissimilarity were lowest for *C. umpquaensis* in the forest habitat for both transition years (Table IV.8). The meadow habitat population structure differed most from stable, averaging 19.9. Differences were greatest during the first transition (1989-1990) for *C. umpquaensis*, but were markedly lowest for *C. coxii* during 1990 to 1991, when data from both sites were combined. The average index of dissimilarity for the Smith and Bilger Creek Road sites were 21.8 and 13.1, respectively.

**Table IV.5.** Size-classified transition matrix analysis by habitat for *Calochortus umpquaensis* for two transition years: 1989-1990 and 1990-1991. Category 1 = seedlings with leaves up to 3 mm wide, 2 = plants with leaf widths greater than 3 mm and no greater than 6 mm, 3 = plants with leaf widths greater than 6 mm. Each number in the matrix is the proportion of plants which transfer from the column category (year 1) to the row category (year 2). Reproduction is incorporated into first row, as the percent of seedlings produced per individual in each reproductive category. Mortality is the percent in plants in each category which failed to appear during the second year. Initial category distributions (%) are based on the numbers of plants in each category the first year (e.g. Init89); stable distributions (%) and lambda values were calculated using DEMOG. See text for further explanation.

## 1989-1990

Ecotone			
lambda = 1.053			
Category	1	2	3
1	0.444	0.036	0.052
2	0.444	0.643	0.133
3	0.000	0.286	0.842
Mortality	0.000	0.048	0.025
Init89	9	56	158
Stage Distribution (%)			
Initial	4.0	25.1	70.9
Stable	18.2	34.7	47.1

## 1990-1991

Ecotone			
lambda = 0.918			
Category	1	2	3
1	0.214	0.053	0.020
2	0.643	0.539	0.144
3	0.000	0.289	0.771
Mortality	0.143	0.118	0.085
Init90	14	76	153
Stage Distribution (%)			
Initial	5.8	31.3	63.0
Stable	4.2	32.2	63.6

Forest			
lambda = 0.998			
Category	1	2	3
1	0.611	0.161	0.062
2	0.222	0.613	0.062
3	0.000	0.226	0.923
Mortality	0.167	0.097	0.015
Init89	18	31	65
Stage Distribution (%)			
Initial	15.8	27.2	57.0
Stable	18.2	20.3	61.4

Forest			
lambda = 0.948			
Category	1	2	3
1	0.714	0.026	0.014
2	0.286	0.737	0.087
3	0.000	0.158	0.855
Mortality	0.000	0.079	0.058
Init90	21	38	69
Stage Distribution (%)			
Initial	16.4	29.7	53.9
Stable	7.5	34.2	58.3

Meadow			
lambda = 0.990			
Category	1	2	3
1	0.385	0.019	0.657
2	0.615	0.566	0.239
3	0.000	0.189	0.567
Mortality	0.000	0.189	0.194
Init89	13	53	67
Stage Distribution (%)			
Initial	9.8	39.8	50.4
Stable	26.3	51.0	22.8

Meadow			
lambda = 0.883			
Category	1	2	3
1	0.660	0.058	0.362
2	0.240	0.493	0.121
3	0.000	0.203	0.569
Mortality	0.100	0.246	0.310
Init90	50	69	58
Stage Distribution (%)			
Initial	28.2	39.0	32.8
Stable	44.2	33.9	21.9

**Table IV.6.** Size-classified transition matrix analysis by habitat for *Calochortus coxii* for two transition years: 1989-1990 and 1990-1991. Category 1 = seedlings with leaves up to 3 mm wide, 2 = plants with leaf widths greater than 3 mm and no greater than 6 mm, 3 = plants with leaf widths greater than 6 mm. Each number in the matrix is the proportion of plants which transfer from the column category (year 1) to the row category (year 2). Reproduction is incorporated into first row, as the percent of seedlings produced per individual in each reproductive category. Mortality is the percent in plants in each category which failed to appear during the second year. Initial category distributions (%) are based on the numbers of plants in each category the first year (e.g. Init89); stable distributions (%) and lambda values were calculated using DEMOG. See text for further explanation.

**1989-1990**

Smith site			
lambda = 0.971			
Category	1	2	3
1	0.364	0.048	0.060
2	0.636	0.710	0.121
3	0.000	0.194	0.802
Mortality	0.000	0.065	0.017
Init89	11	62	116
Stage Distribution (%)			
Initial	5.8	32.8	61.4
Stable	8.3	42.8	48.9

Bilger Creek Road site			
lambda = 0.917			
Category	1	2	3
1	0.500	0.000	0.038
2	0.400	0.703	0.019
3	0.000	0.270	0.846
Mortality	0.100	0.027	0.096
Init89	10	37	52
Stage Distribution (%)			
Initial	10.1	37.4	52.5
Stable	6.8	19.3	73.8

Both sites			
lambda = 0.955			
Category	1	2	3
1	0.429	0.020	0.052
2	0.524	0.707	0.087
3	0.000	0.222	0.820
Mortality	0.048	0.051	0.041
Init89	21	99	172
Stage Distribution (%)			
Initial	7.2	33.9	58.9
Stable	7.1	35.2	57.7

**1990-1991**

Smith site			
lambda = 0.925			
Category	1	2	3
1	0.455	0.090	0.017
2	0.273	0.746	0.248
3	0.091	0.104	0.675
Mortality	0.182	0.060	0.060
Init90	11	67	117
Stage Distribution (%)			
Initial	5.6	34.4	60.0
Stable	12.2	58.8	29.0

Bilger Creek Road site			
lambda = 0.871			
Category	1	2	3
1	0.273	0.023	0.041
2	0.455	0.500	0.219
3	0.182	0.295	0.644
Mortality	0.091	0.182	0.096
Init90	11	44	73
Stage Distribution (%)			
Initial	8.6	34.4	57.0
Stable	5.3	39.3	55.4

Both sites			
lambda = 0.904			
Category	1	2	3
1	0.364	0.063	0.026
2	0.364	0.649	0.241
3	0.136	0.180	0.660
Mortality	0.136	0.108	0.073
Init90	22	111	191
Stage Distribution (%)			
Initial	6.8	34.3	59.0
Stable	7.9	50.5	41.6



**Table IV.7.** Summary of lambda values from transition matrix analysis by habitat for *Calochortus umpquaensis* and by site for *C. coxii*.

<i>Calochortus umpquaensis</i>			
Habitat	Ecotone	Forest	Meadow
1989–1990	1.05	1.00	0.99
1990–1991	0.92	0.95	0.88
Mean	0.99	0.97	0.94
S.D.	0.10	0.04	0.08

<i>Calochortus coxii</i>			
Sitename	Smith	Bilger	Both sites
1989–1990	0.97	0.92	0.96
1990–1991	0.93	0.87	0.90
Mean	0.95	0.89	0.93
S.D.	0.03	0.03	0.04

**Table IV.8.** Differences between stable and initial stage distributions (indices of dissimilarity) for *Calochortus umpquaensis* and *C. coxii*. Only positive differences are summed.

<i>Calochortus umpquaensis</i>				
1989 – 1990				
Category	1	2	3	Sum
Ecotone habitat	-14.2	-9.6	23.8	23.8
Forest habitat	-2.4	6.9	-4.4	6.9
Meadow habitat	-16.5	-11.2	27.6	27.6

1990 – 1991				
Category	1	2	3	Sum
Ecotone habitat	1.6	-0.9	-0.6	1.6
Forest habitat	8.9	-4.5	-4.4	8.9
Meadow habitat	-16.0	5.1	10.9	16.0

<i>Calochortus coxii</i>				
1989 – 1990				
Category	1	2	3	Sum
Smith site	-2.5	-10.0	12.5	12.5
Bilger Cr. Rd. site	3.3	18.1	-21.3	21.3
Both sites	0.1	-1.3	1.2	1.3

1990 – 1991				
Category	1	2	3	Sum
Smith site	-6.6	-24.4	31.0	31.0
Bilger Cr. Rd. site	3.3	-4.9	1.6	4.9
Both sites	-1.1	-16.2	17.4	17.4

## DISCUSSION

### Habitat analysis for *Calochortus umpquaensis*

Both *C. umpquaensis* and *C. coxii* are restricted to serpentine-derived soils, but despite the limited occurrence of these soils in southwestern Oregon, a considerable amount of apparently suitable unoccupied habitat remains (Fredricks 1989b). While historical factors are important in explaining present distribution, the current investigation of microhabitats and demography has proven useful in explaining why these species are not more widespread.

For *C. umpquaensis*, differences in reproductive success, recruitment, and survival in forest, meadow, and ecotone habitats may result from limiting resources. By determining what resources are necessary for stable, reproducing populations, we can consider why apparently suitable habitat is unoccupied. Resource limitation may not be the primary cause of rarity in *C. umpquaensis*, but it may be responsible for the affinity of the species to the transition between forest and meadow. Light, moisture, pollen vectors, nutrients, and temperature are among the resources which may be limiting. These potentially limiting resources are considered here in the context of results from this study.

Individuals of *C. umpquaensis* are densest, produce more buds, and are on average larger in the ecotone habitat. The higher density did not seem to result from direct competition, since vegetation cover was highest in the ecotone. Although mossy sites were occupied in greater proportion to their availability in the meadow, the majority of plants had established on litter in the forest and ecotone. *Calochortus umpquaensis* may be most successful in ecotonal habitats because this area affords the combination of adequate moisture and safe sites necessary for seedling survival and light required for adult reproductive success.

Forest habitats produced the fewest buds, flowers, and capsules. The shaded forest habitat may limit floral initiation in this species. The high incidence of capsule abortion in the forest habitat suggests that pollinators may also be less

active in the cooler, shaded forest habitat.

The recruitment of *C. umpquaensis* within the forest is paradoxically high considering the low seed set in this habitat. The density of seedlings in the forest and their sporadic distribution suggests that if seeds are produced, the probability of landing within a safe site is high. In addition, mammalian and insect predation may be lower relative to the other habitats. Leaf width distribution in the forest is skewed toward smaller individuals. This could suggest that plants are on average younger in the forest. A more likely interpretation of the smaller leaf widths is that the forest populations are less robust, with smaller leaf widths for comparable ages. Higher growth rates in meadow and ecotone indicate that light may be limiting to growth, as well as reproduction, in the forest habitat.

While light may limit floral initiation in the forest, the cause of low bud production in the meadow habitat relative to the ecotone is not clear. Inadequate moisture could limit reproduction in this habitat, since it is exposed to greater desiccation than the forest or ecotone. The correlation between spring precipitation and bud production for *C. umpquaensis*, *C. coxii*, and *C. howellii* (Chapter 2) supports the premise that moisture may limit reproduction in these species.

The high mortality observed in the meadow in 1990 and 1991 is also unexplained. The tendency of *C. umpquaensis* to establish on mossy microsites suggests that the moisture-retaining ability of moss could aid recruitment of seedlings, particularly when spring precipitation is low. Actual microsite measurements of environmental parameters including soil temperature, moisture, and macronutrients are necessary to investigate further the consistently lower bud production and higher seedling mortality in the meadow habitat.

Capsule predation is the most important limiting factor in the ecotone habitat. The heavier predation within this habitat (especially evident in 1989 and 1991) may reflect ecotonal grazing preferences by deer. Deer populations in Douglas County are high (Beiderbeck 1993, pers. comm.), due in part to timber harvest, agricultural development, and long-standing declines in predator populations. Because the timber stand in the vicinity of the Ace Williams population provides thermal cover

that is highly limited in the vicinity, it may serve to concentrate deer populations, resulting in artificially high predation.

Soils analysis of 22 elements including the macronutrients calcium, iron, magnesium, phosphorus, and potassium showed little differences among habitats (Chapter 2). Phosphorus was higher in both surface and subsurface soil in the ecotone, than in the forest or meadow, but differences were not statistically significant. Further investigations of this element, as well as nitrogen could reveal habitat differences. While nitrogen generally tends to be low in serpentine soils, due to their low productivity (Brooks 1987), the ample litter and moss layer suggest that nitrogen may not be limiting at *C. umpquaensis* sites. In the meadow, where pH tends to be more alkaline, manganese may leach readily, resulting in deficiencies of this element.

**Limiting factors in *Calochortus coxii*.** While bud production is higher in this species than in the meadow or forest habitats of *C. umpquaensis*, capsule production and recruitment are significantly lower. Grazing and predation of capsules of *C. coxii* contribute to this low fecundity. The high variability (S.D. = 31.5) in seed set may indicate that pollination may also be limited; unlike other species of *Calochortus*, which are frequently visited by beetles and bees, insect visitors to *C. coxii* are rarely observed. The sparseness of flowering individuals may reduce pollination and subsequent seed set.

**Evaluation of population stability for *C. umpquaensis* and *C. coxii*.** Several methods were used to evaluate stability of selected populations of *C. umpquaensis* and *C. coxii*. Leaf-width frequency distributions were illustrated. Current population structure, mortality and recruitment were compared. Transition matrix models were applied to reveal equilibrium population growth rate, stable size distribution, and the degree of sensitivity of various categories to changes.

The bell-shaped size distributions of *C. umpquaensis* and *C. coxii* populations are similar to those observed in *C. howellii* and *C. longebarbatus* var. *peckii*

(unpubl. data). While the paucity of small individuals may at first appear alarming in rare species, slow, steady recruitment of smaller individuals into the population is sufficient to maintain its stability, if mortality does not exceed recruitment.

*Calochortus umpquaensis* has a greater ability to colonize than the other species studied. The recruitment rate of *C. umpquaensis* far exceeded *C. howellii*, particularly in the meadow. However, mortality in that habitat was also higher than for either *C. coxii* or *C. howellii*. The occurrence of this species in slightly disturbed areas and its ability to tolerate a wide range of habitats indicates that *C. umpquaensis* may be more resilient and adaptable than its close relatives with narrower habitat specificity.

Lambda values for *C. umpquaensis* were highest in the ecotone habitat. The minimal seed set occurring in the forest habitat did not appear to influence the equilibrium population growth rate or stable population structure. The average index of dissimilarity was in fact lowest for the forest, indicating that by this measure this habitat had the highest stability.

Lambda values were lowest in 1990 to 1991 for all three habitats of *C. umpquaensis* and both *C. coxii* sites. Late winter to spring precipitation was lowest during these years, which may have affected reproduction and mortality (Chapter 2). Mortality doubled in 1991 for both species (*C. umpquaensis*: 5.7% for 1990 and 12.5% for 1991; *C. coxii*: 3.8% for 1990 and 8.7% for 1991 for *C. coxii*, Table IV.2), which contributed to lower lambdas for the 1990-1991 transition.

The results of the transition matrix analysis indicate that the Ace Williams population of *C. umpquaensis* is stable, based on equilibrium population growth rate, but population structures. While the *C. coxii* population at the Smith site is also near stable ( $\lambda = 0.95$ ), the Bilger Creek Road population is clearly declining ( $\lambda = 0.89$ ).

The average lambda value for *C. howellii* over six transitions (Table III.8, based on empirically-derived size-categories) was 0.99. Average lambda values for two transitions (1982-1984) for three other rare *Calochortus* species were somewhat higher: *C. obispoensis* 1.02, *C. pulchellus* 1.10, and *C. tiburonensis* 1.16 (Fiedler

1987). A fourth common species, *C. albus* had an average value of 1.11. Indices of dissimilarity, which reflect stability of the population structure, were high for three of the four species Fiedler studied--indicating instability; only *C. tiburonensis* values were lower than those of *C. umpquaensis* or *C. coxii*.

Fiedler reported that mean number of seeds per capsule did not differ significantly among the species she studied; the range was from 35 to 40. Mean number of seeds per capsule for two species investigated here were similar: 38.6 for *C. umpquaensis* and 34.4 for *C. coxii*, but *C. howellii* averaged only 21.0 seeds per capsule (Table III.5a). The common species, *C. albus* had a much greater seed output--individuals had a greater probability of survival to reproductive size and produce more capsules per plant.

*Calochortus albus* has the life-history characteristics of a colonizer (Fiedler 1987). Based on observations and analyses, *C. umpquaensis* exhibits a similar capacity to colonize, yet unlike *C. albus*, remains highly localized. It exhibits higher recruitment, appears to persist in slightly disturbed habitats and shows less habitat specificity, and has higher growth rates than the other species studied here. On the other hand, *C. howellii* may be most comparable to *C. tiburonensis* and *C. obispoensis*, which share characteristics of low seedling establishment, low adult mortality, and slow growth. All inhabit serpentine grasslands with extremely limited ranges: *C. tiburonensis* is known only from Ring Mountain on the Tiburon Peninsula near San Francisco, while *C. obispoensis* occurs on at few isolated sites in the Santa Lucia Mountains of central coastal California (Fiedler 1987).

During this study, noteworthy range extensions for *C. umpquaensis* were discovered. This species is now known from widely scattered serpentine areas spanning 80 km (Figure II.1). Most populations are small, but one located on public land is extensive. This large population (Callahan Meadows) and the one at Ace Williams Mountain are particularly critical to the viability of the species, since smaller populations are more vulnerable to stochastic genetic change.

Morphological differences among the widely separated populations indicate that this species may be diverging genetically, lending additional significance to the

protection of these distinct races. Most newly discovered populations occupied ecotonal habitats, but heavily serpentinized, open sites were also located, strengthening the premise of lower habitat specificity for *C. umpquaensis*. While the range is larger than previously believed, the small area inhabited by this species and the documented threats from human activities support its continued status as endangered.

At Ace Williams Mountain, recruitment in *C. umpquaensis* was adequate, during the 1988 to 1990, to balance mortality. Low capsule and seed production do not result in population instability and may be typical for long-lived perennials. The greatest threat to this species is habitat alteration, particularly changes involving soil-moisture relations. By properly maintaining habitat for *C. umpquaensis*, avoiding direct disturbance (e.g. timber harvest, mining, bulb digging) and curtailing additional non-native grazing pressure within its extremely limited range, extinction probability for the species should be minimized.

Analyses indicate that *C. coxii* is at greater risk. Fewer populations are known and none are extensive. Demographic and reproductive data corroborate our prior concerns that the small populations are declining. The differences in leaf-width frequency distributions of *C. coxii* indicate that the heavy predation at the Bilger site may be reducing the recruitment of seedlings over time, skewing the distribution toward larger individuals. Analysis of the data using size-classified transition matrices indicates that the equilibrium population growth rate at the Bilger Creek Road site is perilously low, and the actual category distributions, especially in the 1990-1991 transition were far from stable. These results serve to demonstrate the vulnerability of *C. coxii*, particularly at the Bilger Creek Road site. Remedial measures, such as setting up exclosures or offering special controlled deer hunts to reduce grazing pressure, may be necessary if populations fail to stabilize, particularly if this species is listed as federally endangered.



### **Evaluation of methods and recommendations for continued study**

While use of the mapping table is awkward at times, this method was successful in minimizing impact to the sites and plants. Despite vandalism at one site, which resulted in the PVC pipe markers being removed, it was not difficult to relocate individuals except where densities were very high. In these cases, occasionally I had to compare similar sized individuals and match with previous years data, but it is unlikely that this affected overall results.

It is still uncertain whether the small number of adults appearing in the plots for the first time are actually plants which were previously missed, because they were grazed at ground level, or if a small number of plants may occasionally remain dormant, but the former explanation seems most plausible. Several unanswered questions, such as this, remain. When studying long-lived species in variable environments, long-term studies are essential. The results presented here are only introductory.

Because of the still uncertain future of *C. umpquaensis* and *C. coxii*, scientific data on trends of other populations of these species are still needed. The methods applied here for data collection may be considered too time consuming to apply to additional sites, but a streamlined modification of this approach is recommended in order to provide a more comprehensive monitoring program for these species. Because it is desirable to maximize number of sites and individuals sampled, it may be adequate to record size categories rather than exact leaf widths. This method would save time in the field, in data entry, and in analysis. While the information gained here on growth rates is useful, the comparison of size-classifications (Chapter 3) support this simpler, more efficient approach.

It is hoped that botanists connected with the B.L.M. will continue to collect data on these species, since three years are inadequate to draw strong conclusions or generalizations on population trends, particularly with the high degree of variability evident during the study. It is the responsibility of the land management agencies, including the B.L.M. and the Forest Service, to manage these populations to insure their continued viability.

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## **APPENDICES**

**Appendix II.1.** Associated species of *Calochortus umpquaensis* and *C. coxii* cited in text and figures, including codes and family names (● indicates species included in Tables II.3-6,8).

Species	Code	Family
● <i>Achillea millefolium</i> L.	ACHMIL	ASTERACEAE
<i>Agoseris grandiflora</i> (Nutt.) Greene	AGOGRA	ASTERACEAE
<i>Agrostis microphylla</i> Steud.	AGRMIC	POACEAE
● <i>Aira caryophyllea</i> L.	AIRCAR	POACEAE
<i>Allium amplexans</i> Torr.	ALLAMP	LILIACEAE
<i>Allium siskiyouense</i> Ownbey	ALLSIS	LILIACEAE
<i>Anthoxanthum aristatum</i> Boiss.	ANTARI	POACEAE
● <i>Arenaria cismontana</i> Meinke & Zika sp. nov.	ARECAL	CARYOPHYLLACEAE
● <i>Arenaria douglasii</i> T. & G.	AREDOU	CARYOPHYLLACEAE
● <i>Aspidotis densa</i> (Brackenr.) Lellinger	ASPDEN	POLYPODIACEAE
<i>Brodiaea congesta</i> Smith	BROCON	LILIACEAE
<i>Brodiaea elegans</i> Hoover	BROELE	LILIACEAE
<i>Bromus carinatus</i> Hook. & Arn.	BROCAR	POACEAE
<i>Bromus mollis</i> L.	BROMOL	POACEAE
<i>Bromus rigidus</i> Roth.	BRORIG	POACEAE
<i>Bromus tectorum</i> L.	BROTEC	POACEAE
<i>Calocedrus decurrens</i> Florin	CALDEC	PINACEAE
<i>Calochortus tolmiei</i> Hook. and Arn.	CALTOL	LILIACEAE
● <i>Camassia quamash</i> (Pursh) Greene	CAMQUA	LILIACEAE
● <i>Cardamine integrifolia</i> (Nutt.) Greene	CARINT	BRASSICACEAE
● <i>Centaureum umbellatum</i> Gilib.	CENUMB	GENTIANACEAE
● <i>Cerastium arvense</i> L.	CERARV	CARYOPHYLLACEAE
● <i>Cerastium viscosum</i> L.	CERVIS	CARYOPHYLLACEAE
● <i>Collinsia grandiflora</i> Lindl.	COLGRA	SCROPHULARIACEAE
● <i>Crepis</i> sp.	CRE	ASTERACEAE
● <i>Cryptantha intermedia</i> (Gray) Greene	CRYINT	BORAGINACEAE
● <i>Cynosurus echinatus</i> H. & A.	CYNECH	POACEAE
● <i>Cystopteris fragilis</i> (L.) Bernh.	CYSFRA	POLYPODIACEAE
● <i>Dactylis glomerata</i> L.	DACGLO	POACEAE
● <i>Danthonia californica</i> Boland.	DANCAL	POACEAE
● <i>Delphinium menziesii</i> DC.	DELMEN	RANUNCULACEAE
● <i>Dodecatheon hendersonii</i> Gray	DODHEN	PRIMULACEAE
<i>Elymus caput-medusae</i> L.	ELYCAP	POACEAE
● <i>Epilobium minutum</i> Lindl.	EPIMIN	ONAGRACEAE
● <i>Eriogonum nudum</i> Dougl.	ERINUD	POLYGONACEAE
● <i>Eriophyllum lanatum</i> (Pursh) Forbes	ERILAN	ASTERACEAE
● <i>Erythronium hendersonii</i> Wats.	ERYHEN	LILIACEAE
<i>Erysimum asperum</i> (Nutt.) DC.	ERYASP	BRASSICACEAE
<i>Eschscholtzia californica</i> Cham.	ESCCAL	PAPAVERACEAE
● <i>Festuca californica</i> Vas.	FESCAL	POACEAE
<i>Festuca idahoensis</i> Elmer	FESIDA	POACEAE
● <i>Festuca rubra</i> L.	FESRUB	POACEAE
<i>Galium ambiguum</i> Wight	GALAMB	RUBIACEAE
● <i>Galium aparine</i> L.	GALAPA	RUBIACEAE
● <i>Galium triflorum</i> Michx.	GALTRI	RUBIACEAE
● <i>Gilia capitata</i> Dougl.	GILCAP	POLEMONIACEAE

Species	Code	Family
• <i>Githopsis specularioides</i> Nutt.	GITSPE	CAMPANULACEAE
• <i>Goodyera oblongifolia</i> Raf.	GOOOBL	ORCHIDACEAE
• <i>Hieracium parryi</i> Zahn.	HIEPAR	ASTERACEAE
<i>Holcus lanatus</i> L.	HOLLAN	POACEAE
<i>Hordeum jubatum</i> L.	HORJUB	POACEAE
<i>Horkelia congesta</i> Hoover	HORCON	ROSACEAE
<i>Hypericum perforatum</i> L.	HYPPER	HYPERICACEAE
• <i>Iris chrysophylla</i> Howell	IRICHR	IRIDACEAE
• <i>Koeleria cristata</i> Pers.	KOECRI	POACEAE
• <i>Lathyrus polyphyllus</i> Nutt.	LATPOL	FABACEAE
<i>Linum angustifolium</i> Huds.	LINANG	LINACEAE
<i>Lithophragma parviflorum</i> (Hook.) Nutt.	LITPAR	SAXIFRAGACEAE
• <i>Lolium multiflorum</i> Lam.	LOLMUL	POACEAE
<i>Lomatium hallii</i> (Wats.) Coult. & Rose	LOMHAL	APIACEAE
• <i>Lomatium nudicaule</i> (Pursh) Coult. & Rose	LOMNUD	APIACEAE
<i>Lomatium utriculatum</i> (Nutt.) Coult. & Rose	LOMUTR	APIACEAE
• <i>Lotus micranthus</i> Benth.	LOTMIC	FABACEAE
• <i>Luzula campestris</i> (L.) DC.	LUZCAM	JUNCACEAE
• <i>Madia elegans</i> D. Don.	MADELE	ASTERACEAE
• <i>Madia madioides</i> (Nutt.) Greene	MADMAD	ASTERACEAE
• <i>Melica geyeri</i> Munro.	MELGEY	POACEAE
<i>Micropus californicus</i> Fisch. & Mey.	MICCAL	ASTERACEAE
• <i>Microsteris gracilis</i> (Hook.) Greene	MICGRA	POLEMONIACEAE
• <i>Mimulus guttatus</i> DC.	MIMGUT	SCROPHULARIACEAE
<i>Orthocarpus hispidus</i> Benth.	ORTHIS	SCROPHULARIACEAE
• <i>Panicum scribnerianum</i> Nash	PANSCR	POACEAE
• <i>Perideridia oregana</i> Nutt.	PERORE	APIACEAE
<i>Phacelia capitata</i> Kruckeb.	PHACAP	FABACEAE
• <i>Pinus jeffreyi</i> Grev. & Balf.	PINJEF	PINACEAE
• <i>Pityrogramma triangularis</i> (Kaulf.) Maxon	PITTRI	POLYPODIACEAE
• <i>Plectritis congesta</i> (Lindl.) DC.	PLECON	VALERIANACEAE
• <i>Poa pratensis</i> L.	POAPRA	POACEAE
• <i>Polystichum munitum</i> (Kaulf.) Presl	POLMUN	POLYPODIACEAE
• <i>Pseudotsuga menziesii</i> (Mirbel) Franco	PSEMEN	PINACEAE
• <i>Ranunculus occidentalis</i> Nutt.	RANOC	RANUNCULACEAE
• <i>Rhus diversiloba</i> T. & G.	RHUDIV	ANACARDIACEAE
<i>Saxifraga integrefolia</i> Hook.	SAXINT	SAXIFRAGACEAE
<i>Scutellaria angustifolia</i> Pursh	SCUANG	LAMIACEAE
<i>Sedum laxum</i> (Britt.) Berger	SEDLAX	CRASSULACEAE
• <i>Sedum stenopetalum</i> Pursh	SEDSTE	CRASSULACEAE
• <i>Sidalcea virgata</i> Howell	SIDVIR	MALVACEAE
• <i>Silene hookeri</i> Nutt.	SILHOO	CARYOPHYLLACEAE
• <i>Sisyrinchium bellum</i> Wats.	SISBEL	IRIDACEAE
<i>Sitanion jubatum</i> Smith	SITJUB	POACEAE
<i>Stellaria jamesiana</i> Torr.	STEJAM	CARYOPHYLLACEAE
<i>Stipa lemmonii</i> (Vasey) Scribn.	STILEM	POACEAE
• <i>Synthyris reniformis</i> (Dougl.) Benth.	SYNREN	SCROPHULARIACEAE
• <i>Thlaspi montanum</i> L.	THLMON	BRASSICACEAE
• <i>Thuja plicata</i> Donn.	THUPLI	CUPRESSACEAE
<i>Thysanocarpus curvipes</i> Hook.	THYCUR	BRASSICACEAE
• <i>Trifolium dubium</i> Sibth.	TRIDUB	FABACEAE

Species	Code	Family
<i>Trifolium eriocephalum</i> Nutt.	TRIERI	FABACEAE
<i>Trifolium howellii</i> Wats.	TRIHOW	FABACEAE
● <i>Trifolium macraei</i> H. & A.	TRIMAC	FABACEAE
<i>Trifolium microcephalum</i> Pursh	TRIMIC	FABACEAE
● <i>Trifolium tridentatum</i> Lindl.	TRITRI	FABACEAE
● <i>Trisetum canescens</i> Buckl.	TRICAN	POACEAE
● <i>Verbascum blattaria</i> L.	VERBLA	SCROPHULARIACEAE
● <i>Vicia americana</i> Muhl.	VICAME	FABACEAE
<i>Vicia sativa</i> L.	VICSAT	FABACEAE
● <i>Viola hallii</i> Gray	VIOHAL	VIOLACEAE
● <i>Viola douglasii</i> Steud.	VIODOU	VIOLACEAE
● <i>Vulpia microstachys</i> Nutt.	VULMIC	POACEAE
● <i>Zigadenus venenosus</i> Wats.	ZIGVEN	LILIACEAE

**Appendix II.2** Associated species data by plot for *Calochortus umpquaensis*, ecotone habitat for 1988. a = Thunder Mt. Road site, b = Little River Road site, c = Ace Williams Mt. site.

ACRONYM	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40			
ACH.MIL	2	1	1	5	6																					2																	
AIR.CAR						T	T	T	1	1	1				1												T	T		1													
ARE.CAL																																											
ARE.DOU																																											
ASP.DEN																																											
BRO.ELE																																											
BRO.HYA																																											
BRO.CAR															1														3	1	1												
CAL.DEC															6																			6					3				
CAM.LEI																																											
CAR.INT																																											
CEN.UMB																																											
CER.ARV																																											
CER.VIS				T	T	T																							T	T													
COL.GRA																																											
CRE																																											
CRY.INT				T																																							
CYN.ECH																																											
CYS.BUL																																											
DAC.GLO				2	2	1										T												T	T	T													1
DAN.CAL	50	15	7	15	10	2	6	5	8	4	4	4	5	8	6	5	5	14	4	4	8	25	15	15	5	5	30	5	15	25	1	5	5	8	6	4			6	2	1		
DEL.MEN																																											
DOD.HEN																																											
EPI.MIN	1																																										
ERI.NUD																																											
ERI.LAN	10	7	7	12	5	6	8	10	20	8	18				8	5	8				1		1	1	4	4	1	4	6	2	6	1				2	1	2					
ERY.ASP																																											
ERY.HEN																																											
FES.CAL																																											
FES.IDA																																											
GAL.APA																																											
GAL.TRI																																											
GIL.CAP																																											
GIT.SPE																																											
GOO.OBL																																											
HIE.PAR																																											
HYP.PER																																											
IRI.CHR																																											
KOE.CRI																																											
LAT.POL																																											
LOL.MUL																																											
LOM.HAL																																											
LOM.NUD																																											
LOT.DUB	1	1	1	1	1	1	1	1	1	1	1																																
LUZ.CAM																																											
MAD.EXI																																											

b.

ACRONYM	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
ACH.MIL		2	1	1						3	2	1					2	1	4	
AIR.CAR																				
ARE.CAL																				
ARE.DOU																				
ASP.DEN				T																
BRO.ELE																				
BRO.HYA																				
BRO.CAR																				
CAL.DEC																				
CAM.LEI																				
CAR.INT																				
CEN.UMB																				
CER.ARV																				
CER.VIS									1											
COL.GRA																				
CRE																				
CRY.INT																				
CYN.ECH																				
CYS.BUL																				
DAC.GLO	1	2	1	1	1	2	1	4	2	6	2	5	5	10	12	20		1	1	1
DAN.CAL				15		6				4		5	2	3	5	2	1		2	1
DEL.MEN																				
DOD.HEN																				
EPI.MIN																				
ERI.NUD																				
ERI.LAN																				
ERY.ASP																				
ERY.HEN																				
FES.CAL																				
FES.IDA																				
GAL.APA																				
GAL.TRI																				
GIL.CAP																				
GIT.SPE																				
GOO.OBL																				
HIE.PAR																				
HYP.PER																				
IRI.CHR				1																
KOE.CRI																				
LATPOL										1				2	2	1	1	1	1	2
LOL.MUL																				
LOM.HAL																				
LOM.NUD																				
LOT.DUB					T	T	1	1	1	1	1			1	T	1		T	T	T
LUZ.CAM																				
MAD.EXI																				
MAD.MAD	1																			
MIC.GRA																				
MIM.GUT																				
ORT.HIS																				
PAN.SCR	8	8	2																40	
PER.ORE																				
PIT.TRI																				
POL.MUN																				
PLE.CON																				
PSE.MEN																				
RAN.OCC	1	1	1	1		1			1	2	4	1	2	2	1	1		1	2	2
SED.STE																				
SID.VIR		1	1		6	8	6	20	14	8	20	1	8	8	10	6	1	1		
SIL.HOO																				
SIS.BEL	20	6	25	24	2	6	1	1	2	4	6	8	4	1	5	8	20	7	16	16
STE.JAM																				
SYN.REN																	2			
THA.MON																				
TRIDUB	1																2	1	10	
TRI.TRI		1	1	1		6		1	2											
TRI.MIC												2	16	10	8					
VER.BLA	2																			
VIC.SAT										1	2	3	2	3	2		1		T	
VIO.DOU																				
VUL.MIC																				
GRASS1																				
GRASS2																				
CAUM%	5	5	5	2	4	5	T			2	2	4	4	2	4	5	9	10	8	8
PLOT#	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
VEG	32	22	32	44	10	23	15	26	22	30	37	25	40	39	46	41	29	14	36	62
MOSS																				
ROCK																				
BARESOIL																				
LITTER	68	78	68	56	90	77	85	74	78	70	63	75	60	61	54	59	71	86	64	38
CAUM#	12	4	11	11	9	5	2			5	5	9	8	4	7	9	12	12	16	11



C.

ACRONYM	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
ACH.MIL								2	3		3	4	1	2	6			2		
AIR.CAR							1	T	2	3	2	T						1		T
ARE.CAL																				
ARE.DOU																				
ASP.DEN																				
BRO.ELE						1	1	T		T	T	1	T	1	1	1	1	2	2	1
BRO.HYA																				
BRO.CAR																				
CAL.DEC					1												T	T	T	1
CAM.LEI		1	1	4	3	1			1	1										
CAR.INT																				
CEN.UMB																				
CER.ARV																				
CER.VIS													8	3			1			
COL.GRA																	1	1		1
CRE		2	3								T									
CRY.INT											T									
CYN.ECH																				
CYS.BUL																				
DAC.GLO	T	2	2	1	1	1				1										
DAN.CAL	1	3	1	2	3	5	3	25	18	5	6	8	5	6	10	8	5	6	4	6
DEL.MEN																				
DOD.HEN																				
EPI.MIN									1											
ERI.NUD																				
ERI.LAN																				
ERY.ASP																				
ERY.HEN																				
FES.CAL	3	1	9	2			4	16	8	T	9									
FES.IDA													1	1		1				
GAL.APA																				
GAL.TRI																				
GIL.CAP																				
GIT.SPE												1								T
GOO.OBL																				
HIE.PAR																				
HYP.PER																				
IRI.CHR																				
KOE.CRI																				
LATPOL																				
LOL.MUL																				
LOM.HAL																				
LOM.NUD																				
LOT.DUB								T			T		1	T		T	T	T		
LUZ.CAM	1	1					2	2	2	2	2	T	1	1	2	1	2	4	2	3
MAD.EXI																				
MAD.MAD																				
MIC.GRA																				
MIM.GUT																				
ORT.HIS																				
PAN.SCR																				
PER.ORE		1	2																	
PIT.TRI																				
POL.MUN																				
PLE.CON								T												
PSE.MEN																				
RAN.OCC	3	2	2	4		4	4	3	3	5	4	10	7	4	4	5	6	7	6	6
SED.STE	T						3	T	T	1	1	2	1	4	1	T	2	2	1	T
SID.VIR																				
SIL.HOO	1		1		2	1	2				2	1	1	1	1	1		T	T	T
SIS.BEL																				
STE.JAM																				
SYN.REN																				
THA.MON										1	1	2	1	T		1	1	T	T	
TRI.DUB																				
TRI.TRI																				
TRI.MIC																				
VER.BLA																				
VIC.SAT																				
VIO.DOU	1		1	1	1			1	2		1		1	T	1	1	1	1	1	1
VUL.MIC		1																		
GRASS1		1	3	3											2				T	
GRASS2	5	5	9	2	3	1					7	18	5	7		8	5	5	6	9
CAUM%	10	5	5	5	8	5	5	5	8	7	1		2	5	5	4	1	3	3	2
PLOT#	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
VEG	10	13	25	20	15	23	28	45	34	29	26	23	30	24	22	22	23	22	17	19
MOSS											62	6	8	7	16	4	4		4	16
ROCK																				
BARESOIL											4	10	12			6			9	10
LITTER	90	87	75	80	85	77	72	55	66	71		61	50	69	62	74	67	78	70	55
CAUM#	34	16	10	8	24	7	11	12	22	17	4		5	10	10	8	3	7	7	6

**Appendix II.3.** Associated species data by plot for *Calochortus umpquaensis*, meadow habitat for 1988. a = Standley Road site, b = Ace Williams Mt. site.

a.

ACRONYM	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
ACH.MIL																				
AIR.CAR	1	1					T	T		1	T							T		
ARE.CAL	1	6	3	T			2	5	12	6	4	2							T	2
ARE.DOU												15	8	16	18	4				
ASP.DEN		8	3	4	3	10	1			2	12							5	3	2
BRO.ELE																				
BRO.HYA																				
BRO.CAR																				
CAL.DEC																				
CAM.LEI																				
CAR.INT																				
CEN.UMB			T	1	T	T			T	T	T						T			T
CER.ARV																				
CER.VIS										T		T				T	T			
COL.GRA						T			T		T									
CRE																				
CRY.INT	T				T		T	T			T						T		T	T
CYN.ECH																				
CYS.BUL																				
DAC.GLO																				
DAN.CAL	65	8	6	12	18	15	50	16	15	25	16	16	2	5	25	65	40	40	35	8
DEL.MEN																				
DOD.HEN				T																
EPI.MIN	T				T	T	T	T	T	T	T	T	1						T	T
ERI.NUD	T																			
ERI.LAN																				
ERY.ASP																				
ERY.HEN																				
FES.CAL																				
FES.IDA		1			T	T	T	2		T	T	1								
GAL.APA														1						
GAL.TRI																				
GIL.CAP									1	T	1									
GIT.SPE		T		T			T	T	T	T	T	T					T			T
GOO.OBL																				
HIE.PAR																				
HYP.PER																				
IRI.CHR																				
KOE.CRI																				
LAT.POL																				
LOL.MUL															1					
LOM.HAL																				
LOM.NUD																				
LOT.DUB																				
LUZ.CAM													T	T				T		T
MAD.EXI																				
MAD.MAD			T	T						T				T					T	
MIC.GRA																				
MIM.GUT	3	7	3	8	5	2					1	7	1				T		T	1
ORT.HIS																				
PAN.SCR																				
PER.ORE				T	T														T	T
PIT.TRI																				
POL.MUN																				
PLE.CON			T	1						T	1							T		T
PSE.MEN																				
RAN.OCC	6	2	2	1	4	6	4	10	12	7	2	8	8	1	4	6	4	3	4	5
SED.STE																				
SID.VIR												4								
SIL.HOO																		1	1	
SIS.BEL	1						1										4	4	2	5
STE.JAM																				
SYN.REN																				
THA.MON																				
TRI.DUB																				
TRI.TRI																			T	
TRI.MIC																				
VER.BLA																				
VIC.SAT																				
VIO.DOU																				
VUL.MIC																				T
ZIG.VEN																				
Unknown1												2	3	16						
Unknown2																				4
CAUM%		1	4	2		1	1	T	T	1	1	2		1				1	1	T
PLOT#	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
VEG	77	34	23	27	30	37	64	38	38	54	46	38	44	26	33	75	48	52	46	27
MOSS				75	63										6					
ROCK				2	10	8	6			3	2			45	61		7		4	
SOIL	23	66				62	57	36	62	59	46	48	62	29		21	45	48	50	73
LITTER												4		56			4			
CAUM#		3	13	8		1	3	1	1	2	6	7		3	1	2	3	3	4	3



**Appendix II.4.** Associated species data by plot for *Calochortus umpquaensis*, forest habitat for 1988. a = Ace Williams Mt. site, b = Watson Mt. site.

[illegible]



**Appendix II.5.** Probability values for differences in elemental concentrations with depth for *Calochortus coxii* (CACO), *C. howellii* (CAHO), and *C. umpquaensis* (CAUM), and all species combined, based on t-test procedure.

Element	CACO	CAHO	CAUM	ALL
pH	0.13	0.47	0.28	0.44
Al	0.38	0.43	0.70	0.37
Ba	0.00	0.55	0.02	0.00
Ca	0.82	0.20	0.14	0.07
Cd	1.00	0.20	0.61	0.96
Co	0.38	0.50	0.19	0.37
Cr	0.05	0.41	0.23	0.75
Cu	0.02	0.30	0.30	0.30
Fe	0.49	0.42	0.89	0.46
K	0.01	0.10	0.00	0.01
Mg	0.64	0.95	0.69	0.75
Mn	0.32	0.74	0.02	0.13
Mo	1.00	0.76	0.10	0.51
Na	0.49	0.97	0.30	0.26
Ni	1.00	0.23	0.62	0.72
P	0.21	0.24	0.01	0.09
Pb	0.05	0.37	0.00	0.01
Si	0.69	0.42	0.02	0.52
Sr	0.10	0.70	0.99	0.37
V	0.70	0.53	0.44	0.81
Zn	0.42	0.10	0.27	0.24
Ca:Mg	0.96	0.32	0.97	0.85



**Appendix II.6.** Elemental soil ANOVA and Tukey-Kramer separation of means test for soils inhabited by three rare *Calochortus* species. Commas separate species for which means were significantly different. H = *C. howellii*, U = *C. umpquaensis*, C = *C. coxii*.

Sorted by Element			Sorted by p-value		
Element	p	Tukey	Element	p	Tukey
pH	0.0001	H,UC	pH	0.0001	H,UC
Al	0.2665	HUC	Ni	0.0001	H,U,C
Ba	0.5871	HUC	Cd	0.0001	U,CH
Ca	0.1432	HUC	Mn	0.0001	U,CH
Cd	0.0001	U,CH	K	0.0001	U,CH
Co	0.0002	H,UC	Mo	0.0001	H,UC
Cr	0.6974	HUC	Sr	0.0001	H,UC
Cu	0.0010	HC,U	Mg	0.0001	H,UC
Fe	0.4843	HUC	V	0.0001	H,UC
K	0.0001	U,CH	P	0.0001	H,UC
Mg	0.0001	H,UC	Co	0.0002	H,UC
Mn	0.0001	U,CH	Cu	0.0010	HC,U
Mo	0.0001	H,UC	Ca:Mg	0.0020	H,UC
Na	0.0049	UC,CH	Pb	0.0025	H,UC
Ni	0.0001	H,U,C	Na	0.0049	UC,CH
P	0.0001	H,UC	Si	0.0326	HUC
Pb	0.0025	H,UC	Ca	0.1432	HUC
Si	0.0326	HUC	Zn	0.2082	HUC
Sr	0.0001	H,UC	Al	0.2665	HUC
V	0.0001	H,UC	Fe	0.4843	HUC
Zn	0.2082	HUC	Ba	0.5871	HUC
Ca:Mg	0.0020	H,UC	Cr	0.6974	HUC

**Appendix II.7. Monthly precipitation at Cave Junction weather station.**

YEAR	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1963	12.57	16.10	18.31	22.73	12.55	1.12	0.08	0.00	0.43	9.83	34.01	10.46	138.20
1964	37.82	2.03	12.04	1.45	2.16	1.52	0.43	0.15	0.05	2.62	31.47	76.61	168.35
1965	0.00	4.01	1.83	17.32	0.53	1.65	0.05	4.44	0.00	4.80	23.83	33.30	91.77
1966	41.45	7.14	26.67	6.58	0.05	0.41	0.66	0.38	3.61	2.39	32.79	28.65	150.77
1967	39.32	5.38	19.79	11.20	3.02	1.24	0.00	0.00	1.32	13.13	9.37	17.78	121.56
1968	36.14	18.01	14.91	1.32	5.26	0.13	0.05	9.37	1.78	8.86	24.43	40.67	160.93
1969	40.31	14.60	2.97	4.93	0.00	1.37	0.25	0.00	3.12	13.36	5.92	38.74	125.58
1970	63.02	7.19	6.86	5.51	2.59	0.20	0.00	0.00	0.00	10.03	46.08	36.04	177.52
1971	36.04	8.56	29.24	15.32	2.24	3.33	0.00	0.94	6.96	2.92	29.08	21.26	155.88
1972	26.44	25.12	20.52	11.66	0.00	2.11	0.00	1.35	0.00	0.00	0.00	36.14	123.34
1973	30.91	12.67	14.68	0.69	1.37	0.58	0.00	0.08	7.67	12.32	76.53	44.22	201.73
1974	43.41	29.08	35.89	10.64	2.24	0.08	0.66	0.00	0.00	3.86	10.31	23.80	159.97
1975	19.61	42.27	41.25	9.75	3.45	0.18	0.43	0.89	0.71	21.36	18.92	17.09	175.92
1976	13.69	22.56	12.57	3.45	1.47	0.69	1.80	6.91	1.47	2.41	4.75	2.95	74.73
1977	7.19	15.29	12.07	1.70	6.50	0.13	0.64	1.47	16.43	7.14	34.85	49.07	152.48
1978	32.82	32.21	11.63	15.72	5.38	0.46	0.53	4.22	14.66	0.00	7.44	5.26	130.33
1979	16.05	36.30	4.98	9.73	13.13	0.79	1.17	1.85	1.50	26.67	27.23	32.94	172.34
1980	30.56	21.74	18.64	12.85	3.10	2.06	0.00	0.00	0.03	7.42	19.48	32.64	148.51
1981	13.03	13.77	13.56	5.18	2.11	1.88	0.38	0.00	4.98	21.49	46.36	68.61	191.34
1982	25.20	27.74	26.92	33.27	0.00	4.90	0.00	0.69	1.85	21.84	25.43	47.12	214.96
1983	35.38	53.85	49.07	9.35	5.11	1.07	3.56	8.20	1.45	5.05	46.81	43.03	261.92
1984	4.39	28.47	23.19	12.78	5.99	3.56	0.00	0.23	0.36	15.24	66.32	7.65	168.17
1985	1.35	15.65	17.86	2.29	2.16	4.01	0.43	0.00	5.00	9.02	15.32	14.20	87.27
1986	33.91	57.33	21.87	3.63	9.86	0.23	0.18	0.00	16.03	9.37	11.23	14.71	178.33
1987	33.32	20.14	24.71	1.63	2.57	0.05	1.80	0.00	0.00	0.18	10.67	42.77	137.85
1988	32.64	0.33	4.27	9.42	6.27	5.97	0.00	0.00	0.33	0.46	52.58	16.94	129.21
1989	11.48	10.44	34.39	10.11	5.99	0.97	0.15	0.13	2.90	16.64	8.18	4.72	106.10
1990	30.40	16.41	7.77	2.74	23.24	1.57	1.14	4.83	0.23	7.32	7.57	4.85	108.08
1991	12.22	11.43	30.73	10.24	4.50	1.60	1.93	0.71	0.00	4.60	13.28	12.09	103.33
Mean	26.23	19.86	19.28	9.08	4.58	1.51	0.56	1.62	3.20	8.98	25.53	28.42	148.84
Minimum	0.00	0.33	1.83	0.69	0.00	0.05	0.00	0.00	0.00	0.00	0.00	2.95	74.73
Maximum	63.02	57.33	49.07	33.27	23.24	5.97	3.56	9.37	16.43	26.67	76.53	76.61	261.92

**Appendix II.8.** Monthly precipitation at Little River weather station.

YEAR	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1964	37.24	7.57	20.80	7.21	5.21	7.95	0.97	1.52	1.60	3.07	24.69	56.16	173.99
1965	29.74	9.30	2.72	9.78	5.44	2.03	0.23	4.11	0.10	7.11	15.54	20.68	106.78
1966	25.96	9.53	14.78	3.00	1.42	2.54	4.29	0.76	4.75	10.64	30.73	0.00	108.41
1967	22.45	9.98	14.07	11.20	6.63	1.04	0.00	0.00	5.31	12.62	6.07	14.71	104.09
1968	12.90	12.50	8.99	4.98	7.47	1.14	0.79	11.33	5.23	13.79	30.28	0.00	109.40
1969	25.93	9.58	12.70	0.00	0.00	8.74	0.00	0.00	3.53	14.20	6.65	0.00	81.33
1970	0.00	4.67	0.00	13.94	7.34	4.83	0.00	0.00	0.00	12.62	27.51	15.11	86.03
1971	29.77	19.28	20.40	13.18	7.82	0.00	0.00	1.63	9.47	9.42	29.08	30.76	170.82
1972	30.20	16.89	25.93	13.84	6.02	4.09	0.00	1.96	4.29	7.04	11.73	0.00	122.00
1973	14.00	3.02	16.05	10.77	3.45	2.79	0.08	1.22	8.20	10.97	53.16	21.77	145.49
1974	26.04	19.71	25.20	11.71	5.54	3.02	0.58	0.23	0.08	5.89	17.30	32.33	147.62
1975	23.22	15.49	19.20	12.75	6.38	2.01	1.63	5.03	1.09	18.29	19.58	27.97	152.63
1976	20.50	13.46	14.81	11.43	3.38	1.85	3.23	12.40	2.34	4.29	3.40	3.51	94.59
1977	4.67	6.86	18.64	6.45	16.71	0.51	0.00	5.38	10.97	7.92	28.85	24.33	131.32
1978	12.90	13.61	6.02	11.40	9.55	4.98	2.34	6.10	10.80	1.19	12.27	19.30	110.46
1979	13.89	26.72	12.62	18.67	7.39	4.29	1.24	4.85	2.08	15.72	15.11	14.10	136.70
1980	16.76	9.93	15.24	10.06	7.75	5.82	0.61	0.10	2.69	6.38	18.67	21.82	115.82
1981	4.95	9.68	9.42	8.79	11.13	6.48	1.27	0.00	6.88	11.43	17.45	45.36	132.84
1982	24.10	13.26	12.60	11.02	0.97	5.49	2.18	1.22	10.06	17.15	13.26	22.89	134.19
1983	11.76	24.36	21.21	12.07	7.87	5.08	7.80	4.52	0.91	3.89	28.30	32.16	159.92
1984	11.30	23.98	20.60	16.13	9.35	8.94	0.61	0.81	2.21	19.58	36.68	19.30	169.49
1985	2.46	13.00	14.99	8.10	4.72	7.85	1.68	1.55	5.79	15.67	18.59	6.60	101.02
1986	15.75	29.21	14.15	9.32	9.27	2.34	2.08	0.00	16.23	6.68	28.02	5.64	138.68
1987	17.88	12.80	10.74	5.08	0.00	1.07	10.44	0.10	0.10	0.00	14.96	22.20	95.38
1988	17.91	5.44	13.00	13.33	12.90	8.69	0.00	0.00	5.26	0.00	42.16	14.38	133.07
1989	22.91	7.09	25.86	10.44	7.72	1.85	0.84	8.23	2.62	7.54	10.13	5.94	111.18
1990	23.19	15.95	10.67	11.40	8.94	5.23	1.60	4.22	1.68	14.55	24.00	13.06	134.49
1991	8.05	10.67	19.00	15.70	3.48	2.87	1.35	0.00	0.00	12.17	24.94	13.74	111.96
Mean	18.09	13.34	15.02	10.42	6.57	4.05	1.64	2.76	4.44	9.64	21.76	17.99	125.70
Minimum	0.00	3.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.40	0.00	81.33
Maximum	37.24	29.21	25.93	18.67	16.71	8.94	10.44	12.40	16.23	19.58	53.16	56.16	173.99

## Appendix II.9. Monthly precipitation at Riddle weather station.

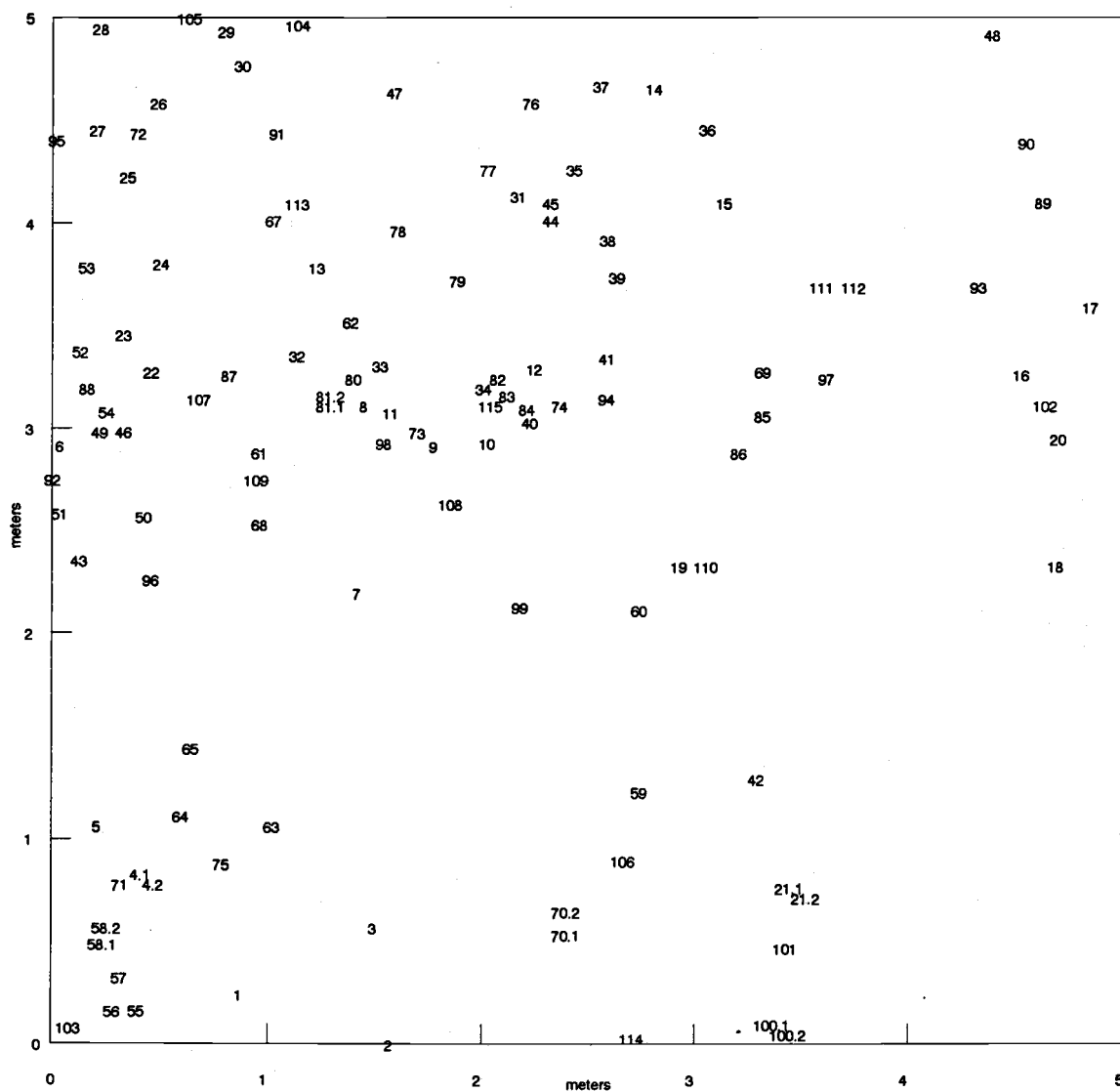
YEAR	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1900	9.96	3.99	3.30	3.66	6.73	5.33	0.00	0.00	2.29	10.57	3.71	15.24	64.77
1901	18.19	9.45	7.19	6.91	2.11	2.16	0.00	3.28	5.74	5.33	9.96	8.59	78.89
1902	3.71	22.35	9.35	9.07	5.26	0.51	1.40	0.00	0.64	0.99	20.88	18.85	92.99
1914	29.92	3.99	4.32	4.24	2.95	2.16	0.03	0.00	5.94	8.00	7.77	4.11	73.43
1915	8.41	11.30	3.23	3.48	6.27	0.74	2.16	0.00	0.51	1.52	15.88	13.89	67.39
1916	18.19	9.22	12.42	5.66	4.88	1.98	4.57	0.43	0.38	0.15	10.80	8.97	77.65
1917	4.50	12.80	6.93	4.93	5.59	0.61	0.00	0.00	1.04	0.13	17.63	6.38	60.53
1918	9.27	12.85	5.66	2.79	1.78	0.18	1.83	3.61	1.75	3.56	9.37	5.79	58.45
1919	22.68	15.95	10.11	7.26	2.06	0.89	0.00	0.10	6.50	5.08	9.19	13.94	93.78
1920	1.22	3.33	5.82	4.37	0.43	2.49	1.65	0.38	7.59	10.72	15.16	16.64	69.80
1921	12.29	9.75	3.86	5.23	3.68	1.60	0.00	0.10	0.94	5.74	16.08	4.62	63.91
1922	10.19	11.53	11.63	4.57	2.06	3.73	0.00	2.24	1.42	7.01	5.44	16.18	76.00
1923	15.29	3.23	3.02	3.89	4.27	2.46	0.94	0.41	2.59	8.69	3.94	9.40	58.12
1924	1.91	6.83	5.00	1.45	0.30	1.30	0.00	1.12	2.08	21.46	17.96	12.50	71.91
1925	13.74	18.36	2.31	10.06	7.72	1.93	0.00	1.07	2.82	0.33	9.68	8.38	76.40
1926	8.10	17.63	0.15	2.92	3.23	0.00	0.00	3.00	1.27	10.08	23.22	11.94	81.53
1927	13.74	21.77	6.10	4.50	3.61	2.41	0.00	0.05	6.02	3.86	12.85	8.61	83.52
1928	7.59	4.37	16.28	8.64	0.28	0.99	0.00	0.00	2.21	3.86	9.19	11.91	65.30
1929	9.75	4.17	5.59	7.26	1.04	6.99	0.10	0.00	0.00	4.22	1.09	29.69	69.90
1930	8.69	10.24	2.79	6.86	5.26	1.80	0.00	0.00	3.99	1.73	9.40	7.67	58.42
1931	12.85	6.17	8.33	5.87	0.25	8.28	0.00	0.00	1.27	8.15	11.91	17.98	81.08
1932	10.26	3.40	11.28	7.75	7.39	2.49	0.13	0.00	0.00	2.77	12.75	14.22	72.44
1933	15.95	4.37	5.99	2.24	5.84	1.17	0.00	0.08	1.27	3.33	2.74	16.23	59.21
1934	10.59	3.89	5.03	4.62	2.57	3.91	0.51	0.10	1.50	10.57	17.30	14.61	75.18
1935	9.83	7.70	8.64	9.70	0.89	0.48	0.00	1.24	0.28	9.12	4.85	9.75	62.48
1936	24.03	10.64	4.32	4.60	5.72	3.56	0.00	0.00	0.00	0.00	0.00	0.00	52.86
1937	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.46	1.91	4.62	17.65	16.36	41.00
1938	10.26	20.24	18.64	4.32	1.04	0.00	0.38	0.00	7.26	3.76	14.53	7.16	87.60
1939	8.46	10.72	8.18	0.74	5.26	2.62	0.89	1.52	1.24	5.99	0.84	22.81	69.27
1940	7.49	24.99	10.59	3.28	3.35	1.45	0.66	0.00	8.20	8.23	10.29	21.21	99.75
1941	8.33	7.87	1.85	6.43	5.54	6.73	0.18	1.37	3.28	4.19	13.18	25.04	84.00
1942	12.60	0.00	3.43	4.57	0.00	1.83	0.00	0.00	2.59	3.89	25.02	23.60	77.52
1943	19.48	4.70	8.18	5.21	3.76	4.42	0.20	1.37	0.99	11.94	8.15	4.67	73.08
1944	5.97	6.30	6.93	0.00	0.00	0.00	0.00	0.00	0.00	3.68	9.27	4.57	36.73
1945	7.52	14.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.47	20.32	17.55	64.19
1946	13.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.55	8.15	15.62	5.21	44.22
1947	5.97	5.69	8.08	3.12	3.56	7.04	6.15	0.99	0.36	15.93	9.53	8.74	75.13
1948	15.60	13.61	8.66	6.68	4.80	4.62	0.30	0.94	2.54	2.92	12.07	19.41	92.15
1949	4.06	13.18	5.61	2.08	3.94	0.15	0.00	0.00	2.29	7.24	5.46	9.70	53.72
1950	25.65	7.72	10.29	1.68	1.37	7.85	0.00	0.18	1.30	29.59	13.03	11.43	110.08
1951	19.84	9.04	7.54	2.08	2.03	0.00	0.00	0.23	1.57	11.51	13.64	21.46	88.95
1952	12.65	6.63	7.62	2.03	1.57	7.04	0.03	0.00	1.93	1.07	2.67	22.02	65.25
1953	19.41	9.80	7.49	5.05	9.12	4.93	0.00	1.65	2.51	5.99	19.46	11.00	96.42
1954	27.81	9.83	5.79	5.13	0.33	4.19	0.00	3.73	3.05	2.54	5.08	13.94	81.43
1955	9.80	5.69	7.21	10.01	1.04	0.61	0.91	0.00	1.70	8.15	12.47	39.09	96.70
1956	26.92	18.14	5.56	1.32	7.75	1.88	0.23	0.00	1.42	12.75	3.07	9.40	88.44
1957	8.38	12.70	17.22	4.39	4.39	0.46	0.20	0.13	2.97	8.20	8.71	21.13	88.90
1958	18.59	22.33	6.99	4.22	2.57	6.17	1.42	0.00	2.13	5.21	14.12	7.37	91.11
1959	22.17	15.01	5.56	1.45	4.85	0.84	0.18	0.03	1.80	4.19	1.75	6.78	64.41
1960	10.39	14.66	15.54	3.66	6.48	0.00	0.00	0.43	1.57	3.61	19.00	6.12	81.46
1961	4.85	13.06	17.40	2.24	4.70	0.99	0.33	0.30	1.73	12.09	20.80	9.09	87.58
1962	4.45	7.37	9.37	3.56	3.48	0.97	0.00	1.93	2.24	21.23	13.87	7.67	76.12
1963	4.34	10.87	10.64	10.57	12.07	2.87	0.53	0.00	1.70	4.04	14.33	4.11	76.07
1964	23.34	1.93	11.07	2.79	1.04	2.82	0.41	0.08	1.04	1.65	13.54	39.50	99.21
1965	17.83	3.71	0.64	6.65	1.19	0.61	0.05	2.67	0.00	3.81	11.99	22.68	71.83
1966	15.80	3.15	7.39	1.88	0.51	1.30	2.29	0.53	3.73	4.65	21.03	12.57	74.83
1967	15.54	2.84	8.61	3.51	2.34	0.84	0.00	0.00	0.89	5.59	4.14	13.13	57.23
1968	16.61	6.88	4.85	2.64	2.41	0.36	0.30	4.72	3.53	9.47	13.77	17.63	83.19
1969	23.39	4.98	2.34	3.20	4.78	3.05	0.00	0.00	2.26	7.62	3.12	25.02	79.76
1970	23.83	4.34	5.08	5.28	1.35	1.27	0.00	0.05	2.67	4.37	15.98	15.04	79.25
1971	16.15	11.84	13.23	6.20	3.89	2.46	0.03	1.17	5.38	3.18	18.42	17.98	99.92
1972	15.72	8.61	11.56	7.52	2.29	2.03	0.00	1.78	1.68	5.03	6.32	10.29	72.82
1973	10.08	3.68	7.14	4.24	2.49	1.07	0.03	0.51	3.84	7.24	38.76	14.55	93.60
1974	24.92	11.94	15.32	7.54	1.83	0.56	1.22	0.20	0.00	4.65	8.79	16.18	93.14
1975	13.34	12.57	14.25	4.78	1.24	0.61	0.91	2.13	1.70	10.54	10.49	14.22	86.79
1976	9.88	5.28	8.81	2.77	0.76	2.13	1.19	5.72	3.07	1.42	0.79	2.11	43.94
1977	3.91	5.56	7.95	2.01	7.16	0.25	0.00	3.38	8.28	3.48	16.26	12.22	70.46
1978	11.38	10.95	5.38	4.83	2.67	2.59	0.46	3.02	8.66	0.38	3.48	5.11	58.90
1979	8.13	12.90	5.41	10.84	3.81	1.27	0.56	3.12	1.68	12.75	8.99	14.99	84.25
1980	14.12	8.20	6.15	7.09	2.06	1.57	0.97	0.00	0.71	4.67	10.92	20.12	76.58
1981	4.67	7.72	8.86	3.02	4.88	2.21	0.00	0.00	5.00	4.42	20.29	28.93	90.02
1982	10.72	6.73	9.63	9.32	0.71	3.45	2.03	1.45	3.73	11.33	8.26	22.68	90.04
1983	14.35	23.55	17.40	6.55	2.72	1.70	3.35	7.82	0.91	1.50	24.99	16.79	121.64
1984	2.01	19.56	9.25	8.51	3.73	2.31	0.00	0.15	0.99	7.14	32.21	9.93	95.78
1985	2.01	8.05	8.51	2.62	2.13	2.13	0.13	0.66	3.33	5.87	10.24	6.27	51.94
1986	10.97	20.32	8.59	1.93	3.76	0.36	1.30	0.00	11.46	6.43	16.79	4.06	85.95
1987	10.08	11.10	5.87	3.15	1.85	1.22	3.78	0.18	0.00	0.08	8.53	22.45	68.30
1988	12.12	1.24	5.11	7.77	5.36	3.81	0.00	0.25	1.37	0.33	19.71	8.43	65.51
1989	9.07	4.22	14.02	6.98	3.12	0.99	0.03	2.24	2.13	5.05	4.90	3.25	56.01
1990	13.87	7.70	3.68	1.70	3.84	0.79	1.91	4.09	0.30	8.94	8.56	6.30	61.67
1991	4.27	5.97	13.13	6.45	7.57	2.67	2.06	0.41	0.03	4.04	11.58	5.94	64.11
Mean	12.75	9.98	7.89	4.94	3.43	2.35	0.59	1.02	2.53	6.48	12.23	13.96	75.75
Minimum	1.22	1.93	0.15	0.74	0.25	0.00	0.00	0.00	0.00	0.13	0.79	2.11	36.73
Maximum	29.92	24.99	18.64	10.64	12.07	8.28	6.15	7.82	11.46	29.59	38.76	39.50	121.64

# Appendix II.10. Monthly precipitation at Sexton Summit weather station.

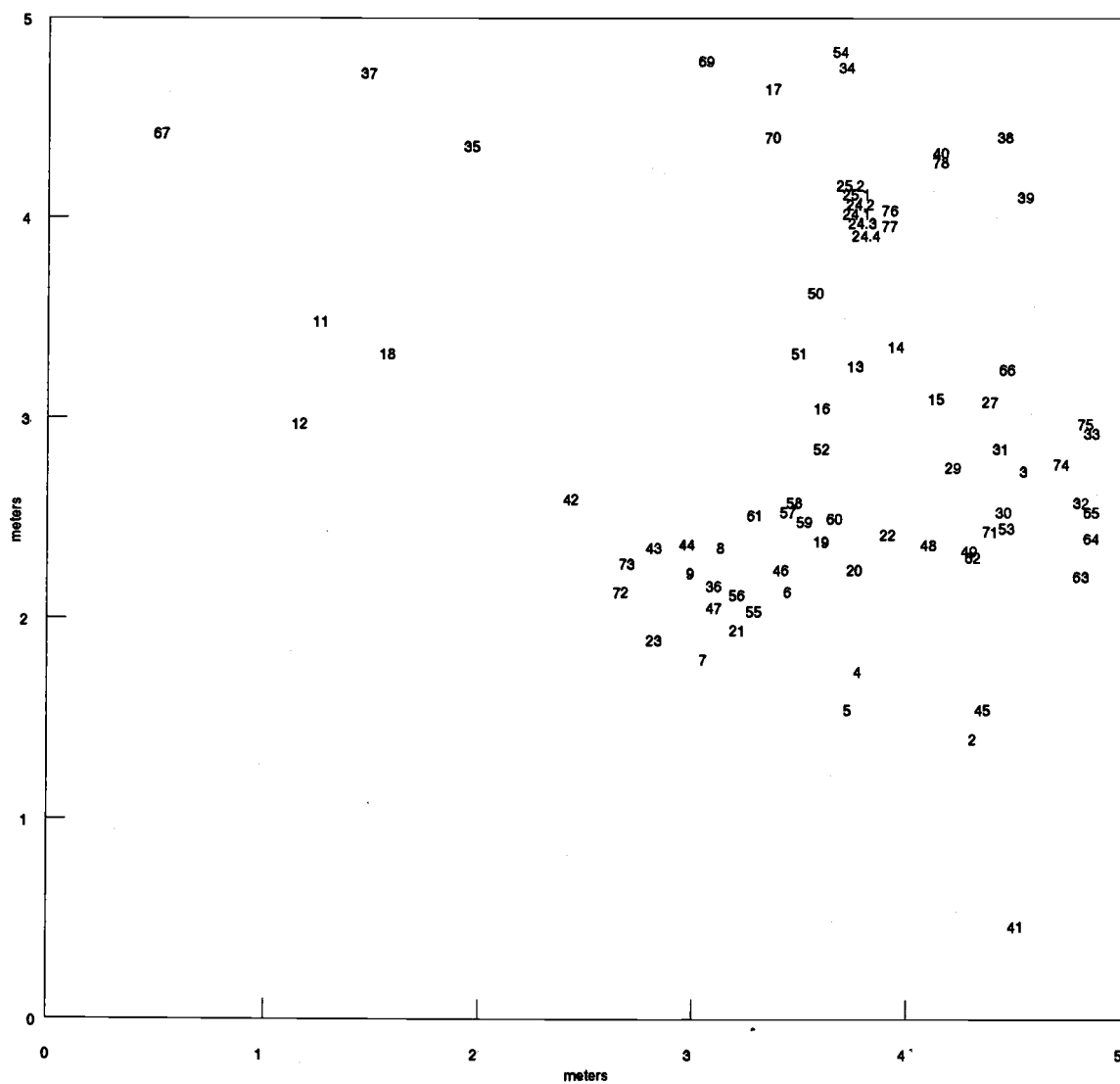
YEAR	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1942	10.08	6.63	2.44	4.60	12.73	1.91	0.05	0.00	1.88	2.64	23.06	20.17	86.18
1943	14.55	3.68	7.77	6.58	2.82	2.82	0.15	1.45	0.71	12.90	7.37	3.48	64.29
1944	5.59	5.79	4.29	4.98	2.49	5.97	0.28	0.84	1.88	5.05	11.51	4.27	52.93
1945	6.48	14.71	9.80	3.15	12.24	0.69	0.20	0.05	2.44	8.48	21.46	16.59	96.29
1948	20.42	11.43	9.73	14.68	7.75	7.80	2.79	2.16	2.92	4.06	9.45	13.26	106.45
1949	2.82	13.03	7.14	1.83	6.96	0.38	0.00	0.00	2.92	3.56	5.56	7.06	51.26
1950	23.57	6.76	12.98	3.91	2.41	5.77	0.00	0.20	2.95	35.23	11.23	15.60	120.60
1951	16.61	13.13	7.34	2.31	4.98	0.00	0.00	0.43	3.10	15.70	16.61	20.60	100.81
1952	18.90	8.94	9.88	2.36	2.57	8.13	0.15	0.58	2.26	0.89	4.29	19.10	78.05
1953	25.76	9.60	7.52	6.68	11.05	4.22	0.00	5.36	2.29	7.92	20.78	9.07	110.24
1954	26.57	8.81	6.65	7.09	0.64	4.22	0.00	1.88	4.80	3.30	8.84	11.15	83.95
1955	7.70	5.33	6.20	9.75	1.73	0.99	0.56	0.00	3.35	7.21	12.83	37.36	93.01
1956	25.40	13.36	6.32	1.52	7.16	2.57	3.05	0.18	1.75	18.69	2.29	8.38	90.68
1957	8.86	13.06	18.01	2.84	6.40	0.61	0.97	0.10	6.22	8.38	8.46	18.08	92.00
1958	21.39	23.77	9.09	4.22	2.95	7.24	0.61	0.05	1.93	4.32	7.37	8.79	91.72
1959	21.51	9.30	5.00	1.75	3.68	1.73	0.00	0.18	7.14	3.86	1.45	6.83	62.43
1960	11.46	21.01	22.78	4.65	14.12	0.00	0.03	0.84	0.91	5.41	27.51	9.91	118.62
1961	12.29	26.26	22.58	4.47	9.60	2.87	0.89	0.69	3.38	13.56	29.92	11.28	137.80
1962	4.60	15.16	9.65	4.62	4.60	0.97	0.00	5.61	4.27	24.82	17.45	12.50	104.24
1963	10.03	17.09	13.13	19.15	18.44	3.73	0.89	0.00	1.37	7.59	29.85	7.19	128.47
1964	26.19	2.06	8.51	1.91	1.65	3.61	1.57	0.03	0.69	2.26	20.78	50.88	120.12
1965	16.28	2.90	0.66	11.18	1.30	1.14	0.13	3.38	0.00	2.26	11.94	17.65	68.81
1966	14.55	3.53	10.59	2.87	0.48	2.13	2.41	1.17	4.62	2.36	24.84	14.05	83.62
1967	14.38	3.07	8.64	4.42	2.72	0.71	0.00	0.00	1.57	6.38	3.38	7.52	52.78
1968	13.74	10.74	5.13	1.80	3.48	0.46	0.15	6.15	2.29	9.68	13.08	19.30	86.00
1969	33.27	6.40	2.41	4.47	6.78	4.19	0.48	0.00	3.18	11.73	3.53	35.69	112.14
1970	48.34	7.32	6.17	6.40	1.60	1.85	0.00	0.00	0.84	8.33	29.97	19.13	129.95
1971	23.98	9.65	18.69	9.53	3.99	4.29	0.38	1.50	5.56	3.33	24.08	24.08	129.06
1972	25.45	17.96	18.21	7.29	3.51	2.36	0.00	2.29	2.51	6.25	8.43	21.49	115.75
1973	16.89	6.40	10.92	2.59	1.12	1.09	0.36	0.25	7.87	16.26	61.19	23.52	148.46
1974	44.02	12.98	18.44	4.98	1.24	0.48	1.17	0.05	0.00	5.99	8.59	14.96	112.90
1975	10.59	18.34	18.64	6.22	1.70	0.81	0.97	2.03	1.78	12.70	12.95	11.58	98.32
1976	4.47	6.68	7.90	3.28	1.47	0.86	3.35	10.74	3.20	1.50	1.88	1.24	46.58
1977	2.59	5.97	7.57	2.57	10.31	0.86	0.56	1.68	10.82	4.62	13.13	13.87	74.55
1978	8.69	11.46	7.34	4.80	2.82	7.11	0.58	5.31	9.50	0.08	6.25	2.84	66.78
1979	8.08	12.09	4.72	9.55	7.52	1.63	1.24	3.07	2.26	16.74	11.61	14.25	92.76
1980	10.64	8.71	7.59	7.59	2.44	2.59	0.00	0.00	0.43	7.77	10.69	16.79	75.26
1981	3.71	7.85	7.77	2.44	3.63	3.23	0.41	0.00	4.17	12.67	21.01	25.50	92.38
1982	7.54	9.09	9.25	10.11	0.28	3.76	0.15	0.38	3.63	12.93	9.32	16.61	83.06
1983	9.75	21.56	17.73	4.83	2.41	1.93	4.60	7.34	0.58	4.24	22.20	17.07	114.25
1984	0.46	14.71	8.15	5.49	2.69	1.93	0.10	1.02	1.83	6.40	30.81	6.78	80.37
1985	0.00	6.05	7.44	1.85	1.52	3.58	0.53	0.28	3.10	2.29	6.12	3.96	36.73
1986	10.95	21.06	8.03	2.36	3.33	1.50	0.23	0.00	9.07	7.52	11.38	5.11	80.52
1987	11.99	10.52	8.64	2.44	0.69	1.91	2.82	0.00	0.03	0.18	5.56	19.51	64.26
1988	9.65	0.71	5.05	7.92	6.25	2.26	0.00	0.10	0.71	0.03	20.35	8.05	61.09
1989	9.25	5.38	13.67	7.85	2.39	1.14	0.13	2.57	4.14	6.10	2.92	2.62	58.14
1990	13.21	8.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.62	5.72	4.78	43.10
1991	4.50	7.98	13.49	5.38	6.48	1.93	1.75	0.76	0.00	2.57	0.94	M	45.77
Mean	14.54	10.56	9.58	5.28	4.56	2.54	0.72	1.47	2.98	7.86	14.16	14.16	88.41
Minimum	0.00	0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.94	1.24	36.73
Maximum	48.34	26.26	22.78	19.15	18.44	8.13	4.60	10.74	10.82	35.23	61.19	50.88	148.46

**Appendix III.1.** Maps illustrating locations of individuals of *Calochortus howellii* within the five permanent plots at Mariposa Meadow. See Figure III.1 for plot locations.

*Calochortus howellii* Permanent Plots  
Plot 1 Mariposa Meadow

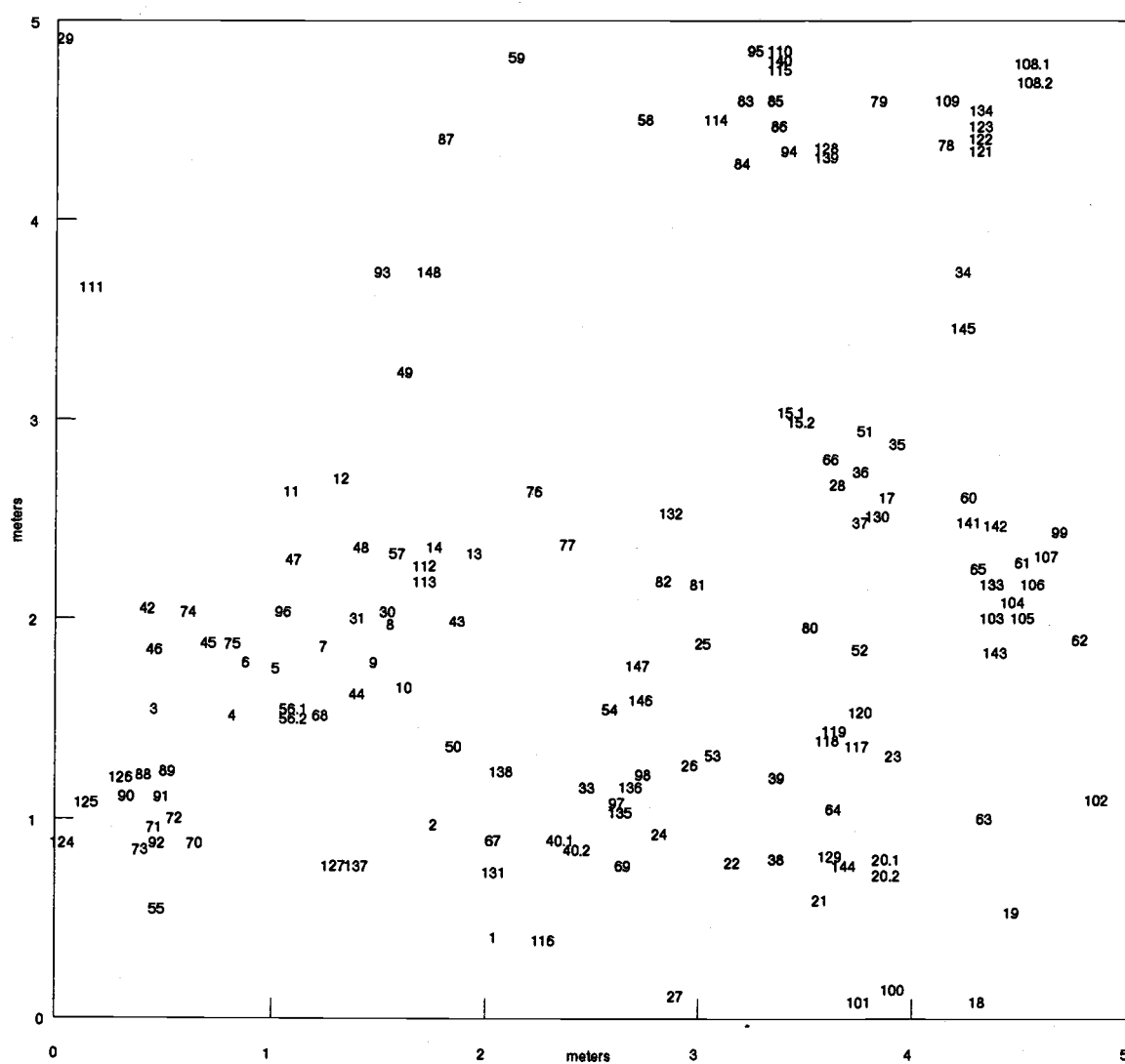


*Calochortus howellii* Permanent Plots  
Plot 2 Mariposa Meadow





*Calochortus howellii* Permanent Plots  
Plot 3 Mariposa Meadow





*Calochortus howellii* Permanent Plots  
Plot 5 Mariposa Meadow

