Demographic perspectives on the rarity and persistence of two mariposa lilies (*Calochortus*) from southern British Columbia

by

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B.A., Queen's University at Kingston, 1989

A Dissertation Submitted in Partial Fulfilment of the
Requirements for the Degree of

DOCTOR OF PHILOSOPHY

in the Department of Biology

Abstract

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The dynamics of peripheral populations provide insight into range limits and rarity. I studied sympatric populations of two species of mariposa lilies with contrasting distributions: *Calochortus lyallii*, a regional endemic of central Washington and southern British Columbia, and *C. macrocarpus*, a more widespread taxon. Marked plants were monitored for five years in the Okanagan highlands, at the northern range limit for *C. lyallii* and near the elevational limit for *C. macrocarpus*. Life table data were used to generate stage-classified matrix population models for three populations of each species and, for *C. lyallii*, different microsites and plant densities. My objectives were to evaluate the demographic variation of *C. lyallii* among populations, microsite types and density classes, and to identify demographic differences between *C. lyallii* and *C. macrocarpus* that might contribute to their differing occurrence patterns.

Annual population growth rates (lambdas) for *C. lyallii* ranged from 0.89 to 1.07 among populations, 0.87 to 1.29 among microsite types, and 0.86 to 1.07 among density classes. Life table response experiment analyses showed that inter-population and inter-microsite variances in lambda resulted mostly from variance in large adult fecundity, whereas the variance in lambda among density classes was mostly due to variance in vegetative stasis. Although differences were not significant, lambda tended to be highest in high density plots, arguing against a density-dependent equilibrium.

Stochastic projections yielded long-term growth rates of near 1 for *C. lyallii*, whereas two of three *C. macrocarpus* populations were projected to decline rapidly in size. In both species, prolonged bulb dormancy was common (lasting up to 4 yr) and helped buffer population fluctuations. The relatively higher lambda of *C. lyallii* resulted primarily from higher flowering frequency. On average, *C. macrocarpus* had higher fruit set and more seeds per capsule than *C. lyallii*, but experienced higher fruit predation and had lower seedling establishment. Seedlings of *C. lyallii* were predicted to live longer, flower sooner, flower more frequently, and leave more offspring than *C. macrocarpus* seedlings. I conclude that differences in the local distribution and abundance between the two species can largely be explained by subtle differences in life history and demography.

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Acknowledgements

For overseeing this project from its inception, and for intellectual guidance, editorial assistance, countless stimulating conversations, and many potlucks, I am deeply indebted to my co-supervisors Geraldine Allen and Joe Antos. Committee members Pat Gregory and Dave Duffus also gave generously of their time and advice, for which I am very grateful.

I thank Peggy Fiedler, who provided the original inspiration for this study through her own PhD research on *Calochortus* demography. I owe a debt of gratitude to Evelyn Hamilton, who listened with an open ear to my first unformed research ideas, then offered useful suggestions about how I might obtain funding to pursue them.

I have had the good fortune to be blessed with great friends, without whose steadfast encouragement (and relentless egging-on) I could not have seen this project through. You are too numerous to name, but you know who you are. A special thanks to Allan Hawryzki, for blazing the way; to Anthony Neilson and Janet Brygger, for providing me with mountain memories and a cool haven on their Okanagan lake; to Jeff Goodyear and Kaaren Lewis, for always making me feel at home; to Brenda Costanzo, for help and company in the lab; to Nancy Mahony, for teaching me about sparrows; to Purnima Govindarajulu, for her commiserating calls and crocodile tales; to Matt Fairbarns, for sending odd jobs my way so that I could continue to pay the rent; and to Erica Wheeler, for sustaining me with endless grub and good cheer.

Rob Webster showed me generous hospitality at Kilpoola Lake. Harry Nielson has crusaded tirelessly to conserve the Lyall's mariposa lily and its habitat at East Chopaka. Both were invaluable sources of local information.

Hal Caswell patiently put up with my pestering questions about matrix models, and Brett Sandercock helped in developing some of the MATLAB code. I am grateful to both.

Parts of the manuscript have been reviewed by Purnima Govindarajulu, Res Altwegg, and Pat Gregory. I appreciate their many useful comments.

Financial support for this research was provided in part by Forest Renewal British Columbia Grant HQ-96265-RE, which I gratefully acknowledge. The Nature Trust of BC kindly made accommodations available to me at Kilpoola Lake.

No graduate student could ever hope to navigate successfully through the bureaucratic process on their own. Many thanks to Eleanore Floyd for efficiently smoothing the way.

Lastly, I offer a special thanks to my parents and the rest of my family for patiently (or not) bearing with me over the years, through thick and thin.

Dedication

To my parents, Mary Helen and Roland,
who taught me to wander in the sholas

Chapter 1: General Introduction

Rarity has long been recognised as a predictor of vulnerability and a precursor to extinction. Over a century ago, Darwin (1872) suggested that establishing the causes of rarity was essential to understanding extinction patterns. He also acknowledged that the factors determining the relative abundances of species, and hence their susceptibility to extinction, were likely to be as obscure as they were diverse:

> Whenever we can precisely say why this species is more abundant in individuals than that; why this species and not another can be naturalised in a given country; then, and not till then, we may justly feel surprise why we cannot account for the extinction of any particular species or group of species (Darwin 1872).

The precipitous rise in extinction rates during the last century has heightened the motivation to identify these factors. If we knew what predisposes a species towards rarity, we might be able to slow extinction down. Yet, despite a rapidly growing body of literature on the biology (see reviews by Gaston 1994, Kunin and Gaston 1997) and management (e.g., Soule 1986) of rare species, a general understanding of the relationship between rarity and persistence remains elusive. A hierarchy of factors interacting at many levels—earth history, evolutionary history, genetics, and ecology—may be needed to explain rarity in any given case (Fiedler 1986, Fiedler and Ahouse 1992).

Regardless of its root cause, the rarity of a species ultimately is expressed in the dynamics of its local populations (Bradshaw and Doody 1978, Menges 1986, Lande 1988, Schoener and Spiller 1992, Doak et al. 1994, Schemske et al. 1994, Byers and Meagher 1997, Fiedler et al. 1998). Extinction is, by definition, a demographic event—the population-level outcome of a terminal imbalance among birth rates, death rates, and dispersal rates. To evaluate threats to, and improve management of, endangered or rare species, we first need to understand the factors that influence population growth within a species (Mehroff 1989, Schemske et al. 1994, Menges 1998). The demographic rates of a population, as well as its composition and its capacity for growth, are in turn consequences of the life history traits of its individual organisms (Cole 1954, Roff 1992).

Rabinowitz (1978) and others (e.g., Hodgson 1986, Fiedler 1987, Karron 1987, Arita et al. 1990, Hedderson 1992, Hodgson 1993, Pantone et al. 1995, Kunin and Shmida 1997) have investigated life history characteristics that could account for the contrasting

population densities and distributions of rare and common species. Comparative studies of taxonomically related rare and common species have succeeded individually at isolating differences relating to breeding systems, reproductive investment, dispersal patterns, body size, ecological specialisation, and numerous other biological attributes. Nevertheless, generalisations about rare-common differences and the mechanisms responsible for creating and maintaining them have proven difficult (Cotgreave 1993, Kunin and Gaston 1993, Fiedler et al. 1998). Part of the difficulty is that there are many types of rarity. Rabinowitz's (1981) now classic paper on the different forms of plant rarity highlighted some of the manifold ways in which rarity is manifest at different spatial scales. For example, a taxon may be wide-ranging but consistently sparse, or locally abundant but restricted geographically, or both locally rare and restricted geographically (Rabinowitz 1981). Rarity is a relative state, and we must be clear about precisely how we are using the word.

It can also be difficult to separate pattern from process when proposing explanations for rarity (Fiedler and Ahouse 1992, Kunin and Gaston 1997). Kunin (1997) cautions against the temptation to automatically view rare-common differences as evolved adaptations to cope with the condition of rarity. He suggests several alternative but equally plausible mechanisms that could have resulted in the disproportionately high incidence of self-compatibility that exists among rare plant taxa. For example, it might be a consequence of either selective speciation (propagules from self-compatible lineages may be more likely to become established after long-distance dispersal events and to speciate into rare endemics) or selective extinction (the reproductive difficulties associated with rarity could result in the extinction of sparse populations of sexually outcrossing species before that of self-compatible ones, biasing the set of rare species). Thus, even when consistent differences are identified, elucidating the processes that produced them is not straightforward (Kunin 1997).

Although the causes of rarity vary, some types of life histories, or combinations of life history traits, may be more liable than others to render species susceptible to extirpation or to be associated with rarity. Thus, knowledge of a species' life history can help us make predictions concerning its potential vulnerabilities. For example, numerous attempts have been made to classify species according to broadly-defined demographic

'strategies' (e.g., Pianka 1970, Grime 1977, Whittaker and Goodman 1979, Saether et al. 1996). One important distinction is between short-lived, fast growing organisms and long-lived, slow growing ones, which differ in the frequency of natural disturbances during an organism's life span and the extent of population fluctuation in time and space. The distinction has received emphasis in the conservation literature, where much of the focus has been to quantify threats to species posed by environmental perturbations, particularly those resulting from human interference (Meffe and Carroll 1994). Ecological theory predicts that species with low intrinsic rates of population increase, large population fluctuations, and short life spans should have higher extinction rates (Goodman 1987). However, interactions among life history traits make certain combinations of these traits, such as long life times and fast population growth rates, unlikely. Other things being equal, a population of a long-lived species would have a lower risk of extinction from demographic accidents *per se* than would a short-lived species. However, if it is also likely to recover more slowly from a severe reduction in density, it will remain longer at risk from those same demographic accidents (Pimm et al. 1988). Consequently, it is difficult to anticipate *a priori* the net effect of a trait such as life span on the length of time a population is likely to survive.

Nevertheless, there is a concern that many long-lived organisms exhibit a suite of coevolved traits that makes it especially difficult for them to respond to sudden environmental disruptions or population declines (Meffe and Carroll 1994). For example, life span and age at maturity positively covary across many taxa (Roff 1992). Delayed maturity has at least two important implications for long-lived species: first, generation times are relatively long, which means that (other things being equal) population growth will be relatively slow (Gotelli 1998); second, the level of survivorship, particularly yearly juvenile survivorship, required to maintain a stable population is likely to be high. For example, Blanding's turtles, which may live for nearly a century and do not become sexually mature until around 17 years of age (Congdon et al. 1993), rely on high juvenile and adult survivorship to compensate for delayed reproduction and low life time fecundity. Juvenile survival must exceed 70% to maintain a stable population, irrespective of annual reproductive success. Under all simulated conditions, moreover, any slight reduction of adult survival rates (such as through harvest or accidental killing)

raised the already high required juvenile survival levels to much higher ones (>85%), suggesting that the species possesses little demographic latitude for responding to chronic increases in mortality at any stage (Congdon et al. 1993). Other long-lived chelonians of conservation concern, such as sea turtles and desert tortoises, appear similarly constrained (Crouse et al. 1987, Doak et al. 1994). This finding suggests that programs aimed at 'head-starting' young juveniles or protecting nesting sites alone will not be sufficient to conserve these organisms (Frazer 1992).

At the opposite end of the demographic spectrum, small-bodied, short-lived organisms generally mature faster, have higher reproductive rates, and possess higher intrinsic rates of increase (Roff 1992). Populations of these organisms are more likely to recover rapidly from sudden reductions in population size than larger, slower-growing species, which should, in theory, make them relatively less prone to extinction. However, theory also predicts that such populations are more likely to undergo large and rapid fluctuations in density, rendering them more susceptible to extinction (Pimm et al. 1988).

Field studies seem to bear out this second prediction. In the Florida scrub, for example, herbaceous species are more extinction-prone than longer-lived shrubs (Quintana-Ascencio and Menges 1996). For birds on small islands off the coast of Britain, Pimm et al. (1988) found a significant relationship between mean temporal coefficients of variation in population size and local extinction risk. Similar results were obtained by Karr (1982) for the avifauna of Barro Colorado Island, Panama. Comparisons of species still extant on the island with species absent from the island but present in nearby mainland forest demonstrated that population variability is in fact a more powerful predictor of extinction probability than rarity *per se* (Karr 1982).

Other factors likely to be associated with high risk of extinction include habitat specialisation or narrow endemism (Menges 1990, Foufopoulos and Ives 1999), complex habitat requirements (Lomolino and Creighton 1996, Marvier and Smith 1997), limited dispersal ability (Laurance 1991, Tilman et al. 1997), and low competitive ability (Pimm 1991). These are the same factors commonly invoked to explain rarity (Kunin and Gaston 1997). In both cases, the challenge lies in separating the effects that intrinsic biological attributes (e.g., rate of natural increase) and extrinsic phenomena (e.g., fluctuating rainfall patterns) exert on observed patterns of abundance. However, the two

are often so inextricably intertwined that making isolated generalisations about either one may not be useful (Mace and Kershaw 1997).

Because the set of rare species is likely to be biased by the selective elimination of species that cannot persist at low abundances (Kunin and Gaston 1993), another approach to studying the relationship between rarity and persistence is to ask what life history or ecological characteristics allow species to persist at low numbers. The utility of this approach is that it focuses attention on those components of the life cycle likely to have a disproportionately large impact on population dynamics in a particular environment. Thus, in the case of Blanding's turtles, Congdon et al. (1993) suggest that naturally high juvenile and adult survival rates served historically to counterbalance the negative effects of slow growth and low lifetime fecundity—a circumstance that, ironically, may now be contributing to the vulnerability of that species. Likewise, Rabinowitz et al. (1986) found that sparse species of prairie grasses tend to have a less variable reproductive output than common species in the same habitat. This is achieved through growth and flowering during a season when rainfall is more predictable, and may compensate for demographic stochasticity, thus reducing the chance of local extinction.

Growth form and habit can also affect plant response to periodic disturbances. Menges and Kohfeldt (1995) documented life history strategies of Florida scrub endemics, a group consisting mostly of gap specialists, in relation to fire. Demographic mechanisms of post-fire recovery include obligate seeding, resprouting, resprouting plus seeding, and resprouting plus clonal spread. The relative frequency of these strategies depends on fire frequency. In areas with long fire-return intervals, the modal mechanism of recovery tends to be seedling recruitment, whereas in areas with more frequent fires, species relying on resprouting and/or vegetative spread tend to predominate. Accordingly, Menges and Kohfeldt (1995) recommend that fire management in Florida scrub avoid overly regular fire regimes, as well as the intense fires usually following fire suppression (which might lead to extirpations of resprouters).

Two other important life history characteristics are dispersal and prolonged dormancy. Much of the discussion in conservation biology during the past decade has concerned the dynamics of metapopulations and especially the critical role of dispersal in maintaining a balance between local extinctions and colonisations (Meffe and Carroll

1994). Dispersal also contributes to sustaining populations that would otherwise be demographically inviable (Pulliam 1988). The current enthusiasm for metapopulation theory amongst conservationists has tended to obscure the fact that the metapopulation concept was originally proposed for highly mobile animals living in well-defined habitats (Levins 1969, Hanski and Gilpin 1991). Metapopulations in a strict sense, i.e., systems of local populations connected by dispersing individuals (Hanski and Gilpin 1991) may not occur in many organisms. Nevertheless, evidence from various empirical studies supports the idea that this phenomenon is relatively common in plants. For example, Eriksson (1996) suggested that short-lived or highly habitat-specialised plants with good dispersal tend to form metapopulations; a well-known example is *Pedicularis furbishiae* (Menges 1990). However widely applicable the metapopulation and source-sink paradigms turn out to be in practice, as a heuristic tool they have served to highlight the double-edged significance of dispersal for all species with locally ephemeral populations. Greater dispersal should, in the long run, make for greater population stability, but the greater the reliance on dispersal, the more magnified will be the effect on a species when habitat alteration inhibits movements among suitable sites (e.g., Lande 1988).

For many less vagile species, the connectivity of populations in space may be less important than their ability to persist locally (Wolf et al. 1999). This is an important distinction for plants especially, since many rare plants are thought to be dispersal limited (Quinn et al. 1994, Kunin and Gaston 1997). For some species, an alternative solution to the problem of environmental uncertainty is to disperse through time, rather than through space. As discussed by Eriksson (1996), two traits enabling plants to tolerate periods of unfavourable conditions or reproductive failure are clonal propagation (cf. Wiegleb et al. 1991, Lantz and Antos 2002) and persistent seed banks (cf. Kalisz and McPeek 1992). Indeed, a general trade-off between seed dormancy and seed dispersal has been found (Rees 1993). Information on seed banks can be crucial to the management of threatened plant species (Pavlik et al. 1993). For the rare serpentine sunflower *Helianthus exilis*, Wolf et al. (1999) determined that the availability of additional suitable habitat, and not dispersal ability, is the primary factor limiting distribution. The ubiquity of *H. exilis* on suitable habitat patches is apparently due to a very low rate of local extinction, which Wolf et al. (1999) attributed in part to the existence of a highly persistent seed bank.

Consequently, they recommended that attempts to conserve this species focus on identifying and protecting populations in high-quality habitats, rather than on mitigating the spatial isolations of patches *per se* (Wolf et al. 1999).

Populations of species unspecialised for either temporal or spatial dispersal may face a high likelihood of being eliminated by stochastic demographic or environmental events, especially when coupled with alterations to critical habitat. For example, *Aster kantoensis* of Japan is a short-lived perennial of gravelly flood plains that lacks a persistent seed bank and persists by colonising new openings created by fluvial disturbance (Washitani et al. 1997). However, recent flood control management and eutrophication have reduced the density of available safe sites to the point where dispersal between them now rarely occurs, resulting in a rapid decline in the number of extant colonies. Human-aided dispersal of seeds to artificial safe sites appears to be the only short-term option for preserving the species (Washitani et al. 1997). Primack and Miao (1992) suggest that lack of dispersal ability may be one of the major factors that prevents angiosperms from modifying their distribution in response to global climate change.

Individual organisms are born, grow, reproduce, and eventually die. The timing of these processes and the rates at which they occur together determine the structure and dynamics of the population (Caswell 2001). Characterising the mechanics of this relationship is relevant for both life history theory (Kalisz and McPeek 1992, McGraw and Caswell 1994) and management (Crouse et al. 1987, Schemske et al. 1994). Accordingly, those charged with the task of formulating conservation strategies for sensitive species are increasingly turning to population models that integrate information on demographic structure and the life cycle to assist them in choosing where best to direct resources in specific cases (Schemske et al. 1994, Fiedler and Kareiva 1998), as well as in developing guidelines for conservation management across taxa (Silvertown et al. 1996, Heppell 1998).

Population projection matrices have become the model of choice in demographic studies because they are well suited to a range of complex life cycles and because matrix analysis yields a number of informative statistics. Comparisons of finite rates of population increase (λ), sensitivities and elasticities, and stable stage (or age) distributions make it possible to identify the effects of changes at different stages of the

life cycle (e.g., altered germination or fecundity) and can reveal important differences among species, populations within species, habitats, and years.

Comparative matrix models have been used to estimate the effects of different conservation strategies. For example, Silva et al. (1991) evaluated the effects of individual fires and fire frequency on population growth in a savannah grass. Similarly, extinction thresholds have been modeled for various harvesting levels in American ginseng (*Panax quinquefolium*) and wild leek (*Allium tricoccum*) (Nantel et al. 1996). Menges (1990) used stochastic matrix simulations to compare population viability of Furbish's lousewort (*Pedicularis furbishiae*) across different habitat patches in various stages of succession. Silvertown et al. (1993) used the additive property of elasticities to investigate the relative importance of growth (*G*), survival (*L*), and fecundity (*F*) in 66 species of perennial plants representing a wide range of life histories and habitats. By ordinating the *G/L/F* ratios for the various species on a triangular plot, they were able to demonstrate distinctive patterns in the relative values of *G/L/F* among different functional groups (but see Enright et al. 1995). Alternatively, single elasticity terms can be summed to assess the impact of different potential 'loops' or pathways through the life cycle (van Groenendael et al. 1994).

The vital rate that contributes most to the variability in population growth rate is not necessarily the one to which population growth rate is most sensitive (Horvitz et al. 1997, Pfister 1998). Life table response experiment (LTRE) analysis can determine the extent to which an observed change in population growth rate is actually due to variance in one transition and not another (Caswell 1989, 2000). Whereas elasticities predict the population response to changes that could occur, LTRE analysis focuses on changes that have actually occurred. This approach has not been used widely for conservation purposes, but could complement analyses of sensitivity and elasticity in directing management efforts.

The genus *Calochortus* is a useful plant group in which to explore plant life histories and questions of rarity using projection matrices (Fiedler et al. 1998). The species are well suited to demographic studies because individual plants are easy to identify and follow over time, and the basal leaf provides a reliable and convenient measure of plant size (Fiedler 1987). To date ten species in this genus, most of these rare

endemics, have been studied using transition matrix methods (Fiedler 1987, Fredricks 1992, Knapp 1996).

My research uses a demographic approach to explore the relationships among life history, population dynamics, and habitat variability in *Calochortus lyallii* Pursh and *C. macrocarpus* Dougl. *Calochortus lyallii* ranges from Yakima Co. in central Washington to the US-Canada border (Hitchcock and Cronquist 1973), a distance of only about 300 km, but tends to be abundant where found. The range of *C. macrocarpus* extends from southern British Columbia south to Nevada and California (Fiedler and Zebell 2002) but, unlike *C. lyallii*, *C. macrocarpus* rarely forms dense populations.

The *Calochortus* populations that I studied are peripheral to their main distribution, but in different ways; *C. lyallii* is at its latitudinal range limit, whereas *C. macrocarpus* is close to its altitudinal limit. Geographically peripheral populations comprise a major component of the local plant diversity in many areas of southern Canada (Argus and Pryer 1992) and elsewhere (Bengtsson 1993). In British Columbia, peripherally rare species account for well over half of all the vascular plants listed as threatened or vulnerable (Douglas et al. 1998).

In **Chapter 2,** I focus on two aspects of the autecology of *C. lyallii* and *C. macrocarpus*: extended bulb dormancy and sexual reproduction. In **Chapter 3**, I use matrix projection techniques to investigate demographic variation in *C. lyallii* at three different levels of observation: among microsites, among patches of varying density, and among populations. In **Chapter 4**, I use a range of analytical techniques (e.g., stochastic projections, LTREs, prospective perturbation analysis, and transient analysis), to explore whether subtle divergences in life history between *C. lyallii* and *C. macrocarpus* are sufficient to account for their strongly contrasting patterns of occurrence on the landscape. By combining a species-specific demographic approach with a comparative approach, I have attempted (1) to isolate those factors most critical to the conservation of *C. lyallii*, and (2) to contribute to the detection of broader patterns in the population dynamics of rarity.

Chapter 2: Dormancy and flowering in two mariposa lilies (*Calochortus*) with contrasting distribution patterns: implications for monitoring

Introduction

Although reproduction and vegetative persistence are both critical to the maintenance of plant populations, the way in which these life history components are combined varies greatly among species. Reproductive attributes such as flower, fruit and seed production can vary markedly in space and time in response to external factors such as weather and pollinator availability. When reproduction fails, populations can only persist through vegetative means, and plants have evolved various modes of coping with unfavourable conditions or with reproductive uncertainty. Clonal propagation is one way in which plants can persist between sexual reproductive episodes (Eriksson 1996, Lantz and Antos 2002). Another is to remain dormant for some portion of the life cycle, e.g., in persistent seed banks (Baskin and Baskin 1978, Kalisz and McPeek 1992) or as dormant bulbs or rhizomes (Boeken 1991, Lesica and Ahlenslager 1996), until conditions become favourable for growth and reproduction.

In recent years, considerable interest has arisen in the evolution of seed dormancy and the influence of seed banks on the demographic structure and dynamics of plant populations. Much less is known about the population-level consequences of extended dormancy at later stages of the life cycle, although this phenomenon is widespread in vascular plants, particularly among geophytes—plants whose perennating structures occur only below ground (Lesica and Steele 1994). For example, orchids may remain underground for extended periods (Mehrhoff 1989, Rasmussen and Whigham 1998). Prolonged dormancy has also been observed in geophytes such as *Silene spaldingii*, *Gentiana pneumonanthe*, and *Allium amplectens* (Oostermeijer et al. 1992, Lesica 1997, Hawryzki 2002). Such underground 'bulb banks' could function to offset the effects of a fluctuating environment in a manner analogous to that hypothesised for seed banks (Pake and Venable 1996). However, dormancy is difficult to detect and measure in short-term studies, especially if it is prolonged or if the duration of dormancy varies within a species

(Lesica and Steele 1994). Detection of dormancy typically requires the monitoring of marked individuals for at least three consecutive years. Therefore, the amount, and even presence, of dormancy is likely to be inadequately recognised in many studies. In such cases, aboveground shoots may not give an accurate indication of plant presence or of individual survivorship, affecting estimates of both population size and population growth rate (Shefferson et al. 2001, Kéry and Gregg 2003).

The chances of a given year being adverse for reproduction are likely accentuated for range-margin populations, where climatic stress could lead to dramatic reductions in seed production, limiting recruitment and increasing the likelihood of local population extinctions (Lawton, 1993, Lesica and Allendorf 1995). Thus plant traits that enhance individual survival are expected to become even more critical for population persistence near the limits of species' geographical ranges. For rare species of conservation concern, information on both reproductive rates and modes of vegetative persistence are essential in this situation.

This paper investigates flowering, fruiting, and dormancy patterns in peripheral populations of two perennial geophytes, Lyall's mariposa lily (*Calochortus lyallii*) and sagebrush mariposa lily (*C. macrocarpus*). *Calochortus lyallii* occurs in grasslands and open forests in central Washington state and extreme southern British Columbia. Although geographically restricted, it occurs at high local densities and often forms patches containing many thousands of individuals. In contrast, *C. macrocarpus* has a much wider geographical range (British Columbia to California) but tends to occur at much lower densities locally. I studied sympatrically occurring populations of the two species in highlands above Osoyoos, BC, at the northern limit of *C. lyallii*'s range and close to the elevational limit for *C. macrocarpus*. I addressed the following specific questions: (i) What proportion of plants undergo prolonged dormancy, and for how long? (ii) Is dormancy synchronised among populations or between species? (iii) Are plants self-compatible? (iv) What proportion of plants flower each year? Do flowering frequency and fruit set vary among sites and years? What is the fate of buds, flowers, and fruits? (v) Are flower and fruit production correlated with climate?

Methods

STUDY SPECIES AND HABITAT

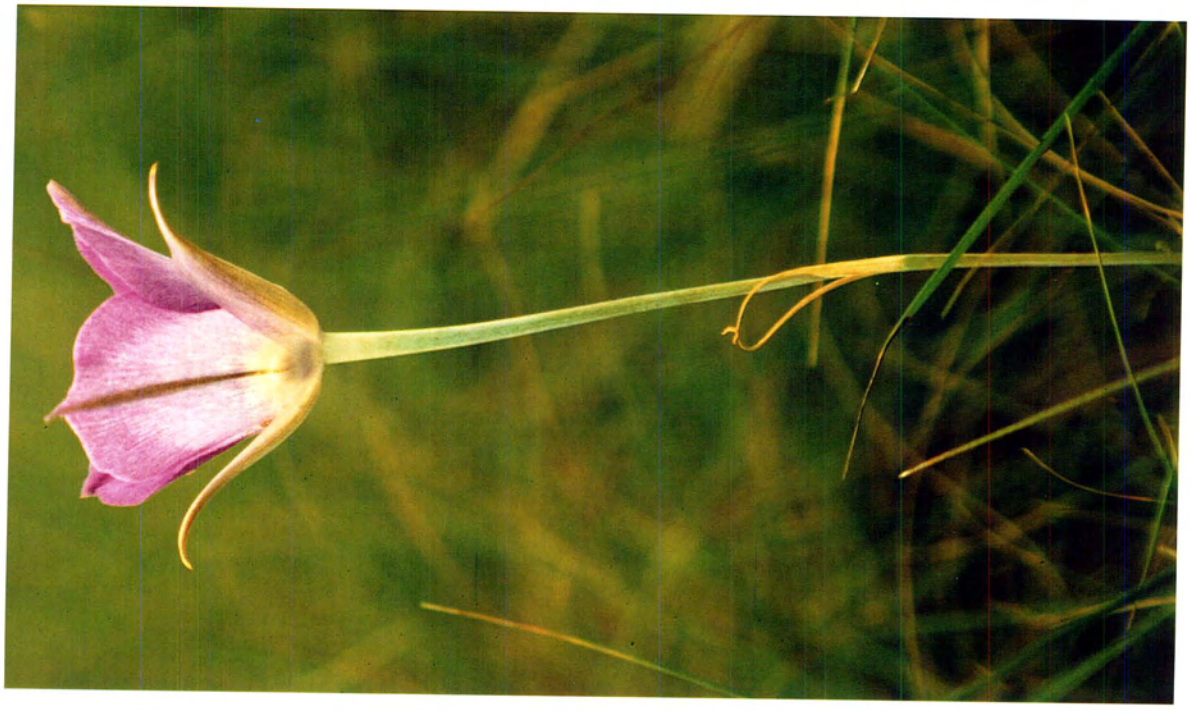
Lyall's mariposa lily (*Calochortus lyallii*) (Fig. 2.1a) and sagebrush mariposa lily (*C. macrocarpus*) (Fig. 2.1b) are perennials growing from bulbs and emerging shortly after snowmelt. *Calochortus lyallii* flowers in late spring, *C. macrocarpus* in midsummer. Vegetative plants of each species produce just a single leaf. Flowering individuals produce a basal leaf and a single scape with usually 1-2 showy flowers, although *C. macrocarpus* occasionally produces up to 4 flowers, and *C. lyallii* may produce up to a dozen. In the latter species, 3- and more-flowered plants may comprise up to 50% of the flowering population in some years. The flowers of *C. lyallii* are white and shallowly tulip-shaped and, at British Columbia sites, are visited primarily by solitary halictid bees (*Duforea* spp.) (Miller and Douglas 1999). *Calochortus macrocarpus* flowers are larger than those of *C. lyallii*, have a lavender, bowl-shaped corolla, and attract a variety of pollinators including Coleoptera and Lepidoptera (Dilley et al. 2000).

Fruits are erect capsules and typically contain 10-50 seeds in *C. lyallii* and 20-250 seeds in *C. macrocarpus*. Seeds are primarily gravity dispersed and germinate the following spring. In late spring, seedlings of both species die back to a buried bulb. In succeeding years, the bulbs increase in size and in depth, eventually descending to *c.* 10 cm below the surface in *C. lyallii* and to *c.* 30 cm in *C. macrocarpus*. Field observations over five years indicate that it takes >3 yr before plants of either species can flower. Although the production of new propagules from bulb offsets has been documented in other mariposa lilies (Fiedler 1987), vegetative reproduction is rare in both *C. lyallii* and *C. macrocarpus*, and plants do not form clonal patches.

Calochortus lyallii inhabits sagebrush slopes, grassy meadows, and open forests along the eastern front of the Cascade Mountains from extreme south central British Columbia to Yakima Co., Washington. In Canada, *C. lyallii* is federally listed as threatened because of its rarity, its highly restricted distribution, and the threats posed by grazing and forestry activities (COSEWIC 2003). *Calochortus macrocarpus* occurs in similar habitats to *C. lyallii*, but with a much larger range that extends from southern BC

Figure 2.1a *Calochortus lyallii.*

Figure 2.1b. *Calochortus macrocarpus.*



south to Nevada and California. My study took place on Black Mt. at East Chopaka, a height of land south of Richter Pass near the Canada-U.S. border, in what is now South Okanagan Grasslands Provincial Park. Here, a continental climate is moderated by the rain shadow cast by the Coast-Cascade Mountains, resulting in warm, dry summers and cool winters (Meidinger and Pojar 1991). The study sites were in grassy meadow openings adjacent to Douglas-fir (*Pseudotsuga menziesii*) forest, at elevations between 1000-1200 m. The meadows are characterised by coarse, well-drained soils and support a diverse herbaceous community, with bunchgrasses dominating over forbs (Miller and Douglas 1999).

FIELD METHODS

I monitored individual plants and reproduction in three populations of each species from 1996-2000. The *C. lyallii* sites chosen were, at the time, the only three known sites in Canada. One *C. macrocarpus* population adjacent to each *C. lyallii* site was identified for comparative study. The three pairs of populations were located on opposite slopes of Black Mt. with differing northerly, easterly, and westerly aspects and are labelled 'NS,' 'ES,' and 'WS,' respectively (Fig. 2.2).

Subsets of each population were monitored in permanently marked 0.5 x 0.5 m (*C. lyallii*) and 3.0 x 3.0 m (*C. macrocarpus*) plots. A larger plot size was used for *C. macrocarpus* to accommodate the lower density of individuals of this species within the study area. I established a total of 95 *C. lyallii* plots (36 at both NS and ES, 23 at WS) and 60 *C. macrocarpus* plots (20 per site), giving initial sample sizes of 1271 and 568 individuals, respectively. Plots were located haphazardly within each population, but were placed so as to encompass the range of microsite variation present at each site. In June 1996, all visible *C. lyallii* and *C. macrocarpus* individuals in each plot were numbered and mapped to the nearest cm. Censuses of all plants were conducted during early June of each year, when I recorded presence or absence of previously marked plants, the width of each basal leaf, the number of flower buds initiated, and herbivore damage; and again in late June (*C. lyallii*), July (*C. lyallii* and *C. macrocarpus*) and September (*C. macrocarpus*) to record flowering and fruit set. Fruit set was not recorded in 2000.

Figure 2.2 Study sites at East Chopaka: NS (a), ES (b), WS (c).

DORMANCY DETERMINATIONS

I found that some plants went undetected for one or more years but then reappeared in subsequent years. Some apparently dormant plants may actually have been grazed at ground level shortly after emergence and thus escaped detection. It is also possible that some small vegetative plants senesced and disappeared before they could be surveyed. In the majority of cases, however, a careful search in the vicinity of the missing plants' mapped locations was sufficient to eliminate these alternative explanations. Thus all plants (other than seedlings) that disappeared for one or more consecutive seasons before reappearing were considered dormant. Seedlings, which are difficult to detect due to their small size and cryptic coloration, and which appear aboveground for only a brief period before senescing, were excluded from dormancy estimations. Because a minimum of two years (three annual censuses) are needed to detect dormancy from census data, estimates of the number of summer dormant plants could be determined only for the middle three time periods (1997, 1998, and 1999). Furthermore, the methods used to calculate dormancy were not the same for each year. The 1997 estimate takes into account any prior-recorded plants that went missing during the period 1997-1999 and reappeared by 2000, but it does not include any plants absent prior to 1997. By comparison, the 1998 estimate takes into account any plants absent in 1998 plus any ones also absent one year before or after 1998; the 1999 estimate includes all plants absent from 1997 up to and including 1999, but does not include any post-1999 absences. Thus there is variation in the bias associated with each of the three estimates.

SELF COMPATIBILITY

Previous studies have shown that several *Calochortus* species are self-compatible but that they usually outcross via insect pollination (references in Dilley et al. 2000). To examine the ability of *C. lyallii* and *C. macrocarpus* to produce seed from self pollen, I compared fruiting success between open-pollinated and self-pollinated flowers. Thirty plants of each species with two buds and similarly sized leaves were haphazardly selected from well outside the demographic plots. I chose plants with two buds because this was the modal inflorescence size for both species. Prior to anthesis in 1997, insect exclosures

consisting of fine mosquito netting sewn into bags were placed over flower buds. The uppermost bud on one of every three plants was enclosed and, following anthesis, hand-pollinated with its own pollen or with pollen from a flower lower down on the same inflorescence. Flowers on another third of the plants were bagged, then left undisturbed. Those of the last third were left open and hand-pollinated with pollen from other plants. Once blooming was complete, bags were removed to allow seed capsules to develop unimpeded; mature capsules were then harvested and seeds counted.

VARIATION IN FLOWERING AND FRUITING

To compare natural flowering and fruiting patterns among populations, years, and species, I computed three indices of reproductive potential for each plot x year combination: ratio of reproductive to vegetative adults; % fruit set (proportion of flowers producing a fruit); and number of seed capsules produced per adult plant. Because the data were non-normally distributed and laden with zeroes, I used randomisation methods (Manly 1997) to test the significance of differences among sites and among years within each species. First, I calculated plot means of each of the indices for each population x year combination (after arcsine-transforming proportional data), together with the standard deviation (*SD*) of the means. To test spatial variation, plots from each year were then randomly permuted among sites to create three new data sets containing the same number of plots as in the original sample; from these data a new *SD* was calculated. Repeating this process 2000 times yielded a set of 2000 *SD* values (test statistic θ) for each year, whose distribution could then be compared against the observed value for that year. If the observed value θ was greater than at least 95% of the permuted values, the difference among sites was considered significant at the alpha 0.05 level. To compare variability in reproductive output over time, the entire process was then repeated by permuting plots among years, for each population separately.

REPRODUCTION IN RELATION TO CLIMATIC FACTORS

Relationships between mean measures of reproductive performance (ratio of reproductive to vegetative adults, % fruit set, and number of seed capsules per flowering

individual) and climatic conditions in each year were investigated using climate data from the Environment Canada weather station at Osoyoos, 10 km E of the site. The data used were monthly rainfall totals and mean monthly temperature from 1995-2000 (April-July of each year). I considered the months April-July as this is the period of active growth and flowering. I used bootstrapping procedures (Efron and Tibshirani 1993) to estimate the strength of correlations between flowering and fruiting patterns and spring and summer weather. For each species in each year, 1000 bootstrap values of each reproductive parameter were generated by pooling plots from all three sites and resampling, with replacement, from the pooled data set. The bootstrapped values were then stacked into a single vector and compared to a corresponding vector of climatic variables by drawing 1000 additional samples, with replacement, from each vector and calculating the correlation coefficient. The significance of a given correlation between a reproductive variable and weather variable was then inferred from the resulting distribution of sample correlation coefficients. For fruit set and capsule production, I examined correlations with both the current and the previous year's weather. For flowering rate, I considered only the previous year's weather because flower primordia are probably initiated prior to the current growing season. In all cases, I considered only months with weather records spanning at least 4 yr. Because rainfall records were unavailable for some month-year combinations, only some of the possible relationships involving reproduction and spring/summer precipitation were tested.

Results

DORMANCY

I detected 263 episodes of prolonged dormancy in *Calochortus lyallii* and 153 episodes in *C. macrocarpus*. Of the plants initially censused in 1996, 21% of *C. lyallii* and 27% of *C. macrocarpus* postponed emergence at least once (Fig. 2.3). Although the distribution of the lengths of dormancy periods was similar for the two species, it was not identical ($\chi^2 = 11.63$, df = 3, $P < 0.01$). The majority of dormancy periods lasted 1 yr, but some plants disappeared for 2 consecutive yr and a few were absent for 3 yr. In addition, several previously unmarked plants appeared in the plots between 1998 and 2000,

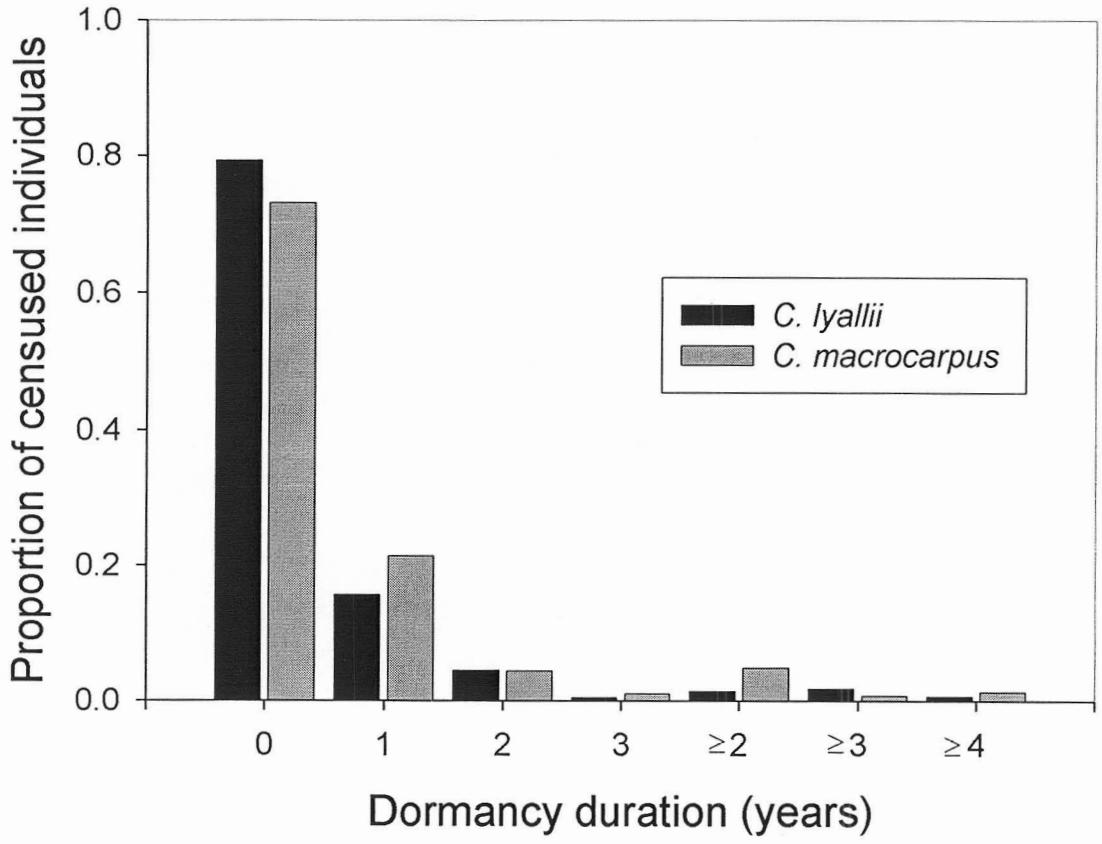


Figure 2.3 Distribution of observed dormancy durations for *C. lyallii* and *C. macrocarpus* (populations pooled). Plants alive at the initial census in 1996 are assigned to the following categories: no dormancy; and 1, 2, or 3 yr dormant. Plants that first 'appeared' in the plots in 1998 or later cannot be assigned an exact dormancy period (only a minimum) and are indicated as ≥ 2, ≥ 3, or ≥ 4 yr dormant.

plots between 1998 and 2000, implying that dormancy may last up to 4 yr, and possibly longer. In this situation I could assign only a minimum dormancy estimate, as there was no way to know if individuals were dormant or not prior to the first census (Fig. 2.3).

Although the actual number of plants dormant each summer could not be determined because the potential length of dormant periods equalled or exceeded the length of the study, it was possible to obtain minimum estimates of the percentage dormant in each sample population for the years 1997-1999 (Fig. 2.4). Overall, prolonged dormancy was more frequent in *C. macrocarpus* than in *C. lyallii* (1997: $\chi^2 = 9.22$, df = 1, $P < 0.01$, sites pooled; 1998: $\chi^2 = 10.70$, df = 1, $P < 0.01$, sites pooled; 1999: $\chi^2 = 18.55$, df = 1, $P < 0.01$, sites pooled). Both species showed a similar pattern of temporal variation, with the highest proportions of dormant plants occurring in 1998. For each year, the highest proportion of dormant individuals for *C. lyallii* occurred at site ES and for *C. macrocarpus* at site WS. Loglinear analyses showed that, for both species, the effects of site and year were highly significant (Table 2.1). However, interactions between location and year were not significant (Table 2.1), implying that annual fluctuations were synchronised across sites.

SELF COMPATIBILITY

Both species showed the ability to set fruit by self-fertilisation. In *Calochortus lyallii*, 30% of self-pollinated flowers set fruit, vs. 22% of control (open-pollinated) flowers. The difference between treatment and control was not significant (Wilcoxon Signed Rank Test, $P = 0.38$). Fruiting capsules developed from open-pollinated flowers generally set more seeds than those from self pollen (21.33 ± 13.69, $n = 6$ vs. 9.38 ± 9.43, $n = 8$), but the difference again was not significant (Student's t-test, df = 12, $P = 0.08$). Results from the corresponding *C. macrocarpus* experiment could not be analysed statistically because most of the bagged plants were browsed by deer. However, seed was set by about half of the bagged flowers not damaged by deer, a proportion very similar to that observed in the unbagged treatment. The number of seeds set per capsule (bagged: 109.20 ± 64.03, $n = 6$; unbagged: 97.40 ± 61.88, $n = 5$) did not significantly differ (Student's t-test, df = 8, $P = 0.77$).

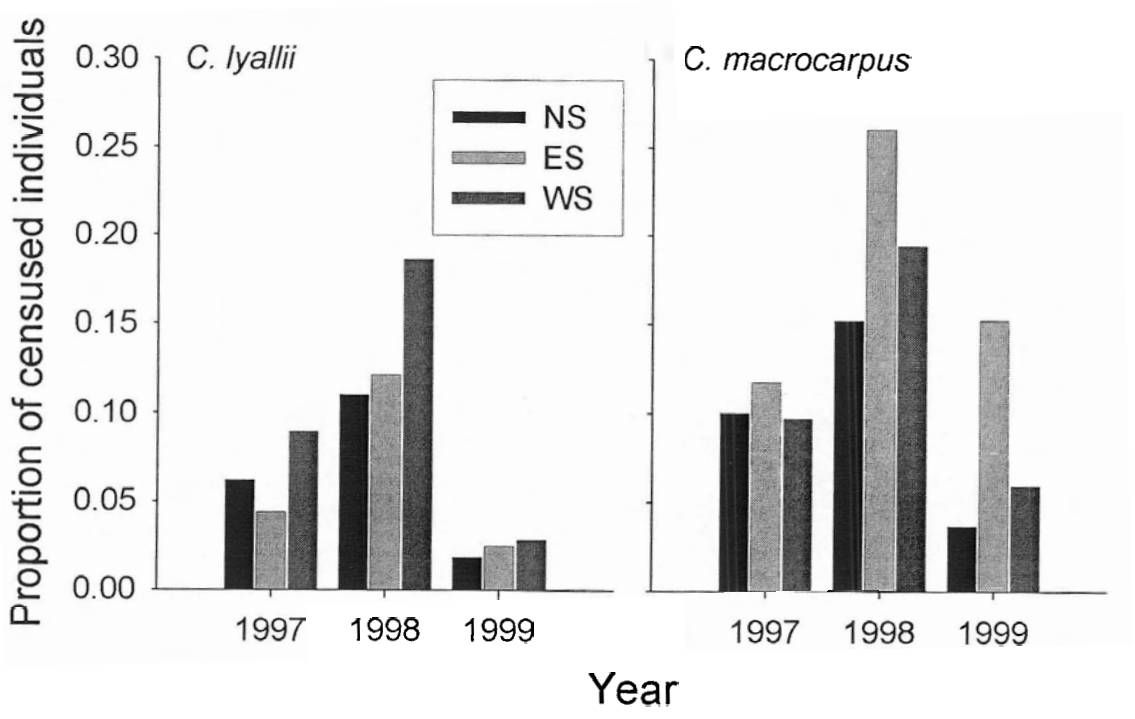


Figure 2.4 Estimated minimum proportion of *Calochortus lyallii* and *C. macrocarpus* plants dormant in each population from 1997-1999, the three years for which dormancy records are available. Sites: north slope (NS), east slope (ES), west slope (WS).

Table 2.1 Loglinear contingency analysis of the effect of year and site on dormancy proportions (P) in *Calochortus lyallii* and *C. macrocarpus* at Black Mt. Years = 1997, 1998, and 1999. Sites = NS, ES, and WS. Data shown are χ^2 approximations using a G^2 test.

	C. lyallii			*C. macrocarpus*		
Model	*df*	G^2	*P*	*df*	G^2	*P*
P, Year x Site	8	212.35		8	72.68	
P x Site, Year x Site	6	190.32		6	55.61	
P x Site	2	22.03	<0.0001	2	17.07	0.0002
P, Year x Site	8	212.35		8	72.68	
P x Year, Year x Site	6	25.59		6	26.31	
P x Year	2	186.76	<0.0001	2	46.37	<0.0001
P x Year, Year x Site	6	25.59		6	26.31	
P x Year, Year x Site, P x Site	4	3.12		4	8.11	
P x Site	2	22.47	<0.0001	2	18.20	<0.0001
P x Site, Year x Site	6	190.32		6	55.61	
P x Year, Year x Site, P x Site	4	3.12		4	8.11	
P x Year	2	187.20	<0.0001	2	47.50	0.0001
P x Year, Year x Site, P x Site	4	3.12		4	8.11	
P x Year X Site	0	0		0	0	
P x Year X Site	4	3.12	0.5380	4	8.11	0.0876

Notes: Contingency analysis test results are based on the log-likelihood test ratio, G^2, which is compared to a χ^2 distribution. The significance of an interaction (P x Site, P x Year, P x Year x Site) is assessed by examining ΔG^2 following the addition of that term to the model. ΔG^2 is distributed as χ^2 with degrees of freedom equal to the difference in degrees of freedom between the two models being compared (Caswell 2001).

Flowers of *C. lyallii* are moderately protandrous, i.e., anthers tend to shed their pollen before the stigma on the same flower becomes receptive (pers. obs.). For self-fertilisation to occur, pollen must be transferred from a pollen-releasing flower lower down in the inflorescence. Consequently, selfing may be uncommon under natural conditions. In contrast, the anthers and stigmas on *C. macrocarpus* flowers mature at about the same time, allowing pollen to be easily transferred from anther to stigma within the same flower. In some bagged flowers, ovaries had already begun to fill with seed by the time I attempted to hand pollinate them, suggesting that self-fertilisation occurs commonly in this species.

VARIATION IN FLOWERING AND FRUIT SET

The average proportion of adult plants initiating flowers was generally much higher for *C. lyallii* than for *C. macrocarpus*. Plot means for a given site and year ranged from 0.51-0.87 and from 0.07-0.79 respectively (Table 2.2). For both species, flowering differed significantly among sites only in 1997 and 1999. However, there was significant variation among years at all sites. Annual variation was most pronounced in *C. macrocarpus*, with much higher flowering rates in 1996 than in any other year (Table 2.2). The proportion of adult *C. macrocarpus* plants in flower (means of all plots per site) never exceeded 0.5 at any site from 1997-2000, whereas the proportion for *C. lyallii* exceeded this value in all years at all sites (Table 2.2).

Fruit set (the proportion of buds maturing to fruit) ranged from 0.10-0.34 in *C. lyallii* and from 0.03-0.68 in *C. macrocarpus* (Table 2.3). There were significant differences among *C. macrocarpus* populations in all years except 1998; in contrast, *C. lyallii* populations differed significantly only in 1997. In *C. macrocarpus*, fruit set varied significantly at two of the three sites, whereas *C. lyallii* showed significant temporal variation at only one site (Table 2.3). Average fruit set across all site-year combinations was 0.24 ($\pm$ 0.06) for *C. lyallii* versus 0.31 ($\pm$ 0.21) for *C. macrocarpus*. In a random sample of capsules from the study area, capsules of *C. macrocarpus* contained significantly more seeds on average than those of *C. lyallii* (23 $\pm$ 14 and 92 $\pm$ 54 seeds, respectively, $P < 0.001$, $n = 42$).

Table 2.2 Flowering plants as a proportion of all adult plants (mean ± SD) in *C. lyallii* and *C. macrocarpus* populations at three sites on Black Mt. over five years (1996-2000), based on observations in 95 *C. lyallii* and 60 *C. macrocarpus* plots. Adult plants were all those with leaf width ≥ that of the smallest fruiting plant in each population. Values shown are plot means (± SD).

	Year				
Site	1996	1997	1998	1999	2000
			C. lyallii		
		*			
NS[†††]	0.66 ± 0.18	0.75 ± 0.18	0.54 ± 0.26	0.86 ± 0.14	0.84 ± 0.21
ES[†††]	0.70 ± 0.27	0.85 ± 0.17	0.61 ± 0.30	0.87 ± 0.13	0.83 ± 0.21
WS[†††]	0.75 ± 0.14	0.74 ± 0.17	0.51 ± 0.26	0.80 ± 0.21	0.80 ± 0.23
			C. macrocarpus		
		**		**	
NS[†††]	0.79 ± 0.16	0.16 ± 0.18	0.22 ± 0.24	0.07 ± 0.13	0.23 ± 0.20
ES[†††]	0.74 ± 0.15	0.40 ± 0.25	0.31 ± 0.28	0.27 ± 0.22	0.47 ± 0.30
WS[†††]	0.75 ± 0.24	0.37 ± 0.26	0.15 ± 0.21	0.35 ± 0.29	0.41 ± 0.27

* Significant difference among sites, by year; $^{*}P < 0.05$, $^{**}P < 0.01$

† Significant difference among years, by site; $^{†††}P < 0.001$

Notes: Significance of effects was tested using non-parametric randomisation procedures applied to individual plots ($n = 2000$ permutations), with standard deviation of flowering proportions as the test statistic.

Table 2.3 Percent fruit set (proportion of flower buds maturing into seed capsules) in *C. lyallii* and *C. macrocarpus* populations at three sites on Black Mt. over four years (1996-2000), based on observations in 95 *C. lyallii* and 60 *C. macrocarpus* plots. Values shown are plot means (± SD).

	Year			
Site	1996	1997	1998	1999
		C. lyallii		
		*		
NS†	0.29 ± 0.17	0.10 ± 0.15	0.20 ± 0.28	0.24 ± 0.22
ES	0.22 ± 0.21	0.26 ± 0.24	0.18 ± 0.31	0.26 ± 0.21
WS	0.34 ± 0.23	0.26 ± 0.28	0.28 ± 0.33	0.27 ± 0.23
		C. macrocarpus		
	*	**		*
NS	0.22 ± 0.24	0.27 ± 0.42	0.5 ± 0.55	0.30 ± 0.45
ES†††	0.03 ± 0.10	0.23 ± 0.29	0.21 ± 0.39	0.60 ± 0.27
WS††	0.18 ± 0.68	0.68 ± 0.30	0.49 ± 0.34	0.04 ± 0.14

* Significant difference among sites, by year; $*P < 0.05$, $**P < 0.01$

† Significant difference among years, by site; $^{\dagger}P < 0.05$, $^{\dagger\dagger}P < 0.01$,

Notes: Significance of effects was tested using non-parametric randomisation procedures (Manly 1997) applied to individual plots (n = 2000 permutations), with standard deviation of % fruit set as the test statistic.

The third measure—number of seed capsules per adult plant—is an integration of the proportion of plants flowering, fruit set, and inflorescence size (Table 2.4). Per capita capsule production (over three sites and four years) averaged 0.29 (± 0.17) for *C. lyallii*, compared to only 0.12 (± 0.11) for *C. macrocarpus*. The highest per capita capsule production was by *C. lyallii* in 1996, at *c.* one capsule for every two adult plants (Table 2.4). However, production varied significantly among years. In *C. macrocarpus*, which underwent heavy browsing of fruit by deer in some years, fruiting success was highly variable, ranging from as low as 0.01 (1 capsule per 100 individuals) to 0.43 depending on year and location. The worst year for fruit production for both species was 1998, which also had below-average proportions of flowering individuals (Table 2.4).

FLOWERING AND FRUITING IN RELATIONSHIP TO CLIMATE

Monthly temperature and precipitation data for Osoyoos from 1995-2000 are shown in Fig. 2.5. Relationships of flowering and fruiting to these variables were similar for both species (Table 2.5). The proportion of adult plants flowering was positively correlated with spring temperatures of the previous year and negatively correlated with precipitation. Fruit set was generally positively correlated with previous-year temperature and precipitation and negatively correlated with current-year precipitation, but showed no clear pattern with respect to current-year temperature. Fruit production (number of fruits per adult plant) was positively correlated with previous-year temperature and negatively correlated with current-year temperature and previous-year precipitation. In *C. lyallii*, fruit production and current-year precipitation were negatively correlated, whereas in *C. macrocarpus* these two variables did not show any consistent correlation.

In general, flowering and fruiting appear to respond favourably to warm dry conditions in the previous year. There was some suggestion, especially in *C. macrocarpus*, that fruit set and per capita fruit production respond in opposite directions to increased rainfall and temperatures during the current year (Table 2.5).

Table 2.4 Number of seed capsules produced per adult plant (mean ± SD) in *C. lyallii* and *C. macrocarpus* populations at three sites on Black Mt. over four years (1996-1999), based on observations in 95 *C. lyallii* and 60 *C. macrocarpus* plots. Values shown are plot means (± SD).

	Year			
Site	1996	1997	1998	1999
		C. lyallii		
		*		*
NS†††	0.46 ± 0.67	0.10 ± 0.13	0.12 ± 0.24	0.16 ± 0.17
ES†††	0.50 ± 0.73	0.50 ± 0.58	0.07 ± 0.20	0.37 ± 0.41
WS†	0.48 ± 0.47	0.31 ± 0.50	0.09 ± 0.16	0.23 ± 0.28
		C. macrocarpus		
	*	**		**
NS††	0.18 ± 0.26	0.02 ± 0.05	0.04 ± 0.09	0.01 ± 0.05
ES††	0.03 ± 0.09	0.11 ± 0.14	0.04 ± 0.13	0.21 ± 0.28
WS††	0.12 ± 0.17	0.43 ± 0.50	0.07 ± 0.16	0.31 ± 0.31

* Significant difference among sites, by year; *$P < 0.05$, **$P < 0.0$

† Significant difference among years, by site; †$P < 0.05$, ††$P < 0.01$

Notes: Significance of effects was tested using non-parametric randomisation procedures applied to individual plots (n = 2000 permutations), with standard deviation of capsules plant^{-1} as the test statistic.

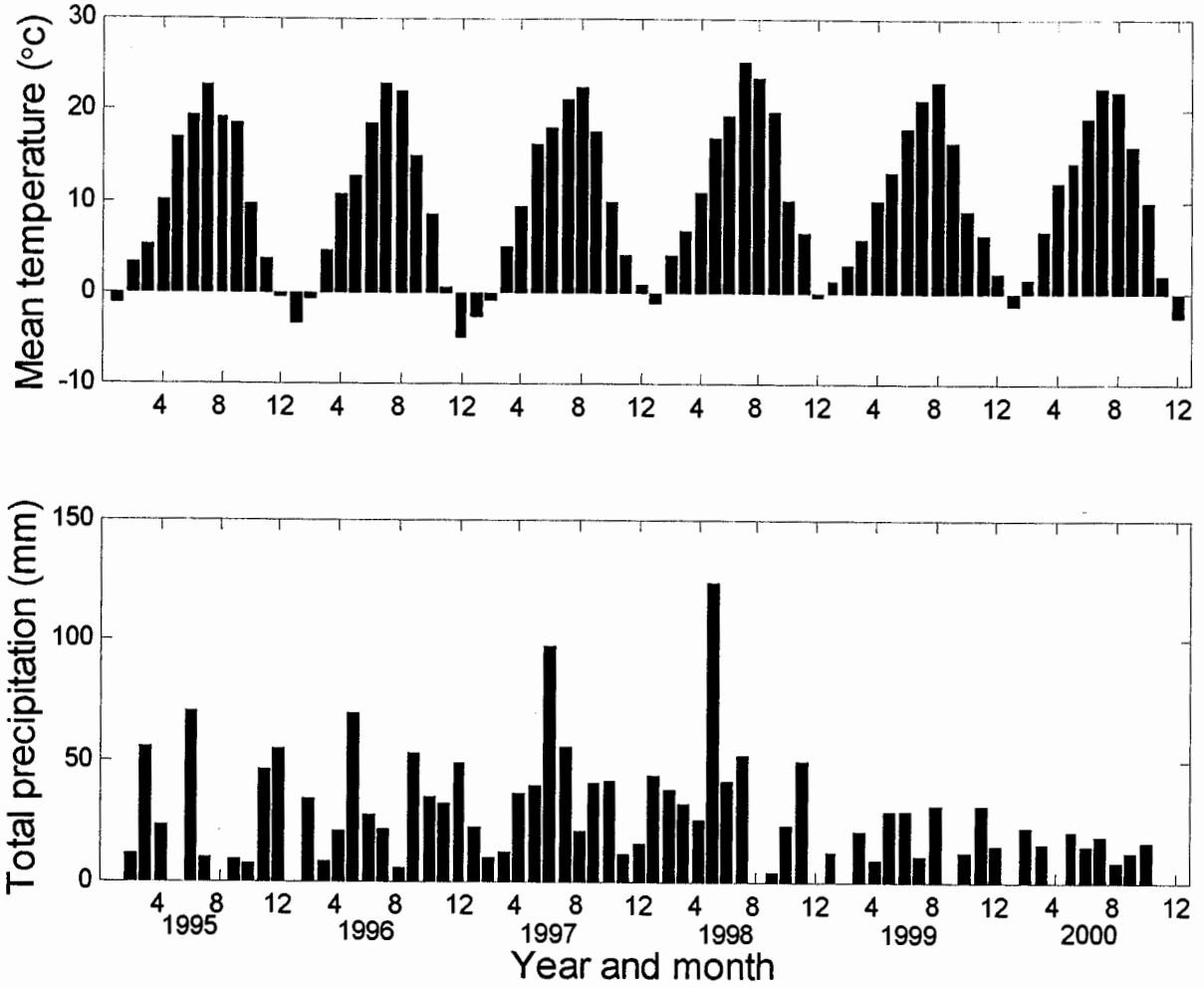


Figure 2.5 Monthly precipitation and mean monthly temperatures for Osoyoos, Canada for the years 1995-2000. Numerals refer to months of the year. Blanks in the precipitation record indicate monthly data are unavailable (i.e., there were no months with nil precipitation).

Table 2.5 Correlation coefficients between climate variables (mean monthly temperature and total monthly precipitation) and three indices of reproductive performance (ratio of flowering to vegetative plants, % fruit set, and total fruits per plant) for *C. lyallii* and *C. macrocarpus*. Each value is the mean (± SD) of the bootstrap distribution of sample correlation coefficients ($n = 2000$). Positive correlations are shown in bold; "--" indicates no analysis attempted (see text for details).

	C. lyallii			*C. macrocarpus*		
Climate variable	Ratio of flowering:vegetative plants	%Fruit set	No. fruits per flowering plant	Ratio of flowering:vegetative plants	%Fruit set	No. fruits per flowering plant
Precipitation in current year						
April	--	--	--	--	--	--
May	--	**0.01 (.01)**	-0.44 (0.01)	--	**0.35 (0.00)**	-0.93 (0.00)
June	--	-0.80 (0.01)	-0.23 (0.01)	--	-0.87 (0.00)	**0.41 (0.01)**
July	--	-0.80 (0.01)	-0.23 (0.01)	--	-0.87 (0.00)	**0.41 (0.01)**
Precipitation in previous year						
April	-0.90 (0.00)	**0.02 (0.01)**	-0.70 (0.01)	-0.94 (0.00)	**0.23 (0.01)**	-0.82 (0.00)
May	--	--	--	--	--	--
June	-0.92 (0.00)	**0.29 (0.01)**	-0.26 (0.01)	-0.89 (0.00)	**0.62 (0.01)**	-0.93 (0.00)
July	-0.92 (0.00)	**0.29 (0.01)**	-0.26 (0.01)	-0.89 (0.00)	**0.62 (0.01)**	-0.93 (0.00)
Temperature in current year						
April	--	**0.51 (0.01)**	-0.08 (0.01)	--	**0.80 (0.00)**	-0.85 (0.00)
May	--	-0.78 (0.01)	-0.79 (0.00)	--	-0.62 (0.00)	-0.35 (0.01)
June	--	-0.05 (0.01)	-0.56 (0.01)	--	**0.29 (0.01)**	-0.92 (0.00)
July	--	**0.09 (0.01)**	-0.39 (0.01)	--	**0.44 (0.01)**	-0.94 (0.00)
Temperature in previous year						
April	**0.68 (0.01)**	-0.09 (0.01)	**0.25 (0.01)**	**0.61 (0.01)**	-0.46 (0.00)	**0.91 (0.00)**
May	-0.47 (0.01)	**0.78 (0.01)**	**0.18 (0.01)**	-0.47 (0.01)	**0.85 (0.00)**	-0.41 (0.01)
June	**0.18 (0.01)**	**0.77 (0.01)**	**0.83 (0.00)**	**0.20 (0.01)**	**0.61 (0.01)**	**0.37 (0.01)**
July	**0.32 (0.01)**	**0.76 (0.01)**	**0.83 (0.00)**	**0.24 (0.01)**	**0.61 (0.01)**	**0.37 (0.01)**

*Significant. A correlation was considered significant if all 2000 bootstrap estimates were either positive or negative (i.e., the bootstrap distribution did not include 0).

FATES OF BUDS, FLOWERS, AND FRUITS

The fates of flower buds over the course of the season (whether aborted, flowered and aborted, damaged/grazed, or matured fruit) varied among years and between species (Fig. 2.6). The proportion of buds successfully maturing to fruit ranged from 0.11-0.26 for *C. lyallii* and from 0.11-0.52 for *C. macrocarpus*. In *C. lyallii*, failure of buds to mature was related primarily to abortion of buds or flowers, and secondarily to damage sustained from insect activities. Damage from other types of herbivory was negligible. In *C. macrocarpus*, abortion of buds or flowers was less common than in *C. lyallii*; however, loss of fruits to predation (primarily by deer) was an important factor limiting seed production in some years. In 1999, when damage from grazing was minimal, > 50% of *C. macrocarpus* buds produced fruit, compared to the observed maximum of 27% for *C. lyallii* (Fig. 2.6).

Discussion

DORMANCY

Substantial proportions of the *Calochortus lyallii* and *C. macrocarpus* individuals in populations on Black Mt. failed to emerge above ground for one or more growing seasons. Such extended dormancy has not been specifically reported for *Calochortus* previously, although Fredericks (1992) reported incidences of extended plant absence during a long-term study of rare *Calochortus* species from Oregon, ascribing these disappearances to ground-level herbivory. The proportion of dormant plants that I observed (ranging from *c.* 2 to 18% in *C. lyallii* and from *c.* 3 to 26% in *C. macrocarpus*) was much less than observed for some orchids (e.g., Tamm 1972, Hutchings 1987, Shefferson et al. 2001) and for the grassland geophytes *Silene spaldingii* (Lesica 1997) and *Allium amplectens* (Hawryzki 2002), but was comparable to, or higher than, the rates recorded for a number of other geophytes (Lesica and Steele 1994). The majority of dormancy episodes lasted 1 yr, and few individuals were dormant longer than 2 yr, consistent with findings for most other species (Lesica and Steele 1994). However, previously unrecorded plants continued to appear in the study plots up until the end of the

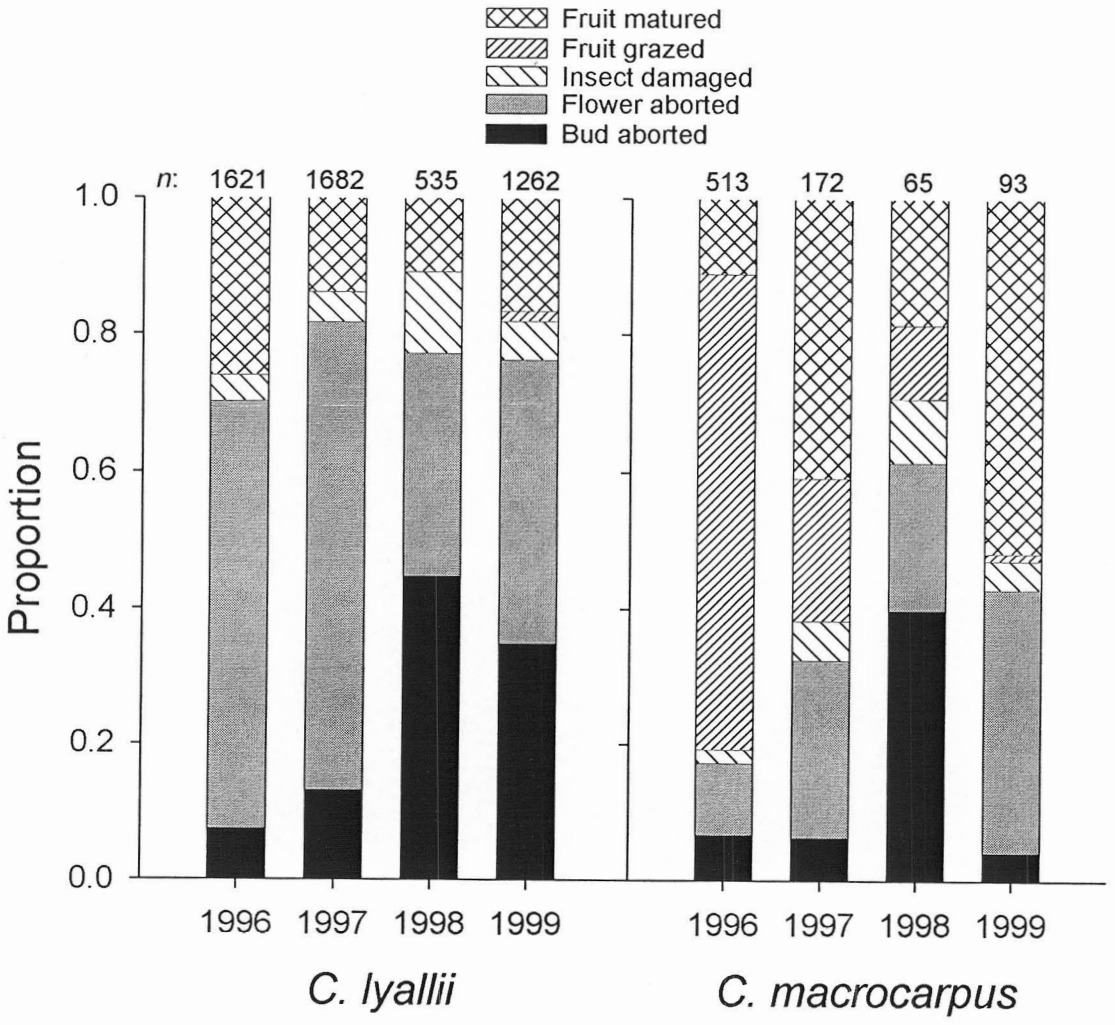


Figure 2.6 Within-year fate of flower buds of *C. lyallii* and *C. macrocarpus*, from 1996-1999, as a proportion of all buds initiated in a given year. Five possible fates were recorded (bud aborted; flower aborted; bud or flower destroyed by insects; fruit grazed; fruit successfully matured). Numbers above bar indicate sample size.

study, and thus the maximum duration of dormancy could be longer than the 3-yr periods I confirmed.

Whole genet dormancy is an often-ignored stage in the life history of plants, and very few studies have obtained simultaneous dormancy data for multiple populations of two related, sympatrically occurring species. Perhaps the most striking thing about my results was the degree of synchronisation in dormancy patterns, both among populations of the same species and between species. The implication is that dormancy was not a random occurrence within populations but a response to the same external factor(s). The annual variation in dormancy rates could be related to climatic factors, but I could not evaluate this possibility because I could only obtain dormancy estimates for three years. Boeken (1991) reported that the failure of *Tulipa systola* plants to emerge above ground during the growing season is the result of early root and shoot abortion in response to soil water deficits, rather than a continuation of the summer resting phase. However, it seems unlikely that dormancy in *C. lyallii* and *C. macrocarpus* is brought on by drought, as the year with the highest dormancy rate was also the year with the wettest spring, whereas the year with the lowest frequency of dormant plants was also the driest of the three years—although it is possible that dormancy was induced by conditions in a previous year (for example, if prior resource acquisition were low). Alternatively, dormancy may have been caused by some synchronised disturbance that affected all sites in a similar way, such as a fungal outbreak or a pulse in subterranean herbivory. Morrow and Olfelt (2003) showed that defoliation by herbivores can induce dormancy lasting up to 10 yr in *Solidago*, and it is possible that non-emergence in *Calochortus* is also related to events occurring during the below-ground phase, i.e., between sprouting of the bulb and emergence of the shoots above ground. However, the actual mechanism(s) responsible for non-emergence in these two species could not be determined from field observations alone.

The consistent differences in dormancy probabilities across sites are presumably related to differences in microsite quality. For example, in this study area, some sites may receive more water from run-off or shed it less effectively, and plants growing there may be less likely to emerge than those in better (drier) sites. If non-emergence is a bet hedging strategy to reduce the risk of sprouting under unfavourable conditions, site-specific consistency would not be expected (Boeken 1991).

Explaining the function of whole genet dormancy in geophytes is a challenging problem. Dormancy could benefit plants by allowing them to conserve energy during harsh periods, thereby enhancing individual survival and future reproduction. However, because dormant plants do not produce photosynthetic tissue, these individuals are prevented from accumulating resources for one or more growing seasons, potentially resulting in reduced survivorship and reproductive opportunity. For example, Shefferson et al. (2003) found that dormant *Cypripedium* plants had a higher mortality rate than ones that emerged every year, and concluded that dormancy was exerting a cost with respect to future survival and reproduction. Likewise, Boeken (1991) was unable to identify any fitness benefits directly associated with non-emergence in the desert perennial *Tulipa systola*. However, detecting fitness trade-offs without experimental manipulation is difficult; greater mortality in plants with high dormancy could simply reflect conditions in poor microsites where mortality might be even greater without dormancy. Furthermore, dormancy could act as a buffer against catastrophic events affecting established plants, in which case this stage would have a positive fitness effect. In subsequent papers, I will attempt to quantify the impact of dormancy on population growth rate itself in *C. lyallii* and *C. macrocarpus*.

The amount of dormancy I found has important implications for population surveys and population monitoring. For example, a survey of *C. macrocarpus* undertaken in 1998 would have underestimated population size by a quarter at minimum, and probably more (given that a proportion of the population was still undetected by 1998). Likewise, a one-year demographic study would have overestimated mortality by a substantial margin. Population surveys involving geophytes should take into account the possibility that the visible population is not necessarily an accurate indication of actual population size, and that a population may not actually be extirpated when no individuals are observed (Lesica and Steele 1994). The stable population structure, calculated from annual transition data using a matrix population model, indicates the proportion of dormant individuals that can be expected under stable conditions (Caswell 2001). However, reliable information on dormancy can only be obtained through long-term monitoring of marked individuals in permanent plots.

REPRODUCTION

Seed production in *Calochortus* is a function of several variables, including (1) the probability that a mature plant will flower; (2) the number of flowers produced; (3) the fraction of flowers that set fruit; and (4) the number of seeds produced in each capsule. The proportion of flowering individuals was greater in *C. lyallii* than in *C. macrocarpus* populations in most years, although flowering was highly variable for both species. However, capsules of *C. macrocarpus* contained more seeds on average than those of *C. lyallii.* Given that seed size is similar, *C. macrocarpus* thus invests more resources than does *C. lyallii* in each seed capsule. In this regard, *C. lyallii* may be more of a bet hedger than *C. macrocarpus*, producing many flowers but investing relatively less energy in each. Because of herbivory by deer, very few of the capsules initiated by *C. macrocarpus* survive long enough to release seeds. However, because of the large number of seeds set per capsule, per capita seed production was actually higher, which may help compensate for the low flowering frequency in this species on Black Mt.

The limitations to seed production differed greatly between the species. High abortion rates in *C. lyallii* do not appear to be related to pollinator availability. In this species the lowest flowers in the inflorescence are often female-infertile (lacking an ovary), suggesting that some flowers are serving a male function (Sutherland and Delph 1984) by increasing pollen production and duration of pollen dissemination. In the related *C. leichtlinii*, most plants produce two hermaphroditic flowers but mature only one fruit (Holtsford 1985), and it is likely that second flowers in that species fulfil a primarily male function. In contrast to *C. lyallii*, low fruit production in *C. macrocarpus* is the result mostly of vertebrate grazing on developing fruits, rather than spontaneous abortion of ovaries. In the absence of browsing by deer, percent of flowers yielding mature fruit would be higher in *C. macrocarpus* than in *C. lyallii*. This is a clear instance of a herbivore causing a reversal of reproductive advantage between two species. To the extent recruitment in *C. macrocarpus* is seed limited, vertebrate herbivory likely plays a major role in its local population dynamics. In both species, invertebrates caused some damage to buds, flowers and developing fruits; for *C. lyallii* this was the only significant type of herbivory that occurred.

Thus it may be necessary to differentiate between potential and realised fruit production when comparing these two species. The higher potential fruit set of *C. macrocarpus* relative to *C. lyallii* could be the result of larger, showier flowers serving as superior pollinator attractants; reduced intraspecific competition for pollinators due to lower plant densities; or a greater ability to set fruit via self-pollination. Self-compatibility could confer an advantage for the sparsely-occurring *C. macrocarpus* if plants are frequently too widely dispersed to be reliably visited by pollinators. Inbreeding can play an important role in seed production even in species with a substantial capacity for both inbreeding and outbreeding (Ohara et al. 2001). This trait may be a factor enabling *C. macrocarpus* to disperse to new habitats, possibly helping to explain its broad geographical distribution. Although self-compatibility is often associated with reduced seed production (Weller 1994), there is little indication that *C. macrocarpus* is experiencing a reduction in this respect relative to *C. lyallii*.

Studies in grassland ecosystems have shown that spring and summer precipitation influences performance of vascular plants (Rabinotwitz et al. 1989, Bengtsson 1993). Although five years of data are insufficient to evaluate conclusively the effects of weather on reproductive performance in *C. lyallii* and *C. macrocarpus*, they can suggest some trends. Flowering and fruiting in the two species correlate most strongly with weather conditions in the previous year. This is not surprising: organ preformation is common in geophytes (Geber et al. 1997, Ohara et al. 2001), and performance in one year is probably closely tied to resource accumulation in the previous season or seasons, when shoot and flower buds are formed. The relationship between reproduction and previous year weather occurs in many herbaceous species (e.g., Bierzychudek 1982), though such a relationship has not been previously demonstrated in *Calochortus*. Warm, dry conditions in the previous year favoured flowering and fruiting in both the species in my study, implying that climatic conditions at the periphery of their range may be a factor limiting their spread.

There is some indication that per capita flower and fruit production was correlated temporally with aboveground emergence rates; the year with the lowest reproductive success (1998) also had the highest proportion of dormant plants. This was also the year with the wettest spring. These findings are consistent with the expectation that marginal

habitats are more likely to be encountered near a species' geographical range limit (or elevational limit) than elsewhere in the range (Nantel and Gagnon 1999, Loewen et al. 2001). At these sites the two species are evidently not limited by a lack of precipitation, but by an excess of it, suggesting that, in the present case, ecological marginality coincides with range marginality.

CONCLUSION

Although both of the *Calochortus* species I studied are near or at the limits of their distribution, factors contributing to population persistence and local distribution differ. The potentially higher seed production of *C. macrocarpus* compared to *C. lyallii* is largely offset by herbivory by deer, implying that an external (and controllable) factor may be greatly limiting population size and density of the former. Major negative impacts on plant populations resulting from high deer abundance have been documented in many areas of North America (Russel et al. 2001). On the other hand, the greater ability of *C. macrocarpus* to self-pollinate may partly reduce the negative effects of reduced pollinator availability stemming from low plant density. Greater dormancy than in *C. lyallii* could possibly also buffer population decline if dormancy reduced mortality in years with especially poor growing conditions. In contrast, *C. lyallii* does not appear to be strongly affected by a specific external factor such as herbivory. Thus, from a practical management point of view, bringing about increases in population size in *C. lyallii* may be more intractable because there is no obvious major external factor to be modified (assuming that control of deer numbers is feasible).

Overall, my study indicates that even closely related taxa growing sympatrically at their geographical (and possible ecological) limits can differ substantially in details of life history, and that extrapolating about the traits contributing to population persistence in one species based on information for another species may therefore be misleading. Furthermore, identifying such differences could be critical to conservation efforts. Traits ranging from protracted dormancy to seed production need to be given due consideration when evaluating the prospects for, and the factors contributing to, population persistence.

Chapter 3: Effects of environmental heterogeneity on the demography of *Calochortus lyallii* (Liliaceae), a bulbous perennial with prolonged dormancy

Introduction

Plants exhibit spatial aggregation at multiple scales (Harper 1977, Greig-Smith 1979, Horvitz and Schemske 1986, Schupp 1995, Fitter et al 2000). Aggregations may consist of a few individuals sharing a common microsite; adjacent patches within a colony; sets of locally connected sub-populations; or isolated populations distributed variously on the landscape, and the total distribution of a species reflects all of these (Quintana-Ascencio and Menges 1996, Hanski and Simberloff 1997, Watkinson et al. 2000). Demographic variation may occur at all scales. For example, adjacent habitat patches may show differences in recruitment, reflecting the availability of safe sites for germination (Thomson et al. 1996), whereas central and peripheral populations might exhibit climate-induced differences in growth and survivorship (Nantel and Gagnon 1999). Furthermore, temporal variation in demographic characteristics can occur at different spatial scales (Pascarella and Horvitz 1998). For example, a major weather event might cause a correlated response over large regions, at the same time a localised disturbance (e.g., herbivory) is producing a separate response within a single population. An appreciation of this interplay of spatial and temporal variation may be critical for the interpretation of demographic studies (Wijesinghe and Hutchings 1997, Pascarella and Horvitz 1998).

At a fine scale, plant density varies within plant populations, and the stability of this density structure may have important demographic implications. Because microhabitat variation is widespread within populations, variations in plant density may result from an environmental mosaic of patches with varying equilibrium densities. Plant numbers could be constant ($\lambda = 1$) within a patch, but the numbers of plants supported would vary. However, variable equilibrium densities within a population could also be the result of source-sink dynamics. A source-sink structure develops when propagules from productive patches ('sources') maintain populations in poor patches ('sinks'), where local

reproductive success fails to keep pace with local mortality (Keddy 1982, Pulliam 1989, Dias 1996). Although often modeled at the landscape or regional level (e.g., Shmida and Wilson 1994), source-sink dynamics can also occur on a local scale (Whittaker and Levin 1977, Shmida and Ellner 1984, Watkinson et al. 1989, Thomson et al. 1996, Kunin 1998; but see Kadmon and Tielborger 1999). For example, Kadmon and Shmida (1990) showed that most seeds (75-99%) of the annual grass *Stipa capensis* were produced in an area covering only 10% of the total patch distribution.

If microhabitats vary in favourability over time, local population dynamics could be represented by a 'shifting mosaic' structure (Bormann and Likens 1979, Clark 1991). Shifting mosaics are common at the landscape level, often driven by disturbance-succession sequences, and frequently include the extremes of population extinction and establishment (Eriksson 1996). Microsite characteristics can also vary over time as a result of local disturbance or succession (Menges 1990, Pascarella and Horvitz 1998, Valverde and Silvertown 1998, Olff et al. 2000). Recruitment occurring in different microsites at different times can result in a local metapopulation comprised of a collection of cohorts, each possessing a unique history and structure (Clark 1991). A shifting mosaic of habitat patches is likely to lead to local variation in population trajectories, with some patches increasing in density as others decrease (Maloney 1988). Shifting mosaic and source-sink dynamics could occur simultaneously within a population, presenting a notable challenge to deciphering population dynamics and causal factors. Furthermore, patch-level variation may be superimposed on overall population trends or fluctuations. A key question is whether changes in the demography of different microsites or areas of differing density occur in tandem, or are weakly related or even negatively correlated.

A complicating factor in the evaluation of population dynamics of some perennial herbaceous plants is the occurrence of prolonged dormancy, in which individuals remain below ground for one or more growing seasons (Lesica and Steele 1994, Shefferson et al. 2001). Dormancy changes the way in which a plant perceives its environment, generally reducing the experienced variability (Venable and Lawlor 1980). For some geophytic species, extended dormancy may be a key to survival during adverse periods, with potentially major consequences for population dynamics (Lesica and Steele 1994). Because the detailed monitoring required for demographic analysis is only rarely

conducted for more than a few years during any given study, both the tracking of dormancy and its incorporation into population models present a special challenge (Shefferson et al. 2001, Hawryzki 2002). If it occurs often, however, prolonged dormancy cannot be safely ignored in demographic analyses (Menges 2000).

Stage-based projection matrices (Lefkovitch 1965, Caswell 2001) provide a powerful tool for evaluating population dynamics of plants, both among and within populations. Empirical studies of intraspecific demographic variation in plants have typically modeled dynamics at a single level, usually that of the population (van Groenendael and Slim 1988, Charron and Gagnon 1991, Ehrlén 1995, Guerrant 1996, Oostermeijer et al. 1996, Ehrlén and van Groenendael 1998, Parker 2000) or habitat patch (Huenneke and Marks 1987, Maloney 1988, Bengtsson 1993, Horvitz and Schemske 1995, Maschinski et al. 1997, Kephart and Paladino 1997, Crone and Gehring 1998, Dammon and Cain 1998, Valverde and Silvertown 1998, Mandujano et al. 2001). Fewer studies have compared patterns of plant response to environmental heterogeneity at multiple spatial or organisational scales (e.g., Alvarez-Buylla 1994, Boeken and Canham 1995, Valverde and Silvertown 1997, Nantel and Gagnon 1999, Wijesinghe and Hutchings 1997, 1999, Menges and Dolan 1998, Menges and Hawks 1998, Pascarella and Horvitz 1998, Watkinson et al. 2000). However, ignoring effects of scale in the analysis of demographic variation can lead to mistaken conclusions about the temporal and spatial dynamics of populations and hinders an understanding of the ecological challenges confronting sensitive species (Menges 1990, Wiens 2000).

This paper documents demographic variability and its relationship to micro-environmental factors in the grassland geophyte *Calochortus lyallii*, a long-lived mariposa lily endemic to central Washington and south-central British Columbia. This species frequently exhibits dormancy during the growing season (*Chapter 2*). Within Canada, *C. lyallii* is known only from *c.* 12 sites in southern British Columbia and is a federally-listed threatened species (COSEWIC 2003).

I analysed variation in population dynamics at three levels of heterogeneity: populations, microsite types, and patches of differing plant density. I used a Lefkovitch stage-based matrix model and associated techniques, including two distinct forms of perturbation analysis—life table response experiment analysis (LTREs; Caswell 2001)

and elasticity analysis (de Kroon et al. 1986)—to address the following questions: (i) How do the demographic properties of these populations (stage-specific probabilities of survival, growth, and reproduction, asymptotic growth rate, stable stage distribution, and stage-specific sensitivities) change through space and time? (ii) Which vital rates and life stages make the largest contributions to spatial variability in fitness, as measured by λ? (iii) Which microsite variables are most likely to influence λ as a consequence of their effect on individual vital rates? (iv) Does extended dormancy act to buffer local population flux? (v) Is there evidence for a stabilising equilibrium within or among populations, or do dynamics exhibit a shifting mosaic structure?

Methods

THE SPECIES AND STUDY AREA

Calochortus lyallii (Liliaceae) is a long-lived perennial geophyte occurring in semi-arid grasslands, open woodlands, and sage scrub in central Washington and adjacent south-central British Columbia. The perennating structure is a subterranean bulb. Shoots emerge soon after snow melt (around the end of April in British Columbia). Each plant produces a single basal leaf and, if reproductive, a single terminal inflorescence bearing 1 to 12 flowers. Flowers are pollinated mainly by halictid bees (Miller and Douglas 1999). Flowering peaks in June, and fruit capsules mature in July, after the leaves have withered. Seeds are gravity-dispersed and germinate the following spring. The single cotyledon, which is about the size and dimension of a 4 cm long toothpick, remains green for about three weeks before dying back to the nascent bulb, at which point the young plant enters dormancy until the following year (Miller and Douglas 1999). The bulb eventually descends to a depth of about 10 cm. Established bulbs may remain dormant for 1 to 4 yr before resuming activity (*Chapter 2*). Although bulbifery (the production of new propagules from bulb offsets) has been documented in other species of *Calochortus* (Fiedler 1987), asexual reproduction in *C. lyallii* has not been observed in British Columbia or reported elsewhere.

Calochortus lyallii shows a highly patchy distribution in British Columbia, with dense populations surrounded by wholly unoccupied areas. All known Canadian

populations of *C. lyallii* occur within 5 km of one another and all are within 5 km of the U.S. border (Miller and Douglas 1999).

Research was conducted at three sites on Black Mt., East Chopaka (49°02'N 119°36'W), near the town of Osoyoos in south-central British Columbia. At the time the study was initiated, these were the only known *C. lyallii* populations in Canada (several more have since been located in the same vicinity). All three populations occur at similar elevations (900-1200 m), but are located on separate slopes. Each is separated from the others by about 2 km of coniferous forest. Populations on the north, east, and west slopes of Black Mt. are referred to as 'NS,' 'ES,' and 'WS,' respectively.

Site NS occurs in an open meadow community of bunchgrasses and forbs approximately 200 x 300 m in area situated on a gentle, undulating slope and surrounded on all sides by Douglas-fir (*Psuedotsuga menziesii*) forest. It is the largest of the three sites in area and also contains the largest *C. lyallii* population. ES is on an open gravelly knoll less than 0.5 ha in size. Although bunchgrasses occur at the site, the dominant species are early spring ephemerals and drought-tolerant forbs such as *Lomatium macrocarpum*, *Lewisia rediviva*, and *Astragalus miser*. WS is located on a small, 50 x 50 m flat bench located amongst cliffs and steep talus on the west side of Black Mt. This area is fully exposed to the prevailing westerly winds and receives slightly more precipitation than either NS or ES. In August 1994, two years prior to the start of the study, all three study sites were burned in a wildfire that incinerated most of the forest on Black Mt. Because monitoring of *C. lyallii* on Black Mt. did not begin until 1996, the immediate impact of the fire on these populations is unknown.

FIELD SAMPLING

I established permanent 50 x 50 cm (0.25 m^2) plots at all sites (36 each at NS and ES, 23 at WS), to attain a sample size of approximately 400 individuals per population. Plots were haphazardly chosen to represent a range of habitat conditions and locations at each site. I fixed the location of plot corners with rebar posts over which a portable plot frame could be inserted. Elastic rubber bands were used to partition the plot frame into 25 grid squares, each 10 x 10 cm. The use of elastic bands allowed me to set the plot

frame in place on the ground without disturbing the vegetation. At the initial census, all *C. lyallii* plants in each plot except for seedlings were tagged with a numbered plastic ring, and their location within the grid recorded on a map. Because seedlings had already senesced by the time of the initial census, I did not begin monitoring the seedling stage until the second year of the study (1997).

Plots were censused three to four times a year from 1996 to 2000 (five growing seasons). Each year, following the germination of *C. lyallii* seeds in April, I counted and mapped all newly-recruited seedlings, and located surviving seedlings from the previous year. At this time I also recorded and mapped any 'new' juvenile plants not observed in previous censuses. Seedlings were generally distinguishable from the smallest juveniles by the presence of a seed coat near the base of the cotyledon. In cases where a seed coat was no longer visible, new germinants were distinguished from second-year juveniles on the basis of leaf width (plants were counted as seedlings if leaves were ≤1 mm wide, as juveniles if leaves were >1 mm wide). Larger juveniles and adults were enumerated during subsequent censuses each year, at which time I recorded the following information: (i) width of the basal leaf, to the nearest 0.1 mm; (ii) number of flower buds initiated; (iii) number of flowers produced; (iv) number of fruits produced; (v) herbivore damage to fruits, flowers, or scapes; and (vi) evidence of bulb predation by pocket gophers. From 1998 onward, any established plants appearing in the plots for the first time were assumed to have been previously dormant. These individuals were also mapped and measured.

To measure germination and test for a persistent seed bank, at each site I buried four nylon mesh bags, each containing a random sample of 25 seeds, just beneath the soil/litter surface in late June, the time of year when capsules naturally begin to dehisce. I checked the bags early the following spring, after the first germination flush, and again in late spring, at which time I recorded the total numbers of germinated seeds. Bags were then replaced beneath the litter and left for another year, to allow any remaining dormant seeds to germinate.

To examine possible relationships between microhabitat and differential success of *C. lyallii* at different life stages, I measured, for each of the 95 plots, slope, aspect, litter depth (cm), % litter cover, % rock cover, soil depth (cm), soil moisture, % exposed soil,

% bryophyte cover, and % vascular plant cover. Slope aspect was rated on a 1 to 5 scale from NNE – NE to SSW-SW. Soil depth was characterised by inserting a steel probe and measuring the depth to obstruction (bedrock or stones) at three separate points in the plot, and recording the average depth. Relative soil moisture content was estimated by inserting a hand-held garden meter approximately 10 cm into the ground at the centre of each plot. I took soil moisture readings at all three sites on the same day (June 29, 1997), three days after the last rainfall, in order to minimize effects of timing and weather on this variable. All cover estimates were made visually to the nearest 1% (if <10%) or to the nearest 10% (if >10%).

To obtain an independent measure of *C. lyallii* recruitment patterns and microhabitat variation within populations, in June 1997 I ran 5 transects at 10 m intervals through each site, beginning from a baseline just outside the population and extending to the opposite side. At ten random points along each transect I established 0.5 x 0.5 m plots (50 plots per population) and recorded the number of *C. lyallii* seedlings, juveniles, and adults present in each, along with the same soil/vegetation parameters as for the demographic plots. These will be referred to as the 'transect' plots to distinguish them from the demographic plots.

DELINEATION OF PLOT GROUPS

To examine patch-level dynamics, I separated the 95 demographic plots into microsite categories. Using all plots from the three sites, I employed detrended correspondence analysis (DCA) to examine variation among plots in microsite characteristics. The DCA (performed using the program PC-ORD; McCune and Mefford 1997) was applied to environmental data from each plot.

Distinct groups of plots did not appear on the ordination (Fig. 3.1), but the 1st and 2nd ordination axes reflected two well-defined gradients, from shallow, rocky soil to deep soil, and from sparse to dense litter/vegetation cover. I divided the plots into four groups by manually partitioning the ordination space into four separate quadrants, each containing approximately the same number of plots (Fig. 3.1). According to the quadrant in which they occurred, plots were then assigned to one of four microsite types: **(A)** exposed ground with deep soil; **(B)** exposed, sloped ground with shallow (rocky) soil; **(C)**

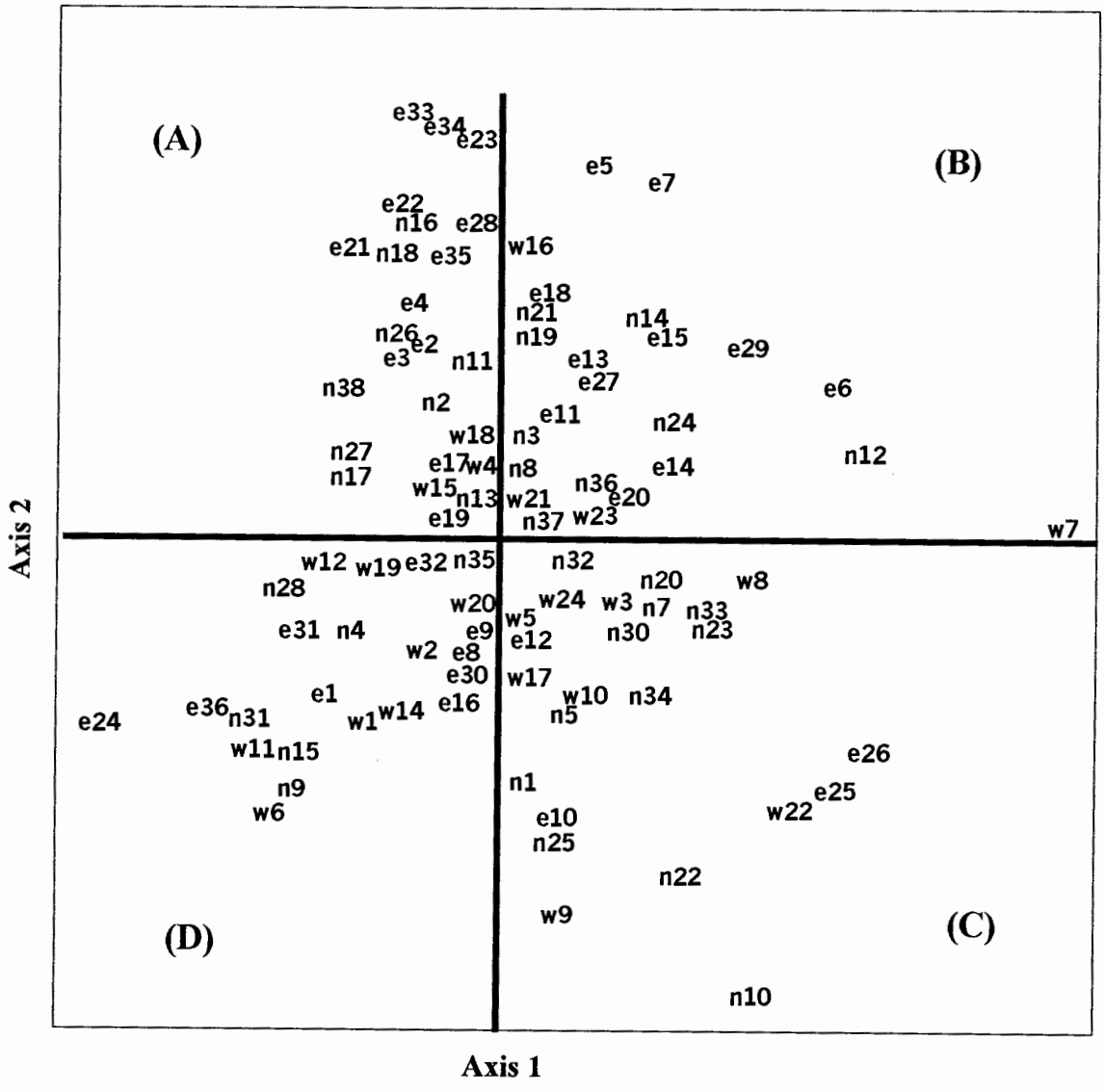


Figure 3.1 Detrended correspondence analysis ordination (axes 1 and 2) of all 95 demographic plots, pooled over three sites. Numbered points refer to individual plots within each population (n = site NS, e = site ES, w = site WS). The intersection of axes lines at the centroid of the cloud of points was used to divide the plot into four quadrants, loosely representing four microsite types: A (low plant cover, deep soil); B (low plant cover, rocky soil); C (high plant/moss cover, rocky soil); D (high plant/litter cover, deep soil).

mossy, with shallow (rocky) soil and high vascular plant cover; (**D**) deep soil, with high litter cover. Plots from the three sites were not separated in this ordination (Fig. 3.1), and all four microsite categories were represented at all sites. Each of these four microsite types was subsequently considered a distinct 'treatment' in the demographic analysis.

To investigate whether *C. lyallii* demography is affected by variation in local population density (or variation in environmental factors associated with population density), I ranked the plots from all three sites according to their mean density (over five yr) of adult *C. lyallii* plants. Plots were then grouped into one of four density classes: Low, Medium-low, Medium-high, and High (Table 3.1). Cut-offs between density classes were such that each class contained approximately the same number of individuals. These density classes became the four 'treatment' levels in the third demographic experiment undertaken to study *C. lyallii* responses to varying conditions.

STAGE CLASSIFICATION

Numerous studies of perennial plants have shown that survival and fecundity rates are closely linked to plant size (e.g., Bierzychudek 1982, Werner and Caswell 1977, Lacey 1986, Hanzawa and Kalisz 1993). In bulbous perennials, plant performance may be strongly related to the size and condition of the perennating organ itself (Fiedler 1987, Hanzawa and Kalisz 1993). However, it was not possible to measure *C. lyallii* bulbs directly without destructively sampling the plots. Thus I used the width of the basal leaf as a relative measure of plant size. Fiedler (1987) found modest ($r = 0.45$ to $r = 0.80$) but significant correlations between bulb wet weight and leaf width in four species of *Calochortus* from California. My own data on *C. lyallii* suggest that reproduction is initiated, and fruits matured, only after certain minimum leaf size thresholds are attained (see below). However, plant size on its own is an insufficient indicator of reproductive state in this species because only a fraction of *C. lyallii* individuals large enough to flower in a given year actually do so. Furthermore, seedlings (plants that germinated in the current year from seed produced the previous year) are best defined not by size but by age. Consequently, I classified individuals by a combination of size, age, and flowering status.

I defined 11 stages (*i*-states, *sensu* Caswell 2001): seedlings, juveniles (two classes), reproductives (four classes), vegetative plants, and dormants (three classes) (Table 3.2). Flowering and fruiting size thresholds were derived retrospectively, from the combined census observations. 'Juveniles' were any established plants below the flowering size threshold. They could be true juveniles or formerly large plants that had regressed in size. The division point between the two juvenile stages was the maximum observed size attained by 2nd year plants. Individuals large enough to flower but too small to set fruit were assigned to the first reproductive class (R1). Above the size threshold for fruit-set, plants were classified according to the number of flower buds (1, 2, or >2) initiated in the spring. To determine if the reproductive class divisions based on bud number were demographically significant, I conducted a chi-squared analysis of the transition data from the first year to test for independence between fate and reproductive state. The chi-squared test was significant ($\chi^2 = 41.53$, $df = 14$, $P < 0.001$), indicating that the fate of reproductive individuals does depend on their initial state, and that these divisions are therefore meaningful.

Individuals that reappeared above ground after an absence of one or more years were classified as dormant for the year or years they failed to appear. I used multiple dormancy classes because the state of a plant after it emerges from dormancy is likely to reflect its state prior to entering dormancy (e.g., if a plant is small when it enters dormancy, it will likely still be small upon re-emerging). One of the central conditions of the matrix projection model is that it describe a first-order Markov process; that is, an individual's fate at time $t + 1$ should depend on its state at time t but not on any state prior to this (Caswell 2001). Seven additional stages would have been needed to include a separate dormant class for every stage in the life cycle having a direct connection to dormancy, which would have necessitated a larger sample of individuals than was available. As a compromise, I assigned dormant plants to one of three classes (DJ, DR, or DV), depending on whether a plant was a juvenile (J1 or J2), a reproductive (R1-R4), or a vegetative adult (V) prior to becoming dormant, respectively (Table 3.2).

The various transitions possible for a *C. lyallii* plant in different stages during a projection interval are shown by the arrows in the life cycle graph (Fig. 3.2). Because *C. lyallii* seeds either die or germinate during the spring following seed shed (see *Chapter*

Table 3.1 Density classes used in evaluating patch-level dynamics.

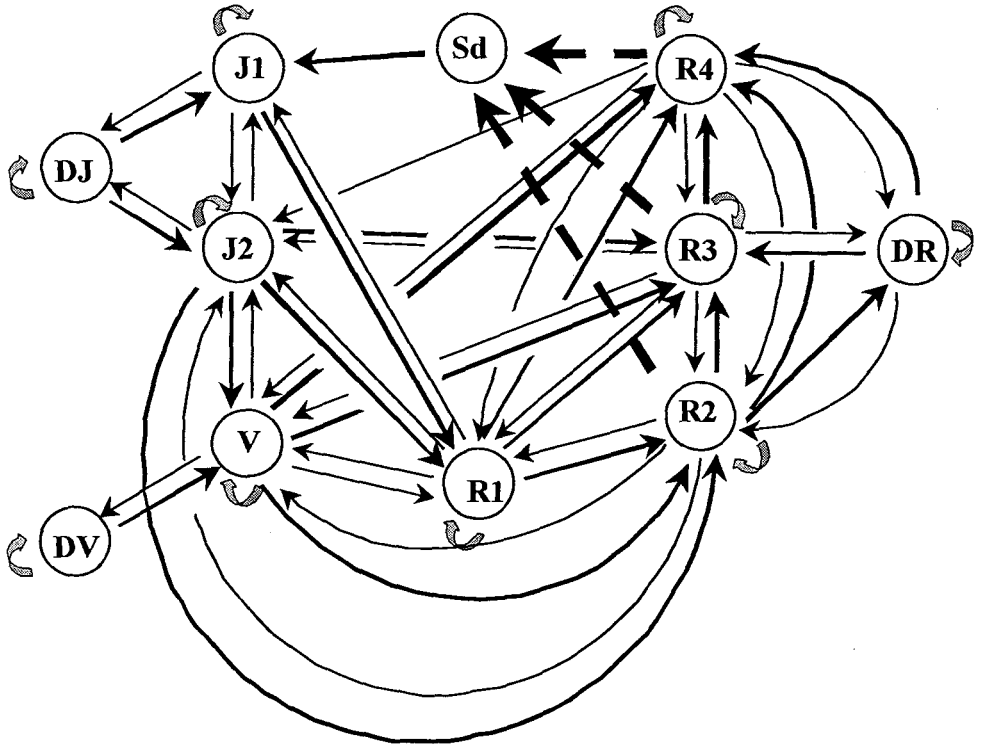
Density class	Annual mean density of adult plants* (number/m^2)	Number of plots
A (low)	1 - 7	44
B (medium-low)	8 - 12	22
C (medium-high)	13 - 17	15
D (high)	18 - 36	14

*Adult plants defined as plants with leaf width > the minimal threshold size for fruiting, i.e., size classes R2, R3, R4, and V (see Table 2).

Table 3.2 Stage categories used to model the population dynamics of *Calochortus lyallii*.

Stage	Category	Plant size (leaf width in mm)	Demographic state
1	seedling (Sd)	< 1.0	cotyledon present
2	small juvenile (J1)	1.0 - 1.9	vegetative leaf
3	large juvenile (J2)	2.0 - 3.6	vegetative leaf
4	pre-reproductive (R1)	3.7 - 4.5	sometimes flowering, but never setting fruit
5	small reproductive (R2)	> 4.5	1 flower bud initiated
6	medium reproductive (R3)	> 4.5*	2 flower buds initiated
7	large reproductive (R4)	> 4.5	> 2 flower buds initiated
8	vegetative adult (V)	> 4.5	no buds initiated (vegetative)
9	dormant juvenile (DV)	\	stage prior to dormancy: 2 or 3
10	dormant reproductive (DR)	\	stage prior to dormancy: 4, 5, 6, or 7
11	dormant vegetative (DV)	\	stage prior to dormancy: 8

*The observed minimum size threshold for fruiting; plants with leaf widths >4.5mm are considered 'adults,' whether they produce flowers or not.



	Sd	J1	J2	R1	R2	R3	R4	V	D1	D2	D3
Sd	0	0	0	0	F_{15}	F_{16}	F_{17}	0	0	0	0
J1	G_{21}	P_{22}	P_{23}	0	0	0	0	0	G_{29}	0	0
J2	0	G_{32}	P_{33}	P_{34}	P_{35}	P_{36}	P_{37}	P_{38}	G_{39}	G_{310}	G_{311}
R1	0	G_{42}	G_{43}	P_{44}	P_{45}	P_{46}	P_{47}	P_{48}	G_{49}	G_{410}	G_{411}
R2	0	0	G_{53}	G_{54}	P_{55}	P_{56}	P_{57}	G_{58}	G_{59}	G_{510}	G_{511}
R3	0	0	G_{63}	G_{64}	G_{65}	P_{66}	P_{67}	G_{68}	G_{69}	G_{610}	G_{611}
R4	0	0	0	G_{74}	G_{75}	G_{76}	P_{77}	G_{78}	G_{79}	G_{710}	G_{711}
V	0	0	G_{83}	P_{84}	P_{85}	P_{86}	P_{87}	P_{88}	G_{89}	G_{810}	G_{811}
D1	0	P_{92}	P_{93}	0	0	0	0	0	P_{99}	0	0
D2	0	0	0	P_{104}	P_{105}	P_{106}	P_{107}	0	0	P_{1010}	0
D3	0	0	0	0	0	0	0	P_{118}	0	0	P_{1111}

Figure 3.2 Life-cycle graph and corresponding generalised matrix model for *C. lyallii* (see Table 3.2 for stage definitions). Circles indicate plant stages and arrows represent the possible transitions between stages. Dark solid arrows represent growth (G); light arrows represent stasis or regression (P); heavy dashed arrows represent fecundity (F).

2), there is no separate category for seeds. Furthermore, because stage 1 (seedlings) is an age class of the same length as the projection interval, it has no self-loop (Caswell 2001).

MATRIX CONSTRUCTION AND ANALYSIS

For each set of plots, I calculated the proportion of individuals in each category experiencing each fate from one year to the next. For non-dormant plants, transition probabilities were calculated directly from the annual census data. I used actual data from each population and year in all cases but 1996-97, when a late start prevented enumeration of seedlings and many of the smaller juveniles (size class J1) before they senesced. I estimated seedling survivorship in 1996-97 from the average survivorship rate for the years 1997-2000, calculated separately from the annual matrices for each plot group. Small juvenile transition probabilities for 1996-97 were calculated after pooling plants from all three populations to obtain a larger sample size. These values were therefore the same for all matrices.

Quantifying transitions into and out of dormancy classes is problematic because *C. lyallii* individuals can remain dormant and out of view for many years. Transitions could only be unequivocally assigned for plants that both entered and emerged from dormancy during the study period; plants that vanished during the study might be either dead or dormant. I assumed the maximum duration of dormancy to be three years, which is an underestimate given that some previously unobserved plants continued to appear in the demographic plots in years 4-5 of the study (*Chapter 2*). However, these instances were rare and had little effect on transition estimates. Thus I could calculate rates of entry into dormancy directly from census data for the first time interval (1996-97). To correct for the occurrence of prolonged dormancy during the latter three transitions, I employed indirect methods (Appendix 3.1).

Some individuals may have been absent at a census for reasons other than physiological dormancy. These plants might have been eaten by herbivores, or senesced and disappeared before they could be surveyed, or I may have failed to observe plants that were actually there. Because the last explanation was the most parsimonious with respect to the smallest individuals in the population (i.e., seedlings and yearlings), absent 2nd year plants were assumed (as long as they reappeared in a subsequent census) to have been

present all along, but unobserved. Thus, the life cycle graph makes no allowance for a seedling to dormant transition (Fig. 3.2). Dormant plants, as defined here, are never recorded as dying, only as re-emerging (or as surviving another year as dormants), effectively fixing survivorship in these stages at 1.0. In reality, mortality likely occurs during dormancy just as in other phases of the life cycle. To correct for this possible overestimation, I assumed that a proportion of all plants (arbitrarily set at 10%, and excluding seedlings) marked as dead actually went dormant first, then died (Appendix 3.1).

Any established plants appearing in the plots *de novo* in a given year were excluded from the life table calculations for that year. However, these individuals were considered in subsequent transitions, and in the estimation of dormancy rates (Appendix 3.1).

Because I did not monitor the fates of seeds in the field, I had to calculate stage-specific fecundities (F_x) indirectly. Fecundity was defined in terms of per capita seedling recruitment. To estimate the reproductive contribution of the various size classes, I first determined the average number of seedlings generated per fruit capsule (F_{cap}) by dividing the total number of seedlings censused at $t+1$ by the total number of mature capsules censused at time t. I then weighted this value by stage, dividing the total number of capsules produced by each reproductive class by the total number of individuals in the class in that year (R_{ind}). I then multiplied R_{ind} by F_{cap} to arrive at an estimate of the number of seedlings produced per individual in each stage. The approach used here is equivalent to that suggested by Caswell (2001) for calculating relative fertilities when reproduction is anonymous. It assumes that seeds produced by plants of different sizes were equally likely to become seedlings and that there was no net dispersal of seeds into or out of the plots.

I used Lefkovitch stage-based matrices (Lefkovitch 1965) to estimate the rate and direction of population growth (Caswell 2001). The basic linear, time-invariant model is given by

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$$

where $\mathbf{n}$ and $\mathbf{n}_{t+1}$ are vectors of stage abundances at time t and $t+1$, respectively, and $\mathbf{A}$ is the population projection matrix, whose elements, a_{ij}, give the contribution of an individual in stage j to stage i over one time step. The asymptotic growth rate is given by

the dominant eigenvalue λ of the matrix **A**. When $\lambda > 1$ the population is expected to grow, and when $\lambda < 1$ the population is expected to decline. The normalized right eigenvector, **w**, represents the stable stage distribution that would result if the conditions given by **A** remained constant indefinitely. Stable stage-specific reproductive values are given by the corresponding left eigenvector, **v**.

The sensitivities of λ to changes in the elements a_{ij} of **A** are given by

$$s_{ij} = \delta\lambda / \delta a_{ij} = \mathbf{v}_i\mathbf{w}_j / \langle \mathbf{w},\mathbf{v} \rangle$$

where $\delta\lambda / \delta a_{ij}$ is the partial derivative of λ with respect to the matrix element a_{ij}, and $\langle \mathbf{w},\mathbf{v} \rangle$ is the scalar product of **w** and **v**. The proportional sensitivities, or elasticities, of λ are given by

$$e_{ij} = (a_{ij} / \lambda)(\delta\lambda / \delta a_{ij}).$$

The elasticities sum to 1, and give the proportional contributions of the matrix elements to λ, enabling comparisons between different species or populations of the same species (de Kroon et al. 1986). Taking the sum across row *i* (or down column *j*) of an elasticity matrix gives the total elasticity of λ to transitions into stage *i* (or out of stage *j*) (van Groenendael et al. 1994). The resulting values can be interpreted as the combined contribution of survival, growth, and fertility elements within each life stage to population growth rate λ (not to be confused with contributions to the *variance* in λ; *cf.* Caswell 2000).

Four projection matrices, one for each transition period, were constructed for each of the three populations, four microhabitat types, and four density classes (a total of 44 matrices). I also calculated the average annual matrix for each plot category. Population growth rate, stable-stage distribution, reproductive values, and sensitivity and elasticity matrices were computed for each matrix using MATLAB (The Mathworks, Inc. 1999).

Projected stable stage distributions (mean matrices) and observed stage distributions from 2000 were compared using Keyfitz's Δ (Keyfitz 1968). For any one treatment level, the distance between the two population vectors n(*t*) and **w** is measured by

$$\Delta(n,w) = \frac{1}{2}\sum_i |n_i - w_i|$$

where both n and w have been scaled so that they sum to 1 (Caswell 2001). The value of Δ varies from 0 to 1.

Pocket gophers have the potential to limit *C. lyallii* abundance locally because they consume the bulbs and are likely to forage where plants are most dense. To test whether gopher predation had a differential impact on estimated population growth rates in plots of varying density, I used simulations to estimate the λ-value that might have been observed for each of the density classes if gophers had consumed no bulbs at all. First I assumed that every *C. lyallii* individual killed by a gopher in a given year in fact survived and remained in the same stage until the following census. I then constructed a new model corresponding to each of the density class-year combinations using this recast data set.

SIGNIFICANCE TESTING AND CONFIDENCE INTERVALS

To determine if the fate of *C. lyallii* individuals of a given stage differed among plot groups and years, I conducted three separate loglinear analyses, one each for plots grouped by population, microsite, and plant density. For each four-way contingency table I used either actual count data (i.e., the number of individuals observed making the transition from state *j* to fate *i*) or, in the case of transitions into and out of dormancy, estimates of counts derived from post-hoc adjustments to the mortality rate (see Appendix 3.1). Death was included as a fate category. Models including and excluding time and/or plot effects were then ranked according to the *Akaike information criterion* (*AIC*; Akaike 1973, Burnham and Anderson 1998), as suggested by Caswell (2001). Relative *AIC* values, scaled so that *AIC* for the saturated model was zero, were computed as $AIC = G^2 - 2(df)$.

Because there is no general method for obtaining the distribution of λ and other demographic statistics in terms of the a_{ij}, I used a bootstrap resampling procedure in conjunction with the percentile method (Efron and Tibshirani 1993, Caswell 2001) to construct nonparametric confidence limits on λ, elasticities, **w**, and **v**. Calculations were carried out in MATLAB using a bootstrap sample size of 3000. When bootstrapping demographic data, it is important that the model used to generate the bootstrap sample reflect as closely as possible the sampling scheme employed in the field (McPeek and Kalisz 1993, Efron and Tibshirani 1993). Because I estimated stage transitions by

observing different sets of individuals in a variety of plot arrangements, the appropriate resampling unit for the bootstrap procedure was a single demographic plot from a group of plots (population, microsite type, or density class). Each bootstrap sample contained the same number of plots as the original data set, with the plots selected randomly with replacement from the original set of plots. For each of the 3000 bootstrap samples, a separate stage-classified matrix was generated as for the original data. Eigenanalyses of each new projection matrix thus obtained yielded a set of bootstrap values that was then used to estimate the distribution, and from this distribution the upper and lower 95% confidence limits, of λ and other demographic properties calculated from the projection matrix.

While bootstrap tests are useful for testing the hypothesis that λ equals some specified value (e.g., 1.0), they cannot be used to compare λ among treatments (Caswell 2001). To test the statistical significance of differences in λ among plot groups, I used nonparametric randomisation tests (Manley 1991; see Brault and Caswell [1993] and Levin et al. [1996] for demographic applications, and Caswell [2001] for a review of the method). As in the bootstrap test, the resampling units were entire plots. As test statistics I used the standard deviations SD(λ), SD(**w**), and SD(**v**). Nine separate randomisation tests were carried out, one for each combination of year (1997-98, 1998-99, 1999-00) x plot type. Because some elements of the 1996-97 matrices consisted of pooled data, these matrices were excluded. For each test, I used a random sample of 2000 permutations (see Appendix 3.1 for details). Each test was carried out as a single routine in MATLAB.

LIFE TABLE RESPONSE EXPERIMENT (LTRE) ANALYSIS

Spatial variance in λ was decomposed into contributions from the variances in, and covariances among, each of the stage-specific vital rates using the methods of Brault and Caswell (1993) and Horvitz et al. (1997). The contribution of any one matrix element to the variance in λ is a direct function of the sensitivity of λ to that entry and the variability of the entry. Let $C(ij,kl)$ denote the covariance of a_{ij} and a_{kl}. The variance in λ among treatments, $V(\lambda)$, is then given by

$$V(\lambda) \approx \sum_{ij} \sum_{kl} C(ij,kl) s_{ij} s_{kl}$$

where s_{ij} and s_{kl} are the sensitivities of the mean matrix. Each of the terms in this summation is the contribution made by the covariance between one pair of vital rates to $V(\lambda)$. As the contributions are additive, summing across the rows (or columns) of the resulting contribution matrix gives a measure of the total contribution to $V(\lambda)$ made by each of the a_{ij} after all variances and covariances, both negative and positive, are taken into account (Horvitz et al. 1997).

These calculations were repeated three times, once for each set of plot groupings. To average out temporal heterogeneity whilst preserving the differences among plots, I substituted the mean annual matrix from each plot group in place of the four yearly matrices. Analyses were thus applied to a set of three transition matrices in the case of the population grouping, and to sets of four matrices in the case of the microsite and density groupings.

Once the vital rates that contribute most to the spatial variability of λ have been identified, the next step is to identify the source of the vital rate variation. For this analysis, I relied on the 10 soil/cover parameters used to distinguish microsite types (see FIELD SAMPLING) to provide an approximation of some of the environmental differences that might influence *C. lyallii* at the plot level. First, for each of the 95 demographic plots sampled, four separate transition matrices were computed from the annual census data from that plot. These matrices were then averaged, yielding 95 individual mean estimates (hereafter referred to as plot estimates) of each vital rate that could then be compared against the 10 microsite variables. Only those transitions making a substantial net contribution (positive or negative) to $V(\lambda)$ were considered. To avoid compounding estimation error, I excluded from this analysis any entries from 1996-97 that were themselves averages of other estimates (i.e., all entries corresponding to the survival and growth of seedlings, small juveniles, and dormants). Correlations ($n = 95$) between matrix parameters and microsite variables were estimated with Spearman rank correlation coefficients because some of the variables were scored with categorical values and most data were not normally distributed.

Results

HABITAT-ABUNDANCE RELATIONSHIPS

Each of the measured microhabitat variables differed significantly among the three *C. lyallii* sites (Kruskal-Wallis, $H \geq 6.47$, $P < 0.05$; Table 3.3). The soil at ES was rockier, drier, more exposed, and shallower than that at either NS or WS. WS had the highest litter cover, litter depth, vascular plant cover, soil moisture, and soil depth, and the lowest bryophyte cover. Microsite conditions at NS were generally intermediate between those at the other two sites (Table 3.3).

At ES, transect plots with seedlings present had significantly more plant cover, deeper soil, and more soil moisture than plots that lacked seedlings. At both ES and WS, plots containing seedlings had more plant litter and less rock cover than those without seedlings. Among the variables measured, only one was strongly associated with seedling presence at all three sites: density of adult *C. lyallii* plants was consistently much greater in plots with seedlings (Fig. 3.3).

GERMINATION

Seeds buried in nylon mesh bags in the fall exhibited 36 – 100% germination (mean germination rate = 0.75 ± 0.20, n = 12) by the following spring. Bags buried underground for a second year showed no additional germination of the remaining seeds. Consequently, it was assumed that all seedlings appearing in the demographic plots came from seed produced during the preceding year (i.e., there was no seed dormancy).

TRANSITION PROBABILITIES

Although transition probabilities varied among years and plot groups, general patterns are evident (average transition matrices are shown in Table 3.4; annual matrices are presented in Appendix 3.2). Mortality was high for seedlings, around 50%, but decreased rapidly in all later stages, usually remaining below 15%. Juveniles and adults, despite their differences in size, exhibited similar mortality rates, as did flowering and vegetative genets. However, among flowering plants fecundity was strongly size-

Table 3.3 Mean (±SD) of habitat variables at the 3 study sites (NS, ES, and WS), based on the 50 transect plots at each site. Differences among the sites are evaluated with the Kruskal-Wallis rank sum test. *H*: Kruskal-Wallis statistic. Significance determined by chi-squared approximation.

	Site			
Habitat variable	NS	ES	WS	*H*
relative soil moisture***	2.44 (0.66)	2.22 (0.67)	2.95 (0.91)	97.07
%moss cover**	27.86 (24.76)	26.74 (27.1)	14.5 (22.37)	14.42
%rock cover***	9.82 (13.32)	21.6 (19.87)	12.5 (22.95)	20.23
soil depth (cm)*	25.54 (14.1)	20.34 (13.31)	27.24 (12.64)	7.82
slope (degrees)*	20.46 (8.31)	16.88 (7.17)	20.56 (8.28)	6.47
relative aspect***	2.12 (0.94)	1.82 (0.72)	4.22 (0.58)	97.07
%bare soil***	9.66 (12.39)	21.46 (22.8)	7.14 (10.96)	20.12
%litter cover***	44.4 (28.83)	14.62 (13.43)	53.6 (31.64)	46.05
litter depth (cm)***	2.28 (2.66)	0.75 (0.49)	2.66 (3.14)	52.29
%total veg. cover*	52.26 (22.23)	50 (35.14)	63.28 (29.47)	7.27

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

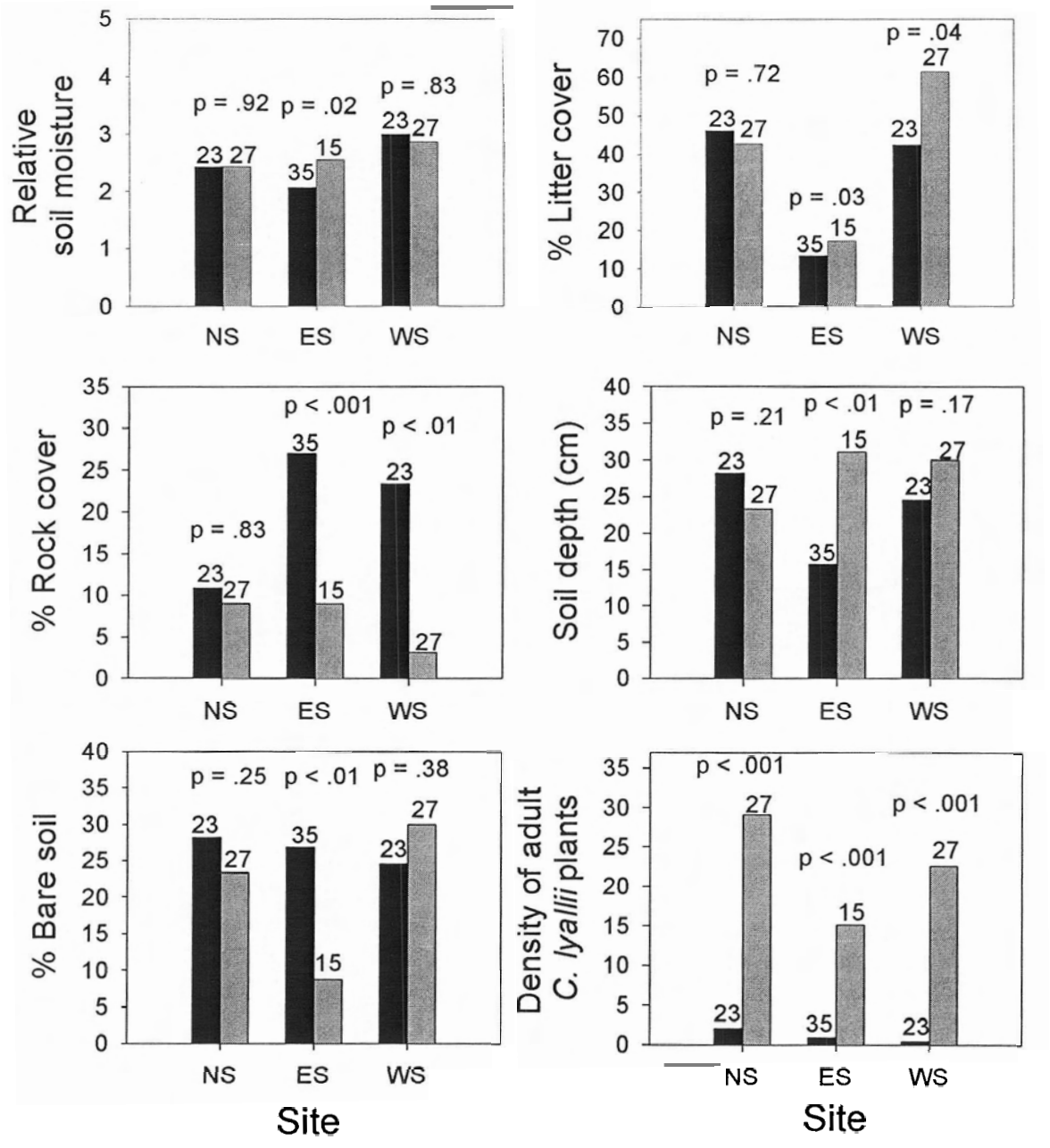


Figure 3.3 Mean values for microhabitat characteristics in transect plots with seedlings (filled bars) vs. plots without seedlings (stippled bars), at three locations on Black Mt. The relative density of mature *C. lyallii* individuals is also shown. Comparisons made by Mann-Whitney *U* test. Values directly above bars are the sample size *n*. Results of tests involving litter depth, % cryptogrammic cover, slope, and aspect were not significant and are not displayed.

Table 3.4 Mean annual transition matrices with their dominant eigenvalues (λ) for *Calochortus lyallii*, for a) populations (NS, ES, WS), b) microsite types (A, B, C, D), and c) densities classes (Low, Med-low, Med-high, High). The mean matrices are derived from the 4 transition periods 1996-97, 1997-98, 1998-99 and 1999-00. Stage classes reflect plant size and/or demographic state (Table 2). Bolded entries are the fecundity terms; other values represent transition probabilities between stages.

a)

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	λ
NS												
Sd	0	0	0	0	**0.2871**	**0.6813**	**1.9048**	0	0	0	0	
J1	0.5209	0.4226	0.0259	0.0045	0	0	0.0036	0.0019	0.0972	0.0092	0.0010	
J2	0	0.3021	0.4568	0.1075	0.0249	0.0224	0.0115	0.0490	0.3174	0.1479	0.2435	
R1	0	0.0166	0.2022	0.2766	0.0675	0.0656	0.0522	0.0457	0.0443	0.1383	0.0403	
R2	0	0	0.0055	0.0338	0.1649	0.0888	0.1040	0.1125	0.0010	0.0350	0.0673	
R3	0	0	0.0155	0.1109	0.2350	0.3039	0.2165	0.2296	0.0010	0.0433	0.0673	0.9817
R4	0	0	0	0.0162	0.1249	0.1233	0.2499	0.0923	0.0010	0.0177	0.0010	
V	0	0	0.0767	0.2202	0.2101	0.1712	0.1694	0.2595	0.0667	0.1817	0.2501	
DJ	0	0.1675	0.1371	0	0	0	0	0	0.3908	0	0	
DR	0	0	0	0.1033	0.0859	0.1029	0.0508	0	0	0.2331	0	
DV	0	0	0	0	0	0	0	0.0883	0	0	0.1622	
ES												
Sd	0	0	0	0	**0.0893**	**0.4915**	**0.9394**	0	0	0	0	
J1	0.4817	0.4522	0.0248	0.0199	0	0.0048	0	0	0.0507	0.0701	0.0615	
J2	0	0.2534	0.4449	0.0989	0.0162	0.0188	0.0081	0.0358	0.4425	0.1023	0.0987	
R1	0	0.0594	0.1773	0.3279	0.0356	0.0658	0.0248	0.0906	0.1043	0.0821	0.0665	
R2	0	0	0.0177	0.0666	0.1802	0.1244	0.1132	0.1266	0.0343	0.0358	0.0176	
R3	0	0.0042	0.0370	0.1035	0.2236	0.2451	0.2295	0.2450	0.0010	0.0980	0.0733	0.9901
R4	0	0	0	0.0276	0.1885	0.1636	0.3321	0.1344	0.0010	0.0739	0.0010	
V	0	0	0.0497	0.1970	0.2174	0.2275	0.1686	0.2125	0.0174	0.1603	0.2656	
DJ	0	0.1406	0.1806	0	0	0	0	0	0.3253	0	0	
DR	0	0	0	0.0756	0.0643	0.0590	0.0299	0	0	0.1537	0	
DV	0	0	0	0	0	0	0	0.0691	0	0	0.2639	

a)

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	λ
WS												
Sd	0	0	0	0	**0.2809**	**0.6359**	**1.6274**	0	0	0	0	
J1	0.5990	0.4260	0.0224	0.0031	0	0.0034	0.0357	0.0053	0.0729	0.0141	0.0108	
J2	0	0.3595	0.3893	0.1082	0.0309	0.0591	0.0041	0.0443	0.3578	0.1878	0.1600	
R1	0	0.0119	0.2063	0.2671	0.1062	0.0922	0.0299	0.0534	0.0770	0.1097	0.0709	
R2	0	0.0027	0.0040	0.0351	0.1189	0.1111	0.0669	0.0877	0.0200	0.0393	0.0176	
R3	0	0.0022	0.0265	0.1612	0.1698	0.2418	0.2404	0.1896	0.0010	0.0527	0.0765	1.0156
R4	0	0	0.0112	0.0796	0.1158	0.1403	0.3253	0.1464	0.0010	0.0539	0.0010	
V	0	0	0.0674	0.1566	0.1666	0.1445	0.1244	0.2427	0.1059	0.1712	0.1886	
DJ	0	0.1045	0.1704	0	0	0	0	0	0.3313	0	0	
DR	0	0	0	0.1035	0.1292	0.1084	0.0928	0	0	0.2748	0	
DV	0	0	0	0	0	0	0	0.1177	0	0	0.3636	

Table 3.4, continued Mean annual transition matrices with their dominant eigenvalues (λ) for *Calochortus lyallii*, for a) populations (NS, ES, WS), b) microsite types (A, B, C, D), and c) densities classes (Low, Med-low, Med-high, High). The mean matrices are derived from the 4 transition periods 1996-97, 1997-98, 1998-99 and 1999-00. Stage classes reflect plant size and/or demographic state (Table 2). Bolded entries are the fecundity terms; other values represent transition probabilities between stages.

b)

	Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	λ
A													
	Sd	0	0	0	0	**0.1763**	**0.4109**	**3.7259**	0	0	0	0	
	J1	0.5091	0.4406	0.0134	0.0053	0	0	0.0035	0	0.0849	0.0501	0.0010	
	J2	0	0.2843	0.4496	0.0953	0.0130	0.0239	0.0085	0.0477	0.4908	0.0985	0.2567	
	R1	0	0.0097	0.1940	0.3338	0.0433	0.0630	0.0296	0.0807	0.0118	0.0855	0.0338	
	R2	0	0	0.0134	0.0414	0.1762	0.1369	0.1172	0.1112	0.0808	0.0161	0.0176	
	R3	0	0.0045	0.0295	0.0921	0.2404	0.2792	0.2298	0.2135	0.0010	0.0663	0.0638	1.0465
	R4	0	0	0	0.0261	0.1526	0.1778	0.3277	0.1109	0.0010	0.0462	0.0010	
	V	0	0	0.0821	0.1860	0.2061	0.1790	0.1572	0.2319	0.0662	0.1764	0.2422	
	DJ	0	0.1855	0.1652	0	0	0	0	0	0.2255	0	0	
	DR	0	0	0	0.0762	0.1219	0.0574	0.0592	0	0	0.2938	0	
	DV	0	0	0	0	0	0	0	0.0943	0	0	0.1597	
B													
	Sd	0	0	0	0	**0.1547**	**0.5188**	**0.8953**	0	0	0	0	
	J1	0.4886	0.4468	0.0135	0.0139	0	0	0	0	0.0740	0.0565	0.0010	
	J2	0	0.3378	0.4115	0.1416	0.0010	0.0284	0.0053	0.0459	0.4038	0.0912	0.2702	
	R1	0	0.0097	0.1924	0.2767	0.0930	0.0833	0.0377	0.0660	0.0362	0.0955	0.0853	
	R2	0	0	0.0062	0.0790	0.1876	0.1165	0.0856	0.0950	0.0668	0.0395	0.0451	
	R3	0	0	0.0113	0.0962	0.1393	0.2177	0.2146	0.1943	0.0010	0.0315	0.0451	0.9544
	R4	0	0	0	0.0235	0.1339	0.1526	0.3528	0.0998	0.0010	0.0251	0.0010	
	V	0	0	0.0473	0.1714	0.2340	0.1998	0.1362	0.2587	0.0540	0.2240	0.2128	
	DJ	0	0.1402	0.2359	0	0	0	0	0	0.3301	0	0	
	DR	0	0	0	0.0707	0.0810	0.0980	0.0349	0	0	0.2552	0	
	DV	0	0	0	0	0	0	0	0.0936	0	0	0.2046	

b)

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	λ
C												
Sd	0	0	0	0	**0.2568**	**0.7305**	**1.5198**	0	0	0	0	
J1	0.5507	0.4300	0.0357	0	0	0	0.0250	0.0027	0.0707	0.0031	0.0010	
J2	0	0.3325	0.4338	0.1255	0.0178	0.0415	0.0059	0.0401	0.3332	0.1716	0.0803	
R1	0	0.0233	0.2159	0.2415	0.0559	0.0661	0.0300	0.0445	0.0575	0.0770	0.0673	
R2	0	0	0.0089	0.0429	0.1886	0.0980	0.1443	0.1526	0.0193	0.0552	0.0176	
R3	0	0.0015	0.0316	0.1375	0.2130	0.2712	0.2085	0.2075	0.0010	0.0805	0.1986	1.0130
R4	0	0	0.0116	0.0638	0.1066	0.1211	0.2495	0.1309	0.0010	0.0573	0.0010	
V	0	0	0.0776	0.2028	0.1695	0.1600	0.1604	0.2640	0.0987	0.1758	0.1577	
DJ	0	0.1184	0.1287	0	0	0	0	0	0.3667	0	0	
DR	0	0	0	0.0913	0.0972	0.1360	0.0580	0	0	0.2000	0	
DV	0	0	0	0	0	0	0	0.0910	0	0	0.3019	
D												
Sd	0	0	0	0	**0.2795**	**0.4949**	**1.4688**	0	0	0	0	
J1	0.5309	0.4062	0.0281	0.0150	0.0000	0.0090	0.0132	0.0056	0.0618	0.0360	0.0509	
J2	0	0.3069	0.4203	0.0815	0.0640	0.0404	0.0147	0.0445	0.3991	0.2110	0.2463	
R1	0	0.0297	0.2105	0.2820	0.0945	0.0721	0.0343	0.0623	0.0924	0.1514	0.0759	
R2	0	0.0030	0.0025	0.0282	0.0960	0.0819	0.0550	0.0798	0.0010	0.0151	0.0337	
R3	0	0.0012	0.0235	0.1571	0.1422	0.2802	0.2465	0.2450	0.0010	0.0562	0.0500	0.9876
R4	0	0	0.0035	0.0411	0.1500	0.1335	0.3465	0.1418	0.0010	0.0483	0.0010	
V	0	0	0.0688	0.1964	0.2659	0.1948	0.1510	0.1984	0.0454	0.1559	0.1490	
DJ	0	0.1510	0.1249	0	0	0	0	0	0.3557	0	0	
DR	0	0	0	0.1147	0.0591	0.0715	0.0625	0	0	0.2071	0	
DV	0	0	0	0	0	0	0	0.0951	0	0	0.2635	

Table 3.4, continued Mean annual transition matrices with their dominant eigenvalues (λ) for *Calochortus lyallii*, for a) populations (NS, ES, WS), b) microsite types (A, B, C, D), and c) densities classes (Low, Med-low, Med-high, High). The mean matrices are derived from the 4 transition periods 1996-97, 1997-98, 1998-99 and 1999-00. Stage classes reflect plant size and/or demographic state (Table 2). Bolded entries are the fecundity terms; other values represent transition probabilities between stages.

c)

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	λ
Low												
Sd	0	0	0	0	**0.0908**	**0.7053**	**1.2506**	0	0	0	0	
J1	0.5204	0.3533	0.0372	0.0167	0	0.0046	0.0216	0	0.0959	0.0031	0.0010	
J2	0	0.3486	0.4684	0.0708	0.0091	0.0253	0.0055	0.0325	0.3900	0.1428	0.0829	
R1	0	0.0332	0.1665	0.2501	0.0906	0.0516	0.0217	0.0451	0.0358	0.0512	0.1527	
R2	0	0.0012	0.0049	0.0306	0.1709	0.1025	0.0948	0.0948	0.0244	0.0729	0.0176	
R3	0	0.0027	0.0191	0.1670	0.1928	0.2873	0.2354	0.2422	0.0010	0.0934	0.0388	0.9702
R4	0	0	0.0126	0.0404	0.1938	0.1721	0.3464	0.1647	0.0010	0.0620	0.0010	
V	0	0	0.1052	0.2049	0.1295	0.1771	0.1234	0.2390	0.1110	0.1909	0.2233	
DJ	0	0.1588	0.1297	0	0	0	0	0	0.2956	0	0	
DR	0	0	0	0.0942	0.0647	0.0751	0.0461	0	0	0.1813	0	
DV	0	0	0	0	0	0	0	0.0853	0	0	0.3652	
Med-low												
Sd	0	0	0	0	**0.1594**	**0.3691**	**1.0713**	0	0	0	0	
J1	0.5497	0.3875	0.0139	0.0068	0	0	0	0.0021	0.0906	0.0094	0.0010	
J2	0	0.3661	0.4707	0.1023	0.0193	0.0452	0.0010	0.0475	0.3084	0.1658	0.3130	
R1	0	0.0114	0.2075	0.2135	0.0562	0.0567	0.0099	0.0600	0.0541	0.1221	0.0389	
R2	0	0	0.0035	0.0476	0.1827	0.1174	0.0734	0.1047	0.0172	0.0289	0.0315	
R3	0	0	0.0102	0.1506	0.1996	0.2871	0.2434	0.1959	0.0010	0.0375	0.0739	0.9814
R4	0	0	0.0079	0.0604	0.1261	0.1462	0.3534	0.1179	0.0010	0.0377	0.0010	
V	0	0	0.0719	0.2355	0.2381	0.1625	0.1605	0.2108	0.0910	0.1832	0.2173	
DJ	0	0.1139	0.1895	0	0	0	0	0	0.4168	0	0	
DR	0	0	0	0.1060	0.0716	0.0944	0.0700	0	0	0.3004	0	
DV	0	0	0	0	0	0	0	0.1291	0	0	0.1922	

c)

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	λ
Med-high												
Sd	0	0	0	0	**0.2636**	**0.6916**	**2.3312**	0	0	0	0	
J1	0.5347	0.5237	0.0271	0	0	0.0040	0	0.0029	0.0906	0.0564	0.0972	
J2	0	0.2509	0.4293	0.1267	0.0281	0.0257	0.0066	0.0318	0.4322	0.1370	0.1121	
R1	0	0.0233	0.1780	0.2770	0.0322	0.0824	0.0540	0.0651	0.1284	0.0496	0.0613	
R2	0	0	0.0145	0.0464	0.1727	0.0981	0.1471	0.1426	0.0321	0.0095	0.0176	
R3	0	0	0.0402	0.0875	0.2182	0.2153	0.1672	0.2244	0.0010	0.0550	0.0511	1.0093
R4	0	0	0.0000	0.0231	0.1726	0.1578	0.2415	0.1210	0.0010	0.0243	0.0010	
V	0	0	0.0610	0.2212	0.2247	0.2213	0.2088	0.2544	0.0174	0.1372	0.1935	
DJ	0	0.1179	0.1650	0	0	0	0	0	0.2532	0	0	
DR	0	0	0	0.0993	0.1106	0.0766	0.0547	0	0	0.2486	0	
DV	0	0	0	0	0	0	0	0.0697	0	0	0.2735	
High												
Sd	0	0	0	0	**0.2571**	**0.4966**	**2.4010**	0	0	0	0	
J1	0.5389	0.4482	0.0210	0.0101	0	0	0	0.0050	0.0501	0.0111	0.0010	
J2	0	0.3051	0.3705	0.1178	0.0262	0.0268	0.0377	0.0764	0.3100	0.1209	0.3454	
R1	0	0.0157	0.2282	0.3695	0.0685	0.1343	0.0910	0.0827	0.0747	0.2171	0.0447	
R2	0	0.0063	0.0051	0.0399	0.2048	0.1226	0.0553	0.0962	0.0010	0.0817	0.0515	
R3	0	0	0.0234	0.1086	0.2450	0.2660	0.3274	0.2358	0.0010	0.0445	0.1198	1.033
R4	0	0	0	0.0437	0.0139	0.0749	0.2202	0.0610	0.0010	0.0610	0.0010	
V	0	0	0.0522	0.1243	0.2491	0.1859	0.1580	0.2539	0.1334	0.1312	0.1685	
DJ	0	0.1781	0.1501	0	0	0	0	0	0.3690	0	0	
DR	0	0	0	0.0968	0.0973	0.0912	0.0270	0	0	0.2134	0	
DV	0	0	0	0	0	0	0	0.0804	0	0	0.1359	

dependent: plants with larger leaves tended to produce more flower buds in the spring ($r = 0.71$, $P < 0.001$), which in turn were more likely to mature into fruit and release seed. Fecundity values for all reproductive stages were highest in 1996-97 and 1998-99, and lowest in 1997-98 and 1999-00. Although highly variable, the overall rate of recruitment was low, averaging fewer than 1 seedling per flowering individual per year.

Although plants were capable of undergoing drastic size changes (both decreases and increases) from one year to the next, most transitions were between adjacent size classes (Appendix 3.2). The largest transition probabilities were for stasis in the juvenile phase (J2 and J3), reflecting the many years it takes *C. lyallii* to grow from a seedling to reproductive maturity (out of the 687 seedlings initially tallied in 1997, none had progressed beyond stage J2 by 2000, the final year of the study). In contrast, transitions between different flowering classes, and between vegetative and reproductive states, were common. In 'good' years (i.e., years with positive λ), reproductive plants tended to remain reproductive, and plants that were previously vegetative often flowered. In 'poor' years, the opposite trend occurred: vegetative plants tended to remain in the same class, whereas plants that had previously flowered often failed to do so.

For all plot groupings (i.e., population, microsite, and density), the effects of time and plot group on fate were both significant, although their interaction was not (Table 3.5). The effect of time was particularly evident ($P < 0.0001$), whether it was evaluated against a background excluding or including plot group. Although ΔG^2 within years was significant, the relative *AIC* values clearly identify the model *STL,STF*, which includes time but excludes plot group, as the most parsimonious model in all cases (Table 3.5).

The contribution of each stage class to the overall time effect is obtained by decomposing the three-way S x F x T table into separate F x T tables, one for each initial state (Caswell 2001) (Table 3.6). Demographic fate differed significantly with time in all stage class-treatment combinations but one (DV, microsite). Relative to the null model *TL,F* (independence of fate and time), models containing the time effect also produced low relative *AIC* values. Exceptions were stage DJ for population and for density, which were more efficiently explained by the null model, and stage DV, which yielded large (and hence non-significant) *AIC* values for all three plot groupings (Table 3.6).

Table 3.5 Log-linear contingency analysis of the effect of location and year on the demographic fate of *C. lyallii*, for three separate plot groupings (population, microsite, and density). For each plot grouping, goodness-of-fit G^2 values were calculated by fitting the saturated model (*SFTL*)* to stage-classified transition data (after adding 0.5 to each cell; Fingleton 1984) from 3 time periods (1997-98, 1998-99, and 1999-00) and either 3 (population) or 4 (microsite and density) treatment levels (see text for details). Models are ranked according to the Akaike information criterion (*AIC*), where Δ *AIC* is measured relative to the *AIC* for the best model (*STL,STF* in all 3 cases) (after Burnham and Anderson 1998).

	G^2			*df*			*P*		
Model	Population	Microsite	Density	Population	Microsite	Density	Population	Microsite	Density
1. *STL, SF*	1637.00	1820.08	1786.47	880	1210	1210	< .0001	< .0001	< .0001
2. *STL,STF*	688.65	883.75	838.05	660	990	990	0.2131	0.9931	0.9998
3. *STL, SLF*	1350.34	1437.18	1397.26	660	880	880	< .0001	< .0001	< .0001
4. *STL, STF, SLF*	408.59	493.52	454.70	440	660	660	0.8560	1.0000	1.0000
5. *SFTL*	0.00	0.00	0.00	0	0	0	1.0000	1.0000	1.0000

		ΔG^2			Δdf			*P*		
Effect	Contrast	Population	Microsite	Density	Population	Microsite	Density	Population	Microsite	Density
T	2 vs. 1	948.35	936.33	948.42	220.00	220.00	220.00	< .0001	< .0001	< .0001
T	4 vs. 3	941.75	943.66	942.56	220.00	220.00	220.00	< .0001	< .0001	< .0001
L	3 vs. 1	286.66	382.90	389.21	220.00	330.00	330.00	0.0017	0.0236	0.0137
L	4 vs. 2	280.06	390.23	383.35	220.00	330.00	330.00	0.0038	0.0125	0.0228
T X L	5 vs. 4	408.59	493.52	454.70	440.00	660.00	660.00	0.8560	1.0000	1.0000

	AIC			ΔAIC		
Model	Population	Microsite	Density	Population	Microsite	Density
1. *STL, SF*	-123.0	-599.9	-633.5	508.4	496.3	508.4
2. *STL,STF*	-631.4	-1096.3	-1142.0	0.0	0.0	0.0
3. *STL, SLF*	30.3	-322.8	-362.7	661.7	773.4	779.2
4. *STL, STF, SLF*	-471.4	-826.5	-865.3	159.9	269.8	276.7
5. *SFTL*	0.0	0.0	0.0	631.4	1096.3	1142.0

* *S* = initial state, *T* = year, *L* = location, *F* = fate.

Table 3.6 Decomposition of G^2 for *C. lyallii* into separate tests, one for each initial state, of the effect of year on fate. The null hypothesis (independence of fate and time), represented by the model *TL,F**, is compared to a model containing the *FT* interaction (*TL,TF*). As in Table 4, results for three treatment types (population, microsite, and density) are presented. Models are ranked according to the Akaike information criterion (*AIC*), where Δ *AIC* is measured relative to the *AIC* for the best model (shown in bold).

		G^2			*df*			*P*			ΔAIC		
Stage	Model	Population	Microsite	Density	Population	Microsite	Density	Population	Microsite	Density	Population	Microsite	Density
Sd	*TL, F*	130.47	116.50	116.84	80	110	110	< 0.0001	< 0.0001	< 0.0001	57.20	46.35	53.51
	TL, TF	33.27	30.15	23.33	60	90	90				**0.00**	**0.00**	**0.00**
J1	*TL, F*	152.09	152.09	155.08	80	110	110	< 0.0001	< 0.0001	< 0.0001	47.95	51.23	45.71
	TL, TF	64.14	60.86	69.37	60	90	90				**0.00**	**0.00**	**0.00**
J2	*TL, F*	136.07	163.5	144.61	80	110	110	< 0.0001	< 0.0001	< 0.0001	22.49	24.64	22.51
	TL, TF	73.58	98.86	82.1	60	90	90				**0.00**	**0.00**	**0.00**
R1	*TL, F*	154.95	177.1	183.1	80	110	110	< 0.0001	< 0.0001	< 0.0001	46.90	44.43	43.54
	TL, TF	68.05	92.67	99.56	60	90	90				**0.00**	**0.00**	**0.00**
R2	*TL, F*	143.80	192.94	181.56	80	110	110	< 0.0001	< 0.0001	< 0.0001	46.06	45.71	45.23
	TL, TF	57.74	107.23	96.33	60	90	90				**0.00**	**0.00**	**0.00**
R3	*TL, F*	283.15	308.53	298.65	80	110	110	< 0.0001	< 0.0001	< 0.0001	155.57	154.31	156.07
	TL, TF	87.58	114.22	102.58	60	90	90				**0.00**	**0.00**	**0.00**
R4	*TL, F*	158.32	176.65	156.18	80	110	110	< 0.0001	< 0.0001	< 0.0001	42.44	42.44	41.30
	TL, TF	75.88	94.21	74.88	60	90	90				**0.00**	**0.00**	**0.00**
V	*TL, F*	202.73	210.05	206.14	80	110	110	< 0.0001	< 0.0001	< 0.0001	69.41	68.84	69.47
	TL, TF	93.32	101.21	96.67	60	90	90				**0.00**	**0.00**	**0.00**
D1	*TL, F*	79.15	101.34	102.04	80	110	110	0.0074	0.0016	0.0054	**0.00**	3.74	**0.00**
	TL, TF	40.51	57.60	62.29	60	90	90				1.36	**0.00**	0.25
D2	*TL, F*	125.65	136.83	159.57	80	110	110	< 0.0001	< 0.0001	< 0.0002	25.86	23.59	35.18
	TL, TF	59.79	73.24	84.39	60	90	90				**0.00**	**0.00**	**0.00**
D3	*TL, F*	70.61	84.55	79.02	80	110	110	0.0162	0.0554	0.0385	**0.00**	**0.00**	**0.00**
	TL, TF	34.80	53.49	46.55	60	90	90				4.19	8.94	7.53

* *T* = year, *L* = location, *F* = fate.

POPULATION PROJECTIONS

Projected population growth rates varied considerably among year-plot group combinations, with λ ranging from 0.893 to 1.074 for the 12 population matrices, from 0.874 to 1.290 for the 16 microsite matrices, and from 0.842 to 1.146 for the 16 density class matrices (Fig. 3.4; Appendix 3.3). Projected growth rates across all treatments were highest in 1996-97 and 1998-99 and lowest in 1997-98 and 1999-00. Annual variation among plots appeared periodic, with 'good' years ($\lambda > 1$) generally followed by 'poor' years ($\lambda < 1$) and vice versa, although λ-values for several of the matrices were statistically indistinguishable from 1. In general, there was more variation among years than among plot groups within a year.

Among the three populations, WS showed the most frequent positive growth, with a λ-value significantly >1 in 1996-97 and 1998-99, significantly <1 in 1997-98, and not different from 1 in 1999-00. Site NS, with the largest *C. lyallii* population, showed the greatest year-to-year fluctuations, with growth projected for 1998-99 and declines projected for both 1997-98 and 1999-00. Among the four microsite types (Fig. 3.1), only A (low plant cover and deep soil), C (high plant cover and rocky soil), and D (high plant/litter cover and deep soil) produced λ -values significantly >1 on one or more occasions; confidence intervals for microsite B (low plant cover and rocky soil) either overlapped the equilibrium point or fell below it. The large positive λ of plots in microsite A in 1998-99 was due primarily to a large flush of new recruits during this period. The relatively large uncertainty in this estimate is because most of the recruited plants occurred in only a few of the plots within microsite A. Thus variability among random samples of plots from this data set was high for fecundity terms, resulting in bootstrap estimates with a larger than average deviance. Among density classes, low density plots tended to show lower λ than high density plots in all years. The lower 95% confidence limit for the low density class did not exceed 1 at any time, whereas for the high density plots λ significantly exceeded 1 in three out of four transitions. Only plots belonging to the medium-high and high density classes had $\lambda > 1$ for 1996-97, whereas

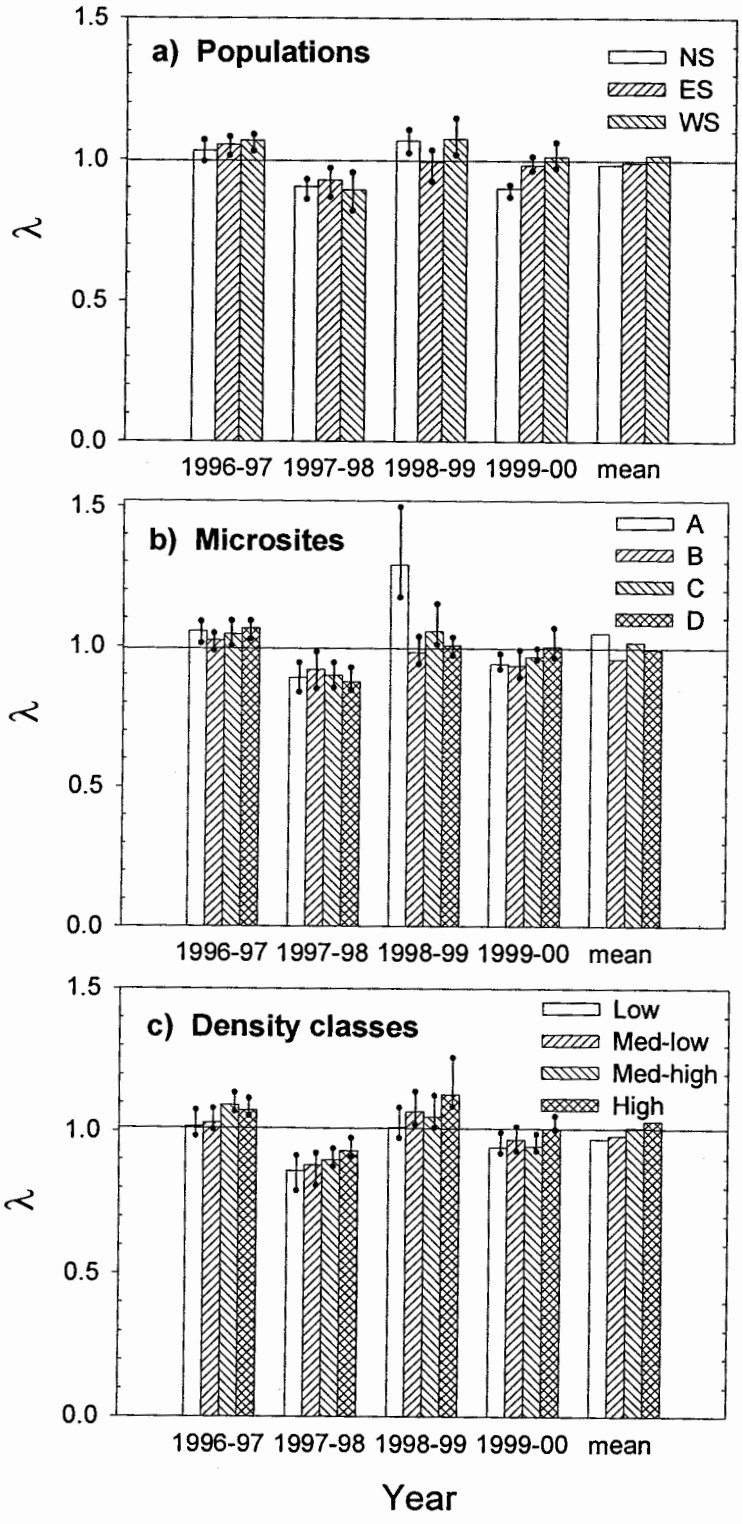


Figure 3.4 Estimates of λ, the projected population growth rate of *C. lyallii*, for different plot groups and years, and the 95% bias-corrected bootstrap confidence intervals of those estimates. Also shown are λ-values derived from the mean annual matrices. Rates of increase were estimated as the dominant eigenvalue of an 11-stage matrix model for each of 3 populations (a), 4 microsite types (b), and 4 density classes (c).

only the high density class yielded a λ significantly above 1 for both of the last two transitions.

Contrary to expectations, predation on bulbs had a greater effect on λ in low than in high density plots (Fig. 3.5). When predation pressure was removed, low density plots were more likely than high density plots to show an increase in λ, which reduced the apparent disparity in λ between low and high density plots (Fig. 3.5).

Randomisation tests of population, microsite, and density effects on λ indicated that significant variation in λ occurred only for microsite differences in 1998-99 (Table 3.7). Fig. 3.6b shows the distribution, obtained by randomly permuting plots among microsite types, of the inter-microsite standard deviation of λ in 1998-99. The observed deviance, $SD(\lambda)_{obs}$, is 0.1425; such large differences occur <1% of the time under the null hypothesis of no microsite effect. In all other treatment-year combinations, $SD(\lambda)_{obs}$ was not significantly greater than that expected under the null hypothesis of random assortment of plots among groups (Fig. 3.6; Table 3.7), and therefore the null hypothesis could not be rejected.

POPULATION STRUCTURE AND STABLE STAGE DISTRIBUTIONS

The size structure of the population, as it existed in 2000, reflects clearly the capacity of this species to recruit successfully from seedlings (Fig. 3.7). The two juvenile classes (J1 and J2) dominate, together comprising 37-50% of established (i.e., post-seedling) plants. A second peak, corresponding to adult flowering plants (classes R2 to R4) and composed primarily of individuals in Class R3, comprises 21-32% of established plants. In contrast, vegetative adults (stage V) represent only 5-10% of established individuals in each plot group. A slightly greater percentage (6-14%) of all individuals occur as dormant bulbs, the majority of which are in the juvenile size class.

In all plot groups analysed, the population structure in 2000, the final census year, corresponded quite closely to the stable stage distribution from the mean annual matrix for that treatment (Fig. 3.7), with Δ values ranging from 0.078 (density class D) to 0.159 (microsite B). Overall, the correspondence between the actual and projected stable stage distribution was greatest (i.e., lowest Δ) for plots arranged according to plant density,

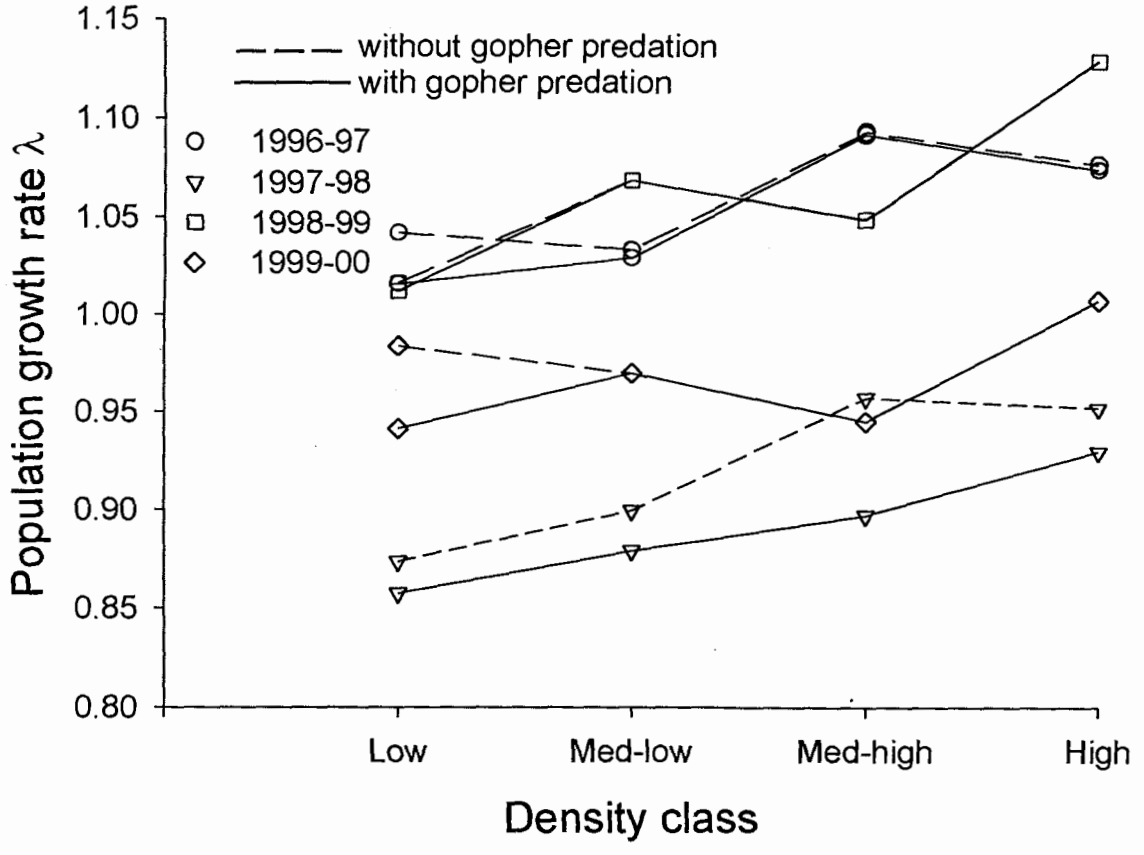


Figure 3.5 Population growth rate λ at different average adult plant densities in the presence and absence of predation (bulbivory) from pocket gophers, in four different transitions. Shown are the observed λ-values, and the λ obtained from the corresponding transition matrix after the mortality due to bulbivory is excluded from the model. See Table 1 for density class definitions. Years: 1996-97 (circles), 1997-98 (triangles), 1998-99 (squares), 1999-00 (diamonds).

Table 3.7 Standard deviations (*SD*) of λ for different plot groups and years, and the probability *P* that a deviation of that magnitude would be observed by chance. For permutation tests plots were randomly assigned among populations, microsite types, or density classes. $n = 2000$ permutations per test.

Observation level	Year	$SD_{(obs)}$	*P*
Population			
	1997-98	0.0171	0.8151
	1998-99	0.0475	0.1584
	1999-00	0.0581	0.0880
Microsite			
	1997-98	0.0180	0.9175
	1998-99	0.1425	< 0.001
	1999-00	0.0300	0.6827
Density class			
	1997-98	0.0302	0.7156
	1998-99	0.0487	0.3173
	1999-00	0.0304	0.7226

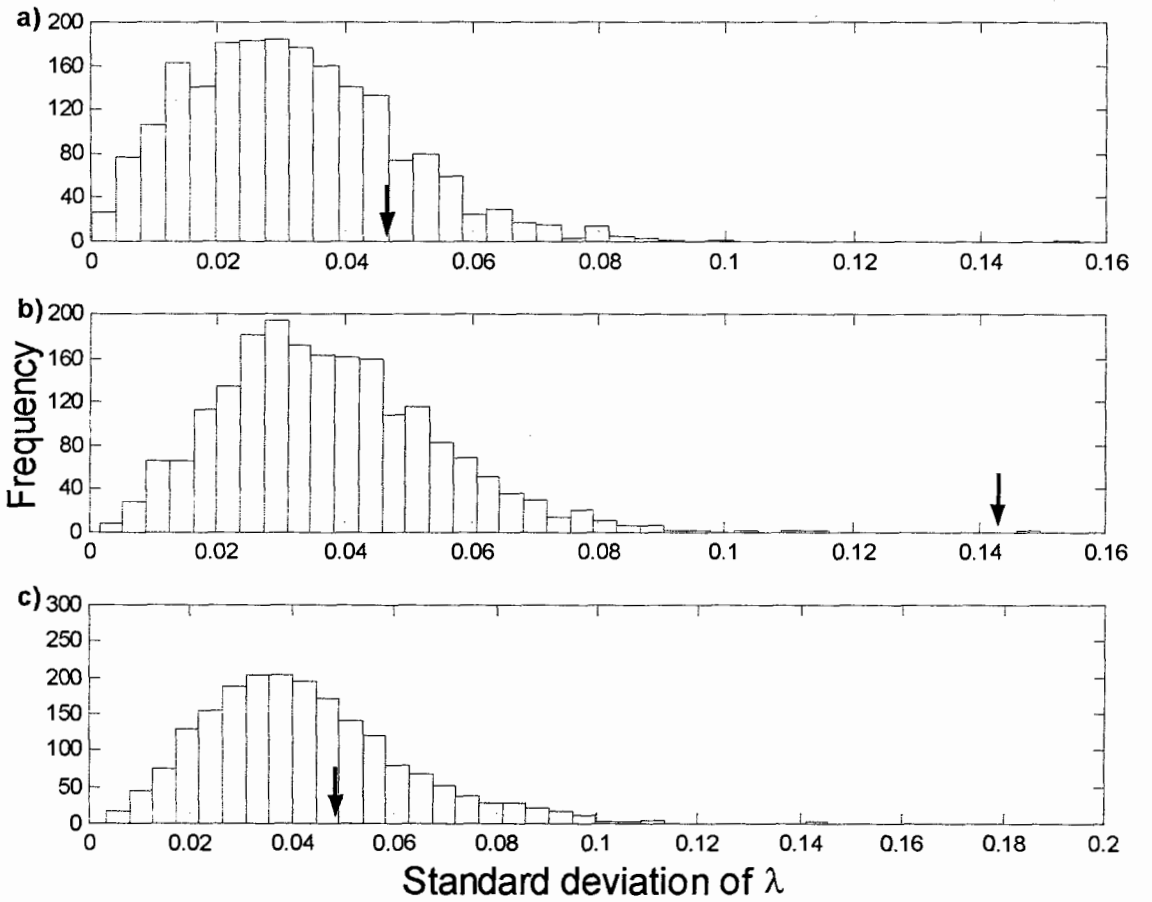


Figure 3.6 Randomisation distributions of $SD(\lambda)$, the standard deviation of population growth rate, λ, among plot groups representing different populations (a), different microsite types (a), and patches of differing intraspecific density (c), under the null hypothesis of no plot group effect. The arrows indicate the observed $SD(\lambda)$. Distributions are based on 2000 random permutations of demographic data for 1998-99, the only year in which any significant difference was observed.

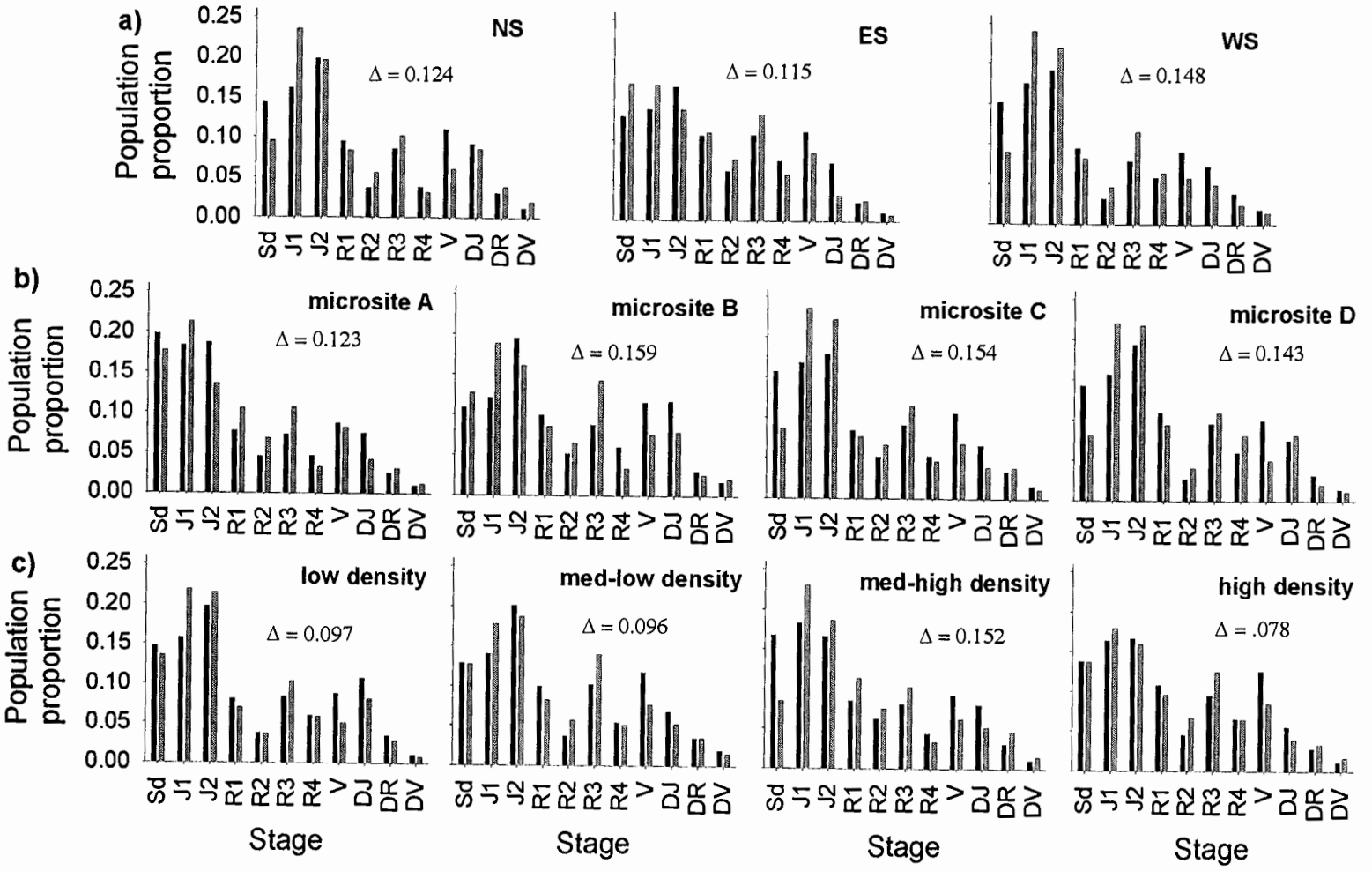


Figure 3.7 Frequency distributions of *C. lyallii* life stages recorded in 2000, the final census year, and projected stable stage distributions calculated from the mean matrices derived from the annual matrices for the periods 1996-97, 1997-98, 1998-99 and 1999-00. Results are shown for 3 populations (a), 4 microsite types (b), and 4 density classes (c). Light bars: observed population structures; dark bars: projected stable stage distributions. For each plot group, the distance between the observed and stable stage distribution is estimated by Keyfitz's Δ (Keyfitz 1968).

lowest for plots grouped by microsite type, and intermediate for entire populations. Nevertheless, the relative stability of these populations, regardless of how they were divided up, implies that the population projection results provide a reasonably accurate measure of current population trends.

Randomisation tests showed that the projected relative frequency of large juveniles (J2) varied significantly among populations in 1997-98 ($P[SD(v) \geq SD(v)_{obs} \mid H_o] = 0.0265$) and 1998-99 ($P = 0.0400$), whereas the relative frequency of small dormants (DJ) varied significantly across sites in 1999-00 ($P = 0.0470$). In contrast, environmental conditions at the microsite level significantly affected the projected frequencies of seedlings and small reproductives (R2) ($P = 0.0005$ and 0.0230, respectively) in 1998-99, and the projected frequency of large flowering adults in 1999-00 ($P = 0.0015$). Plant density, on the other hand, had little discernible effect on stable population structure. An exception occurred in 1999-00, when high density plots appeared to have a higher proportion of two-flowered individuals (R2) than low density plots ($P = 0.0115$).

REPRODUCTIVE VALUES

Reproductive values were generally highest for large reproductives (stage class R4) and lowest for seedlings (Appendix 3.2, last column). Few differences in stage-specific reproductive values occurred among populations, as indicated by randomisation tests. Exceptions were small juveniles, which showed a higher reproductive value relative to seedlings at ES than at NS and WS in 1997-98 ($P[SD(v) \geq SD(v)_{obs} \mid H_o] = 0.012$); and small dormants, which had a higher relative value at ES 1998-99 ($P = 0.043$). In contrast, there were numerous differences in stage-specific reproductive values among microsite types. Measured relative to the reproductive value of seedlings (which does not vary) , values of stage class J1 in 1997-98; classes J2, R1-R4, V, and DR in 1998-99; and classes R1-R3, V, and DR-DV in 1999-00 all varied significantly ($P < 0.05$) among microsites. The most pronounced difference occurred in 1998-99, when a flush of recruits into microsite A resulted in unusually large reproductive values for all four classes of flowering plants, as well as for other established individuals. Permutations of plots among density classes, on the other hand, yielded no significant results; the density of *C.*

lyallii adults within a plot appeared to have little effect on the reproductive values of individuals within the plot.

LTRE ANALYSIS

Although projected growth rates differed little among populations, microsites, or density classes, it is still pertinent to ask how these differences are produced (Brault and Caswell 1993). The LTREs decompose the observed variance in λ, $V(\lambda)$, into contributions from variances in, and covariances among, each of the matrix entries.

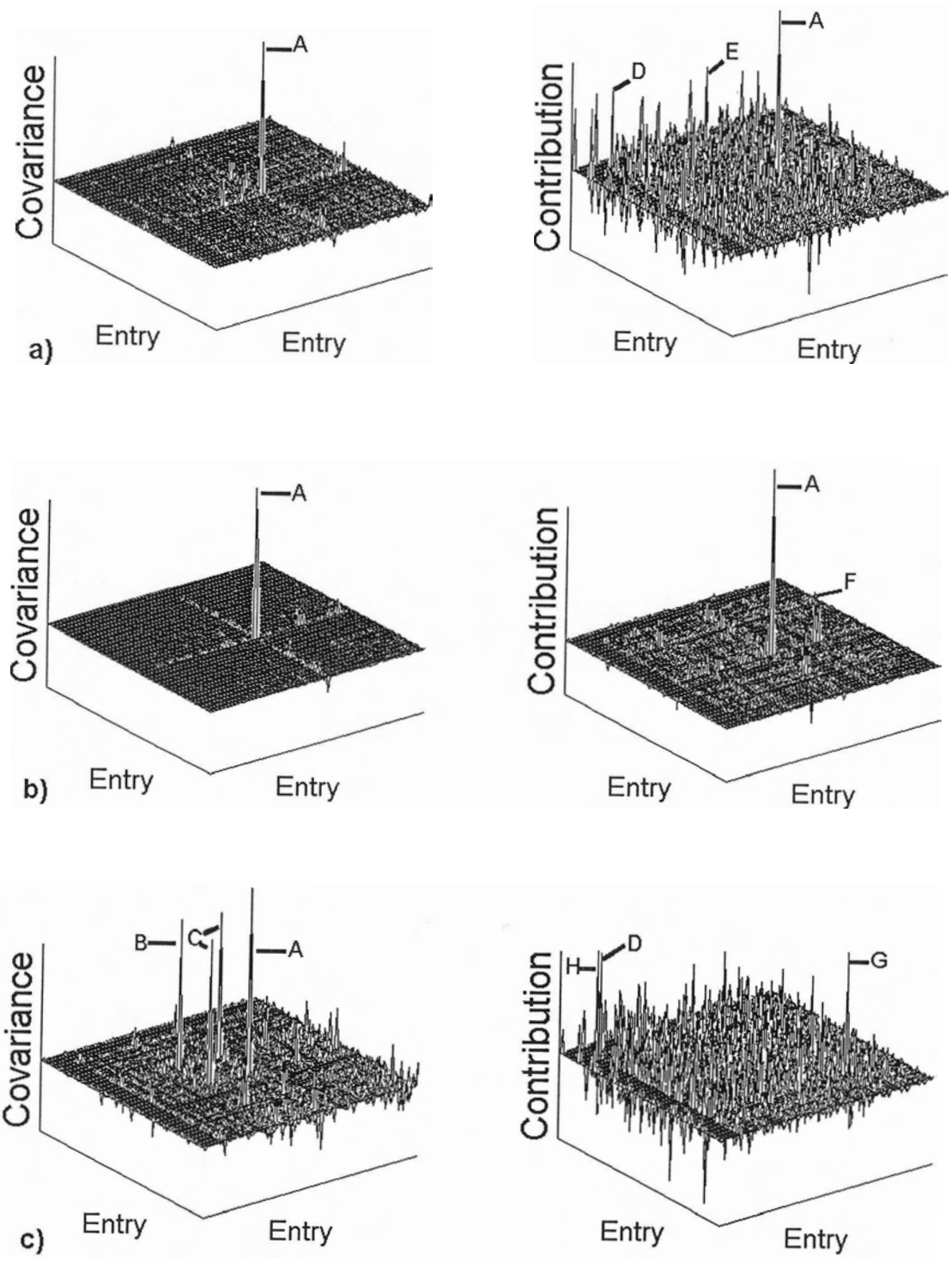
Variance in a_{17} (fecundity of large reproductives) dominated the variance-covariance matrices for all three plot groupings, and contributed overwhelmingly to $V(\lambda)$ among microsites (Fig. 3.8). Although variance in this entry also made the largest contribution to $V(\lambda)$ among populations, variance in a_{32} (growth of small juveniles), and covariance between a_{32} and a_{17}, contributed almost as much to the effect on λ. Among density classes, the largest contributions to $V(\lambda)$ came from variances in a_{59} (transition from dormant to reproductive state), a_{22} (survival of small juveniles), and a_{32} (growth of small juveniles).

Among populations, the largest net contributions to $V(\lambda)$, once individual contributions for all the covariances (and variances) involving each rate are summed, come from a_{21} and a_{32} (growth of seedlings and small juveniles), and from a_{74} (rapid growth of pre-reproductives) (Fig. 3.9a). The transition from vegetative to reproductive state (a_{78}) and the re-emergence of small dormants as vegetative adults (a_{83}) also make substantial net contributions to $V(\lambda)$. The largest negative net contributions to $V(\lambda)$ come from a_{92} (small juveniles entering dormancy) and from a_{33} (stasis of large juveniles).

In contrast, differences among microsites are due almost entirely to covariances involving the fecundity of large reproductives, whereas seedling survival contributes little to $V(\lambda)$ (Fig. 3.9b). Notable negative contributions are made by prolonged juvenile dormancy (a_{99}) and large juveniles entering dormancy (a_{93}).

Among density classes, the largest positive net contributions to $V(\lambda)$ come from stasis of small juveniles (a_{22}), followed by vegetative stasis (a_{88}) and rapid growth of pre-reproductives (a_{74}) (Fig. 3.9c). Covariances involving the transition from reproductive to

Figure 3.8 *Left:* Surface plot of the covariances of the matrix elements a_{ij} and a_{kl} among populations (a), microsites (b), and density classes (c), where a_{ij} and a_{kl} are the mean matrix values calculated over four annual transitions (1996-00). Variances appear on the diagonal; off-diagonal entries are covariances. Important peaks are identified by letter. A = the variance in a_{17} (R4 fecundity); B = the variance in a_{15} (R2 fecundity); C = the covariance between R2 and R4 fecundity. *Right:* The contributions of the covariances to the variance in λ, where λ is the dominant eigenvalue of the mean projection matrix. Important peaks are identified by letter. A = the variance in R4 fecundity; D = the variance in J1 growth; E = the covariance between R4 fecundity and J1 growth; F = the covariance between R4 fecundity and a_{39} (emergence of small dormants); G = the variance in a_{59} (emergence of D1 as flowering plants); H = the variance in J1 stasis.


Covariance
A
Entry
Entry
a)
Contribution
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A
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Entry
Covariance
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Entry
Entry
b)
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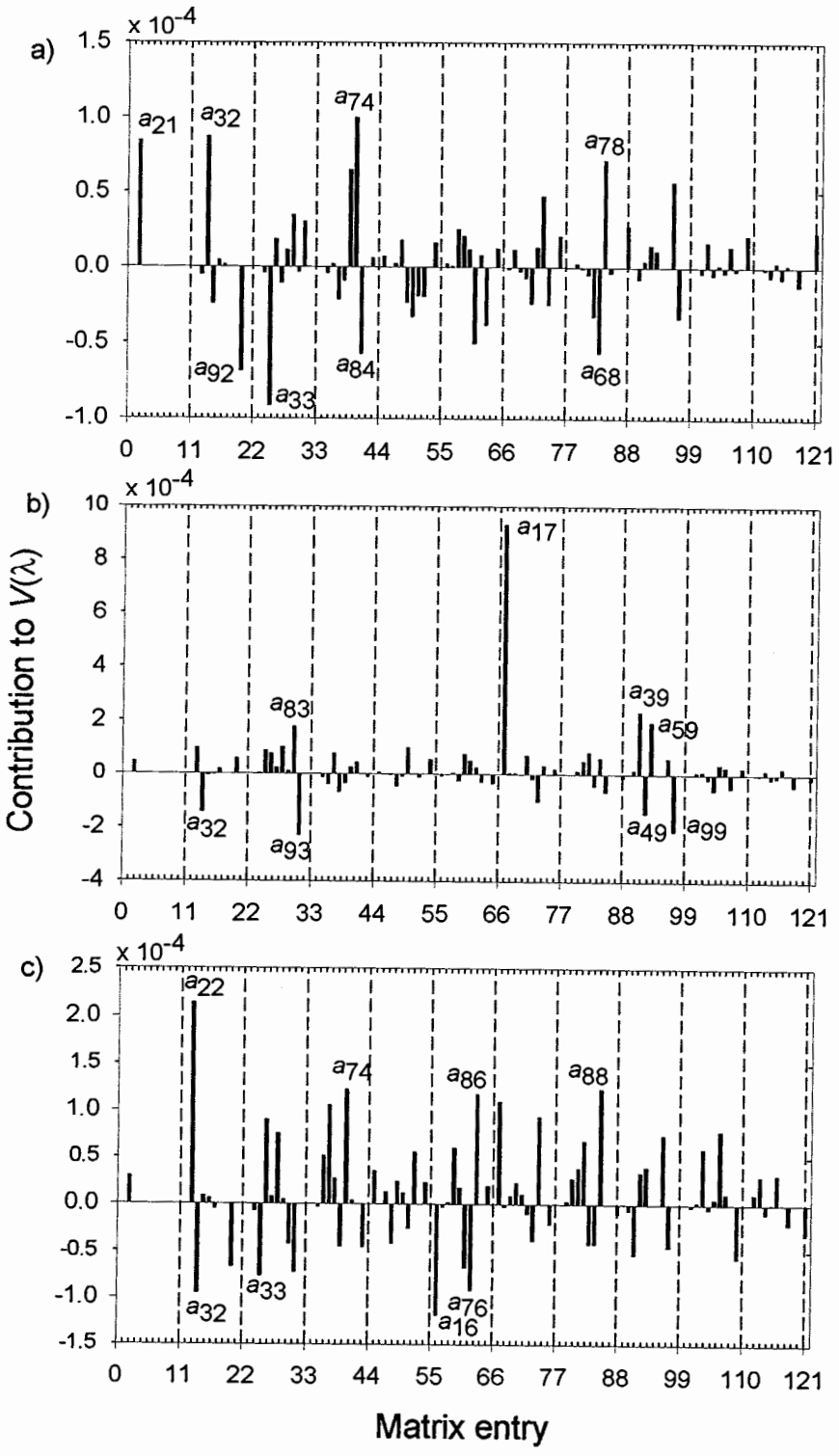

Figure 3.9 The net contribution of the matrix entry a_{ij} to the variance $V(\lambda)$ among a) populations, b) microsites, and c) density classes, obtained by summing over the variance contributions in Figure 10. The 121 entries of the 11 x 11 matrix are arranged in column order: fates of seedlings ($a_{11},\ldots,a_{111}$), fates of small juveniles ($a_{12},\ldots,a_{112}$), etc. Matrix subscripts are indicated for the most conspicuous peaks.

vegetative state (a_{86}) and large reproductive fecundity also make substantial positive contributions, while growth of small juveniles actually makes a net negative contribution to $V(\lambda)$. Also acting to reduce differences among density classes are covariances involving fecundity and growth of medium-sized reproductives (a_{16} and a_{76}).

Of the 19 top-contributing matrix entries identified by the LTRE analysis, those corresponding to growth and survival of seedlings and juvenile plants showed the closest correlation with microsite conditions (Table 3.8). Fecundity of large reproductives, one of the main contributors to $V(\lambda)$, was significantly correlated with only two variables: soil depth (positive) and percent rock cover (negative). Seedling survival was positively correlated with soil depth and with both vascular and non-vascular plant cover, and negatively correlated with both percent bare soil and percent rock cover. Values for small juvenile growth (a_{32}) and large juvenile dormancy, survival and growth (a_{92}, a_{33}, and a_{83}) were positively correlated with soil depth and negatively correlated with percent bare soil. Survival rates of juveniles also tended to increase with increasing plant cover. There was a positive association between soil moisture and the probability of regressing from a flowering to a vegetative state. Two habitat variables, slope inclination and litter depth, showed no significant relationships (Table 3.8).

ELASTICITY ANALYSIS

The elasticity matrices for each plot group-year combination are presented in Appendix 3.4. In general, the elasticity of fecundity elements was low; survival and growth of young/small individuals and stasis of large reproductives tended to make larger proportional contributions to λ. Nevertheless, elasticity patterns varied among matrices, with no single transition dominating. Depending on plot group and transition period, the matrix entry with the highest elasticity was either a_{21} (seedling survival), a_{22} (stasis of small juveniles), a_{33} (stasis of large juveniles), a_{77} (stasis of large reproductives), a_{88} (stasis of vegetative adults), a_{99} (stasis of small dormants), or a_{1111} (stasis of large dormants). Most of these peaks occurred in 1997-98 (Appendix 3.4), when λ was negative for all plot groups. Randomisation tests showed that, within this transition

Table 3.8 Significant Spearman rank correlations between selected habitat variables and plot estimates for the matrix entries a_{ij} with the largest contributions to $V(\lambda)$ among microsite types (Fig. 3.9b). Both positive and negative contributions were considered. Matrix values were the averages over four transition periods (1996-2000) in each demographic plot. $n = 95$ plots.

	Habitat variable									
Matrix entry	Aspect	%bare soil	%litter cover	Litter depth	Soil moisture	%bryophyte cover	%vascular plant cover	%rock cover	Soil depth	Slope
a_{21}		-0.229*				0.267**	0.256*	-0.224*	0.368***	
a_{22}		-0.211*	0.213*				0.257*			
a_{32}		-0.339***				0.284**			0.419***	
a_{92}	-0.207*	-0.219*							0.297**	
a_{33}		-0.320**					0.239*		0.244*	
a_{83}		-0.277**			0.230**				0.205*	
a_{93}		-0.255*								
a_{74}	0.254*									
a_{84}		-0.205*			0.268**					
a_{16}										
a_{76}										
a_{86}					0.282**					
a_{17}								-0.214*	0.246*	
a_{68}		-0.249*								
a_{88}										
a_{39}		-0.312**								
a_{49}										
a_{59}										
a_{99}										

*P < 0.05, **P < 0.01, ***P < 0.001

period, individual elasticities were more likely to vary significantly among populations than among microsite types or density classes (results not shown).

The combined elasticities for individual stage classes were compared by summing down the columns of elasticity matrices associated with the mean annual transition matrix for each plot group (Fig. 3.10). The distribution of elasticities across stages was the same for all plot groups, regardless of the data set being analysed ($\chi^2 \leq 14.5$, df = 20-30, $P \geq 0.99$). Interestingly, elasticity patterns closely resembled the predicted stable stage distributions (Fig. 3.7), with one peak composed of the summed elasticities of large juveniles and a second, smaller peak corresponding to the summed elasticities of large adults. In fact, the two patterns were statistically indistinguishable for every plot group ($\chi^2 \leq 16.4$, $df = 10$, $P \geq 0.09$).

Discussion

VARIATION IN TRANSITION MATRICES AND IN λ

The comparison of transition matrices from three populations, four microsite types, four density classes, and three transition periods (1997-00) showed that effects of year outweighed either location or density in determining demographic vital rates. The relative lack of demographic differentiation at either the inter- or intra-population level is reflected in the similar λ-values within years among plot groups; the only significant difference in λ was among microsites in 1998-99, when λ ranged from 0.9782 to 1.2896 (Table 3.6). Variation in λ among populations and density classes was never significantly greater than would be expected on the basis of the null hypothesis. These results suggest that factors operating at the regional level (e.g., climate) influence population dynamics more than local factors. This is consistent with results of Bengtsson (1993), who detected a significant effect of year but no effect of site on the demographic fate of *Fumana procumbens*. However, it is in contrast to findings for several other perennial herbs (Silva et al. 1991, Oostermeijer 1996, Kephart and Paladino 1997, Valverde and Silvertown 1998, Nantel and Gagnon 1999). In these cases, spatial variation in growth or survival was often attributable to changes in the environment brought about by natural succession

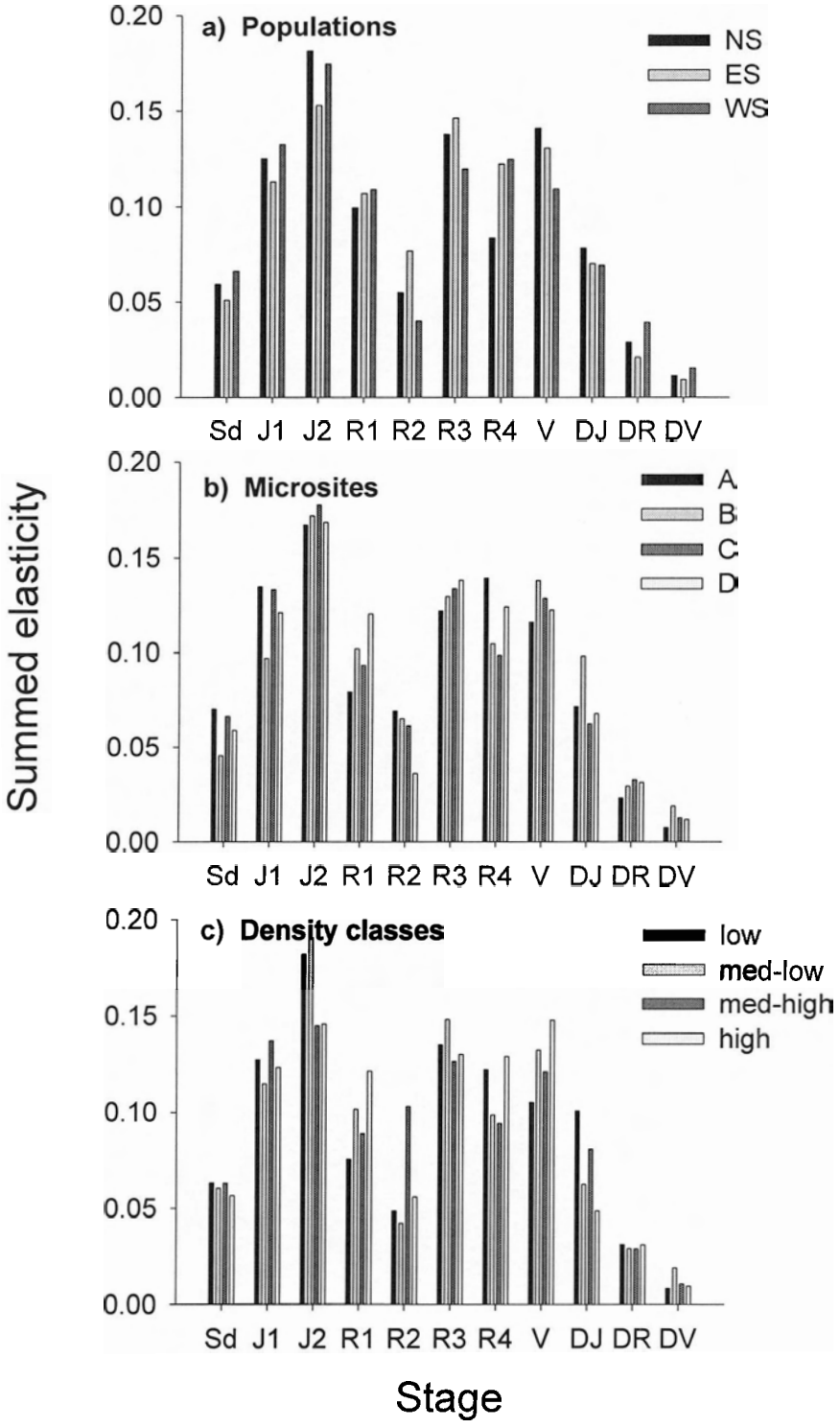

Figure 3.10 Summed elasticities, by stage, corresponding to the mean annual matrix for each of 3 populations (a), 4 microsite types (b), and 4 density classes (c).

or human disturbance, factors that may not have been important at the temporal and spatial scales considered in this study.

Although the spatial variation in λ was not statistically significant in most cases, there were important qualitative differences among plot groups in the sign and direction of annual growth trajectories. For example, the population at site NS had the greatest frequency of transition intervals with λ significantly <1, whereas site WS had the greatest frequency of transition intervals with λ significantly >1. A potential location x year interaction was also evident when plots were grouped according to microsite characteristics, with microsite A (open, deep soils) and C (high plant cover, shallow soils) both showing positive λs in 2 out of four intervals, and microsite B (exposed, rocky ground) failing to have a λ significantly >1 in any interval. Among density classes, high-density plots were more likely to have positive population growth rates than low-density plots. In a stable environment, the difference between λ <1 and λ >1 represents the difference between exponential decline and exponential growth; hence, any change in the direction of λ will by definition have a major impact on population trajectories. These results suggest that *C. lyallii* dynamics may be sensitive to environmental heterogeneity at the levels of organisation examined here, even if absolute differences in λ are small. It is thus relevant to enquire how that variation was produced, and to what extent the factors contributing to differences in λ are scale-dependent.

Among populations, the largest contribution to the variance in λ (dominant eigenvalue of the mean matrix) came from variance in the fecundity of large reproductive plants. This resulted from a combination of the sensitivity of λ to fecundity and the amount of variation in fecundity. However, this entry made only a small net contribution to $V(\lambda)$, because positive and negative covariances tended to cancel out. The largest net contributions came instead from covariances involving growth of small plants and the progression from a non-reproductive to a reproductive state.

In contrast, the variance in λ among microsites was overwhelmingly due to variance in fecundity. On average, large reproductives in microsite A produced over twice the number of recruits per capita as similarly-sized individuals in microsite B. Microsite C and microsite D (high litter cover and deep soil) showed intermediate values for this term.

Although population growth rate was more sensitive to other parameters, particularly the rapid growth of large juveniles, no other parameter varied as much among microsites. Variation in this rate may also help to account for the difference in sign in average growth rates between microsites A and B. Because fecundity terms are themselves functions of both seed production (i.e., fertility) and post-dispersal seed survival and germination, further attempts to explain the variation in λ at this scale should probably focus on factors affecting these lower-level parameters. Given the high germination rates observed for seeds inside buried seed packets, this low recruitment rate cannot be ascribed to poor seed germinability. Rather, seed set, availability of safe sites, and rates of seed loss to post-dispersal predation likely combine to determine differential success of *C. lyallii* at the local microsite scale.

A somewhat different pattern emerges from the variance decomposition analysis of patches grouped by density. In this case, variance in λ was due largely to covariances involving vegetative stasis; variance in fecundity actually made a negative contribution to $V(\lambda)$. Although I could not distinguish between density-specific effects and effects stemming directly from differences in patch quality, this result is consistent with expectations if density-dependent fecundity were acting to regulate population growth. At the least, population and patch effects on λ appear to be mediated by different sets of vital rates. My results emphasise that widely different demographic results can be obtained depending on the organisational scale examined, and therefore that attempts to infer regional patterns from local processes and vice versa may produce erroneous results.

This conclusion differs somewhat from that of Watkinson et al. (2000), who analysed the population dynamics of the annual grass *Vulpia ciliata* at different scales ranging from the regional population down to small (10 x 10 cm) subplots. They found that the most salient features of dynamics at the regional scale (the persistence and very small spatial size of individual populations) could be explained by processes operating at much smaller scales (Watkinson et al. 2000). In that system, population growth was strongly regulated by density-dependent seedling recruitment and λs within patches were consistently low, which, in combination with restricted seed dispersal, was sufficient to account for the limited spatial extent of populations at the regional scale (Watkinson et al. 2000). A similar combination of low λs and restricted dispersal may also help explain the

relatively small areas of most *C. lyallii* populations on Black Mt. (generally much <1 hectare). Indeed, there is growing evidence that seed dispersal limits recruitment in many grassland species (Primack and Miao 1992, Eriksson and Jacobsson 1998).

VARIATION IN STABLE STAGE DISTRIBUTIONS

As with λ, variation in the projected stable stage distribution reflects variation in the vital rates and is an important aspect of a plant's overall response to environmental heterogeneity (Valverde and Silvertown 1998). Together with the stage-specific reproductive values, the stable stage distribution is also one of the components determining the sensitivities and elasticities; as a stage increases in stable frequency, so does the sensitivity of λ to transitions that affect the number of individuals entering and remaining in that stage. I found that the stable stage distribution varied with both population and patch, and that the pattern, and sometimes the direction, of variation differed from year to year, suggesting a temporal interaction as well. Among populations, stable stage frequencies varied most in the expected proportion of smaller established individuals, in particular juveniles and small dormants. With the exception of 1997-98, when the pattern was reversed, these stages made up a greater proportion of the population at the relatively cool, moist site NS than in the drier, rockier conditions at site ES. The differences in population structure among sites indicate that vital rates are affected by processes occurring at the landscape level, even if these effects do not necessarily lead to large changes in λ. Different *C. lyallii* populations could be converging on similar λs through different combinations of life history events. Thus, persistence of the population on the east slope of Black Mt. may rely more on the survival of older, established individuals, whereas persistence in other locations may be more closely tied to high juvenile survival.

In contrast, differences in the stable stage distribution at the microsite level were mostly due to differences in the relative frequencies of reproductive adults and seedlings, especially during the 1998-99 transition. In that year the proportion of seedlings projected for microsite A (37%) far exceeded that of any other microsite type. This plot group x year combination also had the highest projected λ (1.2896) out of all the

treatments. The sudden flush of recruits into these plots could reflect an actual difference in patch quality relative to other microsites, or could be due to chance. Nevertheless, the strong positive correlation between the projected frequency of seedlings for a given microsite-year combination and λ for that year ($r^2 = 0.92$, $P < 0.0001$, $n = 16$) suggests that population structure in *C. lyallii* could serve as a rough gauge of local population growth in cases where more detailed demographic data are lacking. For example, a known relationship between seedling frequency and λ could be used to make an initial, rapid assessment of relative population potential in previously unstudied sites or habitat patches from just a single census of *C. lyallii* individuals taken in the spring—provided the population of concern was at or near its stable stage distribution at the time of censusing.

Although truly stable populations rarely occur in the wild, the relatively modest differences in this study between the stable distributions generated by the mean matrices (1996-2000) and the actual observed distributions in 2000 imply that, overall, vital rates during this period were similar to those that have operated over time to produce the current distributions. Keyfitz's Δ, which estimates the distance or dissimilarity between the two population vectors, was largest when plots were grouped according to microsite (0.145) and smallest when grouped by density (0.106). Values of Δ were substantially lower for *C. lyallii* than for three of the four *Calochortus* species studied by Fiedler (1987) in California, and were within the range of values reported by Fredricks (1992) for the two Oregon endemics *C. umpquaensis* and *C. coxii*. The low Δ values are somewhat surprising given the severe scorching incurred by all three *C. lyallii* sites only two years prior to the commencement of the study. It suggests either that (a) the fire had negligible physical impact on individual plants (a reasonable hypothesis given that the plants had already become dormant for the season when the fire occurred); or (b) that the time required for convergence to a stable distribution following fire is relatively short. The first alternative invokes the concept of resistance, the second, that of resilience (Pimm 1991). In *Chapter 4*, I explore these concepts further in the context of a comparative demographic study between *C. lyallii* and a sympatric congener, *C. macrocarpus*.

PROLONGED BULB DORMANCY

In all three retrospective analyses, the summed contributions of regression into, and stasis via, dormancy were negative, indicating that the patterns of variability relative to this life stage generally acted to reduce the variability of λ. In other words, the probability of becoming and/or remaining dormant declined with increasing environmental favourability. This effect was especially strong for juveniles. The presence of persistent seed banks has been shown to help to ensure the continuation of isolated populations in the absence of regular seed production (Cohen 1966, Baskin and Baskin 1978, Venable and Lawlor 1980, Brown and Venable 1986, Parker et al. 1989, Kadmon and Shmida 1990) or provide a buffer against catastrophic events that affect established plants (Kalisz and McPeek 1993, Pavlik et al. 1993). Kalisz and McPeek (1992) found that dormant seeds of the annual herb *Collinsia verna* were patchy in their distribution, and that spatial variation in seedbank age structure significantly affected the estimates of population dynamics and age structure along different transects within a single population. The population-level consequences of prolonged dormancy at later stages of the life cycle has received much less study (*Chapter 2*). Recently, Shefferson et al. (2003) found that prolonged dormancy in the rare orchid *Cypripedium calceolus* occurred at a cost to future survival and reproduction, and concluded that dormancy was unlikely to be adaptive in *C. calceolus* except possibly as a bet-hedging strategy under catastrophic conditions. My study is one of the first to show quantitatively that underground 'bulb banks' could function to offset the effects of a spatially varying environment, in a manner similar to that hypothesised for dormant seed banks (Kalisz and McPeek 1992). This result lends support to the idea that an important source of persistence for many plants is the buffering provided by the spatial structure within populations (Watkinson et al. 2000).

The factors leading to non-emergence in *C. lyallii* are unclear, although there is indirect evidence that it may be linked to weather patterns or to soil moisture content (*Chapter 2*). For geophytes such as *C. lyallii* that lack a persistent seedbank and have restricted seed dispersal, delaying emergence aboveground until conditions are suitable for growth and reproduction could provide an alternative means of sampling the environment in space and in time (*sensu* Venable and Lawlor 1980). Analytical models

show that, for any population, extinction probability increases as λ decreases and as the variance of λ or of population number with time increases (Lande 1993). Any trait that helps to maximise λ or reduce $V(\lambda)$ should thus be favoured by selection. In the case of bulb dormancy, a trade-off could be expected between the benefits accruing from avoiding emergence during adverse years and the cost incurred from sacrificing current growth and reproduction. As with the seedbank in a temporally varying environment (Cohen 1966), the exact dormancy rate that maximises fitness would presumably be determined by the probability of occurrence of different suites of environmental conditions and the λ realised from emergence under each set of conditions.

HABITAT RELATIONSHIPS

The LTRE analyses identify the vital rates that contribute most to the observed variability of λ; however, they do not indicate what environmental factors caused the rates themselves to vary. Generating hypotheses about the latter is the logical next stage of demographic diagnosis (Caswell 2001). Separate analysis of transition probabilities for individual 0.25 x 0.25 m^2 plots showed that microsite conditions had a significant influence on several 'key' life history transitions (e.g., seedling and juvenile survivorship and growth), but only a weak association with others (e.g., adult survival and flowering). The most marked relationships were a consistent positive correlation of soil depth and a consistent negative correlation of the amount of bare soil with survivorship/growth during the earliest life stages.

Because my analysis does not account for partial correlations or for possible spatial autocorrelations among variables that may exist when samples are spatially constrained (Thomson et al. 1996), these relationships need to be interpreted cautiously. However, they do point towards two interesting possibilities. First, local differences in λ (where these exist) may be more likely to be mediated by fine-scale differences in soil substrate than by other microsite characteristics such as slope, aspect, and litter depth. Secondly, soil depth and exposure may affect *C. lyallii* demography mainly through their effects on the very earliest life stage transitions, i.e., those relating to recruitment and establishment. In contrast, later stages are relatively insensitive to fine-scale differences in

microenvironmental conditions. This is probably because the bulbs of older individuals are deeper in the ground and hence less likely to be affected by physical conditions at or near the soil surface. Even on rocky substrates bearing many *C. lyallii* individuals, I found that bulbs of large plants were usually restricted to deep soil pockets or to crevices in the bedrock. From a management perspective, such individuals would be poor choices for use in bioassays relying on general edaphic characteristics alone to provide demographically relevant measures of habitat suitability (such as one might wish to have before embarking on population enhancements or reintroductions). Instead, these results indicate that more useful information could be obtained by focusing on investigations of the factors causing spatial patchiness in seedling and juvenile abundance and survivorship.

The significant positive correlation I observed between recruitment rate, a_{17}, and soil depth is consistent with the picture of recruitment safe sites that emerges from directly comparing cover plots containing seedlings with those lacking seedlings. In that case, however, there were significant differences in soil depth, soil moisture, and percent bare soil between the two 'types' of plots at site ES but not at NS or WS, indicating the presence of a patch x site interaction. Such a result might be expected if overall habitat conditions at one of the locations were more marginal, rendering recruitment at that location more sensitive to minor variations in local substrate quality. Site ES, on the east slope of Black Mt., appears to present a generally more hostile environment to *C. lyallii* seeds and seedlings than does either NS, on the north slope, or WS, on the west slope. Not only is the soil shallower than that at either of the other two locations, it is also significantly rockier, drier and more exposed (Table 3.3), features that might have little effect on established plants but that could contribute to the premature desiccation of seedlings as well as increase vulnerability to seed predators. These factors could also help to account for the slightly reduced stage-specific fecundity rates I observed at site ES compared to either NS or WS. Furthermore, once germination occurred, seedlings at ES had a lower average annual survival through the first year ($p = 0.49$) than seedlings at either NS ($p = 0.52$) or WS ($p = 0.58$). The importance of favourable microsites for seed germination and seedling establishment is well established (e.g., Harper 1977, Fowler 1988, Aguiar and Sala 1997). In a study of rare Ca*lochortus* species from southern

Oregon (Fredricks 1992), seedlings of both *C. umpquaensis* and *C. coxii* were found to be more likely to establish on mossy microsites or on litter than on bare soil, suggesting that exposure is a major factor contributing to early mortality in this genus in general.

Of course, the occurrence of a positive correlation of seedling density with soil depth is not proof of causation; the association could actually be a spurious one driven by some other spatial process. Thompson et al. (1996) proposed that an apparent negative correlation between flowering and soil moisture in *Erythronium grandiflorum* was spurious and that the apparent 'preference' of *E. grandiflorum* for drier sites was not related to dryness *per se* but was driven by patchiness in gopher predation, which was explained by the rock content of the soil. In the case of *C. lyallii*, the only variable measured that was consistently associated with seedling presence at all three sites was the density of adult conspecifics. This contrasts with the pattern seen in *E. grandiflorum*, which was characterised by a lack of association between the number of flowers initiated and the number of seedlings, but is consistent with expectations given the limited seed dispersal abilities of these two species. The often high density of *Calochortus* patches in the three study sites suggests that safe sites also serve as suitable microhabitats for plants in later stages of the life cycle. Alternatively, if recruitment patterns are determined primarily by seed availability rather than by seedling establishment, as has been demonstrated for some arid and semiarid environments (e.g., Aguiar and Sala 1997), then the spatial distribution of seedlings is more likely to reflect local patterns of seed production and dispersal than the frequency of safe sites *per se*.

ELASTICITY ANALYSIS

Elasticity is fairly uniformly distributed among life cycle components, with no single transition dominating. Juvenile survival made the most consistent contribution to population growth, followed by seedling survival and the fecundity and stasis of large reproductive plants. The combined fates of dormant plants accounted for *c.* 10% of population growth, which was similar to the total contribution from medium-sized reproductive (R2) plants. The most notable deviations from this general pattern occurred in 1997-98, when λ-values were unusually low. From a management standpoint, the lack of concentration of elasticity on any one life cycle event is both comforting and sobering.

On the one hand, my results do not indicate any obvious Achilles heel for *C. lyallii*, such that an isolated perturbation to one vital rate or transition would have a strong impact on population trajectories. Rather, *C. lyallii* appears to possess a relatively stable life history that may help buffer it from stochastic environmental variation. On the other hand, these results also suggest that there is no obvious or easy management strategy likely to yield a substantially increased population growth rate for this species, should such a need arise. Instead, successful management intervention will likely require a focus on preserving and enhancing all life cycle processes simultaneously.

Although there was considerable variation in detail among individual elasticity matrices, combined elasticity estimates associated with the mean vital rates were qualitatively invariant, regardless of the spatial backdrop against which they were evaluated. Thus the strength of selection acting on different life stages appears to be similar among habitats at the scales studied here. From the standpoint of management, this result suggests that the elasticity projections are robust to differences in habitat conditions both within and among sites, once temporal variation is factored out. At the same time, it is clear that attention must be paid not only to the elasticity values themselves but to the environmental context generating them. Management prescriptions based entirely on transition data from a single year or sub-population run the risk of targeting inappropriate stages in the life cycle, if the data are not representative of the target population as a whole.

RELEVANCE TO SPATIAL MODELS OF DYNAMICS

Overall, my data provide little support for a shifting mosaic model of population dynamics at the regional scale. Among the populations studied, dynamics appear to be, for the most part, spatially stable. Temporal variation does exist, but it tends to be synchronised at the spatial scales examined.

My results also appear inconsistent with a local source-sink structure, although my analysis cannot distinguish between this model and a stable system with varying equilibrium densities within populations. This is because for obligately sexual plants such as *C. lyallii*, the dispersal of individuals from 'good' to 'poor' habitats that would indicate a source-sink dynamic is entirely due to seed movement among patches; the

lower-than-expected densities in favourable sites are a result of seed dispersal into less favourable sites, which therefore are able to maintain higher-than-expected densities. However, because tracking seeds is difficult, and sometimes impossible, in natural populations (Wang and Smith 2002), a necessary assumption of demographic analysis in most studies (mine included) is that plots are closed systems (i.e., no net import of seeds). Consequently, the projection matrix will not distinguish between recruitment occurring from seed produced inside the patch and that due to seed originating from elsewhere. Teasing apart these conditions conclusively is probably intractable except via experimentation (Kadmon and Tielborger 1999). However, a source-sink dynamic would be implicated if there were a major discrepancy between the number of new recruits found inside a patch and the number or proportion predicted by the stable stage distribution. In theory, a patch that is functioning as a reproductive sink should have an excess of recruits relative to that predicted for the stable distribution, because most of the propagules inside the patch will die before they can reproduce (Pulliam 1988). However, I found little evidence for such a pattern in *C. lyallii*. In general, the proportion of seedlings observed was the same as or less than that predicted for a stable population.

Despite annual fluctuations in λ over the five years of the study, long-term growth rates (estimated by the dominant eigenvalue of the mean annual matrix) all tended to converge on 1 regardless of plot group, suggesting that density-dependence may be acting to maintain these populations at a stable equilibrium. However, λ increased with density in a given year, which would argue against a density-dependent equilibrium. Such patterns need to be interpreted carefully, particularly in mensurative studies, as patchiness in the favourableness of the environment can often mask effects of competition (Fowler 1988). For example, a positive relationship between density and λ might occur if high resource levels have not been constant long enough for the density of plants in more favourable patches to reach carrying capacity, but have persisted long enough for an increase in density to have begun (Fowler 1988). Such a situation could have arisen following the extremely hot wildfire that burned through the study area in 1994, an event that could have led to reductions in plant density over the short term at the same time that it wrought dramatic, localised changes in the soil nutrient regime.

My matrix simulations revealed that the reduction in growth rate from high- to low-density patches was due in part to an asymmetry in foraging pressure from northern pocket gophers (*Thamomys talpoides*), fossorial rodents that harvest *C. lyallii* bulbs by tunnelling through the soil. These animals, which primarily targeted large, mature *C. lyallii* bulbs, tended to be most active within less favourable, low-density patches. Bulbivory by pocket gophers has also been cited as one of the primary sources of mortality in rare mariposa lilies of southern Oregon (Fredericks 1992). Because reproduction in *C. lyallii* does not occur below a certain size threshold, a decrease in the proportion of large-sized bulbs due to bulbivory reduces seed production. Thus predation, rather than regulating population size, may actually be amplifying density gradients over small spatial scales. This contrasts with the effects of gophers on local distribution patterns of *Erythronium grandiflorum* (Thomson et al. 1996). In that system, gopher activity was concentrated in the same microsites (deep-soil patches) where most *E. grandiflorum* seeds germinated, resulting in higher mortality and lower adult density in these sites than in less physiologically favourable, adjacent rocky areas. The result was a net source-sink flow of seeds from 'poorer' (i.e., rocky) microsites to 'better' (i.e., deep-soil) microsites, where the plants eventually perished (Thomson et al. 1996).

The apparent decline in low-density plots combined with the increase in high-density plots in *C. lyallii* populations suggests that they are not in a state of internal equilibrium. On the contrary, local colonies at the patch level may be going extinct frequently even though the population in total shows little fluctuation. At this scale, the shifting mosaic model of population dynamics thus appears valid.

Chapter 4: Comparative demography of two sympatric species of *Calochortus* (mariposa lily) with contrasting distribution patterns

Introduction

Major differences in the abundance patterns of related sympatric plants are a common but puzzling phenomenon. In particular, the co-occurrence of locally rare and/or geographically restricted species alongside locally abundant and/or widespread congeners has long intrigued scientists (Darwin 1872, Gleason 1924, Harper 1977, Grime 1979, Brown 1984, Kruckeberg and Rabinowitz 1985, Bradshaw 1987, Gaston and Kunin 1997, Pimm 1993, Belville and Louda 1999). The factors contributing to the persistence of these differing abundance patterns are multifarious and complex (Stebbins 1980, Fiedler and Ahouse 1992) and include, to varying degrees, geologic and evolutionary history (Cwynar and MacDonald 1987, Kirkpatrick and Barton 1997), species interactions (Bruelheide and Scheidel 1999, Walck et al. 2001, Lloyd et al. 2002), population genetic structure (Young and Brown 1996, Gitzendanner and Soltis 2000), habitat specificity (Fiedler 1985, Witkowski and Lamont 1997), and land-use history (Hodgson 1986, Menges and Hawkes 1998, Donohue et al. 2000). At the same time, there is a general perception that species' abundances are, in the most proximate sense, an emergent property of their population dynamics (Kunin and Gaston 1997, p. 3), and that to understand variation in the former it is first necessary "...to identify characteristics of life history that determine fitness (or lack of fitness) in particular habitats" (Grime 1979, p. v). Further, Bradshaw (1987) stated, "...we can have no idea about the significance of a particular species' distribution unless we have one for a second species with which to compare it."

Rabinowitz (1978) provided one of the first evaluations of the properties of plants in relation to their population densities and distributions, using a comparison of diaspore weights in seven sparse and common prairie grasses. She found a strong positive correlation between species abundance and the size of dispersal units, and hypothesised that rare grasses may be 'fugitive' species, relying on long-range dispersal to take advantage of spatially and temporally rare microsites suitable for growth. Subsequently,

many studies have focused on isolating differences in the fitness components of rare versus common species (Bevil and Louda 1999). These studies have generally contrasted autecological attributes among multiple species (e.g., Karron 1987a, Kelly and Woodward 1996, Kunin and Shmida 1997, Eriksson and Jakobsson 1998, Cadotte and Lovett-Doust 2002) or between pairs of related, ecologically similar species that vary in abundance (e.g., Karron 1987b, Karron 1989, Baskin et al. 1997, Walck et al. 2001).

The comparative approach has yielded a number of generalisations regarding rarity patterns in plants. For example, there is growing evidence that rare species are disproportionately likely to be self-compatible or asexual (Kunin and Gaston 1993, Kunin and Shmida 1997; but see Weller 1994). Many rare plants also appear to possess poor dispersal abilities (Primack and Miao 1992, Quinn et al. 1994), poor competitive and colonisation abilities (e.g., Rabinowitz et al. 1984, Baskin and Baskin 1988, Snyder et al. 1994, Walck et al. 2001), or lowered reproductive output (e.g., Banks 1980, Pantone et al. 1995) relative to common species. However, generalisations from rare-common comparisons can be obscured (Kunin and Gaston 1993) because there are many types of rarities, from narrow endemics, to geographically peripheral populations, to chronically sparse species with wide geographic distributions. The term 'rare' encompasses a broad spectrum of spatial and temporal patterns of abundance that can be classified by differences in local abundance, geographic range, and habitat specificity (Rabinowitz 1981); many multi-species studies do not adequately differentiate among these disparate phenomena. In addition, variation in the response variables measured can limit generalisations about rare-common differences (Bevil and Louda 1999). Quantitative estimates of demographic vital rates (i.e., age- or stage-specific birth, growth, and survival rates), required for projecting and comparing changes in population size and persistence, can form a consistent basis for comparison among species. However, most studies employing intensive demographic methods to identify limiting factors for a particular, threatened taxon (e.g., Menges 1990, Bengtsson 1993, Aplet et al. 1994, Nault and Gagnon 1993, Kephart and Paladino 1997, Lesica 1997, Menges and Dolan 1998, Kaye et al. 2001, *Chapter 3*) have not included a direct comparison to common related or co-occurring species. Consequently, we lack the information needed to link these

observed life history differences directly to differences in population growth rate (λ), the most appropriate measure of population fitness (Stearns 1992).

In the intensive demographic approach, data indicating transition probabilities between stages of the life cycle are summarised in stage-based population projection matrices (Leslie 1945, Lefkovitch 1965, Tuljapurkar and Caswell 1997, Caswell 2001) that are then used to project the dynamics of a population or set of populations through time. Perturbation analyses (e.g., elasticity; de Kroon et al. 1986, Caswell 2001), which quantify the effect of changes in age- or size-specific demographic rates on population growth, have become an important tool both for the study of natural selection and life history evolution (e.g., Caswell and Werner 1978, Pfister 1998) and for evaluating the effectiveness of management prescriptions aimed at conserving sensitive species (e.g., Crouse et al. 1987, Schemske 1994, Oostermeijer et al. 1996) or at controlling pest species (e.g., McEvoy and Coombs 1999, Parker 2000). Perturbation analysis has also been used to explore life history differences among closely related plants (e.g., Svensson et al. 1993, Silva et al. 2000), as well as to compare the population dynamic traits of species from widely differing taxa, life forms and habitats (e.g., Silvertown et al. 1993, 1996, Nantel and Gagnon 1999). For example, Silvertown et al. (1993, 1996) utilised the additive property of elasticities to compare the relative contribution of fecundity, growth, and stasis (survival without growth) to λ, finding notable differences among plant structural and functional groups (semelparous herbs, iteroparous herbs of open habitats, iteroparous herbs of forested habitats, and long-lived woody species). Recently, some authors have adopted a similar approach in exploring the demographic basis of rare-common differences *per se* (Fiedler 1987, Byers and Meagher 1997, Fiedler et al. 1998). However, few systematic differences with respect to either λ or elasticity patterns have been detected that would account for the differing distribution and abundance patterns among species (Fiedler et al. 1998).

One reason for this may be that the dominant eigenvalue λ of the transition matrix yields the projected, asymptotic growth rate of the population under current conditions, whereas current patterns of distribution and abundance are inevitably linked to conditions or events in the past. Sensitivity and elasticity calculations are *prospective* analyses (*sensu* Caswell 1997). They predict the results of future changes in the vital rates, but say

nothing about how rates varied before, nor about which vital rates were responsible for past changes in λ (Caswell 1997, 2000). Thus, they do not on their own reveal anything about what biologically might have limited a population's past success.

Such questions are more appropriately addressed through a second class of perturbation techniques known as retrospective, or decomposition, analyses (e.g., life table response experiment analysis; LTRE) (Caswell 2000). The goal of these analyses is to decompose the overall treatment effect on λ into contributions from the effect on each stage-specific vital rate. The 'treatments' in an LTRE may be mensurative (e.g., different locations or years) or manipulative. In contrast to prospective analyses, which are prescriptive in nature, retrospective analyses are inherently diagnostic (Caswell 2001). They ask: 'Where in the life cycle has a treatment had the most impact with respect to λ?' Previous applications of this approach include ecotoxicology (e.g., Levin et al. 1996) and assessment of fire as a management tool (Silva et al. 1991, Caswell and Kaye 2001). Because retrospective analyses involve comparisons, they require substantially more data than their prospective counterparts. Only a few studies have used LTRE analysis to compare demographic traits among plant species (e.g., Caswell 2000, Kiviniemi 2002).

Asymptotic rates may differ substantially from short-term predictions of changes in populations not at a stable stage distribution (Fox and Gurevitch 2000). Furthermore, demographic momentum can cause a population to over- or undershoot its equilibrium density following a perturbation, leading to oscillations in population size (Keyfitz 1971). Conditions often do not remain constant long enough for a population's asymptotic properties to be expressed; in this case, transient dynamics may be more important than asymptotic dynamics in predicting differences in patterns of distribution and abundance. Using numerical projection, the fates of populations starting from a specified initial condition can be compared (Caswell and Werner 1978, Satterthwaite et al. 2002). Alternatively, the time required for different models to converge to the stable stage distribution can be estimated analytically from the damping ratio (Grant and Benton 1996). Life histories that result in slow convergence to equilibrium may be especially sensitive to the frequency of environmental perturbations, potentially leading to reductions in population density over time (Pimm 1991).

Ecological theory predicts that stochastic variation in demographic parameters slows population growth, decreases population size, and increases the probability of extinction (Tuljapurkar and Orzack 1980, Lande 1993). As environmental stochasticity increases, the importance of mean population growth rate as a predictor of population dynamics declines (Menges 1998, Caswell 2001). An alternative approach is to employ stochastic models (Caswell and Kaye 2001, Satterthwaite et al. 2002). Environmental variability is typically incorporated into projection models either by drawing each non-zero matrix element separately from a probabilistic distribution for each time step of a simulation ('element selection' model) (Beissinger 1995, Menges 1998) or by drawing entire matrices at random from the available pool of environmental states before projecting forward in time ('matrix selection' model) (Bierzychudek 1982, Kaye et al. 2001). The stochastic growth rate, $\log\lambda_s$, is equal to the time-averaged growth rate over a long simulation (Caswell 2001). Unlike λ, $\log\lambda_s$ does not depend on a stable population structure. However, like λ, $\log\lambda_s$ is an asymptotic measure; it does not indicate a population's past, but only whether it is likely to become smaller or larger in the future. A major difference between λ and $\log\lambda_s$ implies that environmental variability has a large effect on population dynamics.

In this paper, I compare the demography of two species of *Calochortus*: *C. lyallii* and *C. macrocarpus*. Both species inhabit dry grassland, sagebrush-steppe, and open-canopy coniferous forest in the Columbia Plateau region of western North America. *Calochortus macrocarpus* occurs from southern British Columbia south to Montana, Idaho, Nevada, and California. The range of *C. macrocarpus* encompasses that of *C. lyallii*, which is limited to central Washington east of the Cascade Mountains and extreme southern British Columbia. Although limited in distribution, *C. lyallii* is abundant where it grows, often occurring in densities exceeding 100 plants m^{-2}. In contrast, *C. macrocarpus* is widespread but tends to occur in much lower concentrations. Densities rarely exceed 15-20 individuals m^{-2} and are often considerably less; sometimes many metres separate individual plants.

Permanent quadrats were established in three populations of each species in southern British Columbia, and individual plants followed for five years. The purpose of my study was to examine whether subtle differences in life history and demography are

sufficient to account for observed differences in local distribution and abundance between the two species. I used a combination of numerical and analytical approaches—deterministic and stochastic population projections, prospective and retrospective perturbation analyses, transient analyses, and life cycle comparisons—to address the following questions: (1) Do the two species exhibit similar population dynamics? (2) What demographic parameters contribute to variation in fitness (λ) over time within species? (3) Which vital rates are responsible for the differences in population performance between species? (4) What stages of the life cycle have the greatest influence on population maintenance and growth? (5) How do the two species differ in terms of overall life style (e.g., generation time, net reproductive rate, survivorship and life expectancy, and stage durations), and do these differences help to explain the great contrast in their occurrence patterns?

Methods

STUDY SPECIES

Calochortus lyallii (Lyall's mariposa lily) and *C. macrocarpus* (sage-brush mariposa) are geophytic, polycarpic perennials with showy insect-pollinated flowers and gravity-dispersed seeds. Plants emerge early in the spring, following snowmelt, and die back to a dormant bulb during the summer. In both species the major photosynthetic organ is a solitary basal leaf that, in reproductive plants, subtends the single flowering scape. In non-flowering (vegetative) individuals, this leaf is the only aboveground structure produced. Seeds are shed from erect capsules during the summer and germinate the following spring. Persistent seed banks have not been documented; however, bulbs of both species are able to remain dormant for one or more years before re-emerging (*Chapter 2*).

Although they share similar life histories, the two species differ with respect to both phenology and morphology (Owenby 1940). *Calochortus lyallii* is a smaller plant (up to 30 cm tall), with an inflorescence of 1 to 12 flowers, and commences flowering in late May. *Calochortus macrocarpus* is larger (up to 1 m tall) and more robust, but produces only 1 to 3 (occasionally 4) flowers that do not usually open until July, when *C. lyallii* is

setting seed. *Calochortus macrocarpus* capsules, which are larger than those of *C. lyallii*, also take a longer time to mature and do not dehisce until late August or September.

I conducted demographic studies on three populations of each species at Black Mt., British Columbia from 1996-2000. The *C. lyallii* sites chosen were, at the time, the only three sites known in Canada (several more have since been identified). One *C. macrocarpus* population close to each *C. lyallii* site was chosen for comparative study.

FIELD SAMPLING AND STAGE CLASSIFICATION

Subsets of each population were monitored in permanently marked 0.5 x 0.5 m (*C. lyallii*) and 3.0 x 3.0 m (*C. macrocarpus*) plots. A larger plot size was used for *C. macrocarpus* to accommodate the lower density of individuals of this species within the study area. For *C. macrocarpus*, seedling recruitment and survival were monitored within a smaller (1.0 x 0.7 m) subplot at the centre of each plot. I established a total of 95 *C. lyallii* quadrats (36 at both NS and ES, 23 at WS) and 60 *C. macrocarpus* quadrats (20 per site), containing initially 1271 and 568 individuals, respectively. Plots were located haphazardly within each population, but were placed so as to encompass the range of microsite variation present at each site (see *Chapter 3* for details).

All visible *C. lyallii* and *C. macrocarpus* individuals in each plot were numbered and mapped to the nearest cm during June of 1996. Censuses of all plants were conducted during early June of each year, when I recorded the width of each basal leaf and the number of flower buds initiated, and again in late June (*C. lyallii*), July (*C. lyallii* and *C. macrocarpus*) and September (*C. macrocarpus*) to record flowering and fruit set (fruit set was not recorded in 2000). Because the 1996 June census occurred too late in the season to record seedlings and most small juveniles before they senesced, beginning in 1997 an additional census, targeting only the smallest plants, was carried out each May. Individual plants were identified from maps made the previous year. Relocating plants by this method was straightforward except in a few instances where two or more plants re-emerged in virtually the same spot. In these cases, I could not make positive identifications using map locations and instead made the most parsimonious assignment based on the size/state of each plant the previous year.

For demographic analysis, individuals were classified into nine categories according to a combination of age, size, and reproductive state. The categories used were (1) seedlings (= young of the year); (2) small juveniles (yearlings, plus established plants with basal leaf width <2 mm); (3) large juveniles (leaf width ≥2 but ≤3.6 mm—the minimum threshold fruiting size); (4) small reproductives (one flower bud initiated); (5) large reproductives (≥ two flower buds); (6) vegetatives (non-flowering adults, with leaf width ≥ minimum threshold fruiting size); (7) dormant juveniles; (8) dormant reproductives; and, (9) dormant vegetatives. The term 'dormant' was applied, post-hoc, to any previously-marked individuals that went unobserved for one or more years before reappearing (*Chapter 3*). Dormants were assigned to category based on the individual's demographic state prior to becoming dormant (*Chapter 3*)

The number of stage classes employed here contrasts with the 11 *i*-states used in an earlier analysis of demographic variation in *C. lyallii* (*Chapter 3*). One of those states (pre-reproductives) was not clearly defined for *C. macrocarpus*; another (reproductives with > two buds) occurred too rarely to justify a separate stage class. For this analysis, these plants were placed with stage classes three and five, respectively.

Calochortus seedlings are the approximate size and dimension of a toothpick, and in *C. macrocarpus* can always be distinguished from older individuals (yearlings) by the presence of a cotyledon in addition to the first true leaf. In *C. lyallii*, the cotyledon had usually withered by the time of censusing, making it difficult to identify seedlings based on this feature alone. Instead, seedlings were defined as any plant with leaf width ≤ 1.0 mm, the most frequent cut-off size observed during associated field trials of seed germination rates (*Chapter 2*). The minimum threshold size for reproduction was determined by the leaf width of the smallest seed-producing individual in each population. Plants smaller than this were considered juveniles; larger plants were classified as either reproductives or vegetatives, depending on whether they initiated a flowering scape. By this definition very small plants that flowered but did not produce fruits were classified as juveniles.

DEMOGRAPHIC ANALYSIS

Projection matrix model

Over the course of the five years of this study, I mapped and recorded the fates of >2,600 individual *C. lyallii* and >1,000 individual *C. macrocarpus*. The life cycles of the two species are sufficiently similar to be represented by a single life cycle graph (Fig. 4.1). Demographic data were summarised in a stage-based projection matrix model (Lefkovitch 1965) of the form

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$$

where $\mathbf{n}$ and $\mathbf{n}_{t+1}$ are vectors of stage abundances at time t and $t + 1$, respectively, and $\mathbf{A}$ is a matrix of transition probabilities that describes the contribution of each stage class to all the others, for the time interval t to $t + 1$. The dominant eigenvalue λ of $\mathbf{A}$ represents the asymptotic finite rate of increase at the stable stage distribution. The projection equation thus satisfies $\mathbf{Aw} = \lambda\mathbf{w}$, where $\mathbf{w}$ is the dominant right eigenvector of $\mathbf{A}$ and is equivalent to the stable stage distribution. The normalised left dominant eigenvector of $\mathbf{A}$, $\mathbf{v}$, represents stable stage specific reproductive values. Reproductive values include current reproduction and expected future reproduction of individuals presently in each stage (Caswell 2001).

Matrix elements were determined directly from the observed proportion of individuals passing between stages in a year, with the exception of dormancy and fecundity. Dormancy rates were estimated indirectly, following procedures in *Chapter 3* and Appendix 3.1. Stage-specific fecundities (the first row of $\mathbf{A}$) represent the average number of seedlings recruited per individual, and were calculated as: (number of seedlings emerging at time t) × (proportion of seed capsules produced at t - 1 attributed to each class of reproductive plants) / (number of individuals in each class) (see *Chapter* 3 for details). This method assumes that seeds produced by plants of different sizes were equally likely to become seedlings and that there was no net dispersal of seeds into or out of the plots. Because seedlings were not censused until 1997, seedling survivorship in 1996-97 was estimated using the average value from the three subsequent matrices. Small initial sample sizes made it necessary to use a similar method to estimate transition rates for small juveniles (class J1) of *C. macrocarpus* during 1996-97 and 1997-98.

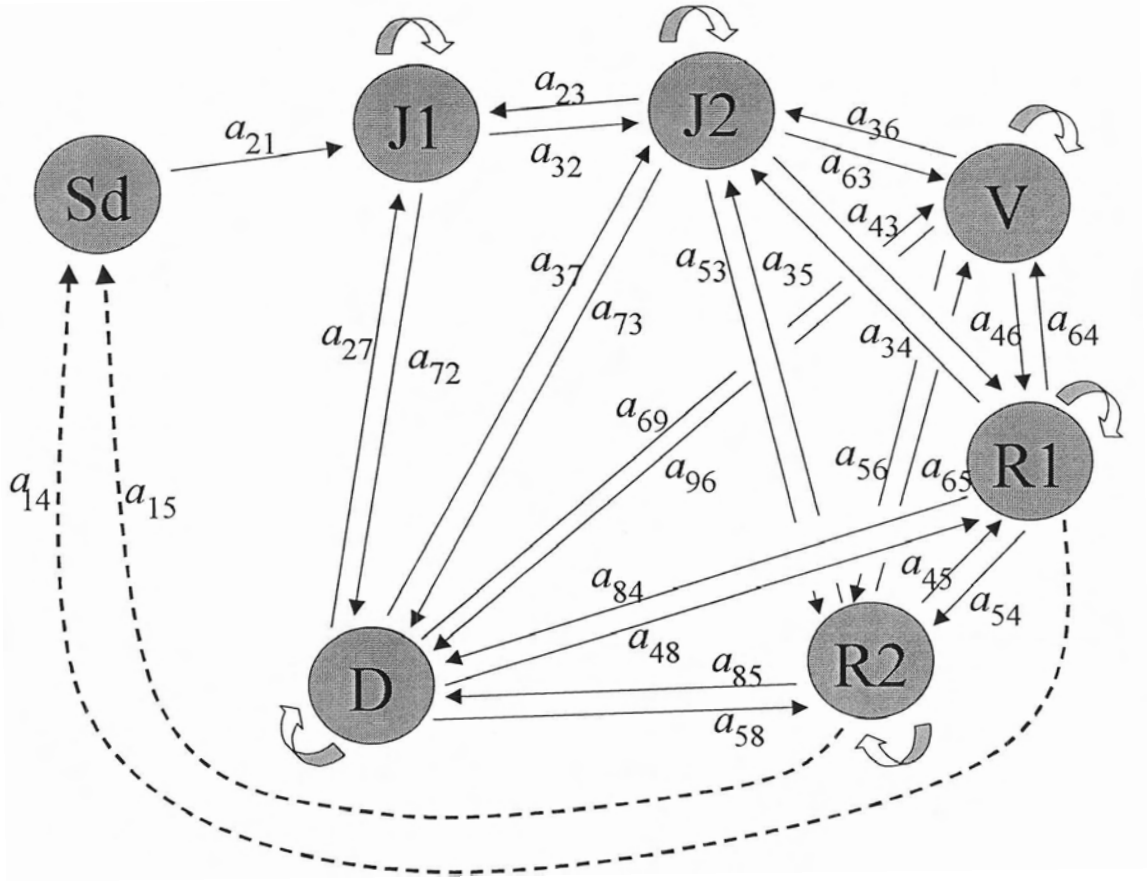

Figure 4.1 Generalised life-cycle graph for *Calochortus lyallii* and *C. macrocarpus*. For clarity, only a single dormancy stage is depicted. The coefficients a_{ij} correspond to the probability that an individual in stage j at time t has made the transition to stage i at $t + 1$. Stages: (1) Sd: seedlings; (2) J1: small juveniles; (3) J2: large juveniles; (4) R1: small reproductive plants; (5) R2: large reproductive plants; (6) V: vegetative adults; (7-9) D: dormant plants. Dashed arrows indicate reproduction.

For each species, I constructed four matrices for each of the three sites (NS, ES, WS), one for each transition period (a total of 24 matrices). An earlier loglinear contingency analysis of *C. lyallii* transition rates based on 11 life stages (*Chapter* 3) showed that most of the variation among matrices in *C. lyallii* was explained by effects of year rather than site. The same analysis showed a similar pattern for *C. macrocarpus* (Appendix 4.1), thus I pooled data from the three populations of each species to construct eight new matrices with higher sample sizes than the original, site-specific matrices.

I used the pooled projection matrices to calculate λ for each combination of year and species. To obtain confidence intervals for λ I used a bootstrap procedure (Efron and Tibshirani 1993, McPeek and Kalisz 1993, Caswell 2001). Individual quadrats were resampled with replacement (using a bootstrap sample size of 3000) from the pooled set of quadrats, and a new projection matrix for each resampling calculated using programs in MATLAB (The MathWorks 1998). Eigenanalyses were performed on each new matrix (also in MATLAB) and bias-corrected, 95% percentile intervals for λ were then generated from the resulting distribution of bootstrap estimates (Efron and Tibshirani 1993). Confidence intervals were obtained for elements of **w** and **v** in the same manner.

To incorporate environmental stochasticity into the projection models, I also calculated the stochastic growth rate, $\log\lambda_s$, following the numerical simulation method outlined in Caswell (2001: 396). The environment was assumed to fall into one of four states, corresponding to the four transitions observed in the study. The sequence of environments was assumed to be independently and identically distributed (iid) (Caswell 2001: 378). At each time step of a simulation, one of the four annual matrices was selected at random and post-multiplied by the vector of individual abundances (Bierzychudek 1982, Nantel et al. 1996, Kaye et al. 2001); the log of population growth, averaged over all time steps, is the time-averaged (stochastic) growth rate. This method preserves the observed covariances among the vital rates, and equates, in effect, to sampling from the bootstrap distribution of projection matrices (Caswell 2001). For each species, I calculated the stochastic growth rate for each populations and for the pooled sample. To estimate $\log\lambda_s$ I ran each model for 50,000 time steps, discarding the initial 1000 iterations to eliminate transient effects.

Perturbation analyses

Elasticity analysis (de Kroon et al. 1986, Caswell 2001) was carried out for each of the annual matrices as well as for the composite (mean) matrix for each species. Elasticity e_{ij} quantifies the proportional change in λ that would result from a small proportional change in matrix element a_{ij}, and is given by $a_{ij}/\lambda \times \partial\lambda/\partial a_{ij}$ (Caswell 2001). Bootstrap confidence intervals for the e_{ij}'s were computed as for other demographic parameters. The additive property of elasticities makes it possible to compare regions of the matrix among populations and among species with similar or with different growth rates (Silvertown et al. 1993, Oostermeijer et al. 1996, De Kroon et al. 2000). To facilitate comparison of elasticity structures I divided the different elasticity matrices for each species into three regions corresponding to growth (*G*), stasis and retrogression (*L*), and fecundity (*F*), and used these composite elasticities to construct a triangular plot in *G-L-F* space (Silvertown et al. 1993).

In contrast to elasticity analysis, which projects the impact that a hypothetical change to a matrix element would have on λ, life table response experiment (LTRE) analysis decomposes the observed effect of a treatment factor on λ into contributions from the different vital rates (Caswell 2000, 2001). In *Chapter 3* I used a random design LTRE (Brault and Caswell 1993, Horvitz et al. 1997) to compare patterns of variation in *C. lyallii* performance across a range of spatial scales. Here, I used similar methods to decompose year-to-year variation in λ associated with differences among the pooled annual matrices, then compared the results between species. To decompose interspecific variation in λ, I used a fixed, one-way design LTRE (Levin et al. 1996, Caswell 2001). Let $\lambda^{(l)}$ and $\lambda^{(m)}$ denote population growth rate of *C. lyallii* and *C. macrocarpus*, respectively, within a given year. The contribution of the matrix entry a_{ij} to the difference in population growth rates of the two species is then given by

$$\lambda^{(l)} \approx \lambda^{(m)} + \sum_{ij} (a_{ij}^{(l)} - a_{ij}^{(m)}) \left. \frac{\partial \lambda}{\partial a_{ij}} \right|_{(A^{(l)}+A^{(m)})/2}$$

where $\left.\frac{\partial \lambda}{\partial a_{ij}}\right|_{(A^{(l)}+A^{(m)})/2}$ is the sensitivity evaluated at the matrix midway between $\mathbf{A}^{(l)}$ and $\mathbf{A}^{(m)}$. In this case, the terms in the summation are the contributions of species differences in the matrix entries to the species difference in λ.

Transient dynamics

An alternative way to study the response of a population to perturbations is to consider its short-term, or transient, behaviour. One useful measure of transient dynamics is the damping ratio, ρ, which determines the rate of convergence to the stable population structure and is defined as $\rho = \lambda_1/|\lambda_2|$, where λ_1 is the dominant eigenvalue and λ_2 is the largest subdominant eigenvalue (Caswell 2001). Convergence is said to occur once the contribution of λ_2 has decreased in magnitude relative to that of λ_1 by some arbitrarily defined multiple, say 20×. I computed the damping ratios, and the time t_x required for the contribution of λ_2 to decline to 5% of that of λ_1, for the mean matrices of both species following Caswell (2001). I also computed population momentum M, the fraction by which population size could be expected to increase or decrease before stabilising, if vital rates were changed to equal replacement levels (Caswell 2001). To simulate a set of stationary vital rates, I divided the fertilities in each matrix by R_0, the net reproductive rate (for computation of R_0, see the next section). When $M > 1$, a population growing at a stationary rate of 1.0 will stabilise at a size larger than its size before the vital rates were changed. $M < 1$ indicates the population will shrink before stabilising.

Age-specific traits and lifetime event probabilities

Although stage-structured models are not explicitly linked to the age of individuals, they are derived from census measurements taken over time, and thus time—and age—are implicit components of these models. Cochran and Ellner (1992) and Caswell (2001) show how to extract various age-specific life history traits as well as age-based population parameters from stage-classified data. I used the mean matrix of each species

to calculate age-specific survivorship and fertility, number of years spent in each stage, net reproductive rate R_0, and generation time (Appendix 4.2). Generation time can be measured in several ways, the appropriateness of which will vary depending on the characteristics of the population (Caughley 1977, Gregory 1997). I defined generation time as the time G required for the population to increase by a factor R_0, satisfying $\lambda^G = R_0$ and calculated as $G = \log R_0 / \log \lambda$ (Caswell 2001). This method is valid so long as both λ and $R_0 \neq 1$ (Caughley 1977), conditions that held for both *C. lyallii* and *C. macrocarpus* in this study (see **Results**).

As the population approaches the stable stage distribution, the frequency distribution of ages for individuals of a given size or stage class also approaches a stable distribution, making it possible to estimate $p_{i,a}$, the fraction of those individuals within stage i whose age is a, from the stage-classified model alone (Cochran and Ellner 1992). Extending the analysis of Cochran and Ellner (1992), Caswell (2001) showed that for each stage, the stable age-within-stage distribution can be obtained from the asymptotic formula

$$p_{i,a+1} = \lambda^{-a}\mathbf{T}^a\mathbf{F}\mathbf{w}$$

where **T** is the transition matrix, **F** is the fertility matrix, λ is the dominant eigenvalue of $\mathbf{A} = \mathbf{T} + \mathbf{F}$, and **w** is the corresponding right eigenvector. Because they convert different stage classifications into a single time variable (i.e., age), the stable age distributions allow for comparisons among different populations or species, or among studies that define stages in different ways (Boucher 1997). Here I use this method to compare stable age-within-stage distributions between *C. lyallii* and *C. macrocarpus*.

Results

FATE OF VEGETATIVE VS. FLOWERING PLANTS

There was large variation in stage-specific flowering performance within and between the two species (Fig. 4.2). For all three emergent adult stages (V, R1 and R2), individuals of *C. lyallii* showed a greater propensity to flower the next year than did individuals of *C. macrocarpus*. The effect of species on fate, conditional on initial state, is significant ($G^2 = 327.85$, $df = 6$, $P < 0.0001$). In both species, initial state and

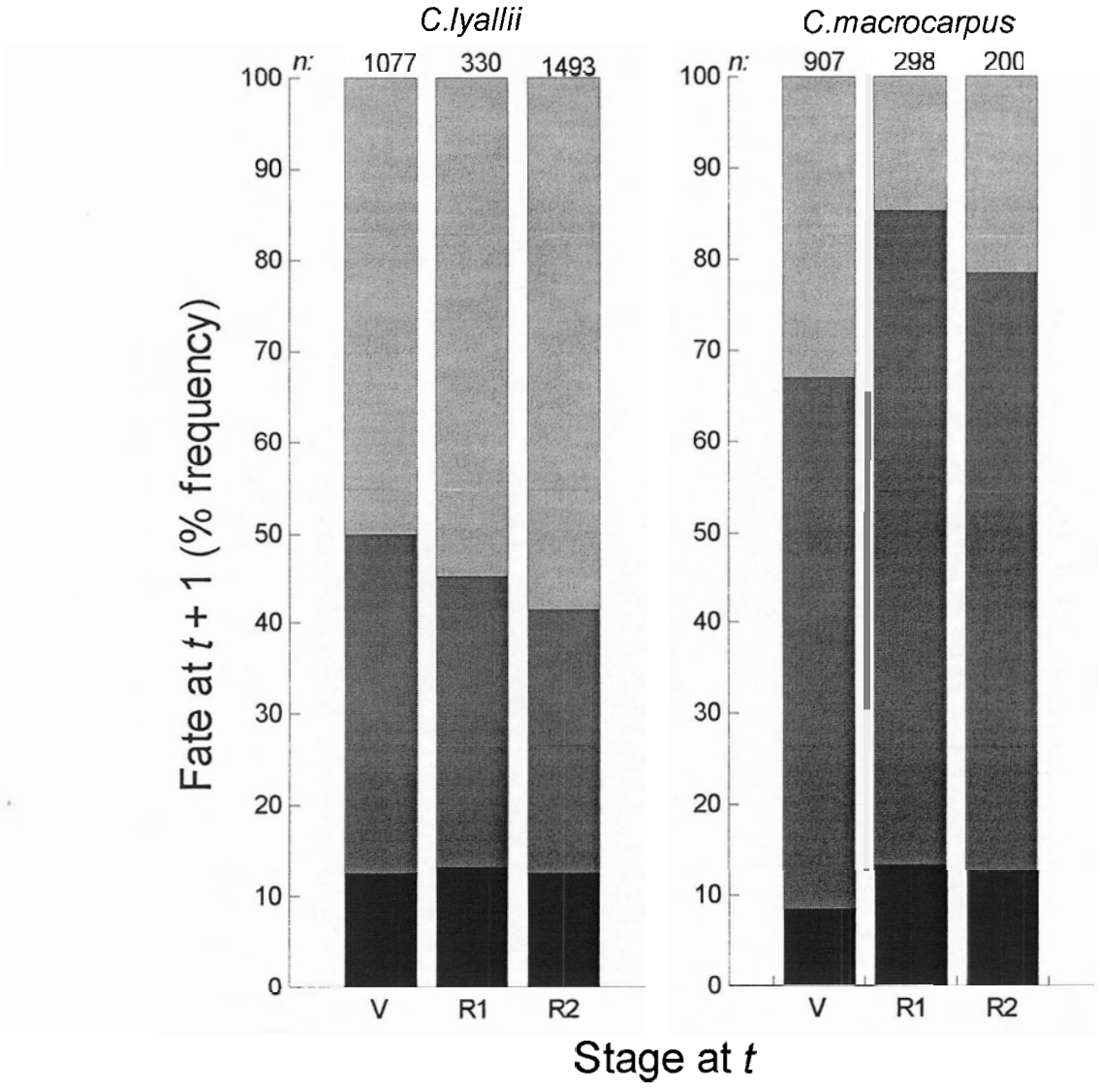

Figure 4.2 Reproductive fate from one year (t) to the next ($t + 1$) of non-flowering and flowering plants of *Calochortus lyallii* and *C. macrocarpus*. V = non-flowering (vegetative) adult; R1 = individuals with one flower; R2 = individuals with two or more flowers. Fates are: dead or dormant (■); non-flowering (▩); flowering (▨).

demographic fate were not independent (*C. lyallii*: $\chi^2 = 22.27$, $df = 4$, $P = 0.0002$; *C. macrocarpus*: $\chi^2 = 43.83$, $df = 4$, $P < 0.0001$). In *C. lyallii*, vegetative plants had the lowest, and large reproductive plants the highest, probability of flowering the following year. Individuals of each stage had a similar likelihood of re-emerging the next spring; slightly more than 10% of plants died or became dormant (Fig. 4.2). In *C. macrocarpus*, however, the pattern of subsequent flowering was reversed: vegetative plants were more likely than reproductives to flower the next year; they were also less likely to fail to reappear, suggesting that reproductive costs associated with flowering are greater for *C. macrocarpus* than for *C. lyallii*.

POPULATION PROJECTION MATRICES

For both *C. lyallii* and *C. macrocarpus*, most elements in the projection matrices (Appendix 4.3) had non-zero values (except for elements in the lower left corresponding to rapid growth of very small individuals), supporting the use of stage-based (Lefkovitch matrix) rather than age-based (Leslie matrix) demographic models for these plant species. In general, projection matrices were dominated by stasis (survival without change in state) and growth, with lower probabilities for retrogression and dormancy. An exception to this were reproductive plants of *C. macrocarpus*, which showed a strong tendency to regress to the vegetative state. Mortality was high for seedlings, but declined rapidly once plants became established. Seedling survivorship tended to be higher in *C. macrocarpus* than in *C. lyallii* ($\overline{X} = 0.64 \pm 0.07$ vs. $\overline{X} = 0.53 \pm 0.17$, $n = 3$, $P = 0.13$), whereas the reverse occurred in the juvenile and adult stages. Fecundity values increased with inflorescence size; for *C. lyallii* especially, seedling recruitment was much greater for R2 than for R1 plants (Appendix 4.3). Although *C. macrocarpus* had lower fruit production than *C. lyallii* (*Chapter 2*), average fecundity values were slightly higher, reflecting the greater seed set in *C. macrocarpus* capsules (and possibly also differences in fecundity components such as over-winter survival of seeds and germination). Stable stage distributions and reproductive values are in Appendix 4.4.

Only *C. lyallii* had a projected value of λ significantly >1.0 during any transition interval and both species had λ-values significantly <1.0 for two out of four transitions

(Table 4.1). For the four *C. lyallii* projection matrices, λ varied from 0.8874 to 1.0440; for the *C. macrocarpus* matrices, λ varied from 0.8857 to 1.0094. *Calochortus lyallii* appeared to alternate between 'good' and 'bad' years, with positive growth projected in 1996-97 and 1998-99 and negative growth projected for 1997-98 and 1999-00. The 95% bootstrap confidence intervals for *C. macrocarpus* were wider but indicated rapid population decline over the first two transitions, a marginal decline in the third transition, and near-equilibrium during the final transition. Estimates of $\log\lambda_s$ for each species (populations pooled) showed a negative stochastic growth rate in both cases, indicating certain (probability of 1) population decline under the observed 5-yr conditions (Table 4.2). The projected annual decline was sharpest for *C. macrocarpus* ($\cong$7%, vs. $\cong$1% for *C. lyallii*). As expected, values of $\log\lambda_s$ were lower, albeit only slightly, than the corresponding values for $\log\mu$, the average growth rate derived from the mean matrix for each species. Within species, $\log\lambda_s$ varied both in quantity and direction among locations. For *C. lyallii*, both NS and ES showed negative long-term trajectories, whereas WS showed slight positive growth. A similar pattern occurred among the three *C. macrocarpus* populations; both NS and ES had negative $\log\lambda_s$, whereas the $\log\lambda_s$ value for WS did not differ significantly from 0. At all three sites (most notably NS and ES) the stochastic growth rate was lower for *C. macrocarpus* than for *C. lyallii* (Table 4.2).

TRANSIENT DYNAMICS

Damping ratios, which measure the rate of convergence to the stable stage distribution, and estimated convergence times were similar for both species (Table 4.3). Estimated time to convergence was greatest (~ 8 yr) in 1997-98, the period of lowest λ for both species. Under average conditions, convergence to equilibrium structure is predicted to take about 5 yr. Thus minor changes in survival and recruitment would not be immediately reflected in the observed population structure.

For *C. lyallii*, replacement fertility levels under conditions of the mean matrix were 0.22 seedlings per small reproductive plant (stage R1) and 1.08 seedlings per large reproductive individual (stage R2), well within the realm of values observed for this species. For *C. macrocarpus*, replacement values were 2.49 and 6.20 seedlings for each

Table 4.1 Estimated population growth rate λ, together with bootstrap standard errors and 95% bias-corrected bootstrap confidence intervals of those estimates, for *Calochortus lyallii* and *C. macrocarpus* over four annual transitions at Black Mt. (sites pooled).

			Bootstrap estimates	
Species	Year	Estimated growth rate λ	*SE*	95% confidence interval
C. lyallii				
	1996-97	1.0440	0.0017	[1.0259, 1.0608]
	1997-98	0.8874	0.0018	[0.8664, 0.9064]
	1998-99	1.0429	0.0020	[1.0206, 1.0654]
	1999-00	0.9626	0.0017	[0.9451, 0.9810]
C. macrocarpus				
	1996-97	0.8868	0.0023	[0.8504, 0.9168]
	1997-98	0.8857	0.0023	[0.8527, 0.9140]
	1998-99	0.9409	0.0032	[0.8913, 1.0156]
	1999-00	1.0094	0.0023	[0.9806, 1.0457]

Table 4.2 Stochastic population growth rate $\log\lambda_s$ (± 95% confidence interval), the same value back-transformed (λ_s), and growth rate of mean population size (λ_m) for *Calochortus lyallii* and *C. macrocarpus*, for the three individual sites (NS, ES and WS) and for the pooled matrices.

Species	Site	$\log\lambda_s$ [a]	λ_s	λ_m [b]
C. lyallii				
	NS	-0.0226 (0.0008)	0.9777	0.9817
	ES	-0.0127 (0.0007)	0.9874	0.9901
	WS	0.0097 (0.0096)	1.0097	1.0156
	pooled	-0.0141 (0.0008)	0.9860	0.9893
C. macrocarpus				
	NS	-0.0893 (0.0008)	0.9146	0.9147
	ES	-0.1132 (0.0015)	0.8930	0.8998
	WS	-0.0016 (0.0021)	0.9984	1.0042
	pooled	-0.0746 (0.0009)	0.9281	0.9296

[a]Stochastic growth rates computed from 50,000-year stochastic projections using four projection matrices.
[b]Calculated as the dominant eigenvalue of the mean population projection matrix.

flowering stage respectively, about two times higher than the highest rates observed during the study. Population momentum *M* was 1.021 for *C. lyallii* and 1.251 for *C. macrocarpus*. Thus, for both species, increasing fertility to replacement levels would lead to an increase in the size of populations before they stabilised. However, the *C. lyallii* population would increase by only about 2%, whereas the *C. macrocarpus* population would undergo a 25% increase before stabilising. In both cases, the response is due to the difference in stable stage distributions before and after the change in fecundity rates (Fig. 4.3). There is an 'excess' of mature and reproductive individuals in the original stable stage distribution; these individuals continue to reproduce after the vital rates are changed, resulting an increase in population size (Caswell 2001). This disparity is more pronounced in *C. macrocarpus*; thus *M* is higher and the population is expected to experience more growth before stabilising.

ELASTICITY ANALYSIS

The elasticity structure was similar among years but differed between species (Appendix 4.5). In *C. lyallii*, the highest elasticity (0.22) was for stasis of large reproductive plants in 1998-99 (a transition with a positive λ). In *C. macrocarpus*, the highest elasticity (0.21) was for vegetative stasis in 1996-97 (negative λ). In both species and all transitions the total elasticity of λ to changes in fecundity in any year was quite small (<10%). In *C. lyallii*, fecundity elasticities of large reproductives were generally an order of magnitude greater than those of small reproductives, whereas in *C. macrocarpus* the two elements made similar proportional contributions to λ. In most years, elasticities of seedling survival/growth were similar to those for fecundity. On average, the combined contributions to λ from dormancy (rows 7-9 of the elasticity matrix) were slightly greater for *C. macrocarpus* (~15%) than for *C. lyallii* (~12%) (Appendix 4.5). The elasticities and sensitivities of the mean matrix were only weakly related (Fig. 4.4). Under these conditions, λ in *C. lyallii* was most sensitive to the rapid growth of large juveniles. However, this transition made only a small proportional contribution to λ; the largest elasticities of the mean matrix were those associated with juvenile stasis and stasis of large reproductives (Fig. 4.4). In *C. macrocarpus*, λ was most sensitive to the fate of

Table 4.3 The asymptotic rate of convergence to the stable stage distribution, represented by the damping ratio, ρ, for four transition periods and for the mean annual matrix, and the expected times to convergence.

	Damping ratio ρ ($\lambda_1 / |\lambda_2|$)		Convergence time*	
Year	*C. lyallii*	*C. macrocarpus*	*C. lyallii*	*C. macrocarpus*
1996-97	2.25	1.85	3.69	4.86
1997-98	1.43	1.41	8.30	8.75
1998-99	1.64	1.82	6.09	5.00
1999-00	1.77	2.01	5.26	4.29
Mean matrix	1.93	1.85	4.55	4.87

*Measured as the time, in years, required for the contribution of the second root (λ_2) to decline to 5% of that of the dominant root (λ_1).

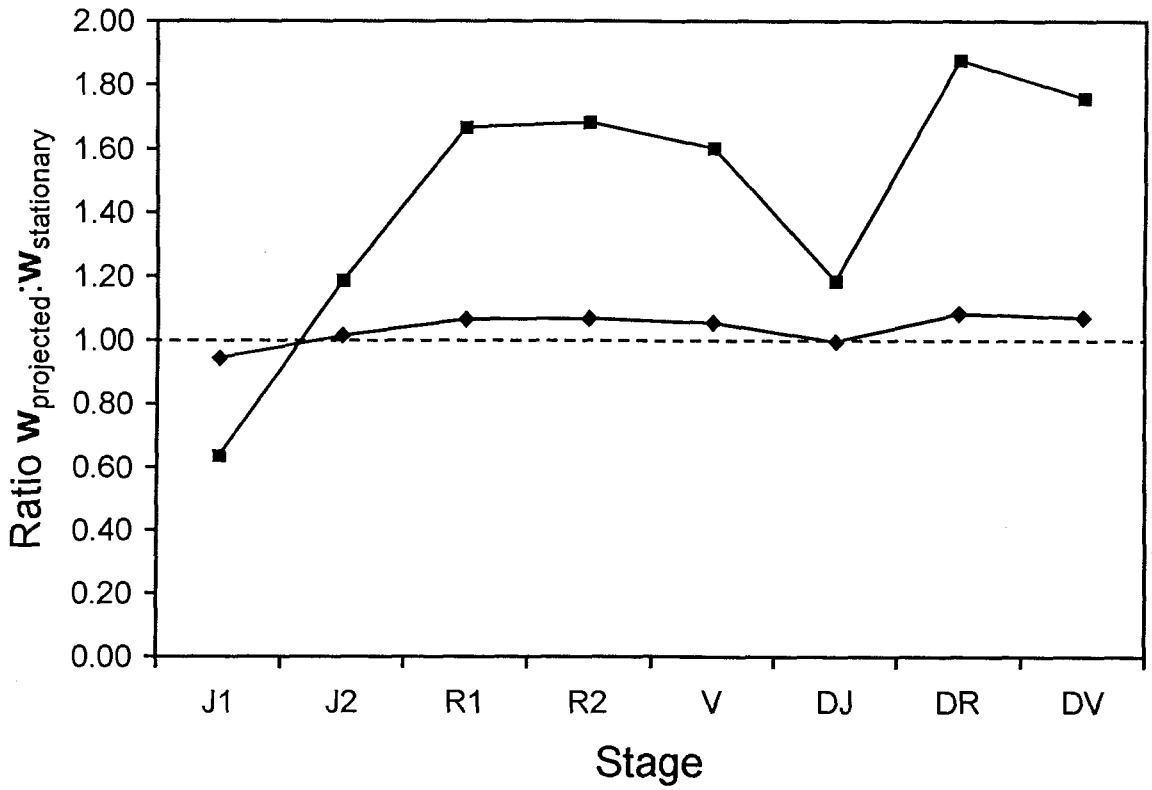

Figure 4.3 Ratios of stable stage frequencies corresponding to the mean observed matrix ($w_{observed}$) vs. stable stage frequencies for a matrix ($w_{stationary}$) in which fertilities have been adjusted to yield a stationary population (i.e., $\lambda = 1$). The dashed line is the line of equality; stages above this line contain an "excess" of individuals in the projected relative to the stationary distribution. Diamonds: *C. lyallii*; squares: *C. macrocarpus*.

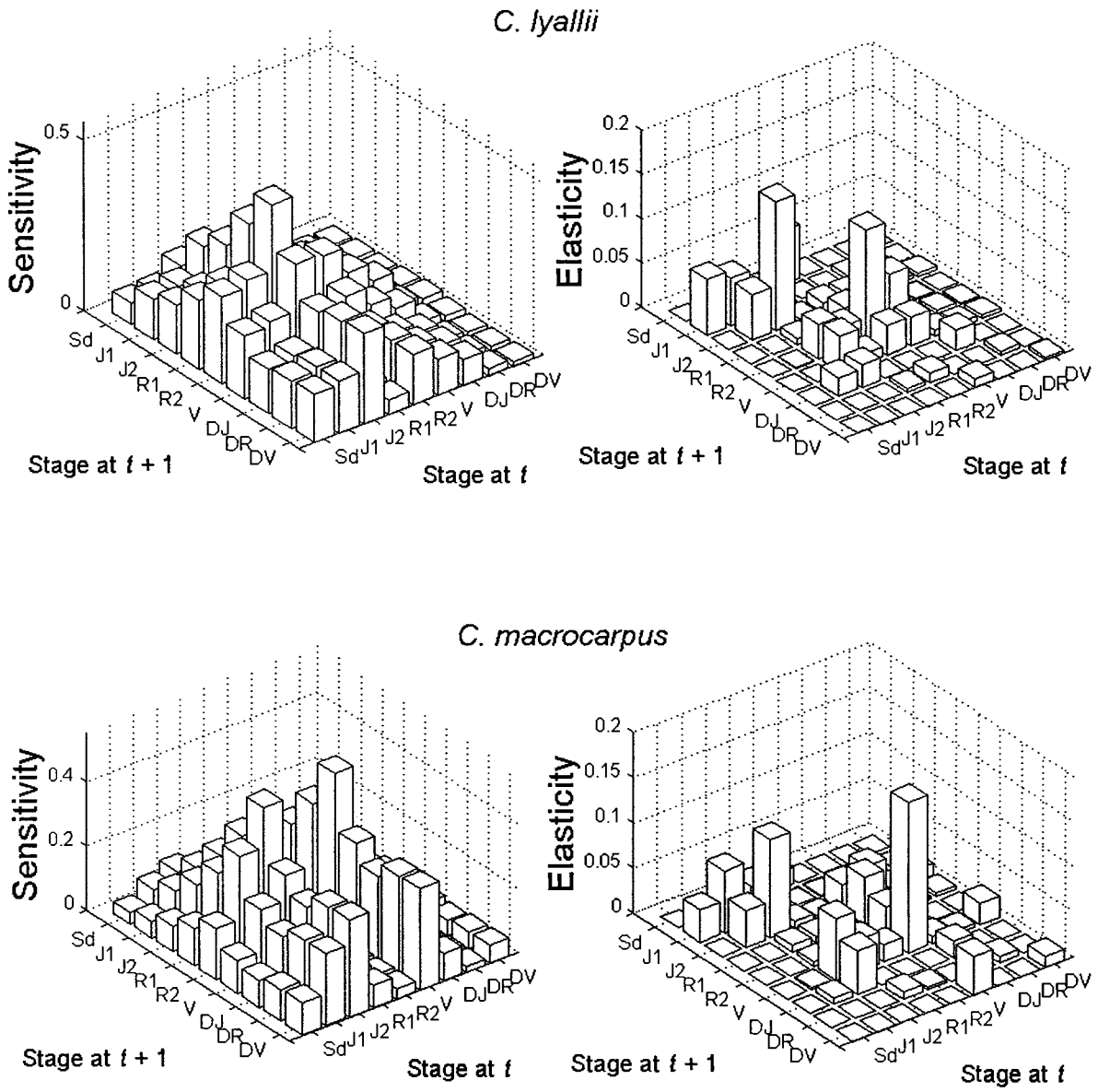

Figure 4.4 The sensitivity matrix (left) and elasticity matrix (right) for *Calochortus lyallii* and *C. macrocarpus*, calculated from the mean transition matrices. Numerals refer to stage categories: (1) seedlings; (2) small juveniles; (3) large juveniles; (4) small reproductives; (5) large reproductives; (6) vegetatives; (7) dormant juveniles; (8) dormant reproductives; (9) dormant vegetatives.

large vegetatives, especially to the transition from vegetative to flowering state. The largest elasticities, however, were e_{66} (vegetative stasis) and e_{33} (juvenile stasis). Thus, on average, proportional perturbations of this species have the biggest impact if they affect the stasis of non-reproductive individuals.

Both species fall into the middle lower right region of the ordination triangle where L (stasis and retrogression) is more important than growth or fecundity (Fig. 4.5), consistent with expectations for iteroparous herbs of late-successional, open habitats (Silvertown et al. 1996). The two species were not noticeably separated on the triangle, indicating similarity at this coarse scale of demographic analysis. For both species, there was a trend of decreasing λ as L increased and F and G decreased, in keeping with theoretical expectations (Silvertown et al. 1996).

LTRE ANALYSIS

Intraspecific variation. In *C. lyallii*, the largest individual contribution to $V(\lambda)$, the annual variance in λ, was from variance in a_{55} (stasis of large reproductives), while a negative covariance between a_{55} and a_{56} (growth from vegetative to large reproductive) was the most important in reducing $V(\lambda)$ (Table 4.4). In *C. macrocarpus*, the largest individual contribution to $V(\lambda)$ came from variance in a_{46} (transition from vegetative to small reproductive); the largest negative contribution was from the covariance between a_{33} (stasis of large juveniles) and a_{56} (transition from vegetative to large reproductive) (Table 4.4). The complete covariance and contribution matrices are shown, as surface plots, in Appendix 4.6.

For *C. lyallii*, entry a_{55} (stasis of large reproductives) also makes the largest net contribution to $V(\lambda)$, once the contributions for all of the variances and covariances (both positive and negative) involving each vital rate are taken into account (Fig. 4.6a). Entries a_{15} (fecundity of large reproductives) and a_{56} (transition from vegetative to large reproductive) also make notable net positive contributions to $V(\lambda)$, while negative variances and covariances involving a_{65} (regression from large reproductive to vegetative) and a_{32} (growth of small juveniles) have the largest role in reducing $V(\lambda)$. Similarly, for

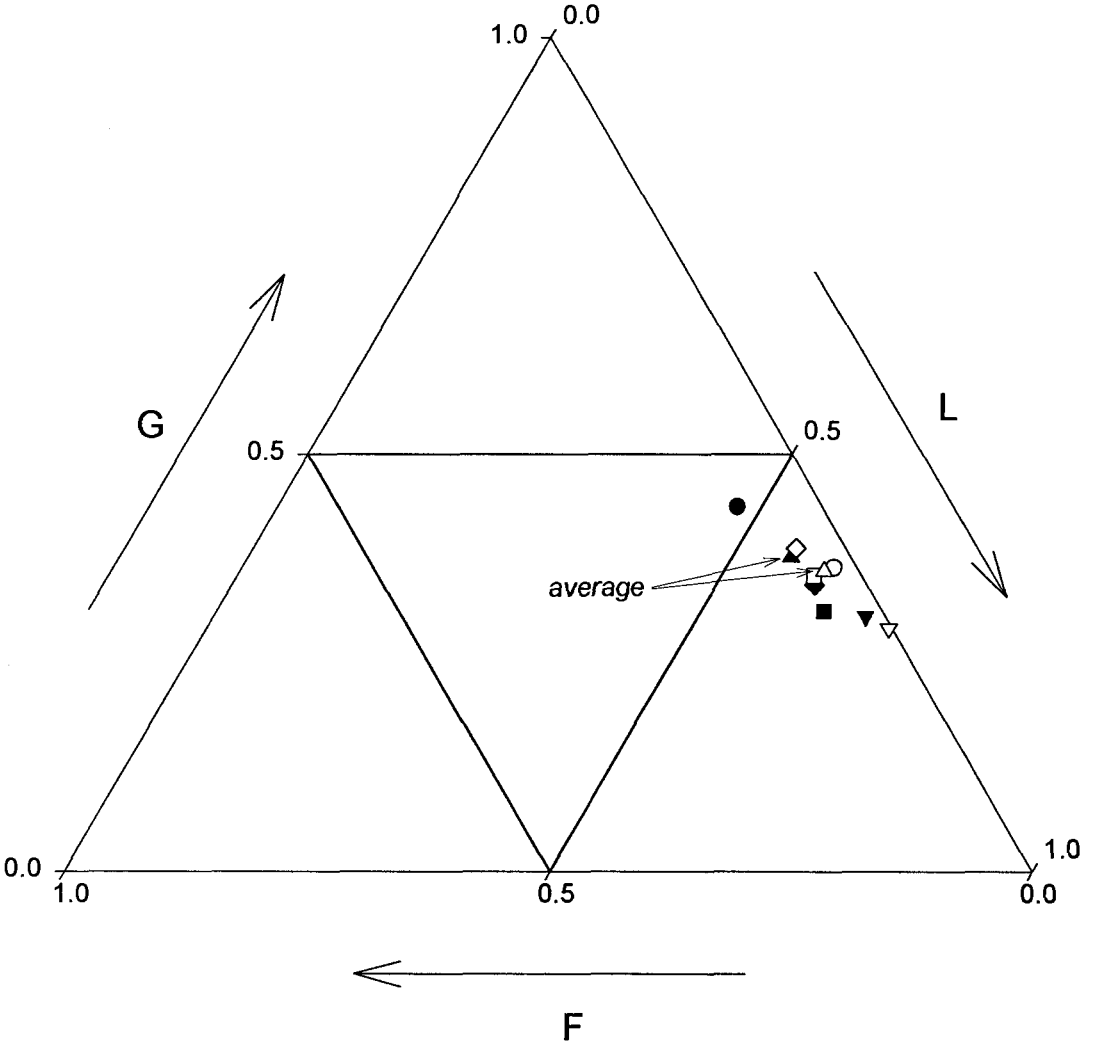

Figure 4.5 Triangle plot of the summed elasticities to stasis/regression (*L*), growth (*G*), and fecundity (*F*) in *Calochortus lyallii* and *C. macrocarpus* over four transition periods. Data pooled across sites. Solid symbols: *C. lyallii*. Open symbols: *C. macrocarpus*. Circles: 1996-97; triangles down: 1997-98; squares: 1998-99; diamonds: 1999-00; triangles up: average (calculated from mean annual matrices).

Table 4.4 Life table response experiments (LTRE) for *Calochortus lyallii* and *C. macrocarpus*. Shown for each species are the top five positive and top five negative LTRE-contributions from covariances among pairs of matrix elements (a_{ij}, a_{kl}) to the inter-year variance in λ, $V(\lambda)$. Single a_{ij} subscripts denote variance in one matrix element; pairs of subscripts denote covariances among two elements.

	C. lyallii		*C. macrocarpus*	
Covariance sign	Matrix element	Contribution ($\times 10^{-3}$)	Matrix element	Contribution ($\times 10^{-3}$)
(+)				
	a_{55}	2.27	a_{46}	1.50
	a_{55},a_{56}	0.96	a_{33}	0.95
	a_{22}	0.95	a_{56}	0.70
	a_{55},a_{15}	0.83	a_{62}	0.66
	a_{55},a_{22}	0.73	a_{96}	0.61
(-)				
	a_{55},a_{65}	-0.81	a_{33},a_{56}	-0.75
	a_{55},a_{32}	-0.72	a_{33},a_{63}	-0.60
	a_{22},a_{32}	-0.69	a_{46},a_{96}	-0.50
	a_{22},a_{72}	-0.52	a_{63},a_{96}	-0.37
	a_{22},a_{73}	-0.44	a_{73},a_{46}	-0.36

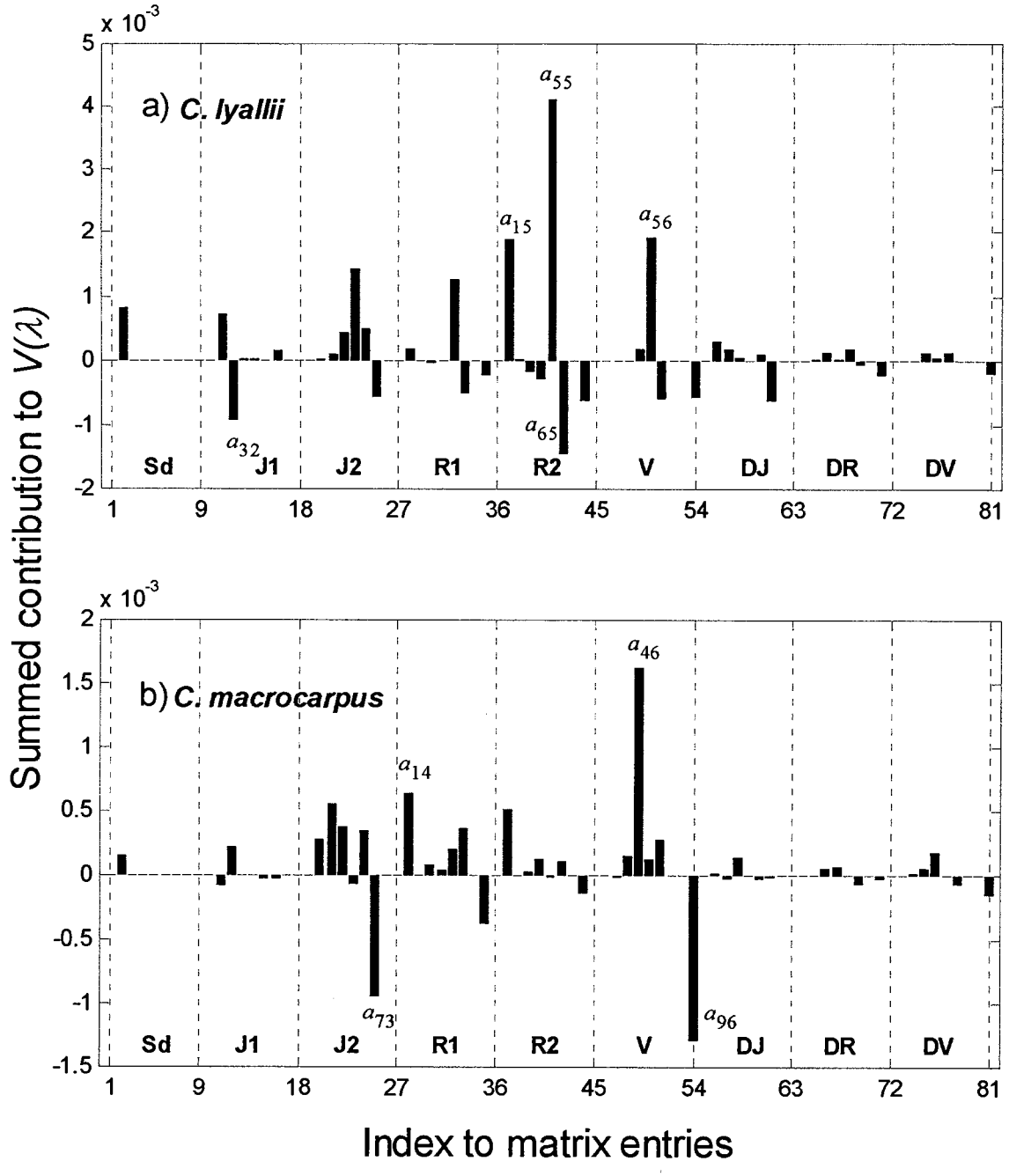

Figure 4.6 The net contribution of matrix entry a_{ij} to the inter-year variance in λ, $V(\lambda)$, calculated by summing the columns of the right-hand (contribution) surfaces in Appendix 7, for *Calochortus lyallii* a) and *C. macrocarpus* b). The 81 entries of the 9 x 9 matrix are arranged in column order along the x-axis: fates of seedlings (1-9), fates of small juveniles (10-18)...fates of dormant vegetatives (73-81).

C. macrocarpus, variances and covariances involving a_{46} (growth from vegetative to small reproductive) outweigh the summed contributions from any other entry (Fig. 4.6b), with the second largest net contribution coming from a_{14} (fecundity of small reproductives). Negative covariances involving a_{96} (transition from vegetative to dormant) and a_{73} (transition from large juvenile to dormant) are the most important overall in reducing $V(\lambda)$ in this species (Fig. 4.6b).

Interspecific variation. Projected rates of increase were higher for *C. lyallii* than *C. macrocarpus* in 1996-97 and 1998-99, similar for both species in 1997-98, and higher for *C. macrocarpus* in 1999-00; this variation relates to species differences in the matrix entries (Fig. 4.7). *Calochortus lyallii* showed a distinct fecundity advantage in 1996-97 (Fig. 4.7a), but this resulted in only a moderate contribution to the difference in λ between species (Fig. 4.7b). This advantage disappeared in 1997-98, and in the last two transitions reversed in favour of *C. macrocarpus*, making a substantial contribution to reducing $\Delta\lambda$ in 1998-99 (Fig. 4.7f). Other notable contrasts were for growth of small juveniles, prolonged juvenile dormancy, stasis of large reproductives, and growth from vegetative to large reproductive state (greater for *C. lyallii*); and seedling survival, stasis of small juveniles, stasis of vegetative plants, and retrogression from reproductive to vegetative (greater for *C. macrocarpus*). After these differences were weighted by their sensitivity, the matrix elements corresponding to fates of large reproductives and vegetative plants were also consistently the most important in terms of explaining $\Delta\lambda$ (Fig. 4.7, right). Analysis of the mean matrices ($\lambda_{C.\ lyallii} = 0.9893$; $\lambda_{C.\ macrocarpus} = 0.9296$) reveals a similar pattern. For the difference in average rate of increase between *C. lyallii* and *C. macrocarpus*, growth of vegetative into large reproductive plants, and ability to flower in successive years, made the greatest contributions (Fig. 4.7j). The exception to this general pattern was 1997-98, when λs were both negative and $\Delta\lambda$ was smallest. The LTRE shows that the small $\Delta\lambda$ in 1997-98 was primarily the result of a balance between the contributions from a_{56} (progression from vegetative to reproductive state) and a_{77} (stasis of dormant juveniles) in *C. lyallii* and from a_{73} (juveniles entering dormancy) and a_{66} (vegetative stasis) in *C. macrocarpus* (Fig. 4.7c-d).

To evaluate further the differences in λ between species, I collapsed the single-element contributions to $\Delta\lambda$ into summed contributions from separate regions of the

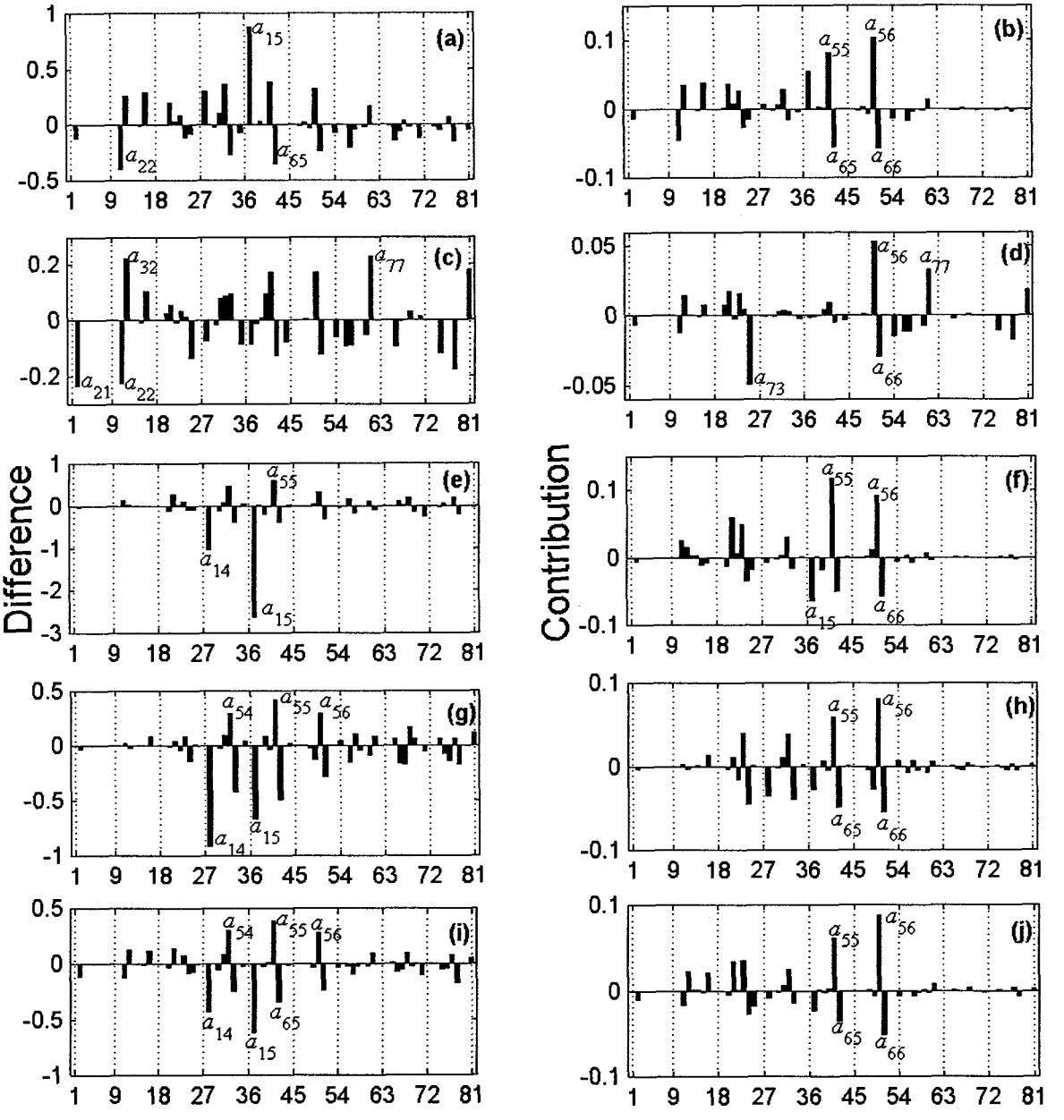

Figure 4.7 *Left*: The differences in stage-specific vital rates between *Calochortus lyallii* and *C. macrocarpus* in separate years. The *C. lyallii* matrix serves as the reference matrix for each year. *Right:* The contributions of those differences to the overall effect of species on λ. Positive values indicate a positive contribution of *C. lyallii* matrix entries relative to *C. macrocarpus* matrix entries. Negative values indicate a disadvantage (or negative contribution to λ) relative to *C. macrocarpus*. Matrices: (a-b) 1996-97; (c-d) 1997-98; (e-f) 1998-99; (f-h) 1999-00; (i-j) mean matrix.

matrix corresponding to stasis, growth and fecundity (*sensu* Silvertown et al. 1993). The advantage of *C. lyallii* with respect to λ was almost entirely due to advantages in growth (Fig. 4.8). Conversely, any *C. macrocarpus* advantage was the result primarily of combined contributions from stasis and fecundity. When $\Delta\lambda$ is small, it is because there is an even balance between contributions from growth in *C. lyallii* and stasis and fecundity in *C. macrocarpus* (Fig. 4.8).

AGE-SPECIFIC TRAITS AND LIFETIME EVENT PROBABILITIES

The fundamental matrix **N** gives the average expected time (in years) that individuals of a given stage will spend in any subsequent stage during the course of their lifetimes (Table 4.5). A *C. lyallii* seedling is expected to spend, on average, 1.05 years as a small juvenile, 1.66 years as a large juvenile, 0.25 years as a small reproductive, and 0.88 years as a large reproductive. By contrast, an adult vegetative plant spends 2.71 years as a large reproductive plant. A plant that survives to the large reproductive stage is forecast to spend, on average, a total of four years in that stage. A *C. macrocarpus* seedling spends only 0.19 and 0.09 years as a small and large reproductive plant, respectively, but spends 0.88 years as a vegetative adult. In contrast to *C. lyallii*, most of the adult (post-juvenile) phase is spent in a vegetative state (Table 4.5).

The average life expectancies (e^x) of individuals in different stages of the life cycle also differ between species (Table 4.6). A newly germinated *C. lyallii* seedling is expected to live for about six years, a *C. macrocarpus* seedling slightly less, and *C. lyallii* continues to maintain a greater average expectancy of further life through most of the life cycle. Individuals of *C. lyallii* are also more likely to flower before they die (Table 4.6); a *C. lyallii* seedling has a 0.24 probability of surviving to reproductive maturity, nearly double that of a *C. macrocarpus* seedling. By the second year of life (small juvenile stage), this probability has increased to 0.45 for *C. lyallii*, compared to only 0.21 for *C. macrocarpus*. Projected average age at maturity was 2.37 yr for *C. lyallii* and 2.52 yr for *C. macrocarpus*. Under average conditions experienced during the study, *C. lyallii* has a net reproductive rate R_0 of 0.85, whereas R_0 for *C. macrocarpus* is 0.25. Generation time,

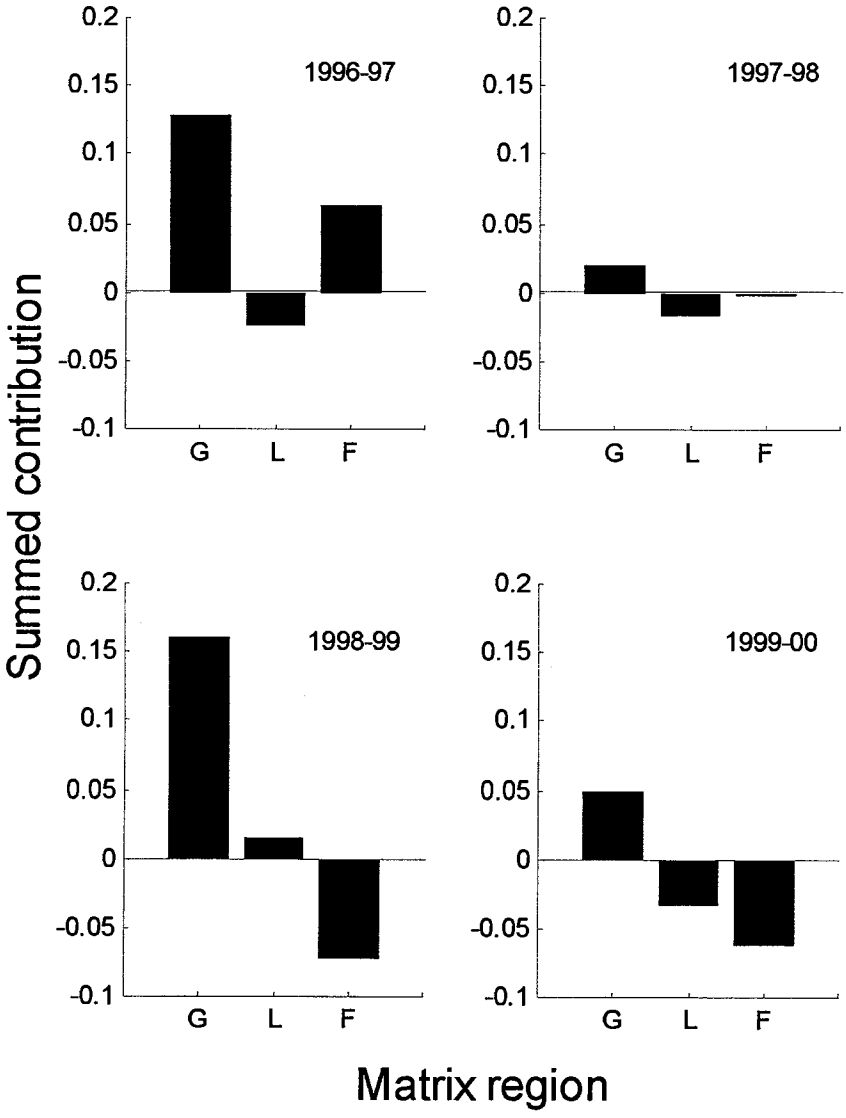

Figure 4.8 The total contributions from growth (*G*), survival (*L*, i.e., stasis or shrinkage), and fecundity (*F*) to the species effect on λ in separate years, calculated by summing over the corresponding regions in Figure A7.1 (appendix). Positive values indicate a positive contribution of *Calochortus lyallii* relative to *C. macrocarpus*, and vice versa.

Table 4.5 The fundamental matrix **N**, together with coefficients of variation (ratio of the standard deviation to the mean) of the mean number of time steps (years) spent in each stage for *Calochortus lyallii* and *C. macrocarpus*, respectively, calculated from the mean annual matrices (pooled across sites). As in the transition matrix, each column corresponds to a different initial state, and each row represents a potential fate. Thus entry 1,1 gives the expected number of years a plant, starting as a seedling, will spend in the seedling stage. Entry 1,9 gives the expected number of years it will spend as a dormant vegetative.

C. lyallii

	Sd	J1	J2	R1	R2	V	DJ	DR	DV
Sd	1.00 (0.00)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
J1	1.05 (1.35)	1.98 (0.70)	0.26 (3.21)	0.17 (4.02)	0.18 (3.92)	0.18 (3.98)	0.41 (2.50)	0.24 (3.40)	0.22 (3.50)
J2	1.66 (1.82)	3.13 (1.13)	4.07 (0.87)	2.00 (1.61)	1.98 (1.61)	2.04 (1.58)	3.21 (1.11)	2.21 (1.49)	2.34 (1.43)
R1	0.25 (3.13)	0.47 (2.17)	0.58 (1.91)	1.86 (0.68)	0.79 (1.56)	0.78 (1.58)	0.55 (1.99)	0.59 (1.90)	0.60 (1.88)
N = R2	0.88 (2.61)	1.65 (1.78)	2.06 (1.53)	2.78 (1.21)	3.93 (0.86)	2.71 (1.23)	1.85 (1.64)	2.04 (1.54)	2.09 (1.51)
V	0.63 (2.43)	1.18 (1.64)	1.45 (1.41)	1.67 (1.27)	1.62 (1.30)	2.68 (0.79)	1.38 (1.47)	1.44 (1.42)	1.57 (1.33)
DJ	0.48 (2.35)	0.90 (1.57)	0.67 (1.91)	0.34 (2.86)	0.34 (2.86)	0.35 (2.83)	2.06 (0.72)	0.39 (2.66)	0.40 (2.60)
DR	0.12 (4.27)	0.22 (3.03)	0.27 (2.68)	0.50 (1.86)	0.48 (1.91)	0.36 (2.28)	0.25 (2.83)	1.61 (0.62)	0.28 (2.66)
DV	0.08 (5.06)	0.15 (3.62)	0.18 (3.24)	0.21 (3.00)	0.20 (3.04)	0.34 (2.29)	0.17 (3.33)	0.18 (3.25)	1.55 (0.60)

C. macrocarpus

	Sd	J1	J2	R1	R2	V	DJ	DR	DV
Sd	1.00 (0.00)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
J1	1.58 (1.23)	2.48 (0.77)	0.53 (2.54)	0.32 (3.38)	0.34 (3.28)	0.35 (3.20)	0.72 (2.13)	0.47 (2.74)	0.44 (2.81)
J2	1.14 (2.05)	1.79 (1.52)	3.45 (0.84)	1.84 (1.48)	1.88 (1.46)	1.98 (1.41)	2.84 (1.04)	2.50 (1.17)	2.43 (1.20)
R1	0.19 (3.42)	0.29 (2.66)	0.53 (1.85)	1.68 (0.64)	0.73 (1.49)	0.80 (1.40)	0.56 (1.80)	0.74 (1.48)	0.74 (1.48)
N = R2	0.09 (3.44)	0.14 (3.49)	0.25 (2.49)	0.34 (2.07)	1.40 (0.53)	0.39 (1.91)	0.24 (2.53)	0.30 (2.22)	0.31 (2.17)
V	0.88 (2.80)	1.38 (2.16)	2.52 (1.45)	3.06 (1.25)	3.29 (1.17)	4.41 (0.88)	2.49 (1.46)	3.00 (1.27)	3.40 (1.14)
DJ	0.32 (2.86)	0.50 (2.20)	0.80 (1.63)	0.43 (2.41)	0.44 (2.38)	0.46 (2.31)	1.96 (0.70)	0.58 (2.01)	0.57 (2.04)
DR	0.04 (7.48)	0.07 (5.94)	0.12 (4.35)	0.33 (2.53)	0.31 (2.64)	0.19 (3.48)	0.13 (4.28)	1.72 (0.65)	0.17 (3.70)
DV	0.14 (4.20)	0.22 (3.30)	0.40 (2.35)	0.48 (2.09)	0.52 (2.00)	0.70 (1.65)	0.39 (2.37)	0.47 (2.11)	1.80 (0.67)

Table 4.6 Average life expectancies (± SD) and flowering probabilities for different life stages of *Calochortus lyallii* and *C. macrocarpus* at Black Mt., based on the mean annual matrices (pooled across sites). For seedlings, this is equal to the mean age at death. *P*(flowering) is the probability of an individual in stage *i* surviving to enter a stage in which reproduction occurs.

Stage	Life expecancy (years)		*P*(flowering)	
	C. lyallii	*C. macrocarpus*	*C. lyallii*	*C. macrocarpus*
Sd	6.14 (± 8.17)	5.38 (± 6.96)	0.24	0.13
J1	9.68 (± 9.04)	6.87 (± 7.67)	0.45	0.21
J2	9.55 (± 9.00)	8.61 (± 8.33)	0.56	0.38
R1	9.51 (± 8.96)	8.48 (± 8.42)	1.00	1.00
R2	9.53 (± 8.96)	8.91 (± 8.46)	1.00	1.00
V	9.42 (± 8.96)	9.27 (± 8.48)	0.74	0.58
DJ	9.88 (± 9.03)	9.32 (± 8.32)	0.51	0.39
DR	8.69 (± 8.93)	9.79 (± 8.45)	0.56	0.51
DV	9.06 (± 8.93)	9.86 (± 8.45)	0.57	0.51

defined as the time it would take the population to increase by the fraction R_0, is 15.50 yr for *C. lyallii* and 19.12 yr for *C. macrocarpus*.

Age-specific survivorship functions derived from the stage-classified model of the two species show the typical, reverse J-shaped curve (Fig. 4.9a). They predict that *C. macrocarpus* has a slight advantage in the first year of life; *C. lyallii* shows a slight advantage once past the seedling stage. Both species are long-lived, with life spans approaching 40 yr. Fertility in both species reaches a maximum between five and 10 years of age, after which it begins to decline. However, the shape of the fertility function varies markedly between species, indicating that for any given age, *C. lyallii* individuals have higher fertility on average than *C. macrocarpus* individuals of comparable age (Fig. 4.9b).

In both species, there is a marked difference among the stage-specific stable age distributions for different stage classes (Fig. 4.10), with a larger number of older individuals in the flowering and large vegetative classes and younger individuals in the juvenile classes. The stable age distributions for larger stages are also flatter and more symmetric than those for smaller stages, reflecting the range of accumulated times taken to pass through the previous stages. However, in *C. lyallii* the age frequency distributions are more strongly skewed towards younger ages compared to those in *C. macrocarpus*, indicating that the latter is an older population, with a greater proportion of old individuals (>15 yr) present in each stage (Fig. 4.10).

Discussion

POPULATION TRENDS AND TEMPORAL VARIATION IN λ

Many factors may interact to constrain the abundance and distribution of species. Some are extrinsic to the life history of the taxon (e.g., land-use history, habitat availability, herbivores, pollinator availability); others are intrinsic and reflect fundamental biological attributes (e.g., fecundity, dispersal mechanisms, competitive ability, genetic variability, habitat specificity). Because they integrate the combined effects of extrinsic and intrinsic factors into a single measure of population fitness, rates

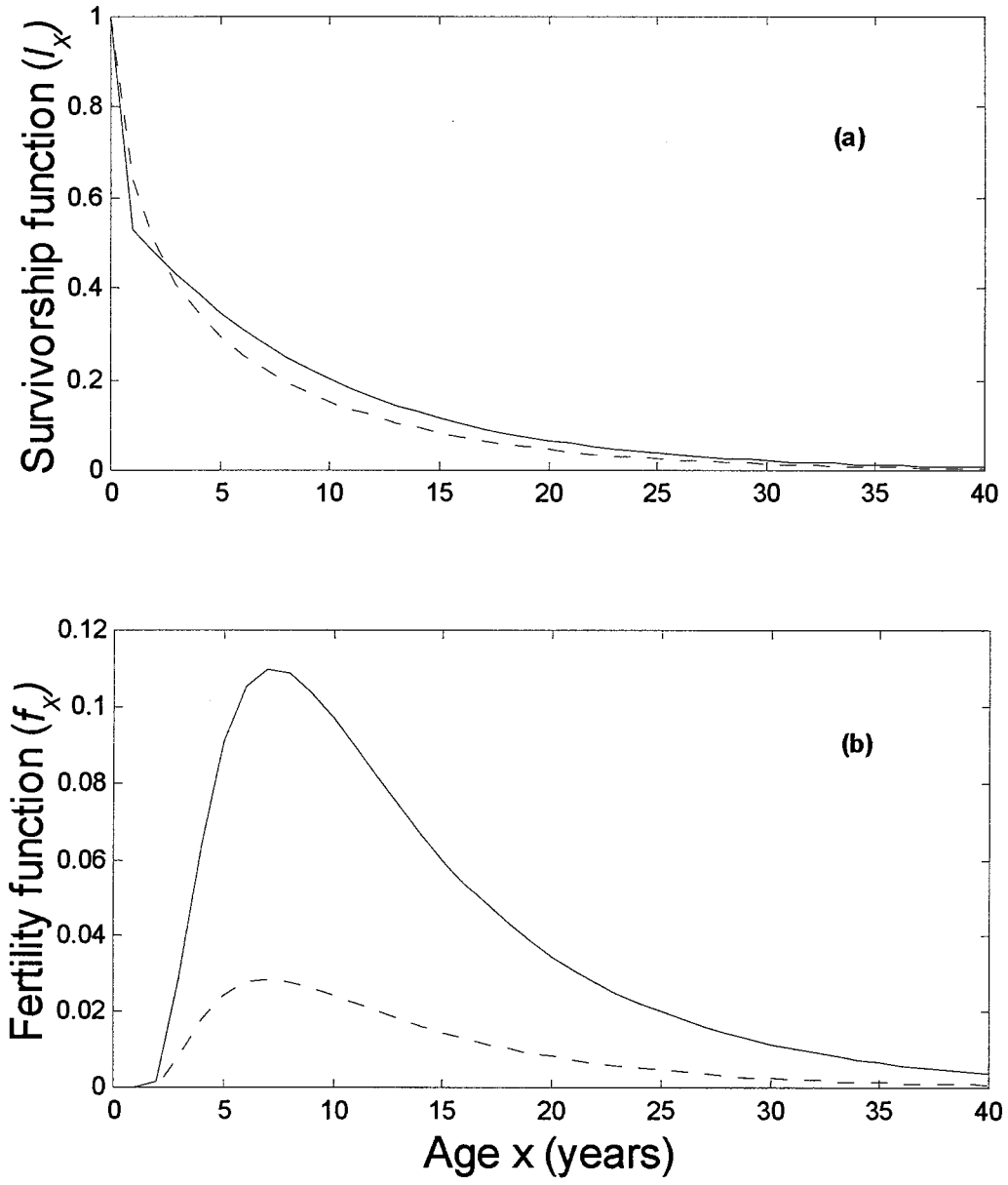

Figure 4.9 (a) Age-specific survivorship (l_x) and (b) maternity (f_x) functions for *Calochortus lyallii* (solid line) and *C. macrocarpus* (dashed line) derived from the stage-classified matrix model for each species (after Cochrane and Ellner 1992).

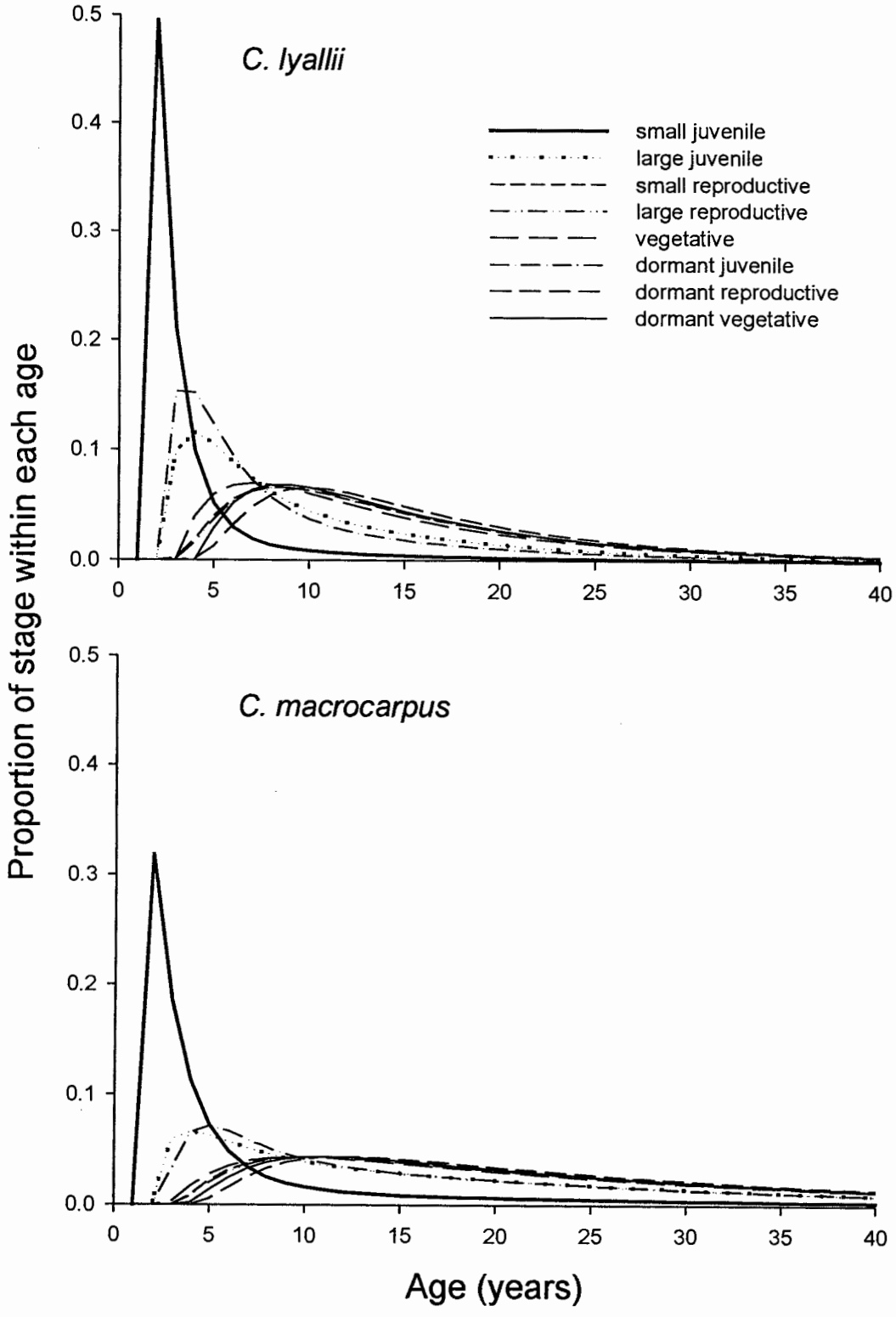

Figure 4.10 Area graph showing the stable age-within-stage distributions for *Calochortus lyallii* and *C. macrocarpus*. The total area under each stage sums to 1. Stage Sd (seedlings) is composed entirely of individuals in age class 1 and is not shown.

of population growth (λ) and its components are well suited for generating hypotheses about the processes underlying species' abundance patterns.

Patterns of population growth in the two mariposa lilies *C. lyallii* and *C. macrocarpus* support the idea that a locally sparse species should, over time, exhibit different population dynamics than a sympatric, locally abundant congener. If the five years of this study are representative of different phases in the dynamics of *C. macrocarpus* on Black Mt., they imply that these populations are typically in a phase of decline punctuated by short bursts of growth. After the sequence of years observed, it would take about 32 years at a growth rate of 1.01 (the 1999-00 matrix) for *C. macrocarpus* to recover to 1996 levels. In contrast, *C. lyallii* appears to fluctuate between 'good' ($\lambda > 1$) and 'poor' ($\lambda < 1$) years while maintaining an overall growth rate close to 1. The stochastic growth rate $\log\lambda_s$ was negative for both species, implying an inability of either to persist locally under prevailing conditions. However, the projected rate of decline was much more rapid for *C. macrocarpus.* Separate stochastic simulations for each of the three sites indicated that the negative trends in long-term growth rate for the pooled data sets could be largely ascribed to low performance at two of the sites (NS and ES); at WS, $\log\lambda_s$ was close to equilibrium in both species.

The relatively low annual growth rates obtained for *Calochortus lyallii* and *C. macrocarpus* appear to be characteristic of species in this genus (Fiedler 1987, Fredricks 1992, Knapp 1996, Fiedler et al. 1998). Previous workers have emphasised reproduction and establishment as the primary factors limiting *Calochortus* populations (Fiedler 1987, Fiedler et al. 1998). Here, the LTREs showed that temporal variation in λ was driven primarily by variation in the transition and flowering behaviour of adults and only secondarily by rates of seed set and seedling establishment. In *C. lyallii*, failure of large reproductive plants to flower in subsequent years was the most important source of reductions in λ. In *C. macrocarpus*, fluctuations in λ mainly reflected changes in the rate at which vegetative plants became reproductive. Thus it appears that local persistence in these species is achieved via different demographic pathways. Whereas *C. lyallii* evidently relies on frequent and regular flowering to produce a steady supply of recruits into the population, reproduction in *C. macrocarpus* tends to be episodic; individuals flower infrequently, and those that do are often grazed before the fruits have a chance to

mature. Nevertheless, the attempt to produce seed may come at a cost with respect to future reproduction; plants of this species generally do not flower two years in succession (Fig. 4.2).

The two species differed in the extent to which bulb dormancy buffered population fluctuations. In *C. macrocarpus*, the effects of low flowering and recruitment were largely countered by increases in below-ground dormancy. In *C. lyallii*, extended dormancy had less of a role in moderating temporal effects on λ, which instead occurred primarily through increases in vegetative growth.

Prolonged dormancy was a common phenomenon in both species of *Calochortus*, with dormant bulbs comprising from 2-24% and 7-27% of the yearly projected stable stage distributions of *C. lyallii* and *C. macrocarpus*, respectively. Although many plants exhibit prolonged dormancy (Lesica and Steele 1994), the logistical challenge of obtaining reliable dormancy estimates for natural populations has meant that impacts of adult dormancy on population dynamics have rarely been quantified (Menges 2000, Shefferson et al. 2001). My study is one of the first to demonstrate that dormancy during juvenile and adult stages could function to offset the effects of a temporally fluctuating environment in a manner analogous to that often hypothesised for soil seed banks (cf. Baskin and Baskin 1978, Kalisz and McPeek 1992). In their review of *Calochortus* demography, Fiedler et al. (1998) note that census data for several *Calochortus* species show patterns of 'episodic mortality' and suggest that these episodes are partly responsible for observed variation in population growth rates. However, most of the data sets cited (from Fiedler 1987, Fredricks 1992, Knapp 1996) span only three years, or two transition periods. It is likely that a portion of the recorded fatalities in these populations actually represent episodes of dormancy not observable within this brief time frame. In the present study, failure to take dormancy into account would have underestimated λ in *C. macrocarpus* by as much as 0.27 over a given transition period (unpubl. results).

In both *C. lyallii* and *C. macrocarpus*, the transitions with the highest LTRE contributions also tended to have the highest elasticity values (Appendix 4.5). This is not always the case; the vital rate that contributes most to the temporal variability in population growth rate is not necessarily the one to which population growth rate is most sensitive (cf. Horvitz et al. 1997, Pfister 1998, Caswell 2000). Elasticities for the mean

matrices (Fig. 4.4) demonstrate that, under average conditions, young/small individuals and old/large individuals made comparable contributions to population growth rate, with no single stage dominating. Among adult stages, stasis of large reproductives made the biggest contribution to λ in *C. lyallii*, whereas in *C. macrocarpus* the highest elasticity by far was for stasis of vegetative plants. Transitions into dormancy and the stasis of dormants together accounted for 10% of the total elasticity in *C. lyallii* but nearly 15% for *C. macrocarpus*. These dormancy elasticities are similar to values reported for another liliaceous geophyte, *Erythronium elegans* (Guerrant 1996), but substantially less than those for the similarly long-lived, grassland geophyte *Silene spaldingii* (Lesica 1997). The higher elasticities for dormancy in *C. macrocarpus* relative to *C. lyallii* are to be expected from life history theory, which holds that for declining populations a delay in reproduction should have a larger positive impact on λ than reproducing early in the life cycle (Stearns 1992).

It has been shown that the position of individual populations in *G-L-F* elasticity space is roughly correlated with life form (Silvertown et al. 1993), but is also influenced by the number of life stages used to classify individuals in the population (Enright et al. 1995), the successional stage of the habitat (Silvertown and Franco 1993, Silvertown et al. 1996), and the population's rate of increase (Oostermeijer 1996, Silvertown et al. 1996). Although not large, variation in the relative contributions of *G* (growth/progression), *L* (stasis/retrogression), and *F* (fecundity) to λ was greater among years than between species (Fig. 4.5), reflecting the fundamental similarity of the life histories of these two species. All of the matrices occurred along the *G-L* axis of the ordination triangle, with low values for *F*, low to intermediate values for *G*, and intermediate to high *L* values. Although this pattern is more generally associated with perennial herbs of forest habitats and woody shrubs than with herbs of open habitats (Silvertown et al. 1996), it is nevertheless consistent with findings for other, long-lived herbaceous geophytes of non-forested habitats (Svensson et al. 1993, Kephart and Paladino 1997, Oostermeijer et al. 1996, Lesica 1997, Hawryzki 2002), including other *Calochortus* species (Fiedler et al.1998). It is not surprising that survival contributes more than reproduction to the maintenance of these slow-growing, late-maturing perennials, particularly in variable and unpredictable environments such as semi-arid

grasslands. However, it would be simplistic to conclude from this that reproduction is 'unimportant' to the long-term dynamics of these species; clearly, for obligately sexual plants such as *Calochortus lyallii* and *C. macrocarpus* to attain $\lambda \geq 1$ requires at least periodic recruitment from seed. Rather, the low F values that appear to characterise this growth form also underscore a potential vulnerability, which is that species that depend heavily on high adult and juvenile survivorship to make up for chronically low recruitment may possess limited demographic latitude for responding to even minor reductions in survival (Congdon et al. 1993). Population resilience—the ability to recover quickly from a major disturbance (Pimm et al. 1988)—may be low in these and similar taxa due to intrinsic life history constraints. From a management standpoint, ignoring reproductive processes in declining populations because F values are low may be precisely the wrong strategy (Silvertown et al 1993).

INTERSPECIFIC VARIATION IN λ

Several studies have found that rare species reproduce less or show more variation among years in reproduction than their widespread congeners (Fiedler 1987, Pavlik et al. 1993, Byers and Meagher 1997, Walck et al. 2001). Decomposition of interspecific differences in λ revealed that the overall higher rate of increase in *C. lyallii* primarily reflected an advantage in the fates of large reproductive and vegetative plants, in particular the stasis of reproductives and the transition of vegetatives into the flowering state. Thus the same set of constraints that distinguished good years from bad in the intraspecific LTREs also distinguished the performance of the two species relative to one another, underscoring the central importance of flowering, and factors influencing flowering, to the long-term dynamics of *Calochortus* species on Black Mt.

Because *C. lyallii* generally produces larger inflorescences than *C. macrocarpus* (*Chapter 2*), the higher propensity for repeated flowering in *C. lyallii* runs counter to the expectation that a larger investment in flowering structures should involve a trade-off cost in future reproduction. However, *C. macrocarpus* blossoms are more than twice as large as those of *C. lyallii*, and their fruits contain over four times the number of seeds on average (*Chapter 2*). It is thus possible that the relative investment (as dry matter, nitrogen and phosphorus) involved in the production of flowers and fruits is not nearly as

different between the species as is implied by the number of flowers per inflorescence. Even so, large absolute differences in size between individuals, and storage of resources between reproductive events, make such costs difficult to demonstrate for most long-lived plants, especially when only natural variation is considered (Ehrlen and van Groenendael 2001). Furthermore, many perennial species differentiate their leaf and flower buds a year or more in advance of their development (Geber et al. 1997, Worley and Harder 1999), which can lead to delayed responses to changes in resource levels, further obscuring the mechanisms underlying different flowering patterns. In *C. lyallii* and *C. macrocarpus*, both flowering frequency and the number of fruits per plant were positively correlated with temperatures during the previous summer and negatively correlated with precipitation the previous summer (*Chapter 2*), suggesting that preformation of flower buds also occurs in this genus. These results also suggest that local limitations on *C. lyallii* and *C. macrocarpus* may be primarily climatic in origin, rather than micro-environmental. Climatic gradients can produce abrupt plant distribution limits even though the physiological responses elicited might appear too small to explain them (Carter and Prince 1981). The regional endemic *C. lyallii* reaches its northern range limit on Black Mt., where it presently occupies only a small fraction of the available habitat. The apparent reliance on drier, hotter conditions for flowering may be one reason why this species has not succeeded in expanding further northward into British Columbia. Although the more widespread *C. macrocarpus* is not at its geographical limit on Black Mt., at 1200 m it is nearing the elevational limit of its distribution. The climate is substantially wetter and cooler there than in the valley bottoms where it is more abundant, and range marginality may also be coinciding with ecological marginality.

Interestingly, the largest *summed* contribution to the interspecific difference in λ came not from fecundity, despite *C. lyallii*'s higher flowering rate, but from the combined effects of growth (Fig. 4.9). In three of the four transition periods the fecundity advantage actually belonged to *C. macrocarpus*. In 1999-00, the one year in which *C. macrocarpus* projected a higher λ than *C. lyallii*, it did so through a combination of higher fecundity and survivorship (i.e., stasis and retrogression). However, the fecundity term estimates the number of seedlings recruited per flowering plant, not the per capita rate of recruitment. Compared to *C. lyallii*, a smaller proportion of *C. macrocarpus*

plants reproduce in any year; hence those that do reproduce would have to recruit proportionately more seedlings per capita in order to achieve the same population-level result. Although *C. macrocarpus* is able partially to accomplish this through the production of larger seed capsules (*Chapter 2*), the stage-specific fecundity rates observed during the study were still substantially less than the estimated replacement fertility values (i.e., the fecundity rates required to sustain a λ of 1 under average conditions). In contrast, replacement fertility rates for *C. lyallii* were well within the range of those observed. Perhaps because flowering in both species occurs only after plants attain a certain size, rapid progression between stages (*C. lyallii*) generally outweighed the advantages of slightly higher recruitment (*C. macrocarpus*).

AGE-BASED TRAITS

Extracting age-based parameters from stage-classified models can reveal useful details about the life cycle not apparent from analysis of the stage-based models alone (Cochran and Ellner 1992), especially for herbaceous perennials whose age characteristics cannot be determined easily by any other means (Morris and Doak 1998). Using such an approach I was able to identify a likely life-span (around 40 yr) for both *Calochortus* species. My analysis also showed that, aside from life-span and age-specific survivorship, *C. lyallii* has a marked advantage over *C. macrocarpus* with respect to nearly every fitness component measured, including net reproductive rate R_0, mean age at maturity, age-specific fertility rate, average life expectancy, generation time, and the likelihood of flowering before dying. A *C. lyallii* seedling is predicted, on average, to live longer (6.14 vs. 5.38 yr), flower sooner, spend more time in a flowering state, and leave more offspring (0.85 vs. 0.25 seedlings) than an equivalent *C. macrocarpus* seedling.

Effects from these life cycle differences on population processes are evident both in the projected stable stage distributions and in the stable age-within-stage distributions. In most years, the stable stage distribution of *C. lyallii* is dominated primarily by juveniles and secondarily by seedlings and large reproductive plants. Juveniles also dominate the stable stage distribution in *C. macrocarpus*; however, the next most abundant plants are in this case vegetative adults. In both species, the distributions of frequency vs. age

within each stage are flatter and more symmetric for adult stages than for sub-adult stages (Fig. 4.10) because of the range of accumulated lag times that develops as individuals pass from stage to stage. This pattern has been reported for a wide range of taxa and is probably widespread in nature (Boucher 1997). However, while substantial proportions of the plants in both species are probably older than their size suggests, the discrepancy between size and age is more marked in *C. macrocarpus* than in *C. lyallii*. In other words, in *C. lyallii* populations, plants that are small in size also tend to be young. In contrast, in populations of *C. macrocarpus* plants are nearly as likely to be old as young. Such results do not on their own explain the marked differences in habitat and distribution, or separate cause from effect in explaining patterns of rarity. Nevertheless, clear demographic differences exist between the restricted but abundant *C. lyallii* and the widespread but sparse *C. macrocarpus*.

As with all models, the transition models used to describe the two species are not a perfect reflection of nature. For example, the models predict ages of maturity at around 2.5 yr, even though no seedling of either species initially censused in 1997 had attained flowering size by 2000, the last year of the study. First-order Markov chain models assume that demographic rates reflect current size and stage but are not influenced by size and stage in previous years (Caswell 2001). However, van Groenendael et al. (1988) suggested, and Ehrlen (2000) subsequently demonstrated, that historical effects can be important in natural populations. My simulations do not test for such effects, but treat all the individuals in a given size class (except for dormants) equally regardless of prior state. For example, 'J1' plants that were seedlings the previous year are assigned the same probability of surviving and advancing to a larger size class as older plants arriving at the same stage via retrogression from an adult size class. Thus some rates (e.g., juvenile growth) may have been overestimated, potentially leading to an underestimate of the number of the years needed to go from germination to flowering. Nevertheless, the values generated by this analysis, although not necessarily absolute, do form a sound basis for comparing life history schedules between the species.

POPULATION DYNAMICS AND RARITY PATTERNS

Theoretical and empirical studies suggest that that as maturation times decrease and reproductive rates increase, intrinsic growth rates should increase and the risk of extinction should decrease (Pimm et al. 1988). However, theory also suggests that these same traits are likely to lead to increased variability in population size, which should increase the risk of extinction (Pimm et al. 1988). My results are consistent with aspects of both predictions. Higher growth and flowering rates in *C. lyallii* resulted in a population growth rate that was higher over the long-term while more variable over the short term. However, population momentum (the fraction by which the population would continue to grow or shrink before stabilising if vital rates were instantaneously brought to stationary levels) was much higher for *C. macrocarpus*, suggesting that this is the species with the more unstable dynamics and also the one most likely to undergo large fluctuations in population size following a perturbation. The sensitivity of marginal populations to environmental stochasticity has not been well studied, but likely depends on many factors (Lesica and Allendorf 1995). Both *C. lyallii* and *C. macrocarpus* appear able to tolerate periodic disturbance (e.g., fire, grazing) to a certain degree, but their degree of tolerance to frequent disturbances may differ considerably.

In a survey of one common and seven narrow-endemic *Calochortus* species from different habitats in the western US, Fiedler et al. (1998) reported λs ranging from 0.54–1.05 in the rare species and from 1.01–1.04 in the common species, detecting no systematic differences between rare and common taxa with respect to population growth rate. Byers and Meagher (1997), comparing a rare and a common species of *Eupatorium*, found that two of three populations of the rare species showed positive λs during the year of study, whereas only one out of three populations of the common species was projected to grow during the same period. The fact that many populations of long-lived plants have λs <1 despite having clearly persisted for a long time is somewhat surprising but not entirely unexpected. Geometric increase and a stable stage distribution are asymptotic characteristics that probably do not occur in many natural populations (Fiedler et al. 1998, Bierzychudek 1999). Although stochastic models provide a more realistic forecast of long-term behaviour, they too can produce misleading results if they fail to capture the

complete range of year-to-year environmental variability experienced by a population (Bierzychudek 1999). All else being equal (e.g., growth form, habitat, weather, community interactions), over time it is generally expected that a locally abundant or widespread species will show, on average, a higher λ, or a less variable λ, than a related rare species inhabiting a similar environment (the implicit assumption being that abundant species are becoming more abundant, and rarer ones more rare). However, over short time scales of one or a few years (i.e., the time scales of most plant demographic studies) we might just as easily find this pattern reversed, or that populations of both species are changing in tandem. Of course, the power of exponential growth is such that, over the long run, every species must maintain an average λ close to 1, otherwise it would soon go extinct or else expand until it filled the world with its numbers (Darwin 1872). No robust empirical link between current λ and 'commonness' or 'rarity' has yet been established, nor is it clear that we should expect one.

Evidence for dispersal limitation has been found for many plants inhabiting fragmented habitats (Primack and Miao 1992). In British Columbia, *C. lyallii* occurs primarily in isolated meadow clearings within coniferous forest (Miller and Douglas 1999). Although the Black Mt. habitat contains many such openings, only a small fraction of these are currently occupied by *C. lyallii*, suggesting that this species may be strongly dispersal limited. Aside from gravity the seeds of *C. lyallii* possess no obvious long range dispersal mechanism, and most seeds probably germinate within centimetres of the parent plant (Miller and Douglas 1999). Although also primarily gravity dispersed, the seeds of *C. macrocarpus* possess broad wings that may aid to some extent in wind dispersal. In addition, the flower stalks of this species, which are several times taller than those of *C. lyallii*, elongate even further after flowering, causing the seed capsules to be raised above the surrounding vegetation (Verbeek and Boasson 1995). Unlike the fruit-bearing stalks of *C. lyallii*, which topple over once the capsules have dehisced, those of *C. macrocarpus* become woody and remain standing, thereby keeping the capsule exposed to the wind until most of the seeds have been released.

The scattered but frequent occurrence of *C. macrocarpus* throughout the study area, as well as its broad geographic distribution, imply that dispersal is probably not a strong limiting factor in the dynamics of this species. Instead, its scarcity at the local scale is

likely due to a combination of factors including low intrinsic growth rate, delayed maturation, a low propensity to flower and set seed once mature, and grazing pressure on seed capsules. In many respects, *C. macrocarpus* resembles a fugitive species (Rabinowitz 1978) subject to frequent population fluctuations and possibly even local extinctions while relying on longer-distance dispersal to sample the environment for safe sites suitable for germination and growth. *Calochortus lyallii*, by comparison, behaves more like a local competitive dominant that persists through vigorous and steady growth, moderate but steady reproduction, and generally stable dynamics.

Chapter 5: Summary and Discussion

The primary aim of this thesis was to investigate the link between population processes and events in the life cycles of *Calochortus lyallii* and *C. macrocarpus*, two related plant species with contrasting patterns of distribution and abundance. Census information collected from three sites over five years provided a basis for describing inter- and intraspecific demographic variability. I tested whether populations show similar growth trajectories, whether the observed dynamics are scale-dependent, and whether the two species persist via similar demographic mechanisms.

Specifically, I found that:

1) Many individuals of both species exhibited prolonged bulb dormancy. Most dormancy episodes lasted 1-2 yr, although unrecorded plants continued to appear in the study plots up until the end of the study, implying a dormancy duration of up to 4 yr.

2) Dormancy episodes were synchronised among populations within species, and also between species, suggesting control by the same external environmental factor.

4) The proportion of plants flowering was usually higher for *C. lyallii*, but flower abortion was lower in *C. macrocarpus*. Low fruit production related primarily to flower and fruit abortion in *C. lyallii*, but to deer herbivory in *C. macrocarpus*.

5) Warm, dry conditions in the previous year favoured flowering and fruiting in both species, implying that climatic conditions at their range peripheries may be limiting their spread.

6) The three *C. lyallii* populations had generally stable dynamics, with projected annual λ-values that fluctuated around 1 but with long-term stochastic growth rates close to equilibrium. By comparison, *C. macrocarpus* exhibited relatively unstable dynamics, with two of three populations studied projected to decline rapidly in size. Prolonged bulb dormancy in *Calochortus* may help to reduce spatiotemporal variation in λ.

7) In *C. lyallii*, variance in λ at the population and patch level were mediated by different sets of vital rates. This emphasises that different demographic results are obtained depending on the scale examined; therefore attempts to infer regional patterns from local processes and vice versa can produce erroneous results.

8) The most important sources of temporal variation in λ were, in *C. lyallii*, changes in the rate at which large reproductive plants flowered, and in *C. macrocarpus*, changes in the rate at which vegetative plants became reproductive.
9) The generally higher λ observed for *C. lyallii* than for *C. macrocarpus* resulted primarily from greater flowering frequency.
10) In *C. lyallii*, the highest elasticities were associated with survival of juveniles and large reproductive plants; in *C. macrocarpus*, they were associated with survival of juveniles and large vegetative plants.

Calochortus lyallii is a slow-growing plant with high survivorship, delayed maturity, low but variable recruitment, a low intrinsic rate of increase, and limited dispersal. Local populations tend to be large, with stage structures that suggest they have persisted for many years. At the regional scale, the pooled populations on Black Mt. had a small but significantly negative stochastic growth rate (~-1% per year). This is likely a conservative projection, as most transition probabilities (e.g., seedling survival) used to model dynamics in this study were low estimates. In any case, the relatively small departure from equilibrium was not substantially greater than the deviance one might expect to observe in a long-lived herbaceous perennial monitored over several years in a variable environment (Erhlén 1995, Kaye et al. 2001).

The dynamics of *C. macrocarpus* populations are more difficult to interpret. In contrast to its congener, this species has undergone a marked decline on Black Mt., in numbers of both emergent plants and numbers of reproductive individuals. Two of the three populations studied projected a strongly negative long-term growth rate, indicating that local extinction is likely under current conditions. Yet the demographic structure of these populations implies that they, like those of *C. lyallii*, have existed for many generations. Thus the current decrease could signify a long-term, deterministic trend, or it could represent a stochastic and temporary fluctuation in the local dynamics of the species.

In the case of *C. lyallii*, it is puzzling that no populations have been found at nearby lower elevations in the Okanagan Valley, where conditions appear more suitable for growth. The most parsimonious explanation is that a long-distance dispersal event led to establishment at the current sites, but that limited dispersal ability, or insufficient time,

has prevented *C. lyallii* from colonising other habitats north of the Similkameen River Valley, which here forms the boundary between Washington and BC and which likely acts as an effective local barrier to further immigration from the south.

Calochortus lyallii conservation and management

The generally stable dynamics exhibited by *C. lyallii* suggest that direct demographic intervention is probably not warranted at present. Instead, efforts to conserve *C. lyallii* populations in Canada should focus first on preserving the structure and function of the grass-forb meadows that contain these populations. This may be difficult. Following a forest fire in 1994, salvage-logging operations cleared away large sections of burnt forest on the north and east slopes, facilitating livestock access to several *C. lyallii* sites. Subsequently, a number of invasive plant species, including hound's tongue (*Cynoglossum offincinale*) and knapweed (*Centaurea diffusa*), have increased in the area and now pose a potential threat to many plant communities on Black Mt. (Miller and Douglas 1999).

In the event that demographic intervention becomes necessary in the future, my analyses indicate that the most effective way to reduce temporal fluctuations in population growth rate is to reduce the variance in the stasis of large flowering plants. On the other hand, effecting an increase in λ will likely require managing for the whole life cycle, with particular attention paid to the factors affecting fecundity/recruitment and the survivorship of seedlings, juveniles and large flowering plants. The most variable matrix element, fecundity, may also be the one most amenable to management. Because many *C. lyallii* seeds do not survive to germinate, a relatively straightforward way to raise fecundity rates would be to collect seeds before the capsules dehisce, and keep them in safe storage until they can be sowed *in situ* the following spring.

The effectiveness of such a strategy would depend on environmental conditions and the structure of the corresponding transition matrix. Using simulations, for example, I have found that a doubling of the per capita recruitment rate from 1 to 2 seedlings a year is usually sufficient to raise λ from slightly <1 to slightly >1, as long as the elasticity of fecundity is sufficiently high (*c.* >0.03). However, in matrices with λ-values close to 0.9,

and with elasticity of fecundity <0.01, fecundity rates would have to be increased by as much as 200 times (a biological improbability) in order to raise λ to 1 (unpubl. results).

Moreover, because elasticities evaluate the consequences of variation in a single matrix entry only, management interventions aimed at augmenting only processes with high elasticities may not be effective if life history traits covary (van Tienderen 1995, Menges 1998). Linkages in transition probabilities can arise because of phenotypic or genetic trade-offs (for instance, current reproduction may be negatively correlated with future survival) or because several matrix elements respond similarly to changes in the environment (van Tienderen 1995). Correlations between matrix elements can reduce the opportunities for spreading risks between life stages, increasing the probability of extinction. For example, in declining populations of *Pedicularis furbishiae*, the highest elasticity terms were for survival, but reducing mortality nevertheless appeared to be a poor management choice because it involved curtailing the disturbances that provide ideal conditions for establishment and growth (Menges 1990).

Conclusions

Results from my study emphasise a fundamental point: the spatial and temporal scales of analysis affect the interpretation of population dynamics (Wiens 1989, Levin 1992). Matching the scale of measurement to the scales of heterogeneity most relevant to the organism can be challenging; hence study at multiple scales may be necessary. In the case of *C. lyallii*, for example, it was necessary to study dynamics at the scale of individual patches to find that intrapopulation variability was partly a function of the variation in soil depth, mediated by its effect on establishment and survival of seedlings and juveniles. It is also evident that conclusions drawn from a single demographic transition can be seriously misleading over longer time intervals, especially if prolonged dormancy is occurring; failure to account for this life history phenomenon in models of population dynamics would clearly produce erroneous results. In my study, an observation span of five years was still insufficient to resolve satisfactorily the dormancy behaviours of *C. lyallii* and *C. macrocarpus*. To do so would likely require monitoring

populations over a length of time greater than is usually seen in demographic studies of herbaceous plants.

A second point is that demographic extrapolations based on taxonomic relatedness, morphological similarity, or habitat overlap may not always be reliable. On the basis of my study, management recommendations for *C. macrocarpus* would differ substantially from those suggested by models of *C. lyallii* dynamics. There has been considerable emphasis recently on defining plant 'functional groups' in order to describe more accurately the relationship between life history variation and population processes (Silvertown et al. 1993), and to develop better guidelines for conservation. This approach is useful; for example, 'bulbous geophytes', which include *C. lyallii* and *C. macrocarpus*, possess a suite of common characteristics (perennial habit, growth from a subterennean bulb, cryptic life stages) that are important to population dynamics. Although such similarities allow for the generation of useful hypotheses, generalisations based on this approach can only be extended so far. In the end, there is probably no substitute for intensive ecological study of critical life history features on a species-by-species basis.

It is axiomatic that rarity precedes extinction; thus the study of rarity is critical for conservation goals as well as for the development of ecological theory. Rarity is of multiple forms, resulting from multiple processes, which has hampered determination of its causes and consequences and its relationships to specific aspects of life history. We now have a good idea about the sorts of life history traits that increase a species' vulnerability to extinction. Examples are large body size, slow growth, low fecundity, low r, variable r, variable population density, and poor dispersal (or profound reliance on dispersal). However, correlations among these traits tend to obscure the nature of their respective roles in delimiting patterns of distribution and abundance. Habitat specialisation, seed banks, complex life cycles, interactions with other species (e.g., pollinators), and other autecological idiosyncrasies must clearly also be considered when attempting to predict susceptibility to extinction; species that have always been rare may be of less concern (as they have already demonstrated, to a certain degree, an ability to persist despite low numbers) than formerly more common ones that are decreasing. In such instances, detailed demographic analyses can provide useful insights into the processes limiting population size and stability. In this study, for example, it is the

comparatively widespread *C. macrocarpus*, rather than the overall rarer *C. lyallii*, that appears to be at greater risk of local extirpation, implying that management may need to focus on both species to prevent loss of local diversity.

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Appendix 3.1 Methods for calculating dormancy rates and performing randomisation tests

Estimating dormancy rates

To estimate dormancy rates for the middle two transitions (1997-98 and 1998-99), I assumed that the probability of an absent plant being dormant (versus dead) did not vary among years. I then used pooled census records from the most complete time sequence available (i.e., 1996-00) to estimate the likelihood that a plant that failed to appear at census t was dormant and not dead, taking into account both its state and the number of years it had already been absent at the time of the current census. The rate at which individuals in stage j became dormant during each transition interval was estimated by

$$p_{d(t+1)j(t)} = c_t * q_j + k(m_j - a) / \sum n_{i(t+1)j(t)} \qquad \text{(A1.1)}$$

where $p_{d(t+1)j(t)}$ represented the transition probability from stage j at time t to dormancy at time t+1; c_t denoted a constant (estimated proportion by which the observed number of dormants underestimated the actual number of dormants in a given year); q_j was the number of dormant stage j plants directly tallied; m_j was the number of stage j plants absent and unaccounted for at time t+1, but excluding any absentees whose fate was unambiguous (i.e., bulbs that had clearly been harvested by pocket gophers or other predators); a was the difference between q and c_t*q_j; k was another constant (estimated proportion of remaining absentees that went dormant for a year, then died—10% in the present case); and $\Sigma n_{i(t+1)j(t)}$ represented the total number of individuals in stage j at time t.

Plants failing to appear for the final census in 2000 could not be distinguished as dead or dormant. In this instance, dormancy rates could only be inferred from patterns observed in previous years. The probability of transition from stage j into dormancy was estimated by

$$\begin{aligned} p_{d(t+1)j(t)} &= \sum (q_j + k(m_j - a)) / (m_j - n_{g(t+1)j(t)})(1/n_t)(m_{j(2000)}) \\ &= h * m_{j(2000)} \end{aligned} \qquad \text{(A3.2)}$$

where h represented the mean likelihood, over the three transition intervals from 1996-99, that an absent 'stage j' plant at census t was, in fact, dormant (calculated as the ratio of [corrected] dormant:total absent in that interval); $n_{g(t+1)j(t)}$ was the number of stage j plants whose bulbs had been excavated by grazers and whose fate (death) was therefore known; and $m_{j(2000)}$ was the total number of absentees in 2000. For $p_{d(t+1)j(t)}$ where j denoted a dormant stage, only the means from the middle two transitions (1997-98 and 1998-99) were used, as dormant to dormant transitions were by definition unavailable for the initial time interval.

To calculate transition probabilities from dormancy back to other stages (i.e., those entries in the 'dormant' columns of the projection matrix), I again assumed that a certain fraction k (10 %) of all plants unaccounted for in the previous census went dormant first for a year, then died. This amount was then added to the current year's total dormant count. Let $p_{i(t+1)d(t)}$ represent the rate of transition from a given dormant class to stage i. Then

$$P_{d(t+1)d(t)} = n_{t(t+1)d(t)} / (\sum n_{i(t+1)d(t)} + \sum k(n_{d(t)j(t-1)})) \qquad \text{(A3.3)}$$

where $n_{i(t+1)d(t)}$ is the observed number of contributions from a given dormant class to stage i at time t+1, and the summation in the denominator represents the (corrected) total count of individuals starting out in that dormant class at time t. This had the effect of increasing the total number of plants contributing to the dormant stages, while reducing, by a corresponding amount, the likelihood that an individual would survive dormancy. The degree of adjustment for a given dormant class was a direct function of the mortality rate in the stages potentially contributing to that class: if no deaths were recorded for a given stage in a given year, then no adjustment was made. This ensured that all rate corrections reflected actual census counts, and that live individuals were not discounted from the census arbitrarily. Because no records of past dormancy existed for the first transition, this retrospective approach was only suited to estimating transition probabilities for the last three time intervals (1997-98, 1998-99, and 1999-00). The

means of these values were used to estimate the corresponding matrix coefficients for 1996-97.

Randomisation tests

The goal of the randomisation tests was to determine whether the observed assortment of demographic plots into populations, microsite types, or density classes produced an observed difference ($\Delta\lambda$) in growth rate (or in any other relevant demographic property) greater than what would be expected from simply observing random subsets of the entire population. The null hypothesis was that the life history events occurring at each plot are independent of the plot group to which it belongs. As test statistics I used the standard deviations SD(λ), SD(**w**), and SD(**v**). The distribution of each test statistic θ under the null hypothesis was obtained by permuting plots--with their full contingent of individual plant histories--among groups, maintaining the sample sizes for each group. Due to the impracticality of examining every permutation, the total number of which is vast, I used a random sample of 2000 permutations. For each permutation of the data I calculated a new matrix model and associated set of demographic parameters, and then calculated θ. The fraction of these permutations in which θ exceeded the observed value of the test statistic represented the probability of obtaining such a large deviation, under the null hypothesis.

Appendix 3.2 Transition matrices

Table A3.2 Annual stage-based transition matrices with their right (w) and left (v) eigenvectors for a) populations NS, ES, WS; b) microsite types A, B, C, D; and c) densities classes Low, Med-low, Med-high, High, for the transition periods 1996-97, 1997-98, 1998-99, 1999-00. Stage classes reflect plant size and/or demographic state (Table 2). Bolded entries are the fecundity terms; other values represent transition probabilities between stages. **w** and **v** represent the projected stable stage distribution and reproductive values, respectively.

a) **Site NS**

Stage	Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1996-97													
Sd	0	0	0	0	**1.0157**	**1.2061**	**2.6109**	0	0	0	0	0.2325	1.0000
J1	0.5209	0.1429	0.0123	0	0	0	0	0	0.0972	0.0092	0.0010	0.1501	1.9793
J2	0	0.4643	0.3086	0.0448	0.0010	0.0010	0.0010	0.0328	0.3174	0.1479	0.2435	0.1590	2.2370
R1	0	0.0357	0.3457	0.1045	0.1053	0.0500	0.0595	0.0492	0.0443	0.1383	0.0403	0.0886	2.4363
R2	0	0	0.0123	0.0597	0.1579	0.0333	0.0476	0.0902	0.0010	0.0350	0.0673	0.0249	4.4877
R3	0	0	0.0370	0.0746	0.2105	0.3167	0.1310	0.2213	0.0010	0.0433	0.0673	0.0656	4.2719
R4	0	0	0	0.0448	0.2105	0.1500	0.3571	0.1639	0.0010	0.0177	0.0010	0.0518	5.9265
V	0	0	0.0988	0.3582	0.1053	0.1167	0.0952	0.2213	0.0667	0.1817	0.2508	0.0935	3.3084
DJ	0	0.3250	0.1074	0	0.0000	0.0000	0	0	0.3908	0.0000	0	0.1028	1.9457
DR	0	0	0	0.0552	0.0684	0.1367	0.0679	0	0	0.2331	0	0.0239	2.1732
DV	0	0	0	0	0	0	0	0.0689	0	0	0.1622	0.0074	2.3826
1997-98													
Sd	0	0	0	0	**0**	**0.5978**	**1.2767**	0	0	0	0	0.0564	1.0000
J1	0.3544	0.2000	0.0532	0	0	0	0.0143	0	0.0926	0.0010	0.0010	0.0687	2.5534
J2	0	0.4000	0.4787	0.1029	0.0690	0.0390	0.0429	0.0879	0.1852	0.0010	0.1190	0.2221	2.8112
R1	0	0.0286	0.1383	0.3235	0.0690	0.0519	0.0143	0.0330	0.0010	0.0529	0.1190	0.0890	2.4476
R2	0	0	0.0010	0.0010	0.1379	0.0909	0.1000	0.0659	0.0010	0.0529	0.0010	0.0303	2.7258
R3	0	0	0.0106	0.0735	0.0690	0.1688	0.1714	0.2198	0.0010	0.0010	0.0010	0.0721	3.1841
R4	0	0	0	0.0010	0.0010	0.0010	0.1714	0.0220	0.0010	0.0010	0.0010	0.0062	4.4223
V	0	0	0.0957	0.2500	0.4483	0.3506	0.3143	0.3407	0.0010	0.2116	0.2381	0.1855	2.6745
DJ	0	0.2014	0.1434	0	0	0	0	0	0.6481	0	0	0.1779	3.0076
DR	0	0	0	0.1265	0.1724	0.1805	0.0657	0	0	0.4233	0	0.0621	1.7703
DV	0	0	0	0	0	0	0	0.0879	0	0	0.3571	0.0298	2.3286

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1998-99													
Sd	0	0	0	0	**0.1329**	**0.5552**	**2.7636**	0	0	0	0	0.1709	1.0000
J1	0.6029	0.7756	0.0313	0.0179	0	0	0	0.0074	0.1522	0.0256	0.0010	0.3842	1.7704
J2	0	0.1154	0.5234	0.1786	0.0010	0.0179	0.0010	0.0444	0.5328	0.1279	0.3000	0.1320	3.6372
R1	0	0.0010	0.2188	0.3929	0.0385	0.0010	0.0667	0.0593	0.0381	0.2046	0.0010	0.0578	4.8528
R2	0	0	0.0078	0.0357	0.1923	0.0714	0.2000	0.1185	0.0010	0.0512	0.2000	0.0309	6.1665
R3	0	0	0.0078	0.1786	0.3462	0.4643	0.2000	0.2815	0.0010	0.1279	0.2000	0.0842	6.9444
R4	0	0	0.0000	0.0179	0.2308	0.2679	0.2667	0.1111	0.0010	0.0512	0.0010	0.0476	8.5844
V	0	0	0.0859	0.1429	0.1154	0.1429	0.2000	0.3111	0.1522	0.3325	0.2000	0.0654	5.6461
DJ	0	0.0276	0.0820	0	0	0	0.0000	0	0.0881	0	0	0.0219	3.3426
DR	0	0	0	0.0357	0.0077	0.0036	0.0067	0	0	0.0272	0	0.0028	4.8285
DV	0	0	0	0	0	0	0	0.0370	0	0	0.0010	0.0023	4.5551
1999-00													
Sd	0	0	0	0	**0**	**0.3660**	**0.9681**	0	0	0	0	0.0518	1.0000
J1	0.6053	0.5720	0.0066	0	0	0	0	0	0.0469	0.0010	0.0010	0.1250	1.4839
J2	0	0.2288	0.5166	0.1039	0.0286	0.0319	0.0010	0.0309	0.2343	0.3148	0.3114	0.2755	1.4074
R1	0	0.0010	0.1060	0.2857	0.0571	0.1596	0.0682	0.0412	0.0937	0.1574	0.0010	0.1167	1.5430
R2	0	0	0.0010	0.0390	0.1714	0.1596	0.0682	0.1753	0.0010	0.0010	0.0010	0.0415	1.9982
R3	0	0	0.0066	0.1169	0.3143	0.2660	0.3636	0.1959	0.0010	0.0010	0.0010	0.0769	2.2952
R4	0	0	0	0.0010	0.0571	0.0745	0.2045	0.0722	0.0010	0.0010	0.0010	0.0190	3.2278
V	0	0	0.0265	0.1299	0.1714	0.0745	0.0682	0.1649	0.0469	0.0010	0.3114	0.0660	1.8435
DJ	0	0.1162	0.2157	0	0	0	0	0	0.4361	0	0	0.1600	1.3802
DR	0	0	0	0.1958	0.0950	0.0907	0.0630	0	0	0.2488	0	0.0538	1.0729
DV	0	0	0	0	0	0	0	0.1593	0	0	0.1286	0.0137	1.3292

a) **Site ES**

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1996-97													
Sd	0	0	0	0	**0.2324**	**0.4613**	**1.2880**	0	0	0	0	0.2018	1.0000
J1	0.4817	0.1429	0.0213	0	0	0	0	0	0.0972	0.0092	0.0010	0.1221	2.1857
J2	0	0.4643	0.2979	0.0968	0.0010	0.0010	0.0010	0.0196	0.3174	0.1479	0.2435	0.1359	2.5656
R1	0	0.0357	0.2128	0.2258	0.0010	0.0494	0.0238	0.0294	0.0443	0.1383	0.0403	0.0602	2.9761
R2	0	0	0.0213	0.0968	0.0952	0.1728	0.1190	0.0980	0.0010	0.0350	0.0673	0.0505	4.0062
R3	0	0	0.0638	0.0645	0.2381	0.2346	0.1825	0.2549	0.0010	0.0433	0.0673	0.0873	3.8582
R4	0	0	0.0000	0.0645	0.3810	0.2222	0.4921	0.2941	0.0010	0.0177	0.0010	0.1245	5.2016
V	0	0	0.1064	0.3226	0.1905	0.1728	0.0952	0.1765	0.0667	0.1817	0.2508	0.0919	3.5525
DJ	0	0.3250	0.2574	0	0	0	0	0	0.3908	0.0000	0	0.1128	2.1277
DR	0	0	0	0.0419	0.0095	0.0370	0.0159	0	0	0.2331	0	0.0100	2.2641
DV	0	0	0	0	0	0	0	0.0284	0	0	0.1622	0.0029	2.4390
1997-98													
Sd	0	0	0	0	**0.0184**	**0.1387**	**0.3452**	0	0	0	0	0.0076	1.0000
J1	0.2244	0.5000	0.0233	0.0270	0	0	0	0	0.0010	0.0010	0.0010	0.0324	4.1299
J2	0	0.2000	0.5349	0.1351	0.0213	0.0116	0.0156	0.0123	0.5634	0.1538	0.0010	0.4390	4.1390
R1	0	0.2000	0.0233	0.3784	0.0213	0.0814	0.0156	0.1111	0.0010	0.1538	0.0010	0.0591	2.3446
R2	0	0	0.0010	0.0010	0.2128	0.1628	0.1563	0.1111	0.0010	0.0010	0.0010	0.0234	2.1193
R3	0	0	0.0233	0.0541	0.1064	0.0465	0.2031	0.1728	0.0010	0.0010	0.0010	0.0359	2.1866
R4	0	0	0	0.0010	0.0426	0.0116	0.1250	0.0247	0.0010	0.0010	0.0010	0.0048	2.5482
V	0	0	0.0010	0.1622	0.4043	0.4651	0.3516	0.3333	0.0010	0.1538	0.3448	0.0836	2.0354
DJ	0	0.1000	0.3042	0	0	0	0	0	0.4225	0	0	0.2713	4.6555
DR	0	0	0	0.0946	0.1128	0.1319	0.0617	0	0	0.1538	0	0.0172	1.7100
DV	0	0	0	0	0	0	0	0.1778	0	0	0.3448	0.0256	1.2362

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1998-99													
Sd	0	0	0	0	**0.0785**	**0.9595**	**1.1880**	0	0	0	0	0.2242	1.0000
J1	0.5263	0.6333	0.0536	0.0526	0	0.0192	0	0	0.1035	0.0709	0.0010	0.3614	1.8782
J2	0	0.0667	0.3393	0.0526	0.0189	0.0192	0.0010	0.0935	0.6210	0.1063	0.1493	0.0688	5.4984
R1	0	0.0010	0.3214	0.2632	0.0010	0.0192	0.0010	0.0791	0.1035	0.0354	0.2239	0.0420	7.0534
R2	0	0	0.0357	0.1316	0.1509	0.0577	0.0010	0.1367	0.0010	0.1063	0.0010	0.0258	7.2969
R3	0	0.0167	0.0357	0.1842	0.2642	0.4038	0.2381	0.3381	0.0010	0.2481	0.2239	0.1092	8.4232
R4	0	0	0	0.0263	0.2830	0.3077	0.4762	0.1295	0.0010	0.1772	0.0010	0.0967	7.8341
V	0	0	0.0536	0.2105	0.1321	0.1154	0.0952	0.1439	0.0010	0.1063	0.2239	0.0459	7.0937
DJ	0	0.0283	0.0482	0	0	0	0	0	0.1798	0	0	0.0168	5.4028
DR	0	0	0	0.0789	0.0830	0.0058	0.0190	0	0	0.0753	0	0.0087	6.5437
DV	0	0	0	0	0	0	0	0.0079	0	0	0.1990	0.0005	7.4611
1999-00													
Sd	0	0	0	0	**0.0281**	**0.4065**	**0.9362**	0	0	0	0	0.0826	1.0000
J1	0.6944	0.5326	0.0010	0	0	0	0	0	0.0010	0.1995	0.2428	0.1463	1.4113
J2	0	0.2826	0.6076	0.1111	0.0238	0.0435	0.0147	0.0179	0.2682	0.0010	0.0010	0.2242	1.5798
R1	0	0.0010	0.1519	0.4444	0.1190	0.1130	0.0588	0.1429	0.2682	0.0010	0.0010	0.1573	1.6108
R2	0	0	0.0127	0.0370	0.2619	0.1043	0.1765	0.1607	0.1341	0.0010	0.0010	0.0662	1.9678
R3	0	0	0.0253	0.1111	0.2857	0.2957	0.2941	0.2143	0.0010	0.0997	0.0010	0.1071	2.3344
R4	0	0	0	0.0185	0.0476	0.1130	0.2353	0.0893	0.0010	0.0997	0.0010	0.0380	3.1740
V	0	0	0.0380	0.0926	0.1429	0.1565	0.1324	0.1964	0.0010	0.1995	0.2428	0.0794	1.8340
DJ	0	0.1092	0.1124	0	0	0.0000	0	0	0.3081	0	0	0.0613	1.6792
DR	0	0	0	0.0870	0.0521	0.0614	0.0228	0	0	0.1526	0	0.0297	1.4524
DV	0	0	0	0	0	0	0	0.0623	0	0	0.3497	0.0079	1.2671

a) **Site WS**

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1996-97													
Sd	0	0	0	0	**0.4294**	**0.7580**	**1.3496**	0	0	0	0	0.1641	1.0000
J1	0.5990	0.1429	0.0172	0	0	0	0	0	0.0972	0.0092	0.0010	0.1206	1.7830
J2	0	0.4643	0.2414	0.0896	0.0010	0.0548	0.0135	0.0353	0.3174	0.1479	0.2435	0.1414	2.1502
R1	0	0.0357	0.3103	0.3284	0.1364	0.1370	0.0676	0.0706	0.0443	0.1383	0.0403	0.1178	2.5978
R2	0	0	0.0010	0.0448	0.2727	0.0822	0.0405	0.0941	0.0010	0.0350	0.0673	0.0358	3.0208
R3	0	0	0.0345	0.1642	0.1364	0.2603	0.2568	0.2118	0.0010	0.0433	0.0673	0.0911	3.4233
R4	0	0	0.0172	0.0896	0.0455	0.1644	0.2838	0.1882	0.0010	0.0177	0.0010	0.0673	4.1777
V	0	0	0.1207	0.2090	0.3182	0.1781	0.1892	0.2706	0.0667	0.1817	0.2508	0.1202	2.7311
DJ	0	0.3250	0.2431	0	0	0	0.0000	0	0.3908	0	0	0.1086	1.7183
DR	0	0	0	0.0478	0.0500	0.0616	0.1122	0	0	0.2331	0	0.0247	1.8180
DV	0	0	0	0	0	0	0.0000	0.0635	0	0	0.1622	0.0084	1.9352
1997-98													
Sd	0	0	0	0	**0.2899**	**0.5828**	**0.8792**	0	0	0	0	0.0292	1.0000
J1	0.4819	0.4444	0.0154	0.0123	0	0.0135	0	0.0109	0.0010	0.0010	0.0010	0.0448	1.8529
J2	0	0.4444	0.3846	0.1481	0.0385	0.0946	0.0010	0.0435	0.3960	0.0585	0.0010	0.1538	1.8062
R1	0	0	0.1077	0.2222	0.0385	0.0541	0.0500	0.0652	0.0010	0.0585	0.0010	0.0530	1.8551
R2	0	0	0.0010	0.0123	0.0769	0.0270	0.0833	0.0217	0.0010	0.0010	0.0010	0.0088	2.3481
R3	0	0	0.0010	0.0247	0.0010	0.1216	0.1333	0.0761	0.0010	0.0010	0.0010	0.0241	2.5570
R4	0	0	0.0000	0.0123	0.0010	0.0135	0.1500	0.0326	0.0010	0.0010	0.0010	0.0108	3.4209
V	0	0	0.0308	0.0988	0.3462	0.1757	0.2167	0.3261	0.1485	0.3509	0.1852	0.2003	2.2880
DJ	0	0.0111	0.2577	0	0.0000	0	0	0	0.4455	0	0	0.0897	2.3850
DR	0	0	0	0.2457	0.2846	0.2408	0.2217	0	0	0.4678	0	0.0558	2.4158
DV	0	0	0	0	0	0	0	0.2506	0	0	0.7407	0.3297	2.8740

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1998-99													
Sd	0	0	0	0	**0.3578**	**0.7952**	**3.3739**	0	0	0	0	0.2346	1.0000
J1	0.5481	0.6731	0.0438	0	0	0	0.1429	0.0104	0.1923	0.0453	0.0402	0.3672	1.9593
J2	0	0.1859	0.4672	0.1277	0.0833	0.0370	0.0010	0.0833	0.3461	0.3173	0.2411	0.1484	3.6099
R1	0	0.0064	0.2044	0.2340	0.1667	0.1111	0.0010	0.0625	0.0769	0.1662	0.2411	0.0563	5.2596
R2	0	0.0064	0.0073	0.0426	0.0010	0.1852	0.0010	0.0833	0.0769	0.0453	0.0010	0.0191	5.7096
R3	0	0	0.0511	0.2128	0.2500	0.1852	0.2857	0.1979	0.0010	0.0907	0.1608	0.0556	6.8253
R4	0	0	0.0146	0.1489	0.3333	0.3333	0.3571	0.1979	0.0010	0.0453	0.0010	0.0596	8.4257
V	0	0	0.0657	0.1702	0.0010	0.0741	0.0714	0.1771	0.1154	0.1511	0.2411	0.0348	5.0402
DJ	0	0.0128	0.0540	0	0	0	0	0	0.1781	0	0	0.0142	3.4232
DR	0	0	0	0.0351	0.0167	0.0741	0.0143	0	0	0.0964	0	0.0074	4.2251
DV	0	0	0	0	0	0	0	0.0844	0	0	0.0536	0.0029	4.4537
1999-00													
Sd	0	0	0	0	**0.0463**	**0.4074**	**0.9070**	0	0	0	0	0.1238	1.0000
J1	0.7671	0.4435	0.0131	0	0	0	0	0	0.0010	0.0010	0.0010	0.1719	1.3172
J2	0	0.3435	0.4641	0.0676	0.0010	0.0500	0.0010	0.0152	0.3717	0.2274	0.1543	0.1866	1.6948
R1	0	0.0043	0.2026	0.2838	0.0833	0.0667	0.0010	0.0152	0.1858	0.0758	0.0010	0.0905	2.2122
R2	0	0.0043	0.0065	0.0405	0.1250	0.1500	0.1429	0.1515	0.0010	0.0758	0.0010	0.0556	1.8947
R3	0	0.0087	0.0196	0.2432	0.2917	0.4000	0.2857	0.2727	0.0010	0.0758	0.0771	0.1390	2.5907
R4	0	0	0.0131	0.0676	0.0833	0.0500	0.5102	0.1667	0.0010	0.1516	0.0010	0.0726	4.0300
V	0	0	0.0523	0.1486	0.0010	0.1500	0.0204	0.1970	0.0929	0.0010	0.0771	0.0627	2.2316
DJ	0	0.0692	0.1269	0	0	0	0	0	0.3106	0	0	0.0508	1.7979
DR	0	0	0	0.0856	0.1653	0.0571	0.0229	0	0	0.3017	0	0.0375	2.1269
DV	0	0	0	0	0	0	0	0.0725	0	0	0.4979	0.0089	1.2543

Table A3.2, continued: Annual stage-based projection matrices with their right (w) and left (v) eigenvectors for a) populations NS, ES, WS; b) microsite types A, B, C, D; and c) densities classes Low, Med-low, Med-high, High, for the transition periods 1996-97, 1997-98, 1998-99, 1999-00. Stage classes reflect plant size and/or demographic state (Table 2). Bolded entries are the fecundity terms; other values represent transition probabilities between stages. w and v represent the projected stable stage distribution and reproductive values, respectively.

b) Microsite A

	Stage												
Stage	Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1996-97													
Sd	0	0	0	0	**0.6105**	**0.9158**	**1.3461**	0	0	0	0	0.2093	1.0000
J1	0.5091	0.1429	0.0175	0	0	0	0	0	0.0972	0.0092	0.0010	0.1319	2.0633
J2	0	0.4643	0.3158	0.1026	0.0010	0.0010	0.0010	0.0341	0.3174	0.1479	0.2435	0.1499	2.4458
R1	0	0.0357	0.2281	0.1795	0.0010	0.0526	0.0488	0.0795	0.0443	0.1383	0.0403	0.0719	2.3765
R2	0	0	0.0175	0.1026	0.2667	0.1404	0.1098	0.1136	0.0010	0.0350	0.0673	0.0527	4.1272
R3	0	0	0.0702	0.0513	0.2000	0.3158	0.2073	0.2500	0.0010	0.0433	0.0673	0.0857	4.3541
R4	0	0	0	0.0513	0.2667	0.2105	0.4024	0.2045	0.0010	0.0177	0.0010	0.0812	5.0575
V	0	0	0.1404	0.2051	0.0667	0.0877	0.0976	0.1932	0.0667	0.1817	0.2508	0.0792	3.4329
DJ	0	0.3250	0.1789	0	0	0	0	0	0.3908	0	0	0.1056	2.0076
DR	0	0	0	0.0974	0.0800	0.0982	0.0573	0	0	0.2331	0	0.0297	2.1476
DV	0	0	0	0	0	0	0	0.0330	0	0	0.1622	0.0029	2.3978
1997-98													
Sd	0	0	0	0	**0.0338**	**0.2314**	**0.5063**	0	0	0	0	0.0138	1.0000
J1	0.2126	0.2500	0.0010	0.0213	0	0	0.0139	0	0.0699	0.0010	0.0010	0.0219	4.1801
J2	0	0.3750	0.5333	0.0851	0.0256	0.0286	0.0139	0.0545	0.4895	0.0010	0.0010	0.2599	3.9625
R1	0	0.0010	0.0889	0.4043	0.0513	0.0571	0.0139	0.0364	0.0010	0.0654	0.0010	0.0856	2.4284
R2	0	0	0.0010	0.0010	0.2051	0.1857	0.1944	0.0909	0.0010	0.0010	0.0010	0.0448	2.7008
R3	0	0	0.0010	0.0213	0.0513	0.0857	0.0694	0.1091	0.0010	0.0010	0.0010	0.0391	2.7399
R4	0	0	0	0.0010	0.0256	0.0286	0.0417	0.0010	0.0010	0.0010	0.0010	0.0034	3.0263
V	0	0	0.0222	0.1915	0.4359	0.4286	0.4028	0.3818	0.1399	0.1961	0.3448	0.2426	2.2763
DJ	0	0.2812	0.2694	0	0	0	0	0	0.2797	0	0	0.1250	4.2046
DR	0	0	0	0.1213	0.1821	0.0743	0.1347	0	0	0.5882	0	0.0728	2.0678
DV	0	0	0	0	0	0	0	0.2046	0	0	0.3448	0.0912	1.4778

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1998-99													
Sd	0	0	0	0	**0**	**0**	**12.0000**	0	0	0	0	0.3674	1.0000
J1	0.6481	0.7091	0.0339	0	0	0	0	0	0.1713	0.0550	0.0010	0.4189	1.9897
J2	0	0.1091	0.4237	0.1026	0.0244	0.0010	0.0010	0.0672	0.6281	0.1100	0.2791	0.0687	6.0712
R1	0	0.0010	0.3051	0.3333	0.0010	0.0010	0.0010	0.0840	0.0010	0.1375	0.0930	0.0239	9.1733
R2	0	0	0.0339	0.0256	0.0732	0.0476	0.0010	0.1176	0.0571	0.0275	0.0010	0.0064	14.4730
R3	0	0.0182	0.0339	0.2051	0.3902	0.4762	0.3333	0.3193	0.0010	0.2200	0.1861	0.0436	16.3594
R4	0	0	0	0.0513	0.3171	0.4286	0.6667	0.1681	0.0010	0.1650	0.0010	0.0395	28.1008
V	0	0	0.1017	0.2564	0.1220	0.0476	0.0010	0.1597	0.0571	0.1925	0.3721	0.0151	11.5253
DJ	0	0.0400	0.0373	0	0	0	0	0	0.0661	0	0	0.0158	4.6523
DR	0	0	0	0.0026	0.0732	0.0010	0.0010	0	0	0.0292	0	0.0005	10.2271
DV	0	0	0	0	0	0	0	0.0252	0	0	0.0010	0.0003	7.7019
1999-00													
Sd	0	0	0	0	**0.0609**	**0.4962**	**1.0514**	0	0	0	0	0.0612	1.0000
J1	0.6667	0.6604	0.0010	0	0	0	0	0	0.0010	0.1353	0.0010	0.1690	1.4077
J2	0	0.1887	0.5256	0.0909	0.0010	0.0652	0.0182	0.0351	0.5281	0.1353	0.5031	0.2573	1.3222
R1	0	0.0010	0.1538	0.4182	0.1200	0.1413	0.0545	0.1228	0.0010	0.0010	0.0010	0.1348	1.0991
R2	0	0	0.0010	0.0364	0.1600	0.1739	0.1636	0.1228	0.2641	0.0010	0.0010	0.0673	1.6288
R3	0	0	0.0128	0.0909	0.3200	0.2391	0.3091	0.1754	0.0010	0.0010	0.0010	0.0798	2.0287
R4	0	0	0	0.0010	0.0010	0.0435	0.2000	0.0702	0.0010	0.0010	0.0010	0.0131	3.0443
V	0	0	0.0641	0.0909	0.2000	0.1522	0.1273	0.1930	0.0010	0.1353	0.0010	0.0831	1.4039
DJ	0	0.0958	0.1752	0	0	0	0.0000	0	0.1653	0	0	0.0792	1.4710
DR	0	0	0	0.0837	0.1525	0.0560	0.0438	0	0	0.3248	0	0.0433	0.9242
DV	0	0	0	0	0	0	0	0.1143	0	0	0.1308	0.0118	0.8367

b) **Microsite B**

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1996-97													
Sd	0	0	0	0	**0.4274**	**0.4662**	**1.1886**	0	0	0	0	0.1596	1.0000
J1	0.4868	0.1429	0.0010	0	0	0	0	0	0.0972	0.0092	0.0010	0.1073	2.0962
J2	0	0.4643	0.2963	0.1212	0.0010	0.0465	0.0010	0.0411	0.3174	0.1479	0.2435	0.1721	2.3254
R1	0	0.0357	0.2593	0.3030	0.2500	0.0698	0.0010	0.0137	0.0443	0.1383	0.0403	0.0960	2.8654
R2	0	0	0.0010	0.0010	0.1250	0.0698	0.0635	0.0822	0.0010	0.0350	0.0673	0.0221	3.3095
R3	0	0	0.0010	0.1515	0.0010	0.2093	0.1587	0.2055	0.0010	0.0433	0.0673	0.0629	3.2706
R4	0	0	0.0000	0.0909	0.2500	0.2326	0.4921	0.2877	0.0010	0.0177	0.0010	0.1045	4.2383
V	0	0	0.0370	0.3030	0.2500	0.1860	0.0794	0.1781	0.0667	0.1817	0.2508	0.0902	2.9152
DJ	0	0.3250	0.4074	0	0	0	0	0	0.3908	0	0	0.1668	2.0234
DR	0	0	0	0.0030	0.0125	0.0581	0.0413	0	0	0.2331	0	0.0108	2.0597
DV	0	0	0	0	0	0	0	0.0726	0	0	0.1622	0.0076	2.1696
1997-98													
Sd	0	0	0	0	**0**	**0.1989**	**0.5579**	0	0	0	0	0.0072	1.0000
J1	0.2800	0.2222	0.0303	0	0	0	0	0	0.0010	0.0010	0.0010	0.0163	3.2763
J2	0	0.5556	0.4545	0.1875	0.0010	0.0010	0.0010	0.0400	0.2290	0.0010	0.0010	0.2901	3.0240
R1	0	0.0010	0.0303	0.2188	0.0010	0.0667	0.0286	0.0600	0.0010	0.0010	0.1887	0.0262	1.3852
R2	0	0	0.0010	0.0010	0.1875	0.1111	0.1143	0.0400	0.0010	0.0010	0.0010	0.0093	1.2982
R3	0	0	0.0303	0.0313	0.1250	0.0889	0.2571	0.1800	0.0010	0.0010	0.0010	0.0283	1.4583
R4	0	0	0	0.0010	0.0625	0.0010	0.1857	0.0010	0.0010	0.0010	0.0010	0.0017	2.0802
V	0	0	0.0010	0.1250	0.3750	0.3778	0.2714	0.3800	0.0010	0.3774	0.3774	0.0647	1.3451
DJ	0	0.1305	0.2653	0	0	0	0	0	0.7634	0	0	0.5136	4.5671
DR	0	0	0	0.1906	0.1313	0.2694	0.0343	0	0	0.3774	0	0.0257	0.9632
DV	0	0	0	0	0	0	0	0.1400	0	0	0.3774	0.0168	1.4446

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1998-99													
Sd	0	0	0	0	**0.1306**	**0.9139**	**0.7833**	0	0	0	0	0.1328	1.0000
J1	0.5208	0.7619	0.0217	0.0556	0	0	0	0	0.1966	0.0806	0.0010	0.3687	1.8782
J2	0	0.1429	0.3696	0.1667	0.0010	0.0010	0.0010	0.0676	0.5408	0.0806	0.3333	0.1316	2.6476
R1	0	0.0010	0.3261	0.1667	0.0010	0.0556	0.0667	0.0676	0.0983	0.2419	0.1111	0.0738	3.0064
R2	0	0	0.0217	0.2778	0.2778	0.1111	0.0010	0.1351	0.0010	0.1209	0.1111	0.0574	2.9392
R3	0	0	0.0010	0.1111	0.1111	0.3333	0.1333	0.2162	0.0010	0.0806	0.1111	0.0630	4.8425
R4	0	0	0.0000	0.0010	0.2222	0.3333	0.5333	0.0405	0.0010	0.0806	0.0010	0.0828	4.2825
V	0	0	0.0870	0.1667	0.1111	0.0833	0.0667	0.2838	0.1475	0.2015	0.2222	0.0649	3.1078
DJ	0	0.0095	0.0957	0	0	0	0	0	0.0010	0	0	0.0165	2.6270
DR	0	0	0	0.0056	0.0278	0.0083	0.0200	0	0	0.0857	0	0.0047	3.1477
DV	0	0	0	0	0	0	0	0.0473	0	0	0.1481	0.0037	3.3466
1999-00													
Sd	0	0	0	0	**0**	**0.3582**	**1.1416**	0	0	0	0	0.0873	1.0000
J1	0.6596	0.4557	0.0010	0	0	0	0	0	0.0010	0.0010	0.0010	0.1216	1.4138
J2	0	0.2658	0.5625	0.0811	0.0010	0.0263	0.0010	0.0010	0.1857	0.0010	0.0010	0.1767	1.7976
R1	0	0.0010	0.0625	0.4054	0.1379	0.1316	0.0323	0.0435	0.1857	0.0010	0.0010	0.1209	2.6737
R2	0	0	0.0156	0.0541	0.2759	0.1053	0.1290	0.1087	0.0010	0.2647	0.0010	0.0733	3.9306
R3	0	0	0.0010	0.1081	0.4138	0.3684	0.3871	0.2826	0.0010	0.0010	0.0010	0.1398	4.2866
R4	0	0	0	0.0010	0.0345	0.1053	0.2258	0.0217	0.0010	0.0010	0.0010	0.0275	5.5322
V	0	0	0.0156	0.0541	0.0345	0.1053	0.0968	0.3043	0.0010	0.2647	0.6916	0.0867	4.0510
DJ	0	0.1415	0.2688	0	0	0	0	0	0.3111	0	0	0.1041	1.3676
DR	0	0	0	0.1062	0.0310	0.0696	0.0355	0	0	0.3101	0	0.0415	3.4201
DV	0	0	0	0	0	0	0	0.1524	0	0	0.2882	0.0205	4.3795

c) **Microsite C**

Stage	Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1996-97													
Sd	0	0	0	0	**0.7612**	**1.2626**	**2.7731**	0	0	0	0	0.2319	1.0000
J1	0.5507	0.1429	0.0213	0	0	0	0	0	0.0972	0.0092	0.0010	0.1580	1.9048
J2	0	0.4643	0.2128	0.0600	0.0010	0.0500	0.0010	0.0141	0.3174	0.1479	0.2435	0.1504	2.1967
R1	0	0.0357	0.3191	0.1400	0.1176	0.1000	0.0714	0.0282	0.0443	0.1383	0.0403	0.0857	2.6335
R2	0	0	0.0213	0.1000	0.2353	0.1000	0.0714	0.1268	0.0010	0.0350	0.0673	0.0396	3.5266
R3	0	0	0.0426	0.1200	0.2353	0.1500	0.1071	0.1831	0.0010	0.0433	0.0673	0.0531	3.8511
R4	0	0	0.0213	0.0800	0.0588	0.1500	0.2857	0.2394	0.0010	0.0177	0.0010	0.0527	5.5820
V	0	0	0.0638	0.2800	0.1176	0.1250	0.1250	0.2535	0.0667	0.1817	0.2508	0.0809	3.4086
DJ	0	0.3250	0.2021	0	0	0	0	0	0.3908	0	0	0.1242	1.8830
DR	0	0	0	0.0220	0.0765	0.1000	0.0982	0	0	0.2331	0	0.0189	2.1020
DV	0	0	0	0	0	0	0	0.0521	0	0	0.1622	0.0048	2.2553
1997-98													
Sd	0	0	0	0	**0.2661**	**0.5914**	**0.9124**	0	0	0	0	0.0508	1.0000
J1	0.4455	0.2778	0.0741	0	0	0	0	0	0.0010	0.0010	0.0010	0.0527	2.0128
J2	0	0.3889	0.4444	0.1064	0.0357	0.0732	0.0204	0.0152	0.3125	0.0840	0.0010	0.1290	2.3872
R1	0	0.0556	0.1852	0.3404	0.0714	0.0244	0.0010	0.0455	0.0010	0.0010	0.0010	0.0685	1.9648
R2	0	0	0.0010	0.0010	0.1429	0.0976	0.1429	0.0758	0.0010	0.0840	0.0010	0.0306	2.0980
R3	0	0	0.0010	0.0638	0.0357	0.1707	0.2245	0.1970	0.0010	0.0010	0.0010	0.0540	2.6197
R4	0	0	0	0.0213	0.0010	0.0010	0.1633	0.0152	0.0010	0.0010	0.0010	0.0060	3.5633
V	0	0	0.1111	0.1915	0.3929	0.2927	0.3469	0.4242	0.1042	0.2521	0.0010	0.1613	1.8824
DJ	0	0.0819	0.1388	0	0	0	0	0	0.5208	0	0	0.0592	2.5397
DR	0	0	0	0.1745	0.1893	0.2457	0.0816	0	0	0.2521	0	0.0489	1.3369
DV	0	0	0	0	0	0	0	0.1803	0	0	0.8108	0.3390	0.1926

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1998-99													
Sd	0	0	0	0	**0**	**0.7813**	**1.6875**	0	0	0	0	0.1793	1.0000
J1	0.5844	0.7273	0.0375	0	0	0	0.1000	0.0109	0.0744	0.0010	0.0010	0.3645	1.8014
J2	0	0.1515	0.5125	0.1579	0.0010	0.0010	0.0010	0.0978	0.3718	0.1676	0.0756	0.1382	3.3651
R1	0	0.0010	0.1875	0.2632	0.0010	0.0010	0.0010	0.0543	0.0744	0.1676	0.2267	0.0408	4.0992
R2	0	0	0.0125	0.0263	0.1429	0.1111	0.2000	0.1413	0.0744	0.1006	0.0010	0.0394	4.0771
R3	0	0	0.0625	0.2105	0.3810	0.4167	0.2000	0.2500	0.0010	0.1341	0.3023	0.0936	5.2355
R4	0	0	0.0250	0.1316	0.3333	0.3056	0.2000	0.1522	0.0010	0.0671	0.0010	0.0685	4.9466
V	0	0	0.0750	0.1842	0.0010	0.0833	0.1000	0.2283	0.2231	0.2682	0.3778	0.0478	4.0378
DJ	0	0.0220	0.0538	0	0	0	0	0	0.1722	0	0	0.0175	3.2980
DR	0	0	0	0.0263	0.0143	0.0625	0.0200	0	0	0.0713	0	0.0090	3.8514
DV	0	0	0	0	0	0	0	0.0293	0	0	0.0010	0.0013	4.0908
1999-00													
Sd	0	0	0	0	**0**	**0.2867**	**0.7060**	0	0	0	0	0.0651	1.0000
J1	0.6222	0.5723	0.0101	0	0	0	0	0	0.1104	0.0010	0.0010	0.1298	1.5472
J2	0	0.3253	0.5657	0.1778	0.0333	0.0417	0.0010	0.0333	0.3313	0.2870	0.0010	0.2727	1.6025
R1	0	0.0010	0.1717	0.2222	0.0333	0.1389	0.0465	0.0500	0.1104	0.0010	0.0010	0.1063	1.6729
R2	0	0	0.0010	0.0444	0.2333	0.0833	0.1628	0.2667	0.0010	0.0010	0.0010	0.0577	1.4873
R3	0	0.0060	0.0202	0.1556	0.2000	0.3472	0.3023	0.2000	0.0010	0.1435	0.4239	0.1205	2.0419
R4	0	0	0	0.0222	0.0333	0.0278	0.3488	0.1167	0.0010	0.1435	0.0010	0.0398	2.9635
V	0	0	0.0606	0.1556	0.1667	0.1389	0.0698	0.1500	0.0010	0.0010	0.0010	0.0767	1.7356
DJ	0	0.0445	0.1201	0	0	0	0	0	0.3829	0	0	0.0665	1.5432
DR	0	0	0	0.1422	0.1088	0.1357	0.0323	0	0	0.2434	0	0.0543	1.6469
DV	0	0	0	0	0	0	0	0.1021	0	0	0.2335	0.0107	1.2023

(B) **Microsite D**

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1996-97													
Sd	0	0	0	0	**0.3509**	**0.6259**	**1.6742**	0	0	0	0	0.1905	1.0000
J1	0.5309	0.1429	0.0182	0	0	0	0	0.0000	0.0972	0.0092	0.0010	0.1210	1.9916
J2	0	0.4643	0.3091	0.0233	0.0010	0.0010	0.0120	0.0260	0.3174	0.1479	0.2435	0.1230	2.3762
R1	0	0.0357	0.3818	0.2791	0.0455	0.0946	0.0602	0.0649	0.0443	0.1383	0.0403	0.1069	2.6868
R2	0	0	0.0010	0.0233	0.0909	0.0946	0.0602	0.0519	0.0010	0.0350	0.0673	0.0274	4.0400
R3	0	0	0.0364	0.1163	0.2273	0.3243	0.2410	0.2727	0.0010	0.0433	0.0673	0.1113	3.8329
R4	0	0	0	0.0465	0.2727	0.1486	0.3976	0.1299	0.0010	0.0177	0.0010	0.0730	5.4636
V	0	0	0.1455	0.3721	0.3636	0.2162	0.1687	0.2597	0.0667	0.1817	0.2508	0.1441	2.9306
DJ	0	0.3250	0.0764	0	0	0	0	0	0.3908	0	0	0.0731	1.9139
DR	0	0	0	0.0744	0.0010	0.0486	0.0386	0	0	0.2331	0	0.0197	2.0358
DV	0	0	0	0	0	0	0	0.0623	0	0	0.1622	0.0100	2.1888
1997-98													
Sd	0	0	0	0	**0.1972**	**0.5254**	**1.0623**	0	0	0	0	0.0414	1.0000
J1	0.3886	0.3929	0.0286	0.0167	0.0000	0.0123	0.0000	0.0108	0.0010	0.0010	0.0010	0.0623	2.2494
J2	0	0.3214	0.4286	0.1500	0.1053	0.0741	0.0448	0.0753	0.6024	0.1000	0.2083	0.3621	2.0246
R1	0	0.0714	0.0857	0.2000	0.0010	0.0864	0.0448	0.1075	0.0010	0.2000	0.0010	0.0932	1.9234
R2	0	0	0.0010	0.0167	0.0526	0.0123	0.0448	0.0538	0.0010	0.0010	0.0010	0.0115	2.2193
R3	0	0	0.0143	0.0667	0.1053	0.1111	0.1791	0.1398	0.0010	0.0010	0.0010	0.0410	2.4549
R4	0	0	0	0.0010	0.0010	0.0010	0.1940	0.0645	0.0010	0.0010	0.0010	0.0117	3.7754
V	0	0	0.0571	0.1500	0.3684	0.2593	0.2239	0.2151	0.0010	0.3000	0.2083	0.1166	2.1326
DJ	0	0.1223	0.2134	0.0000	0.0000	0	0	0	0.3614	0	0	0.1656	2.4077
DR	0	0	0	0.2000	0.1684	0.1947	0.1448	0	0	0.3000	0	0.0527	2.1556
DV	0	0	0	0	0	0	0	0.1646	0	0	0.4167	0.0420	1.9208

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1998-99													
Sd	0	0	0	0	**0.5152**	**0.4722**	**2.2368**	0	0	0	0	0.1581	1.0000
J1	0.5424	0.6783	0.0515	0.0435	0.0000	0.0238	0.0526	0.0118	0.1478	0.0470	0.0654	0.3312	1.8497
J2	0	0.1329	0.4926	0.1087	0.0909	0.0714	0.0010	0.0588	0.3942	0.4226	0.2614	0.1600	3.5101
R1	0	0.0070	0.1912	0.3696	0.2727	0.0476	0.0010	0.0588	0.0986	0.0939	0.2614	0.0830	5.2336
R2	0	0.0070	0.0010	0.0435	0.1818	0.0714	0.0526	0.0706	0.0010	0.0235	0.0654	0.0245	5.6930
R3	0	0	0.0221	0.1957	0.0010	0.3571	0.3158	0.3176	0.0010	0.0939	0.1307	0.0886	6.6019
R4	0	0	0	0.0435	0.0909	0.1905	0.2632	0.1765	0.0010	0.0010	0.0010	0.0466	8.1463
V	0	0	0.0515	0.0870	0.2727	0.2143	0.2105	0.2118	0.0010	0.1409	0.0010	0.0663	5.9788
DJ	0	0.0175	0.0713	0	0	0	0	0	0.3424	0	0	0.0260	3.3282
DR	0	0	0	0.1087	0.0091	0.0024	0.0105	0	0	0.0998	0	0.0110	4.0579
DV	0	0	0	0	0	0	0	0.0588	0	0	0.1743	0.0047	4.4104
1999-00													
Sd	0	0	0	0	**0.0548**	**0.3560**	**0.9019**	0.0000	0.0000	0.0000	0.0000	0.1490	1.0000
J1	0.6618	0.4106	0.0141	0.0000	0.0000	0.0000	0.0000	0.0000	0.0010	0.0867	0.1361	0.1769	1.5090
J2	0	0.3092	0.4507	0.0441	0.0588	0.0149	0.0010	0.0179	0.2822	0.1734	0.2721	0.1636	1.8035
R1	0	0.0048	0.1831	0.2794	0.0588	0.0597	0.0313	0.0179	0.2258	0.1734	0.0010	0.0902	2.6206
R2	0	0.0048	0.0070	0.0294	0.0588	0.1493	0.0625	0.1429	0.0010	0.0010	0.0010	0.0385	2.5286
R3	0	0.0048	0.0211	0.2500	0.2353	0.3284	0.2500	0.2500	0.0010	0.0867	0.0010	0.1175	3.1248
R4	0	0	0.0141	0.0735	0.2353	0.1940	0.5313	0.1964	0.0010	0.1734	0.0010	0.1162	4.4142
V	0	0	0.0211	0.1765	0.0588	0.0896	0.0010	0.1071	0.1129	0.0010	0.1361	0.0461	2.5027
DJ	0	0.1392	0.1385	0	0	0	0	0	0.3282	0	0	0.0705	2.0808
DR	0	0	0	0.0759	0.0580	0.0401	0.0561	0	0	0.1956	0	0.0253	2.4152
DV	0	0	0	0	0	0	0	0.0947	0	0	0.3009	0.0063	1.5039

Table A3.2, continued: Annual stage-based projection matrices with their right (w) and left (v) eigenvectors for a) populations NS, ES, WS; b) microsite types A, B, C, D; and c) densities classes Low, Med-low, Med-high, High, for the transition periods 1996-97, 1997-98, 1998-99, 1999-00. Stage classes reflect plant size and/or demographic state (Table 2). Bolded entries are the fecundity terms; other values represent transition probabilities between stages. w and v represent the projected stable stage distribution and reproductive values, respectively.

(C) **Low density**

Stage	Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1996-97													
Sd	0	0	0	0	**0.2313**	**1.0316**	**1.7633**	0	0	0	0	0.0631	1.0000
J1	0.5204	0.1429	0.0417	0	0	0	0	0	0.0972	0.0092	0.0010	0.1158	1.3092
J2	0	0.4643	0.3750	0.0010	0.0010	0.0200	0.0010	0.0010	0.3174	0.1479	0.2435	0.1687	1.2956
R1	0	0.0357	0.1250	0.2500	0.1538	0.0800	0.0291	0.0119	0.0443	0.1383	0.0403	0.1506	1.7180
R2	0	0	0.0010	0.0313	0.2308	0.1000	0.0874	0.0952	0.0010	0.0350	0.0673	0.0760	1.5510
R3	0	0	0.0010	0.1563	0.0769	0.2800	0.1553	0.2262	0.0010	0.0433	0.0673	0.1597	1.7899
R4	0	0	0.0417	0.0938	0.3846	0.2400	0.4854	0.3095	0.0010	0.0177	0.0010	0.0458	2.5561
V	0	0	0.2083	0.3438	0.0010	0.1400	0.0874	0.1667	0.0667	0.1817	0.2508	0.1090	1.5294
DJ	0	0.3250	0.2083	0	0	0	0	0	0.3908	0	0	0.0605	1.4375
DR	0	0	0	0.0375	0.0154	0.0320	0.0320	0	0	0.2331	0	0.0391	1.7502
DV	0	0	0	0	0	0	0	0.0548	0	0	0.1622	0.0116	1.0895
1997-98													
Sd	0	0	0	0	**0**	**0.4229**	**0.8360**	0.0000	0.0000	0.0000	0.0000	0.0591	1.0000
J1	0.4310	0.1905	0.0465	0.0313	0	0	0.0095	0	0.0010	0.0010	0.0010	0.0547	2.0998
J2	0	0.4286	0.5814	0.1563	0.0010	0.0161	0.0190	0.0156	0.2817	0.1587	0.0010	0.2174	2.2009
R1	0	0.0952	0.1395	0.1563	0.0370	0.0323	0.0010	0.0625	0.0010	0.0010	0.2174	0.0973	1.5702
R2	0	0	0.0010	0.0010	0.0741	0.1290	0.1238	0.0625	0.0010	0.1587	0.0010	0.0425	1.8949
R3	0	0	0.0233	0.0625	0.1111	0.0968	0.2667	0.1875	0.0010	0.0010	0.0010	0.0795	2.0892
R4	0	0	0	0.0313	0.0741	0.0010	0.1905	0.0469	0.0010	0.0010	0.0010	0.0237	3.0849
V	0	0	0.0465	0.1875	0.4444	0.3710	0.2000	0.4219	0.2817	0.1587	0.0010	0.2234	1.9181
DJ	0	0.1678	0.1053	0	0	0	0	0	0.4225	0	0	0.0665	2.4276
DR	0	0	0	0.1375	0.1556	0.1705	0.1000	0	0	0.1587	0	0.0481	1.2911
DV	0	0	0	0	0	0	0	0.0992	0	0	0.6522	0.0877	1.4032

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1998-99													
Sd	0	0	0	0	**0.0952**	**0.8395**	**1.5385**	0	0	0	0	0.1912	1.0000
J1	0.4825	0.6890	0.0517	0.0357	0.0000	0.0185	0.0769	0.0000	0.2844	0.0010	0.0010	0.3483	2.1057
J2	0	0.1341	0.4569	0.0714	0.0010	0.0185	0.0010	0.1122	0.3792	0.0647	0.0010	0.1201	4.1231
R1	0	0.0010	0.2069	0.3214	0.0714	0.0010	0.0385	0.0612	0.0010	0.0647	0.3523	0.0515	5.5104
R2	0	0	0.0086	0.0357	0.1786	0.1111	0.0769	0.1020	0.0948	0.0970	0.0010	0.0328	5.1443
R3	0	0.0061	0.0345	0.2857	0.2500	0.3889	0.1923	0.3163	0.0010	0.1293	0.0010	0.0966	6.7345
R4	0	0	0	0.0357	0.2500	0.2963	0.3462	0.1531	0.0010	0.1293	0.0010	0.0715	6.4993
V	0	0	0.0776	0.1429	0.0714	0.0926	0.1154	0.1735	0.0948	0.3234	0.4697	0.0517	5.7494
DJ	0	0.0250	0.0940	0	0	0	0	0	0.1098	0	0	0.0221	3.5462
DR	0	0	0	0.0554	0.0179	0.0435	0	0	0	0.1375	0	0.0099	5.3448
DV	0	0	0	0	0	0	0	0.0724	0	0	0.1565	0.0044	5.4295
1999-00													
Sd	0	0	0	0	**0.0369**	**0.5272**	**0.8646**	0	0	0	0	0.1307	1.0000
J1	0.6477	0.3907	0.0088	0	0	0	0	0	0.0010	0.0010	0.0010	0.1468	1.5136
J2	0	0.3674	0.4602	0.0545	0.0333	0.0465	0.0010	0.0010	0.5817	0.1998	0.0860	0.2067	1.7978
R1	0	0.0010	0.1947	0.2727	0.1000	0.0930	0.0182	0.0448	0.0969	0.0010	0.0010	0.0946	2.0261
R2	0	0.0047	0.0088	0.0545	0.2000	0.0698	0.0909	0.1194	0.0010	0.0010	0.0010	0.0409	2.3139
R3	0	0.0047	0.0177	0.1636	0.3333	0.3837	0.3273	0.2388	0.0010	0.1998	0.0860	0.1349	3.2599
R4	0	0	0.0088	0.0010	0.0667	0.1512	0.3636	0.1493	0.0010	0.0999	0.0010	0.0642	4.0290
V	0	0	0.0885	0.1455	0.0010	0.1047	0.0909	0.1940	0.0010	0.0999	0.1719	0.0743	2.4831
DJ	0	0.1172	0.1113	0	0	0	0	0	0.2592	0	0	0.0558	1.7411
DR	0	0	0	0.1464	0.0700	0.0544	0.0371	0	0	0.1959	0	0.0337	2.1247
DV	0	0	0	0	0	0	0	0.1149	0	0	0.4897	0.0174	1.7762

(C) **Med-low density**

Stage	Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1996-97													
Sd	0	0	0	0	**0.3379**	**0.4811**	**1.2410**	0	0	0	0	0.1307	1.0000
J1	0.5209	0.1429	0.0010	0	0	0	0	0	0.0972	0.0092	0.0010	0.1468	1.5136
J2	0	0.4643	0.2500	0.0606	0.0010	0.0172	0.0010	0.0440	0.3174	0.1479	0.2435	0.2067	1.7978
R1	0	0.0357	0.3750	0.1818	0.0476	0.0690	0.0125	0.1099	0.0443	0.1383	0.0403	0.0946	2.0261
R2	0	0	0.0010	0.0606	0.2381	0.1034	0.0375	0.1099	0.0010	0.0350	0.0673	0.0409	2.3139
R3	0	0	0.0010	0.0909	0.0952	0.2586	0.1375	0.1978	0.0010	0.0433	0.0673	0.1349	3.2599
R4	0	0	0	0.0909	0.1429	0.2069	0.4875	0.2088	0.0010	0.0177	0.0010	0.0642	4.0290
V	0	0	0.1563	0.3939	0.3333	0.1724	0.0875	0.1648	0.0667	0.1817	0.2508	0.0743	2.4831
DJ	0	0.3250	0.2188	0	0	0	0	0	0.3908	0	0	0.0558	1.7411
DR	0	0	0	0.0091	0.0571	0.0931	0.0975	0	0	0.2331	0	0.0337	2.1247
DV	0	0	0	0	0	0	0	0.0736	0	0	0.1622	0.0174	1.7762
1997-98													
Sd	0	0	0	0	**0.0703**	**0.2876**	**0.5009**	0	0	0	0	0.0242	1.0000
J1	0.3235	0.1538	0.0010	0	0	0	0	0	0.0010	0.0010	0.0010	0.0108	2.8897
J2	0	0.6154	0.6346	0.1176	0.0333	0.0741	0.0010	0.0959	0.2970	0.0010	0.0010	0.2766	3.5664
R1	0	0.0010	0.0962	0.2745	0.0667	0.0556	0.0250	0.0548	0.0010	0.0010	0.0010	0.0666	2.5356
R2	0	0	0.0010	0.0010	0.1333	0.1111	0.1375	0.0274	0.0010	0.0010	0.0010	0.0183	2.5296
R3	0	0	0.0192	0.0392	0.0667	0.1667	0.1500	0.1781	0.0010	0.0010	0.0010	0.0645	2.7522
R4	0	0	0	0.0010	0.0010	0.0185	0.1125	0.0137	0.0010	0.0010	0.0010	0.0056	3.1661
V	0	0	0.0385	0.2941	0.4667	0.2778	0.4125	0.2877	0.0990	0.3401	0.4478	0.2206	2.5214
DJ	0	0.0154	0.1731	0	0	0	0	0	0.5941	0	0	0.1409	3.8812
DR	0	0	0	0.1784	0.1367	0.1703	0.1050	0	0	0.5442	0	0.0664	2.2399
DV	0	0	0	0	0	0	0	0.2329	0	0	0.4478	0.1055	2.3535

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1998-99													
Sd	0	0	0	0	**0.1833**	**0.4293**	**1.8333**	0	0	0	0	0.1584	1.0000
J1	0.6724	0.7937	0.0444	0.0270	0	0	0	0.0084	0.2632	0.0262	0.0010	0.4094	1.6091
J2	0	0.1587	0.5778	0.1892	0.0417	0.0244	0.0010	0.0336	0.1974	0.1836	0.3962	0.1597	2.8202
R1	0	0.0010	0.2000	0.1892	0.0417	0.0244	0.0010	0.0588	0.0658	0.1836	0.1132	0.0435	3.8883
R2	0	0	0.0111	0.1081	0.0833	0.0732	0.0010	0.1176	0.0658	0.0787	0.0566	0.0184	4.2404
R3	0	0	0.0111	0.2432	0.2917	0.4634	0.3333	0.2437	0.0010	0.1049	0.2264	0.0841	5.0609
R4	0	0	0.0222	0.1081	0.2917	0.2683	0.5000	0.1345	0.0010	0.1311	0.0010	0.0719	6.6347
V	0	0	0.0556	0.1081	0.0833	0.1220	0.0833	0.2269	0.1974	0.2098	0.1698	0.0400	3.5958
DJ	0	0.0048	0.0467	0	0	0	0	0	0.2286	0	0	0.0110	2.6202
DR	0	0	0	0.0270	0.0167	0.0024	0.0083	0	0	0.0558	0	0.0022	3.6661
DV	0	0	0	0	0	0	0	0.0345	0	0	0.0010	0.0013	3.2955
1999-00													
Sd	0	0	0	0	**0.0462**	**0.2786**	**0.7099**	0	0	0	0	0.0590	1.0000
J1	0.6818	0.4597	0.0093	0	0	0	0	0	0.0010	0.0010	0.0010	0.0860	1.4703
J2	0	0.2258	0.4206	0.0417	0.0010	0.0649	0.0010	0.0164	0.4220	0.3309	0.6111	0.2536	1.8537
R1	0	0.0081	0.1589	0.2083	0.0690	0.0779	0.0010	0.0164	0.1055	0.1654	0.0010	0.1106	2.0046
R2	0	0	0.0010	0.0208	0.2759	0.1818	0.1176	0.1639	0.0010	0.0010	0.0010	0.0482	2.2579
R3	0	0.0081	0.0093	0.2292	0.3448	0.2597	0.3529	0.1639	0.0010	0.0010	0.0010	0.0960	2.6691
R4	0	0	0.0093	0.0417	0.0690	0.0909	0.3137	0.1148	0.0010	0.0010	0.0010	0.0387	3.8656
V	0	0	0.0374	0.1458	0.0690	0.0779	0.0588	0.1639	0.0010	0.0010	0.0010	0.0491	2.2291
DJ	0	0.1104	0.3196	0	0	0	0	0	0.4539	0	0	0.1797	1.7972
DR	0	0	0	0.2094	0.0759	0.1116	0.0690	0	0	0.3684	0	0.0683	1.5845
DV	0	0	0	0	0	0	0	0.1755	0	0	0.1576	0.0108	1.8367

(C) **Med-high density**

Stage	Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1996-97													
Sd	0	0	0	0	**0.7571**	**1.0716**	**2.8333**	0	0	0	0	0.0590	1.0000
J1	0.5209	0.1429	0.0145	0	0	0	0	0	0.0972	0.0092	0.0010	0.0860	1.4045
J2	0	0.4643	0.2319	0.0952	0.0010	0.0010	0.0010	0.0122	0.3174	0.1479	0.2435	0.2536	1.9642
R1	0	0.0357	0.3333	0.1429	0.0010	0.0588	0.1017	0.0122	0.0443	0.1383	0.0403	0.1106	1.7574
R2	0	0	0.0290	0.0714	0.0625	0.1373	0.1017	0.0732	0.0010	0.0350	0.0673	0.0482	1.9724
R3	0	0	0.0725	0.0476	0.3125	0.2745	0.2203	0.2439	0.0010	0.0433	0.0673	0.0960	2.1241
R4	0	0	0	0.0238	0.3125	0.1765	0.2542	0.1951	0.0010	0.0177	0.0010	0.0387	2.9600
V	0	0	0.0870	0.3333	0.2500	0.1373	0.1525	0.3293	0.0667	0.1817	0.2508	0.0491	1.6860
DJ	0	0.3250	0.1536	0	0	0	0	0	0.3908	0	0	0.1797	2.0336
DR	0	0	0	0.0286	0.0063	0.0569	0.0475	0	0	0.2331	0	0.0683	1.6138
DV	0	0	0	0	0	0	0	0.0232	0	0	0.1622	0.0108	1.5154
1997-98													
Sd	0	0	0	0	**0.1185**	**0.5870**	**1.1007**	0	0	0	0	0.0329	1.0000
J1	0.3021	0.5556	0.0755	0	0	0.0159	0	0	0.0010	0.0010	0.0010	0.1036	2.9206
J2	**0**	0.2222	0.3585	0.1224	0.0800	0.0317	0.0010	0.0130	0.6838	0.0010	0.0010	0.3058	2.9264
R1	0	0.0556	**0**.0566	0.3265	0.0400	0.0476	0.0204	0.0519	0.0010	0.0010	0.0010	0.0588	1.3787
R2	0	0	**0**.0010	0.0204	0.3200	0.1270	0.1429	0.1169	0.0010	0.0010	0.0010	0.0366	1.5980
R3	**0**	0	0.0010	0.0816	0.0400	0.0794	0.0816	0.1558	0.0010	0.0010	0.0010	0.0322	1.9188
R4	0	0	0	0.0010	0.0010	0.0159	0.1224	0.0260	0.0010	0.0010	0.0010	0.0053	2.6362
V	0	0	0.0943	0.1224	0.2800	0.3651	0.3673	0.3117	0.0010	0.1429	0.0010	0.1192	1.1782
DJ	0	0.0708	0.3484	0	0	0	0	0	0.2564	0	0	0.1819	3.2151
DR	0	0	0	0.1796	0.2040	0.1849	0.1347	0	0	0.4286	0	0.0544	0.4003
DV	0	0	0	0	0	0	0	0.2072	0	0	0.5263	0.0693	0.0409

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1998-99													
Sd	0	0	0	0	**0.1788**	**0.6808**	**3.9333**	0	0	0	0	0.2472	1.0000
J1	0.5851	0.6762	0.0172	0.0000	0.0000	0.0000	0.0000	0.0118	0.1390	0.1166	0.0676	0.3886	1.8192
J2	0	0.1238	0.4310	0.1000	0.0303	0.0385	0.0010	0.0824	0.6023	0.3497	0.2029	0.1161	4.5932
R1	0	0.0010	0.2241	0.2333	0.0010	0.0010	0.0010	0.0588	0.0927	0.0583	0.2029	0.0383	6.5414
R2	0	0	0.0172	0.0667	0.0909	0.0010	0.1111	0.1647	0.0010	0.0010	0.0010	0.0198	7.9590
R3	0	0	0.0862	0.1667	0.3030	0.2692	0.1111	0.2824	0.0010	0.1748	0.1353	0.0556	8.2673
R4	0	0	0	0.0667	0.3333	0.4231	0.3333	0.1647	0.0010	0.0291	0.0010	0.0564	10.1669
V	0	0	0.0517	0.2667	0.1515	0.1923	0.2222	0.2000	0.0010	0.1748	0.2029	0.0506	7.0843
DJ	0	0.0324	0.0483	0	0	0	0	0	0.1609	0	0	0.0201	4.0496
DR	0	0	0	0.1000	0.0909	0.0077	0.0222	0	0	0.0310	0	0.0071	5.0197
DV	0	0	0	0	0	0	0	0.0035	0	0	0.1803	0.0002	5.6068
1999-00													
Sd	0	0	0	0	**0**	**0.4269**	**1.4576**	0	0	0	0	0.0504	1.0000
J1	0.7308	0.7200	0.0010	0	0	0	0	0	0.1252	0.0987	0.3193	0.2078	1.3089
J2	0	0.1933	0.6957	0.1892	0.0010	0.0317	0.0233	0.0196	0.1252	0.0493	0.0010	0.3060	1.2774
R1	0	0.0010	0.0978	0.4054	0.0870	0.2222	0.0930	0.1373	0.3757	0.0010	0.0010	0.1439	1.3916
R2	0	0	0.0109	0.0270	0.2174	0.1270	0.2326	0.2157	0.1252	0.0010	0.0010	0.0542	1.6726
R3	0	0	0.0010	0.0541	0.2174	0.2381	0.2558	0.2157	0.0010	0.0010	0.0010	0.0545	2.0137
R4	0	0	0	0.0010	0.0435	0.0159	0.2558	0.0980	0.0010	0.0493	0.0010	0.0171	3.8601
V	0	0	0.0109	0.1622	0.2174	0.1905	0.0930	0.1765	0.0010	0.0493	0.3193	0.0688	1.8621
DJ	0	0.0432	0.1097	0	0	0	0	0	0.2048	0	0	0.0566	1.4153
DR	0	0	0	0.0892	0.1413	0.0568	0.0144	0	0	0.3019	0	0.0364	0.7326
DV	0	0	0	0	0	0	0	0.0450	0	0	0.2250	0.0042	1.3980

(C)						High density						
	Stage											
Stage	Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1996-97													
Sd	0	0	0	0	**0.7549**	**0.5765**	**0.8627**	0	0	0	0	0.0504	1.0000
J1	0.5209	0.1429	0.0164	0	0	0	0	0	0.0972	0.0092	0.0010	0.2078	1.3089
J2	0	0.4643	0.3279	0.1034	0.0010	0.0364	0.0238	0.0769	0.3174	0.1479	0.2435	0.3060	1.2774
R1	0	0.0357	0.2951	0.2759	0.1667	0.1091	0.0714	0.0577	0.0443	0.1383	0.0403	0.1439	1.3916
R2	0	0	0.0010	0.0690	0.1667	0.0727	0.0952	0.0962	0.0010	0.0350	0.0673	0.0542	1.6726
R3	0	0	0.0492	0.1379	0.3333	0.2545	0.3095	0.2692	0.0010	0.0433	0.0673	0.0545	2.0137
R4	0	0	0.0000	0.0690	0.0010	0.1091	0.2143	0.0962	0.0010	0.0177	0.0010	0.0171	3.8601
V	0	0	0.0656	0.1724	0.1667	0.1818	0.2143	0.2308	0.0667	0.1817	0.2508	0.0688	1.8621
DJ	0	0.3250	0.2016	0.0000	0	0	0	0	0.3908	0	0	0.0566	1.4153
DR	0	0	0	0.0948	0.0917	0.1055	0.0500	0	0	0.2331	0	0.0364	0.7326
DV	0	0	0	0	0	0	0	0.0673	0	0	0.1622	0.0042	1.3980
1997-98													
Sd	0	0	0	0	**0.2735**	**0.1854**	**0.6078**	0	0	0	0	0.0079	1.0000
J1	0.2597	0.3636	0.0185	0.0185	0	0	0	0.0200	0.0610	0.0010	0.0010	0.0655	3.2432
J2	0	0.2727	0.2963	0.1296	0.0500	0.0690	0.1250	0.0800	0.3049	0.0690	0.2857	0.2794	1.9142
R1	0	0.0010	0.1296	0.3519	0.0010	0.1207	0.1250	0.1200	0.0010	0.2069	0.0010	0.1255	1.7660
R2	0	0	0.0010	0.0010	0.1000	0.0172	0.0417	0.0400	0.0010	0.0010	0.0010	0.0068	2.2726
R3	0	0	0.0010	0.0185	0.0500	0.1034	0.0833	0.0800	0.0010	0.0010	0.0010	0.0152	2.1790
R4	0	0	0	0.0010	0.0010	0.0010	0.0833	0.0200	0.0010	0.0010	0.0010	0.0032	2.6382
V	0	0	0.0370	0.0741	0.4000	0.3276	0.3333	0.3200	0.0010	0.2759	0.2857	0.0953	1.8975
DJ	0	0.3022	0.2002	0	0	0	0	0	0.6098	0	0	0.3256	3.4048
DR	0	0	0	0.1796	0.2150	0.2008	0.0125	0	0	0.3448	0	0.0545	2.0724
DV	0	0	0	0	0	0	0	0.1230	0	0	0.2857	0.0211	1.9781

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV	w	v
1998-99													
Sd	0	0	0	0	**0**	**1.0571**	**7.4000**	0	0	0	0	0.2236	1.0000
J1	0.6452	0.7500	0.0351	0.0217	0	0	0	0	0.0411	0.0332	0.0010	0.3786	1.7765
J2	0	0.1500	0.3509	0.1304	0.0010	0.0010	0.0010	0.0735	0.6168	0.2656	0.1367	0.0968	2.9854
R1	0	0.0250	0.3333	0.4348	0.0010	0.2143	0.0010	0.1029	0.0822	0.2988	0.1367	0.0903	4.4733
R2	0	0.0250	0.0175	0.0435	0.5000	0.2143	0.0010	0.0735	0.0010	0.0664	0.1367	0.0541	5.1946
R3	0	0	0.0010	0.1087	0.3333	0.3571	0.6667	0.2941	0.0010	0.1328	0.4100	0.0746	7.2017
R4	0	0	0	0.0435	0.0010	0.1429	0.3333	0.1029	0.0010	0.0010	0.0010	0.0240	15.0379
V	0	0	0.1053	0.1739	0.1667	0.0714	0.0010	0.2647	0.1234	0.0664	0.1367	0.0470	5.5789
DJ	0	0.0050	0.0474	0.0000	0	0	0	0.0000	0	0	0	0.0062	2.8528
DR	0	0	0	0.0337	0.0010	0.0010	0.0010	0	0	0.0706	0	0.0030	3.6035
DV	0	0	0	0	0	0	0	0.0397	0	0	0.0010	0.0016	4.7694
1999-00													
Sd	0	0	0	0	**0**	**0.1674**	**0.7333**	0	0	0	0	0.0631	1.0000
J1	0.7297	0.5362	0.0141	0	0	0	0	0	0.0010	0.0010	0.0010	0.1158	1.3092
J2	0	0.3333	0.5070	0.1077	0.0526	0.0010	0.0010	0.0750	0.0010	0.0010	0.7155	0.1687	1.2956
R1	0	0.0010	0.1549	0.4154	0.1053	0.0930	0.1667	0.0500	0.1713	0.2244	0.0010	0.1506	1.7180
R2	0	0	0.0010	0.0462	0.0526	0.1860	0.0833	0.1750	0.0010	0.2244	0.0010	0.0760	1.5510
R3	0	0	0.0423	0.1692	0.2632	0.3488	0.2500	0.3000	0.0010	0.0010	0.0010	0.1597	1.7899
R4	0	0	0	0.0615	0.0526	0.0465	0.2500	0.0250	0.0010	0.2244	0.0010	0.0458	2.5561
V	0	0	0.0010	0.0769	0.2632	0.1628	0.0833	0.2000	0.3426	0.0010	0.0010	0.1090	1.5294
DJ	0	0.0800	0.1513	0	0	0	0	0	0.3801	0	0	0.0605	1.4375
DR	0	0	0	0.0792	0.0817	0.0575	0.0444	0	0	0.2051	0	0.0391	1.7502
DV	0	0	0	0	0	0	0	0.0916	0	0	0.0948	0.0116	1.0895

Appendix 3.3 Estimated λs and confidence intervals

Table A3.3 Estimates of population growth rate, λ, for 44 different *C. lyallii* plot group x year combinations, and the 95% bias-corrected bootstrap confidence intervals of those estimates. For the analysis, demographic plots were sorted by population, microsite type, and intraspecific plant density. See text for plot group definitions.

Observation level	Year	Plot group	Lower 95%	λ	Upper 95%
Population	1996-97	NS	0.9962	1.0310	1.0652
		ES	1.0240	1.0528	1.0803
		WS	1.0414	1.0680	1.0942
	1997-98	NS	0.8607	0.9050	0.9291
		ES	0.8700	0.9267	0.9699
		WS	0.8138	0.8930	0.9547
	1998-99	NS	1.0343	1.0675	1.1136
		ES	0.9362	0.9913	1.0474
		WS	1.0267	1.0739	1.1493
	1999-00	NS	0.8764	0.8982	0.9237
		ES	0.9631	0.9801	1.0183
		WS	0.9868	1.0105	1.0614
Microsite	1996-97	A	1.0179	1.0506	1.0841
		B	0.9898	1.0204	1.0541
		C	1.0107	1.0490	1.0916
		D	1.0231	1.0573	1.0888
	1997-98	A	0.8275	0.8889	0.9311
		B	0.8401	0.9174	0.9739
		C	0.8362	0.8966	0.9272
		D	0.8260	0.8741	0.9130
	1998-99	A	1.1746	1.2896	1.5042
		B	0.9227	0.9782	1.0325
		C	0.9985	1.0528	1.1258
		D	0.9702	1.0032	1.0466
	1999-00	A	0.9202	0.9385	0.9866
		B	0.8767	0.9325	0.9791
		C	0.9518	0.9627	1.0006
		D	0.9687	0.9986	1.0606

Table A3.3, continued

Observation level	Year	Plot group	Lower 95%	λ	Upper 95%
Density class	1996-97	Low	0.9772	1.0154	1.0536
		Med-low	0.9975	1.0288	1.0593
		Med-high	1.0518	1.0911	1.1309
		High	1.0418	1.0736	1.1052
	1997-98	Low	0.7788	0.8575	0.8996
		Med-low	0.8014	0.8788	0.9110
		Med-high	0.8495	0.8967	0.9284
		High	0.8909	0.9289	0.9665
	1998-99	Low	0.9713	1.0117	1.0633
		Med-low	1.0115	1.0683	1.1424
		Med-high	1.0000	1.0481	1.1131
		High	1.0741	1.1280	1.2365
	1999-00	Low	0.9092	0.9407	0.9833
		Med-low	0.9280	0.9691	1.0093
		Med-high	0.9327	0.9443	0.9799
		High	1.0034	1.0066	1.0389

Appendix 3.4 Elasticity matrices

Table A3.4 Annual elasticity matrices for a) populations NS, ES, WS; b) microsite types A, B, C, D; and c) densities classes Low, Med-low, Med-high, High, for the transition periods 1996-97, 1997-98, 1998-99, 1999-00. Stage classes reflect plant size and/or state (Table 2). Bolded entries are the fecundity terms.

a) NS

Stage	Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1996-97											
Sd	0	0	0	0	**0.0103**	**0.0323**	**0.0551**	0	0	0	0
J1	0.0977	0.0173	0.0016	0	0	0	0	0	0.0081	0.0002	0
J2	0	0.0635	0.0447	0.0036	0	0	0	0.0028	0.0298	0.0032	0.0016
R1	0	0.0053	0.0546	0.0092	0.0026	0.0033	0.0031	0.0046	0.0045	0.0033	0.0003
R2	0	0	0.0036	0.0097	0.0072	0.0040	0.0045	0.0154	0.0002	0.0015	0.0009
R3	0	0	0.0103	0.0115	0.0091	0.0362	0.0118	0.0360	0.0002	0.0018	0.0009
R4	0	0	0	0.0096	0.0127	0.0238	0.0447	0.0370	0.0002	0.0010	0
V	0	0	0.0212	0.0428	0.0035	0.0103	0.0067	0.0279	0.0093	0.0059	0.0025
DJ	0	0.0387	0.0135	0	0	0	0	0	0.0319	0	0
DR	0	0	0	0.0043	0.0015	0.0079	0.0031	0	0	0.0049	0
DV	0	0	0	0	0	0	0	0.0063	0	0	0.0012
1997-98											
Sd	0	0	0	0	**0**	**0.0182**	**0.0033**	0	0	0	0
J1	0.0215	0.0148	0.0127	0	0	0	0	0	0.0177	0	0
J2	0	0.0325	0.1259	0.0108	0.0025	0.0033	0.0003	0.0193	0.0390	0	0.0042
R1	0	0.0020	0.0317	0.0297	0.0022	0.0039	0	0.0063	0.0002	0.0034	0.0037
R2	0	0	0.0003	0.0001	0.0048	0.0075	0.0007	0.0140	0.0002	0.0038	0
R3	0	0	0.0032	0.0088	0.0028	0.0163	0.0014	0.0547	0.0002	0	0
R4	0	0	0	0.0002	0	0.0001	0.0020	0.0076	0.0003	0.0001	0
V	0	0	0.0239	0.0250	0.0153	0.0285	0.0022	0.0712	0.0002	0.0148	0.0080
DJ	0	0.0175	0.0403	0	0	0	0	0	0.1460	0	0
DR	0	0	0	0.0084	0.0039	0.0097	0.0003	0	0	0.0196	0
DV	0	0	0	0	0	0	0	0.0160	0	0	0.0104

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1998-99											
Sd	0	0	0	0	**0.0012**	**0.0134**	**0.0378**	0	0	0	0
J1	0.0524	0.1515	0.0021	0.0005	0	0	0	0.0002	0.0017	0	0
J2	0	0.0463	0.0722	0.0108	0	0.0016	0	0.0030	0.0122	0.0004	0.0007
R1	0	0.0005	0.0403	0.0317	0.0017	0.0001	0.0044	0.0054	0.0012	0.0008	0
R2	0	0	0.0018	0.0037	0.0105	0.0107	0.0169	0.0137	0	0.0003	0.0008
R3	0	0	0.0021	0.0206	0.0213	0.0780	0.0190	0.0367	0	0.0007	0.0009
R4	0	0	0	0.0025	0.0176	0.0556	0.0313	0.0179	0	0.0004	0
V	0	0	0.0184	0.0134	0.0058	0.0195	0.0154	0.0330	0.0054	0.0015	0.0007
DJ	0	0.0102	0.0104	0	0	0	0	0	0.0019	0	0
DR	0	0	0	0.0029	0.0003	0.0004	0.0004	0	0	0.0001	0
DV	0	0	0	0	0	0	0	0.0032	0	0	0
1999-00											
Sd	0	0	0	0	**0**	**0.0203**	**0.0133**	0	0	0	0
J1	0.0336	0.0765	0.0020	0	0	0	0	0	0.0080	0	0
J2	0	0.0290	0.1444	0.0123	0.0012	0.0025	0	0.0021	0.0380	0.0172	0.0043
R1	0	0.0001	0.0325	0.0371	0.0026	0.0136	0.0014	0.0030	0.0167	0.0094	0
R2	0	0	0.0004	0.0065	0.0103	0.0177	0.0019	0.0167	0.0002	0	0
R3	0	0	0.0030	0.0226	0.0216	0.0338	0.0115	0.0214	0.0003	0	0
R4	0	0	0	0.0003	0.0055	0.0133	0.0091	0.0111	0.0004	0.0001	0
V	0	0	0.0097	0.0201	0.0095	0.0076	0.0017	0.0145	0.0100	0	0.0057
DJ	0	0.0145	0.0591	0	0	0	0	0	0.0694	0	0
DR	0	0	0	0.0177	0.0031	0.0054	0.0009	0	0	0.0104	0
DV	0	0	0	0	0	0	0	0.0101	0	0	0.0017

a) Site ES

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1996-97											
Sd	0	0	0	0	**0.0040**	**0.0138**	**0.0548**	0	0	0	0
J1	0.0726	0.0130	0.0022	0	0	0	0	0	0.0082	0	0
J2	0	0.0497	0.0355	0.0051	0	0	0.0001	0.0016	0.0314	0.0013	0.0006
R1	0	0.0044	0.0294	0.0138	0	0.0044	0.0030	0.0027	0.0051	0.0014	0.0001
R2	0	0	0.0040	0.0080	0.0066	0.0207	0.0203	0.0123	0.0002	0.0005	0.0003
R3	0	0	0.0114	0.0051	0.0158	0.0270	0.0300	0.0309	0.0001	0.0006	0.0003
R4	0	0	0	0.0069	0.0342	0.0345	0.1089	0.0480	0.0002	0.0003	0
V	0	0	0.0175	0.0236	0.0117	0.0183	0.0144	0.0197	0.0091	0.0022	0.0009
DJ	0	0.0289	0.0254	0	0	0	0	0	0.0320	0	0
DR	0	0	0	0.0020	0.0004	0.0025	0.0015	0	0	0.0018	0
DV	0	0	0	0	0	0	0	0.0022	0	0	0.0004
1997-98											
Sd	0	0	0	0	**0.0001**	**0.0014**	**0.0005**	0	0	0	0
J1	0.0020	0.0194	0.0122	0.0019	0	0	0	0	0.0003	0	0
J2	0	0.0078	0.2810	0.0096	0.0006	0.0005	0	0.0012	0.1829	0.0032	0
R1	0	0.0044	0.0069	0.0152	0.0003	0.0020	0	0.0063	0.0002	0.0018	0
R2	0	0	0.0003	0	0.0031	0.0036	0.0005	0.0057	0.0002	0	0
R3	0	0	0.0065	0.0020	0.0016	0.0011	0.0006	0.0091	0.0002	0	0
R4	0	0	0	0	0.0007	0.0003	0.0004	0.0015	0.0002	0	0
V	0	0	0.0003	0.0056	0.0056	0.0098	0.0010	0.0164	0.0002	0.0016	0.0052
DJ	0	0.0044	0.1798	0	0	0	0	0	0.1543	0	0
DR	0	0	0	0.0028	0.0013	0.0023	0.0001	0	0	0.0013	0
DV	0	0	0	0	0	0	0	0.0053	0	0	0.0031

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1998-99											
Sd	0	0	0	0	**0.0005**	**0.0270**	**0.0296**	0	0	0	0
J1	0.0572	0.1109	0.0018	0.0011	0	0.0010	0	0	0.0008	0.0003	0
J2	0	0.0342	0.0331	0.0031	0.0007	0.0030	0.0001	0.0061	0.0148	0.0013	0
R1	0	0.0007	0.0403	0.0201	0	0.0038	0.0002	0.0066	0.0032	0.0006	0.0002
R2	0	0	0.0046	0.0104	0.0073	0.0119	0.0002	0.0118	0	0.0017	0
R3	0	0.0131	0.0053	0.0168	0.0148	0.0959	0.0500	0.0338	0	0.0047	0.0002
R4	0	0	0	0.0022	0.0148	0.0679	0.0931	0.0120	0	0.0031	0
V	0	0	0.0068	0.0162	0.0062	0.0231	0.0169	0.0121	0	0.0017	0.0002
DJ	0	0.0143	0.0046	0	0	0	0	0	0.0042	0	0
DR	0	0	0	0.0056	0.0036	0.0011	0.0031	0	0	0.0011	0
DV	0	0	0	0	0	0	0	0.0007	0	0	0.0002
1999-00											
Sd	0	0	0	0	**0.0011**	**0.0261**	**0.0214**	0	0	0	0
J1	0.0486	0.0661	0.0002	0	0	0	0	0	0	0.0050	0.0016
J2	0	0.0392	0.1292	0.0166	0.0015	0.0044	0.0005	0.0013	0.0156	0	0
R1	0	0.0001	0.0329	0.0676	0.0076	0.0117	0.0022	0.0110	0.0159	0	0
R2	0	0	0.0034	0.0069	0.0205	0.0132	0.0079	0.0151	0.0097	0	0
R3	0	0	0.0080	0.0245	0.0265	0.0444	0.0157	0.0239	0	0.0042	0
R4	0	0	0	0.0056	0.0060	0.0231	0.0170	0.0135	0.0001	0.0056	0
V	0	0	0.0094	0.0160	0.0104	0.0185	0.0055	0.0172	0	0.0065	0.0021
DJ	0	0.0161	0.0254	0	0	0	0	0	0.0190	0	0
DR	0	0	0	0.0119	0.0030	0.0057	0.0008	0	0	0.0040	0
DV	0	0	0	0	0	0	0	0.0038	0	0	0.0021

a) Site WS

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1996-97											
Sd	0	0	0	0	**0.0064**	**0.0285**	**0.0375**	0	0	0	0
J1	0.0724	0.0127	0.0018	0	0	0	0	0	0.0078	0.0002	0
J2	0	0.0497	0.0303	0.0094	0	0.0044	0.0008	0.0038	0.0306	0.0032	0.0018
R1	0	0.0046	0.0471	0.0415	0.0052	0.0134	0.0049	0.0091	0.0052	0.0037	0.0004
R2	0	0	0.0002	0.0066	0.0122	0.0093	0.0034	0.0141	0.0001	0.0011	0.0007
R3	0	0	0.0069	0.0274	0.0069	0.0335	0.0244	0.0360	0.0002	0.0015	0.0008
R4	0	0	0.0042	0.0182	0.0028	0.0258	0.0330	0.0391	0.0002	0.0008	0
V	0	0	0.0193	0.0278	0.0129	0.0183	0.0144	0.0367	0.0082	0.0051	0.0024
DJ	0	0.0278	0.0244	0	0	0	0	0	0.0301	0	0
DR	0	0	0	0.0042	0.0013	0.0042	0.0057	0	0	0.0043	0
DV	0	0	0	0	0	0	0	0.0061	0	0	0.0011
1997-98											
Sd	0	0	0	0	**0.0012**	**0.0067**	**0.0045**	0	0	0	0
J1	0.0124	0.0175	0.0021	0.0006	0	0.0003	0	0.0019	0	0	0.0003
J2	0	0.0170	0.0507	0.0067	0.0003	0.0020	0	0.0075	0.0304	0.0028	0.0003
R1	0	0	0.0146	0.0104	0.0003	0.0011	0.0005	0.0115	0	0.0029	0.0003
R2	0	0	0.0002	0.0007	0.0008	0.0007	0.0010	0.0048	0	0	0.0004
R3	0	0	0.0002	0.0016	0	0.0036	0.0017	0.0185	0.0001	0	0.0004
R4	0	0	0	0.0011	0	0.0005	0.0026	0.0106	0.0001	0	0.0005
V	0	0	0.0051	0.0057	0.0033	0.0046	0.0025	0.0708	0.0145	0.0212	0.0662
DJ	0	0.0006	0.0448	0	0	0	0	0	0.0452	0	0
DR	0	0	0	0.0149	0.0029	0.0067	0.0027	0	0	0.0299	0
DV	0	0	0	0	0	0	0	0.0684	0	0	0.3328

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1998-99											
Sd	0	0	0	0	**0.0021**	**0.0135**	**0.0615**	0	0	0	0
J1	0.0771	0.1481	0.0039	0	0	0	0.0051	0.0002	0.0016	0.0002	0
J2	0	0.0754	0.0765	0.0079	0.0018	0.0023	0	0.0032	0.0054	0.0026	0.0008
R1	0	0.0038	0.0488	0.0212	0.0051	0.0099	0	0.0035	0.0018	0.0020	0.0011
R2	0	0.0041	0.0019	0.0042	0	0.0180	0.0001	0.0051	0.0019	0.0006	0
R3	0	0	0.0158	0.0250	0.0100	0.0215	0.0355	0.0144	0	0.0014	0.0010
R4	0	0	0.0056	0.0216	0.0164	0.0477	0.0548	0.0177	0	0.0009	0
V	0	0	0.0150	0.0148	0	0.0063	0.0066	0.0095	0.0025	0.0017	0.0011
DJ	0	0.0049	0.0084	0	0	0	0	0	0.0026	0	0
DR	0	0	0	0.0026	0.0004	0.0053	0.0011	0	0	0.0009	0
DV	0	0	0	0	0	0	0	0.0040	0	0	0.0002
1999-00											
Sd	0	0	0	0	**0.0013**	**0.0288**	**0.0335**	0	0	0	0
J1	0.0636	0.0510	0.0016	0	0	0	0	0	0	0	0
J2	0	0.0509	0.0746	0.0053	0	0.0060	0.0001	0.0008	0.0163	0.0073	0.0012
R1	0	0.0008	0.0425	0.0289	0.0052	0.0104	0.0001	0.0011	0.0106	0.0032	0
R2	0	0.0007	0.0012	0.0035	0.0067	0.0201	0.0100	0.0092	0	0.0027	0
R3	0	0.0020	0.0048	0.0290	0.0214	0.0732	0.0273	0.0225	0.0001	0.0037	0.0009
R4	0	0	0.0050	0.0125	0.0095	0.0142	0.0759	0.0214	0.0001	0.0116	0
V	0	0	0.0111	0.0153	0.0001	0.0236	0.0017	0.0140	0.0054	0	0.0008
DJ	0	0.0109	0.0216	0	0	0	0	0	0.0144	0	0
DR	0	0	0	0.0084	0.0099	0.0086	0.0018	0	0	0.0122	0
DV	0	0	0	0	0	0	0	0.0029	0	0	0.0028

Table A3.4, continued Annual elasticity matrices for a) populations NS, ES, WS; b) microsite types A, B, C, D; and c) densities classes Low, Med-low, Med-high, High, for the transition periods 1996-97, 1997-98, 1998-99, 1999-00. Stage classes reflect plant size and/or demographic state (Table 2). Bolded entries are the fecundity terms.

b) Microsite A

Stage	Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1996-97											
Sd	0	0	0	0	**0.0119**	**0.0290**	**0.0404**	0	0	0	0
J1	0.0813	0.0144	0.0020	0	0	0	0	0	0.0078	0.0002	0
J2	0	0.0554	0.0428	0.0067	0	0.0001	0.0001	0.0024	0.0303	0.0040	0.0006
R1	0	0.0041	0.0300	0.0113	0	0.0040	0.0035	0.0055	0.0041	0.0036	0.0001
R2	0	0	0.0040	0.0113	0.0214	0.0183	0.0136	0.0137	0.0002	0.0016	0.0003
R3	0	0	0.0169	0.0059	0.0170	0.0436	0.0271	0.0319	0.0002	0.0021	0.0003
R4	0	0	0	0.0069	0.0263	0.0337	0.0611	0.0303	0.0002	0.0010	0
V	0	0	0.0267	0.0187	0.0045	0.0095	0.0100	0.0194	0.0089	0.0069	0.0009
DJ	0	0.0318	0.0199	0	0	0	0	0	0.0306	0	0
DR	0	0	0	0.0056	0.0033	0.0067	0.0037	0	0	0.0055	0
DV	0	0	0	0	0	0	0	0.0023	0	0	0.0004
1997-98											
Sd	0	0	0	0	**0.0006**	**0.0035**	**0.0007**	0	0	0	0
J1	0.0047	0.0087	0.0004	0.0029	0	0	0.0001	0	0.0140	0.0001	0.0001
J2	0	0.0124	0.2098	0.0110	0.0017	0.0017	0.0001	0.0200	0.0927	0.0001	0.0001
R1	0	0	0.0214	0.0321	0.0021	0.0021	0	0.0082	0.0001	0.0044	0.0001
R2	0	0	0.0003	0.0001	0.0095	0.0075	0.0007	0.0228	0.0001	0.0001	0.0001
R3	0	0	0.0003	0.0019	0.0024	0.0035	0.0002	0.0277	0.0001	0.0001	0.0001
R4	0	0	0	0.0001	0.0013	0.0013	0.0002	0.0003	0.0001	0.0001	0.0001
V	0	0	0.0050	0.0143	0.0170	0.0146	0.0012	0.0806	0.0152	0.0124	0.0274
DJ	0	0.0099	0.1125	0	0	0	0	0	0.0562	0	0
DR	0	0	0	0.0082	0.0064	0.0023	0.0004	0	0	0.0338	0
DV	0	0	0	0	0	0	0	0.0280	0	0	0.0178

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1998-99											
Sd	0	0	0	0	**0**	**0**	**0.0917**	0	0	0	0
J1	0.0917	0.1144	0.0009	0	0	0	0	0	0.0010	0	0
J2	0	0.0537	0.0342	0.0029	0.0002	0.0001	0	0.0012	0.0116	0.0001	0.0001
R1	0	0.0007	0.0372	0.0141	0	0.0001	0.0001	0.0023	0	0.0001	0
R2	0	0	0.0065	0.0017	0.0013	0.0058	0.0001	0.0050	0.0025	0	0
R3	0	0.0241	0.0074	0.0155	0.0079	0.0658	0.0417	0.0153	0	0.0003	0.0002
R4	0	0	0	0.0067	0.0110	0.1017	0.1431	0.0138	0.0001	0.0004	0
V	0	0	0.0156	0.0137	0.0017	0.0046	0.0001	0.0054	0.0020	0.0002	0.0002
DJ	0	0.0151	0.0023	0	0	0	0	0	0.0009	0	0
DR	0	0	0	0.0001	0.0009	0.0001	0.0001	0	0	0	0
DV	0	0	0	0	0	0	0	0.0006	0	0	0
1999-00											
Sd	0	0	0	0	**0.0032**	**0.0305**	**0.0106**	0	0	0	0
J1	0.0443	0.1212	0.0003	0	0	0	0	0	0.0001	0.0064	0
J2	0	0.0325	0.1379	0.0125	0.0001	0.0053	0.0002	0.0030	0.0427	0.0060	0.0060
R1	0	0.0001	0.0335	0.0478	0.0068	0.0096	0.0006	0.0087	0.0001	0	0
R2	0	0	0.0003	0.0062	0.0135	0.0174	0.0027	0.0128	0.0263	0.0001	0
R3	0	0	0.0052	0.0192	0.0337	0.0299	0.0063	0.0228	0.0001	0.0001	0
R4	0	0	0	0.0003	0.0002	0.0081	0.0061	0.0137	0.0002	0.0001	0
V	0	0	0.0179	0.0133	0.0146	0.0132	0.0018	0.0174	0.0001	0.0063	0
DJ	0	0.0184	0.0511	0	0	0	0	0	0.0149	0	0
DR	0	0	0	0.0080	0.0073	0.0032	0.0004	0	0	0.0100	0
DV	0	0	0	0	0	0	0	0.0061	0	0	0.0010

b) **Microsite B**

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1996-97											
Sd	0	0	0	0	**0.0038**	**0.0119**	**0.0503**	0	0	0	0
J1	0.0659	0.0130	0.0001	0	0	0	0	0	0.0138	0.0001	0
J2	0	0.0469	0.0480	0.0110	0	0.0028	0.0001	0.0035	0.0498	0.0015	0.0017
R1	0	0.0044	0.0518	0.0338	0.0064	0.0051	0.0001	0.0014	0.0086	0.0017	0.0004
R2	0	0	0.0002	0.0001	0.0037	0.0059	0.0089	0.0099	0.0002	0.0005	0.0007
R3	0	0	0.0002	0.0193	0	0.0174	0.0220	0.0245	0.0002	0.0006	0.0007
R4	0	0	0	0.0150	0.0095	0.0251	0.0882	0.0445	0.0003	0.0003	0
V	0	0	0.0075	0.0343	0.0065	0.0138	0.0098	0.0190	0.0131	0.0023	0.0023
DJ	0	0.0286	0.0574	0	0	0	0	0	0.0534	0	0
DR	0	0	0	0.0002	0.0002	0.0030	0.0036	0	0	0.0021	0
DV	0	0	0	0	0	0	0	0.0058	0	0	0.0011
1997-98											
Sd	0	0	0	0	**0**	**0.0017**	**0.0003**	0	0	0	0
J1	0.0020	0.0037	0.0089	0	0	0	0	0	0.0005	0	0
J2	0	0.0085	0.1238	0.0046	0	0	0	0.0024	0.1104	0	0
R1	0	0	0.0038	0.0025	0	0.0008	0	0.0017	0.0002	0	0.0014
R2	0	0	0.0001	0	0.0007	0.0013	0.0001	0.0010	0.0002	0	0
R3	0	0	0.0040	0.0004	0.0005	0.0011	0.0002	0.0053	0.0002	0	0
R4	0	0	0	0	0.0004	0	0.0002	0	0.0003	0	0
V	0	0	0.0001	0.0014	0.0015	0.0045	0.0002	0.0103	0.0002	0.0041	0.0026
DJ	0	0.0030	0.1091	0	0	0	0	0	0.5556	0	0
DR	0	0	0	0.0015	0.0004	0.0023	0	0	0	0.0029	0
DV	0	0	0	0	0	0	0	0.0041	0	0	0.0028

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1998-99											
Sd	0	0	0	0	**0.0031**	**0.0236**	**0.0266**	0	0	0	0
J1	0.0532	0.2161	0.0022	0.0032	0	0	0	0	0.0025	0.0003	0
J2	0	0.0571	0.0527	0.0133	0.0001	0.0001	0.0001	0.0048	0.0097	0.0004	0.0013
R1	0	0.0005	0.0528	0.0151	0.0001	0.0043	0.0068	0.0054	0.0020	0.0014	0.0005
R2	0	0	0.0034	0.0247	0.0192	0.0084	0.0001	0.0106	0	0.0007	0.0005
R3	0	0	0.0003	0.0163	0.0127	0.0416	0.0219	0.0278	0	0.0007	0.0008
R4	0	0	0	0.0001	0.0224	0.0368	0.0775	0.0046	0	0.0007	0
V	0	0	0.0146	0.0157	0.0081	0.0067	0.0070	0.0235	0.0031	0.0012	0.0010
DJ	0	0.0038	0.0135	0	0	0	0	0	0	0	0
DR	0	0	0	0.0005	0.0021	0.0007	0.0021	0	0	0.0005	0
DV	0	0	0	0	0	0	0	0.0042	0	0	0.0008
1999-00											
Sd	0	0	0	0	**0**	**0.0202**	**0.0126**	0	0	0	0
J1	0.0328	0.0315	0.0001	0	0	0	0	0	0.0001	0	0
J2	0	0.0234	0.0719	0.0071	0.0001	0.0027	0	0.0001	0.0140	0	0
R1	0	0.0001	0.0119	0.0527	0.0109	0.0198	0.0010	0.0041	0.0208	0	0
R2	0	0	0.0044	0.0103	0.0320	0.0233	0.0056	0.0149	0.0002	0.0174	0
R3	0	0	0.0003	0.0225	0.0523	0.0889	0.0183	0.0423	0.0002	0.0001	0
R4	0	0	0	0.0003	0.0056	0.0328	0.0138	0.0042	0.0002	0.0001	0
V	0	0	0.0045	0.0107	0.0041	0.0240	0.0043	0.0430	0.0002	0.0179	0.0231
DJ	0	0.0095	0.0261	0	0	0	0	0	0.0178	0	0
DR	0	0	0	0.0177	0.0031	0.0134	0.0013	0	0	0.0177	0
DV	0	0	0	0	0	0	0	0.0233	0	0	0.0104

c) **Microsite C**

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1996-97											
Sd	0	0	0	0	**0.0126**	**0.0279**	**0.0609**	0	0	0	0
J1	0.1014	0.0179	0.0025	0	0	0	0	0	0.0096	0.0001	0
J2	0	0.0672	0.0293	0.0047	0	0.0024	0	0.0010	0.0361	0.0026	0.0011
R1	0	0.0062	0.0527	0.0132	0.0051	0.0058	0.0041	0.0025	0.0060	0.0029	0.0002
R2	0	0	0.0047	0.0126	0.0137	0.0078	0.0055	0.0151	0.0002	0.0010	0.0005
R3	0	0	0.0103	0.0165	0.0150	0.0128	0.0091	0.0238	0.0002	0.0013	0.0005
R4	0	0	0.0074	0.0160	0.0054	0.0185	0.0350	0.0451	0.0003	0.0008	0.0000
V	0	0	0.0136	0.0341	0.0066	0.0094	0.0094	0.0292	0.0118	0.0049	0.0017
DJ	0	0.0403	0.0239	0	0	0	0	0	0.0381	0	0
DR	0	0	0	0.0017	0.0027	0.0047	0.0045	0	0	0.0039	0
DV	0	0	0	0	0	0	0	0.0040	0	0	0.0007
1997-98											
Sd	0	0	0	0	**0.0064**	**0.0252**	**0.0044**	0	0	0	0
J1	0.0360	0.0233	0.0152	0	0	0	0	0	0.0001	0.0001	0.0005
J2	0	0.0387	0.1082	0.0138	0.0021	0.0074	0.0002	0.0046	0.0349	0.0077	0.0006
R1	0	0.0046	0.0371	0.0362	0.0034	0.0020	0	0.0114	0.0001	0.0001	0.0005
R2	0	0	0.0002	0.0001	0.0072	0.0087	0.0014	0.0203	0.0001	0.0068	0.0006
R3	0	0	0.0003	0.0091	0.0023	0.0191	0.0028	0.0658	0.0001	0.0001	0.0007
R4	0	0	0	0.0041	0.0001	0.0002	0.0028	0.0069	0.0002	0.0001	0.0010
V	0	0	0.0213	0.0195	0.0179	0.0235	0.0031	0.1018	0.0092	0.0183	0.0005
DJ	0	0.0087	0.0360	0	0	0	0	0	0.0619	0	0
DR	0	0	0	0.0126	0.0061	0.0140	0.0005	0	0	0.0130	0
DV	0	0	0	0	0	0	0	0.0044	0	0	0.0419

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1998-99											
Sd	0	0	0	0	**0**	**0.0253**	**0.0400**	0	0	0	0
J1	0.0652	0.1650	0.0032	0	0	0	0.0043	0.0003	0.0008	0	0
J2	0	0.0642	0.0824	0.0075	0	0.0001	0.0001	0.0054	0.0076	0.0018	0.0001
R1	0	0.0005	0.0367	0.0152	0.0001	0.0001	0.0001	0.0037	0.0018	0.0021	0.0004
R2	0	0	0.0024	0.0015	0.0079	0.0146	0.0193	0.0095	0.0018	0.0013	0.0000
R3	0	0	0.0156	0.0155	0.0272	0.0705	0.0248	0.0216	0.0000	0.0022	0.0007
R4	0	0	0.0059	0.0092	0.0225	0.0489	0.0234	0.0124	0	0	0
V	0	0	0.0145	0.0105	0.0001	0.0109	0.0096	0.0152	0.0055	0.0034	0.0007
DJ	0	0.0091	0.0085	0	0	0	0	0	0.0034	0	0
DR	0	0	0	0.0014	0.0007	0.0078	0.0018	0	0	0.0009	0
DV	0	0	0	0	0	0	0	0.0020	0	0	0
1999-00											
Sd	0	0	0	0	**0**	**0.0215**	**0.0175**	0	0	0	0
J1	0.0390	0.0715	0.0027	0	0	0	0	0	0.0071	0.0001	0
J2	0	0.0421	0.1539	0.0189	0.0019	0.0050	0	0.0026	0.0220	0.0155	0
R1	0	0.0001	0.0488	0.0246	0.0020	0.0174	0.0019	0.0040	0.0076	0.0001	0
R2	0	0	0.0003	0.0044	0.0125	0.0093	0.0060	0.0189	0.0001	0.0001	0
R3	0	0.0010	0.0070	0.0210	0.0147	0.0532	0.0153	0.0195	0.0001	0.0099	0.0058
R4	0	0	0	0.0044	0.0036	0.0062	0.0256	0.0165	0.0001	0.0144	0
V	0	0	0.0179	0.0179	0.0104	0.0181	0.0030	0.0124	0.0001	0.0001	0
DJ	0	0.0056	0.0315	0.0000	0.0000	0.0000	0.0000	0.0000	0.0245	0.0000	0.0000
DR	0	0	0	0.0155	0.0064	0.0168	0.0013	0	0	0.0135	0
DV	0	0	0	0	0	0	0	0.0059	0	0	0.0019

(B) **Microsite D**

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1996-97											
Sd	0	0	0	0	**0.0035**	**0.0256**	**0.0449**	0	0	0	0
J1	0.0741	0.0127	0.0016	0	0	0	0	0	0.0052	0.0001	0
J2	0	0.0491	0.0332	0.0022	0	0.0001	0.0008	0.0033	0.0203	0.0025	0.0021
R1	0	0.0043	0.0464	0.0295	0.0012	0.0104	0.0043	0.0092	0.0032	0.0027	0.0004
R2	0	0	0.0002	0.0037	0.0037	0.0157	0.0065	0.0111	0.0001	0.0010	0.0010
R3	0	0	0.0063	0.0175	0.0088	0.0509	0.0248	0.0554	0.0001	0.0012	0.0010
R4	0	0	0	0.0100	0.0150	0.0333	0.0583	0.0376	0.0001	0.0007	0
V	0	0	0.0193	0.0429	0.0107	0.0260	0.0133	0.0404	0.0053	0.0039	0.0027
DJ	0	0.0277	0.0066	0	0	0	0	0	0.0201	0	0
DR	0	0	0	0.0060	0	0.0041	0.0021	0	0	0.0034	0
DV	0	0	0	0	0	0	0	0.0072	0	0	0.0013
1997-98											
Sd	0	0	0	0	**0.0012**	**0.0117**	**0.0067**	0	0	0	0
J1	0.0197	0.0299	0.0126	0.0019	0	0.0006	0	0.0015	0.0002	0.0001	0.0001
J2	0	0.0220	0.1707	0.0154	0.0013	0.0033	0.0006	0.0097	0.1097	0.0058	0.0096
R1	0	0.0047	0.0324	0.0195	0	0.0037	0.0005	0.0131	0.0002	0.0110	0
R2	0	0	0.0004	0.0019	0.0007	0.0006	0.0006	0.0076	0.0002	0.0001	0.0001
R3	0	0	0.0069	0.0083	0.0016	0.0061	0.0028	0.0217	0.0002	0.0001	0.0001
R4	0	0	0	0.0002	0	0.0001	0.0046	0.0154	0.0003	0.0001	0.0001
V	0	0	0.0240	0.0162	0.0049	0.0123	0.0030	0.0291	0.0002	0.0183	0.0101
DJ	0	0.0100	0.1011	0	0	0	0	0	0.0783	0	0
DR	0	0	0	0.0218	0.0023	0.0093	0.0020	0	0	0.0185	0
DV	0	0	0	0	0	0	0	0.0200	0	0	0.0182

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1998-99											
Sd	0	0	0	0	**0.0037**	**0.0122**	**0.0304**	0	0	0	0
J1	0.0462	0.1212	0.0044	0.0019	0	0.0011	0.0013	0.0004	0.0021	0.0003	0.0002
J2	0	0.0450	0.0806	0.0092	0.0023	0.0065	0.0000	0.0040	0.0105	0.0048	0.0013
R1	0	0.0035	0.0467	0.0468	0.0102	0.0064	0.0001	0.0060	0.0039	0.0016	0.0019
R2	0	0.0038	0.0003	0.0060	0.0074	0.0105	0.0041	0.0078	0	0.0004	0.0005
R3	0	0	0.0068	0.0312	0.0000	0.0609	0.0283	0.0406	0.0001	0.0020	0.0012
R4	0	0	0	0.0086	0.0053	0.0401	0.0291	0.0278	0.0001	0	0
V	0	0	0.0144	0.0126	0.0117	0.0331	0.0171	0.0245	0.0000	0.0027	0
DJ	0	0.0056	0.0111	0.0000	0.0000	0.0000	0.0000	0.0000	0.0086	0.0000	0.0000
DR	0	0	0	0.0107	0.0003	0.0002	0.0006	0	0	0.0013	0
DV	0	0	0	0	0	0	0	0.0050	0	0	0.0011
1999-00											
Sd	0	0	0	0	**0.0009**	**0.0186**	**0.0465**	0	0	0	0
J1	0.0660	0.0486	0.0015	0.0000	0	0	0	0	0	0.0015	0.0006
J2	0	0.0438	0.0590	0.0032	0.0018	0.0014	0.0001	0.0007	0.0159	0.0035	0.0014
R1	0	0.0010	0.0348	0.0293	0.0026	0.0082	0.0042	0.0010	0.0185	0.0051	0
R2	0	0.0010	0.0013	0.0030	0.0025	0.0197	0.0081	0.0074	0.0001	0	0
R3	0	0.0012	0.0048	0.0313	0.0125	0.0535	0.0403	0.0160	0.0001	0.0030	0.0000
R4	0	0	0.0045	0.0130	0.0177	0.0446	0.1209	0.0177	0.0001	0.0086	0
V	0	0	0.0038	0.0177	0.0025	0.0117	0.0001	0.0055	0.0088	0	0.0009
DJ	0	0.0227	0.0209	0	0	0	0	0	0.0214	0	0
DR	0	0	0	0.0073	0.0024	0.0051	0.0070	0	0	0.0053	0
DV	0	0	0	0	0	0	0	0.0029	0	0	0.0013

Table A3.4, continued Annual elasticity matrices for a) populations NS, ES, WS; b) microsite types A, B, C, D; and c) densities classes Low, Med-low, Med-high, High, for the transition periods 1996-97, 1997-98, 1998-99, 1999-00. Stage classes reflect plant size and/or demographic state (Table 2). Bolded entries are the fecundity terms.

(C) Low density

Stage	Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1996-97											
Sd	0	0	0	0	**0.0022**	**0.0229**	**0.0622**	0	0	0	0
J1	0.0873	0.0166	0.0040	0	0	0	0	0	0.0097	0.0001	0
J2	0	0.0600	0.0496	0.0024	0	0.0001	0.0001	0.0001	0.0353	0.0025	0.0009
R1	0	0.0042	0.0331	0.0154	0.0029	0.0040	0.0014	0.0037	0.0045	0.0022	0.0001
R2	0	0	0.0002	0.0037	0.0073	0.0100	0.0097	0.0093	0.0002	0.0009	0.0004
R3	0	0	0.0003	0.0130	0.0114	0.0255	0.0229	0.0346	0.0002	0.0013	0.0004
R4	0	0	0	0.0117	0.0152	0.0290	0.0767	0.0514	0.0003	0.0007	0
V	0	0	0.0396	0.0211	0.0023	0.0143	0.0081	0.0148	0.0109	0.0045	0.0013
DJ	0	0.0369	0.0241	0	0	0	0	0	0.0382	0	0
DR	0	0	0	0.0042	0.0004	0.0038	0.0039	0	0	0.0037	0
DV	0	0	0	0	0	0	0	0.0031	0	0	0.0006
1997-98											
Sd	0	0	0	0	**0.0012**	**0.0170**	**0.0123**	0	0	0	0
J1	0.0305	0.0135	0.0221	0.0024	0	0	0.0004	0	0.0003	0.0002	0.0002
J2	0	0.0350	0.1603	0.0075	0.0001	0.0014	0.0004	0.0154	0.0676	0.0002	0.0002
R1	0	0.0031	0.0134	0.0065	0.0024	0.0006	0	0.0045	0.0002	0.0001	0.0001
R2	0	0	0.0002	0	0.0029	0.0061	0.0019	0.0110	0.0002	0.0076	0.0001
R3	0	0	0.0052	0.0034	0.0037	0.0029	0.0052	0.0280	0.0002	0.0001	0.0001
R4	0	0	0	0.0001	0.0032	0.0017	0.0068	0.0181	0.0004	0.0002	0.0002
V	0	0	0.0036	0.0059	0.0117	0.0149	0.0028	0.0269	0.0322	0.0068	0.0001
DJ	0	0.0179	0.0833	0	0	0	0	0	0.2211	0	0
DR	0	0	0	0.0049	0.0048	0.0043	0.0010	0	0	0.0244	0
DV	0	0	0	0	0	0	0	0.0011	0	0	0.0039

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1998-99											
Sd	0	0	0	0	**0.0011**	**0.0234**	**0.0369**	0	0	0	0
J1	0.0614	0.1569	0.0038	0.0012	0	0.0014	0.0020	0	0.0053	0	0
J2	0	0.0576	0.0631	0.0048	0.0000	0.0027	0.0001	0.0037	0.0167	0.0009	0.0008
R1	0	0.0006	0.0363	0.0163	0.0040	0.0001	0.0001	0.0039	0.0028	0.0010	0.0007
R2	0	0	0.0043	0.0034	0.0105	0.0114	0.0110	0.0083	0.0030	0.0010	0
R3	0	0.0057	0.0051	0.0245	0.0198	0.0672	0.0196	0.0283	0.0001	0.0021	0
R4	0	0	0	0.0041	0.0150	0.0543	0.0594	0.0124	0.0001	0.0015	0
V	0	0	0.0182	0.0065	0.0020	0.0108	0.0157	0.0099	0.0028	0.0022	0.0007
DJ	0	0.0111	0.0196	0	0	0	0	0	0.0065	0	0
DR	0	0	0	0.0050	0.0006	0.0011	0.0021	0	0	0.0008	0
DV	0	0	0	0	0	0	0	0.0023	0	0	0.0004
1999-00											
Sd	0	0	0	0	**0.0019**	**0.0287**	**0.0232**	0	0	0	0
J1	0.0538	0.0497	0.0002	0	0	0	0	0	0.0001	0.0024	0
J2	0	0.0380	0.1325	0.0046	0.0011	0.0058	0.0000	0.0011	0.0398	0.0027	0.0014
R1	0	0.0001	0.0321	0.0336	0.0036	0.0072	0.0009	0.0034	0.0138	0	0
R2	0	0.0010	0.0035	0.0068	0.0085	0.0068	0.0067	0.0080	0.0001	0.0001	0
R3	0	0	0.0005	0.0152	0.0177	0.0610	0.0357	0.0263	0.0002	0.0060	0
R4	0	0	0.0066	0.0003	0.0064	0.0384	0.0350	0.0211	0.0003	0.0001	0
V	0	0	0.0145	0.0246	0.0000	0.0124	0.0055	0.0116	0.0002	0.0041	0.0021
DJ	0	0.0174	0.0372	0	0	0	0	0	0.0429	0	0
DR	0	0	0	0.0098	0.0023	0.0022	0.0011	0	0	0.0128	0
DV	0	0	0	0	0	0	0	0.0035	0	0	0.0018

(C) **Med-low density**

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1996-97											
Sd	0	0	0	0	**0.0052**	**0.0179**	**0.0512**	0	0	0	0
J1	0.0743	0.0135	0.0026	0	0	0	0	0	0.0068	0.0001	0
J2	0	0.0500	0.0358	0.0051	0	0.0015	0.0001	0.0029	0.0251	0.0023	0.0031
R1	0	0.0042	0.0494	0.0198	0.0018	0.0065	0.0049	0.0111	0.0039	0.0024	0.0006
R2	0	0	0.0002	0.0036	0.0095	0.0062	0.0063	0.0184	0.0001	0.0008	0.0012
R3	0	0	0.0002	0.0152	0.0025	0.0501	0.0165	0.0386	0.0001	0.0010	0.0013
R4	0	0	0.0057	0.0049	0.0128	0.0253	0.0768	0.0471	0.0002	0.0005	0
V	0	0	0.0189	0.0550	0.0127	0.0148	0.0126	0.0291	0.0067	0.0036	0.0040
DJ	0	0.0296	0.0132	0	0	0	0	0	0.0262	0	0
DR	0	0	0	0.0009	0.0017	0.0033	0.0050	0	0	0.0032	0
DV	0	0	0	0	0	0	0	0.0102	0	0	0.0019
1997-98											
Sd	0	0	0	0	**0.0005**	**0.0113**	**0.0012**	0	0	0	0
J1	0.0130	0.0036	0.0002	0	0	0	0	0	0.0002	0.0001	0.0002
J2	0	0.0132	0.1314	0.0155	0.0000	0.0037	0.0001	0.0182	0.0485	0.0001	0.0002
R1	0	0	0.0169	0.0171	0.0005	0.0024	0.0001	0.0088	0.0001	0.0001	0.0204
R2	0	0	0.0002	0.0001	0.0006	0.0039	0.0005	0.0063	0.0001	0.0001	0.0002
R3	0	0	0.0043	0.0018	0.0014	0.0038	0.0005	0.0295	0.0001	0.0001	0.0002
R4	0	0	0	0.0022	0.0008	0.0001	0.0003	0.0004	0.0002	0.0001	0.0002
V	0	0	0.0115	0.0162	0.0074	0.0101	0.0012	0.0961	0.0177	0.0205	0.0464
DJ	0	0.0004	0.0664	0	0	0	0	0	0.1107	0	0
DR	0	0	0	0.0135	0.0006	0.0065	0.0004	0	0	0.0197	0
DV	0	0	0	0	0	0	0	0.0679	0	0	0.1014

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1998-99											
Sd	0	0	0	0	**0**	**0.0320**	**0.0296**	0	0	0	0
J1	0.0616	0.1877	0.0026	0	0	0	0	0.0002	0.0010	0.0002	0
J2	0	0.0623	0.1093	0.0111	0.0009	0.0033	0	0.0018	0.0039	0.0017	0.0003
R1	0	0.0006	0.0620	0.0298	0.0012	0.0001	0.0095	0.0028	0.0009	0.0011	0.0003
R2	0	0	0.0002	0.0056	0.0000	0.0124	0.0001	0.0038	0.0008	0	0.0001
R3	0	0	0.0093	0.0424	0.0069	0.0689	0.0405	0.0188	0	0.0003	0.0002
R4	0	0	0	0.0002	0.0112	0.0613	0.0294	0.0068	0	0.0010	0
V	0	0	0.0064	0.0146	0.0024	0.0086	0.0001	0.0094	0.0009	0.0023	0.0003
DJ	0	0.0027	0.0048	0	0	0	0	0	0.0013	0	0
DR	0	0	0	0.0047	0.0005	0.0007	0.0007	0	0	0.0005	0
DV	0	0	0	0	0	0	0	0.0012	0	0	0.0001
1999-00											
Sd	0	0	0	0	**0**	**0.0318**	**0.0258**	0	0	0	0
J1	0.0576	0.0579	0.0001	0	0	0	0	0	0.0001	0	0
J2	0	0.0435	0.0857	0.0074	0.0001	0.0042	0.0000	0.0001	0.0238	0.0117	0
R1	0	0.0013	0.0386	0.0219	0.0034	0.0158	0.0001	0.0001	0.0129	0.0042	0
R2	0	0	0.0002	0.0022	0.0154	0.0280	0.0057	0.0154	0.0001	0.0001	0
R3	0	0.0017	0.0051	0.0344	0.0318	0.0723	0.0246	0.0254	0.0001	0.0001	0
R4	0	0	0.0037	0.0038	0.0066	0.0262	0.0357	0.0131	0.0001	0.0081	0
V	0	0	0.0172	0.0155	0.0076	0.0101	0.0037	0.0212	0.0001	0.0001	0.0084
DJ	0	0.0114	0.0257	0	0	0	0	0	0.0242	0	0
DR	0	0	0	0.0131	0.0022	0.0071	0.0018	0	0	0.0106	0
DV	0	0	0	0	0	0	0	0.0084	0	0	0.0037

(C) **Med-high density**

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1996-97											
Sd	0	0	0	0	**0.0201**	**0.0276**	**0.0443**	0	0	0	0
J1	0.0920	0.0155	0.0017	0	0	0	0	0	0.0092	0.0001	0
J2	0	0.0618	0.0289	0.0078	0.0000	0.0026	0.0000	0.0032	0.0368	0.0018	0.0010
R1	0	0.0060	0.0440	0.0216	0.0060	0.0054	0.0039	0.0010	0.0065	0.0021	0.0002
R2	0	0	0.0050	0.0151	0.0115	0.0145	0.0074	0.0134	0.0003	0.0010	0.0007
R3	0	0	0.0202	0.0154	0.0001	0.0169	0.0141	0.0311	0.0002	0.0010	0.0005
R4	0	0	0	0.0085	0.0193	0.0163	0.0555	0.0386	0.0003	0.0006	0
V	0	0	0.0134	0.0255	0.0116	0.0112	0.0117	0.0297	0.0126	0.0036	0.0017
DJ	0	0.0351	0.0308	0	0	0	0	0	0.0368	0	0
DR	0	0	0	0.0026	0.0002	0.0050	0.0024	0	0	0.0028	0
DV	0	0	0	0	0	0	0	0.0041	0	0	0.0007
1997-98											
Sd	0	0	0	0	**0.0015**	**0.0076**	**0.0035**	0	0	0	0
J1	0.0125	0.0326	0.0077	0	0	0.0018	0	0	0.0001	0.0001	0.0001
J2	0	0.0075	0.0843	0.0116	0.0016	0.0016	0.0002	0.0002	0.0688	0.0067	0.0001
R1	0	0.0001	0.0211	0.0277	0.0016	0.0066	0.0000	0.0133	0.0001	0.0001	0.0001
R2	0	0	0.0003	0.0021	0.0164	0.0144	0.0017	0.0194	0.0002	0.0001	0.0001
R3	0	0	0.0003	0.0041	0.0023	0.0253	0.0036	0.0652	0.0002	0.0001	0.0001
R4	0	0	0	0.0001	0.0001	0.0028	0.0037	0.0115	0.0002	0.0001	0.0001
V	0	0	0.0139	0.0154	0.0254	0.0325	0.0050	0.1138	0.0002	0.0177	0.0314
DJ	0	0.0147	0.0551	0	0	0	0	0	0.0650	0	0
DR	0	0	0	0.0096	0.0059	0.0085	0.0009	0	0	0.0306	0
DV	0	0	0	0	0	0	0	0.0318	0	0	0.0276

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1998-99											
Sd	0	0	0	0	**0.0039**	**0.0120**	**0.0482**	0	0	0	0
J1	0.0641	0.1087	0.0022	0.0006	0	0	0.0024	0.0003	0.0005	0.0004	0
J2	0	0.0625	0.0572	0.0029	0.0016	0.0001	0.0001	0.0057	0.0074	0.0021	0.0003
R1	0	0.0006	0.0410	0.0202	0.0001	0.0068	0.0001	0.0052	0.0006	0.0024	0.0013
R2	0	0	0.0062	0.0129	0.0115	0.0131	0.0101	0.0168	0	0.0013	0.0006
R3	0	0	0.0163	0.0137	0.0274	0.0834	0.0319	0.0213	0	0.0033	0.0018
R4	0	0	0	0.0061	0.0171	0.0625	0.0478	0.0160	0	0.0007	0
V	0	0	0.0154	0.0214	0.0048	0.0182	0.0083	0.0204	0.0006	0.0005	0.0009
DJ	0	0.0075	0.0016	0.0000	0	0	0	0	0.0004	0	0
DR	0	0	0	0.0004	0.0060	0.0030	0.0014	0	0	0.0009	0
DV	0	0	0	0	0	0	0	0.0048	0	0	0
1999-00											
Sd	0	0	0	0	**0**	**0.0206**	**0.0155**	0	0	0	0
J1	0.0361	0.0792	0.0033	0	0	0	0	0	0.0001	0.0072	0
J2	0	0.0309	0.0830	0.0161	0.0001	0.0032	0	0.0024	0.0000	0.0066	0.0033
R1	0	0.0001	0.0187	0.0651	0.0157	0.0169	0.0006	0.0082	0.0000	0.0001	0
R2	0	0	0.0020	0.0074	0.0356	0.0262	0.0068	0.0133	0.0467	0.0090	0
R3	0	0.0013	0.0021	0.0153	0.0551	0.0293	0.0079	0.0240	0.0001	0.0093	0.0046
R4	0	0	0	0.0003	0.0150	0.0074	0.0142	0.0112	0.0001	0.0002	0
V	0	0	0.0038	0.0102	0.0164	0.0261	0.0023	0.0122	0.0001	0.0083	0
DJ	0	0.0144	0.0327	0	0	0	0	0	0.0167	0	0
DR	0	0	0	0.0111	0.0091	0.0193	0.0012	0	0	0.0294	0
DV	0	0	0	0	0	0	0	0.0080	0	0	0.0015

(C) **High density**

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1996-97											
Sd	0	0	0	0	**0.0058**	**0.0241**	**0.0423**	0	0	0	0
J1	0.0722	0.0119	0.0001	0	0	0	0	0	0.0053	0.0002	0
J2	0	0.0473	0.0383	0.0059	0	0.0001	0.0011	0.0054	0.0212	0.0035	0.0006
R1	0	0.0043	0.0456	0.0194	0.0001	0.0098	0.0053	0.0064	0.0035	0.0039	0.0001
R2	0	0	0.0036	0.0089	0.0090	0.0185	0.0118	0.0188	0.0001	0.0012	0.0003
R3	0	0	0.0109	0.0135	0.0318	0.0344	0.0341	0.0381	0.0001	0.0015	0.0003
R4	0	0	0	0.0173	0.0117	0.0482	0.0372	0.0350	0.0001	0.0008	0
V	0	0	0.0152	0.0282	0.0114	0.0235	0.0157	0.0432	0.0056	0.0054	0.0008
DJ	0	0.0261	0.0098	0	0	0	0	0	0.0206	0	0
DR	0	0	0	0.0052	0.0025	0.0059	0.0029	0	0	0.0046	0
DV	0	0	0	0	0	0	0	0.0021	0	0	0.0004
1997-98											
Sd	0	0	0	0	0.0018	0.0052	0.0018	0	0	0	0
J1	0.0088	0.0392	0.0127	0.0033	0	0	0	0.0024	0.0124	0	0
J2	0	0.0318	0.1425	0.0192	0.0029	0.0038	0.0003	0.0141	0.0484	0.0041	0.0206
R1	0	0.0072	0.0419	0.0614	0	0.0052	0.0006	0.0239	0.0001	0.0140	0
R2	0	0	0.0004	0.0002	0.0067	0.0027	0.0011	0.0191	0.0001	0.0001	0
R3	0	0	0.0004	0.0166	0.0025	0.0070	0.0007	0.0335	0.0001	0.0001	0
R4	0	0	0	0.0002	0	0.0001	0.0014	0.0074	0.0002	0.0001	0
V	0	0	0.0290	0.0300	0.0091	0.0252	0.0035	0.0607	0.0001	0.0242	0
DJ	0	0.0007	0.0608	0	0	0	0	0	0.0531	0	0
DR	0	0	0	0.0234	0.0071	0.0118	0.0002	0	0	0.0096	0
DV	0	0	0	0	0	0	0	0.0208	0	0	0

Stage	Stage Sd	J1	J2	R1	R2	R3	R4	V	DJ	DR	DV
1998-99											
Sd	0	0	0	0	**0**	**0.0094**	**0.0597**	0	0	0	0
J1	0.0691	0.1580	0.0023	0.0007	0	0	0	0	0	0	0
J2	0	0.0457	0.0412	0.0105	0	0.0023	0.0001	0.0042	0.0036	0.0006	0.0003
R1	0	0.0069	0.0374	0.0286	0	0.0062	0.0001	0.0065	0.0032	0.0007	0
R2	0	0.0091	0.0002	0.0021	0.0063	0.0121	0.0001	0.0106	0	0.0003	0
R3	0	0	0.0025	0.0125	0.0079	0.0324	0.0385	0.0321	0	0.0008	0.0012
R4	0	0	0.0076	0.0193	0.0194	0.0436	0.0789	0.0312	0	0.0002	0
V	0	0	0.0132	0.0131	0.0070	0.0217	0.0229	0.0219	0.0076	0.0007	0.0005
DJ	0	0.0104	0.0041	0	0	0	0	0	0.0047	0	0
DR	0	0	0	0.0029	0.0001	0.0003	0.0001	0	0	0.0001	0
DV	0	0	0	0	0	0	0	0.0021	0	0	0.0003
1999-00											
Sd	0	0	0	0	**0**	**0.0182**	**0.0342**	0	0	0	0
J1	0.0524	0.0846	0.0017	0	0	0	0	0	0.0051	0	0.0038
J2	0	0.0515	0.0721	0.0105	0.0021	0.0028	0.0012	0.0024	0	0	0.0045
R1	0	0.0002	0.0357	0.0358	0.0001	0.0159	0.0081	0.0051	0.0170	0.0113	0
R2	0	0	0.0002	0.0057	0.0079	0.0160	0.0087	0.0199	0.0001	0	0
R3	0	0	0.0089	0.0297	0.0128	0.0473	0.0211	0.0186	0.0001	0	0
R4	0	0	0	0.0161	0.0045	0.0091	0.0374	0.0184	0.0001	0.0347	0
V	0	0	0.0024	0.0167	0.0156	0.0174	0.0057	0.0165	0.0150	0	0
DJ	0	0.0113	0.0261	0	0	0	0	0	0	0	0
DR	0	0	0.0000	0.0148	0.0156	0.0118	0.0040	0	0	0.0049	0
DV	0	0	0	0	0	0	0	0.0084	0	0	0.0008

Appendix 4.1 Loglinear analysis of transition matrices (*C. macrocarpus*)

To test for effects of site and year on the fate of *C. macrocarpus* individuals, i.e., to show if matrices differed among locations and/or years, I conducted a loglinear contingency analysis. In the analysis the response variable was fate (*F*), and the explanatory variables were state (*S*), time (*T*), and location (*L*). Mortality was included in the analysis as a fate category. Following hypothesis testing, loglinear models were ranked according to the Akaike information criterion (*AIC*) (Akaike 1973, Burnham and Anderson 1998), using procedures outlined in Caswell (2001). Although the loglinear analysis showed significant effects of both site and year (Table A4.1), comparisons of relative *AIC* values revealed that temporal variation in the matrices accounted for most of these effects. Further decomposition of G^2 shows that the lack of the fit of the model *STL, SF* is mostly explained by the interaction of fate and time in all stages except Sd (seedlings) and dormant vegetative plants (DJ and DV) (Table A4.2). Because an earlier analysis of *C. lyallii* matrices based on 11 life stages (see *Chapter* 3, Table 3.5) had revealed a similar pattern, I pooled data from the three populations of each species to construct eight new matrices with higher sample sizes than the original, site-specific matrices. Loglinear analyses were carried out using Statistix, release 1 (Analytical Software 1996).

Table A4.1.1 Loglinear contingency analysis of the effect of location (*L*) and year (*T*) on the demographic fate (*F*) of *Calochortus macrocarpus*, conditional on initial state (*S*) (after Caswell 2001). For each observation type, goodness-of-fit G^2 values were calculated by fitting the saturated model (*STL,SF*) to stage-classified transition data (after adding 0.5 to each cell, as suggested by Fingleton 1984) from three time periods (1997-98, 1998-99, and 1999-00). Models are ranked according to the Akaike information criterion (*AIC*), where Δ *AIC* is measured relative to the *AIC* for the best model (*STL,STF* in all cases).

Model	G^2	*df*	*P*	*AIC*	Δ *AIC*
M1 = *STL, SF*	700.56	512	< .0001	-323.4	182.2
M2 = *STL,STF*	262.36	384	1.0000	-505.6	0.0
M3 = *STL, SLF*	532.11	384	< .0001	-235.9	269.8
M4 = *STL, STF, SLF*	105.36	256	1.0000	-406.6	99.0
M5 = *SFTL*	0.00	0	1.0000	0.0	505.6

Effect	Contrast	ΔG^2	Δ*df*	*P*
T	M2 vs. M1	438.20	128.00	< .0001
T	M4 vs. M3	426.75	128.00	< .0001
L	M3 vs. M1	168.45	128.00	0.0096
L	M4 vs. M2	157.00	128.00	0.0416
T X L	M5 vs. M4	105.36	256.00	1.0000

Table A4.1.2 Decomposition of G^2 for *Calochortus macrocarpus* into separate tests, one for each initial state, of the effect of year (*T*) on fate (*F*). Here, the null hypothesis (independence of fate and time), represented by the model *TL,F*, is compared to a model containing the *FT* interaction (*TL,TF*). Transition rates for stage J1 (small juveniles) were only available for 1998-00 and thus were excluded from the analysis. Models are ranked according to the Akaike information criterion (*AIC*), where Δ *AIC* is measured relative to the *AIC* for the best model.

Stage	Model	G^2	*df*	ΔG^2	Δ*df*	*P*	*AIC*	Δ*AIC*
Sd	*TL, F*	19.58	64	8.15	16	0.9443	-108.42	0.0
	TL, TF	11.43	48				-84.57	23.9
J1	*TL, F*	-	-	-	-	-	-	-
	TL, TF							
J2	*TL, F*	150.6	64	107.46	16	< 0.0001	22.6	75.5
	TL, TF	43.14	48				-52.86	0.0
R1	*TL, F*	99.35	64	74.16	16	< 0.0001	-28.65	42.2
	TL, TF	25.19	48				-70.81	0.0
R2	*TL, F*	47.60	64	34.28	16	0.0050	-80.4	2.3
	TL, TF	13.32	48				-82.68	0.0
V	*TL, F*	224.73	64	132.38	16	< 0.0001	96.73	100.4
	TL, TF	92.35	48				-3.65	0.0
DJ	*TL, F*	57.65	64	24.96	16	0.0705	-70.35	0.0
	TL, TF	32.69	48				-63.31	7.0
DR	*TL, F*	44.17	64	33.06	16	0.0073	-83.83	1.1
	TL, TF	11.11	48				-84.89	0.0
DV	*TL, F*	56.88	64	23.75	16	0.0951	-71.12	0.0
	TL, TF	33.13	48				-62.87	8.3

Appendix 4.2 Calculating age-based parameters and lifetime event probabilities

Cochran and Ellner (1992) and Caswell (2001) show how to extract various age-specific life history traits (e.g., average life expectancy, age at maturity, and net reproductive rate) as well as age-based population parameters (e.g., age-within-stage distributions and generation time) from stage-classified data by decomposing the transition matrix into separate birth and survival matrices and treating the individual life cycle as a Markov chain. Let **T** describe transitions of living individuals and **F** the production of new individuals. The transition matrix can then be written

$$\mathbf{A} = \mathbf{T} + \mathbf{F}$$

and the movement of an individual through its life cycle can be described as an s+1 dimensional Markov chain with transition matrix

$$\mathbf{P} = \begin{pmatrix} \mathbf{T} & \mathbf{0} \\ \mathbf{m} & 1 \end{pmatrix} \text{ of dimension } \begin{pmatrix} s \times s & s \times 1 \\ s \times 1 & 1 \times 1 \end{pmatrix}$$

where s is the number of stages, s + 1 (death) is an absorbing state, and mj is the probability of death for stage j (Caswell 2001). The expected total times spent in each state i prior to absorption (i.e., death), conditional on an individual reaching state j, are given by a matrix

$$E(v_{ij}) = (\mathbf{I} - \mathbf{T})^{-1}$$
$$= \mathbf{N}$$

where **I** denotes the identity matrix and **N** is the fundamental matrix of the Markov chain.

To compute the probability of flowering before death, a new Markov chain, conditioned on absorption in state k ('flowering'), is created having a transition matrix

$$\mathbf{P'} = \begin{pmatrix} \mathbf{T'} & \mathbf{0} \\ \mathbf{M'} & \mathbf{I} \end{pmatrix}$$

Here, **T'** is a matrix of transitions of individuals that neither die nor reproduce, having entries

$$t'_{ij} = (1 - a_j)t_{ij} \qquad i, j \in \mathcal{T}$$

where α_j is the probability that an individual in stage i flowers in the interval $(t, t + 1)$ and $\mathcal{T}$ is the set of transient states; and **M'** is an s x 2 matrix giving the probabilities of

transitions from transient states to death and to the second absorbing state (i.e., 'flowering'), with entries

$$m'_{ij} = \begin{cases} (1-a_j)m_j & i = 1,\ j \in \mathcal{T} \\ a_j & i = 1,\ j \in \mathcal{T} \end{cases}$$

The probability of absorption in each state (i.e., death and flowering) is given, in matrix notation, by

$$\mathbf{B} = \mathbf{M}' (\mathbf{I} - \mathbf{T}')^{-1}$$

with the stage-specific probabilities of flowering before death contained in the second row $\mathbf{b}'_2$ of $\mathbf{B}$ (Caswell 2001).

The mean age at first reproduction (i.e., age at maturity) is equivalent to the expected time to absorption in 'reproduced-before-dying,' conditional on absorption in that state, and is given by

$$(E(n_i^{(c)})) = \mathbf{e}^{\mathrm{T}}(\mathbf{I} - \mathbf{T}^{(c)})^{-1}$$

where

$$\mathbf{T}^{(c)} = \mathrm{diag}\ (\mathbf{b}'_{2.})^{-1}\ \mathbf{T}'\mathrm{diag}\ (\mathbf{b}'_{2.})$$

and $\mathbf{e}^{\mathrm{T}}$ is a vector of ones, transposed. Multiplying the fertility matrix $\mathbf{F}$ by the fundamental matrix $\mathbf{N}$ (the expected number of time steps spent in each transient state) yields a matrix $\mathbf{R}$ containing the expected lifetime production of seedlings of an individual starting out in stage j. Entry r_{11} of $\mathbf{R}$ gives the mean number of offspring produced by a plant starting life in the seedling stage and is equivalent to the net reproductive rate, R_0 (Caswell 2001).

Appendix 4.3 Transition matrices

Table A4.3 Stage-based transition matrices for *Calochortus lyallii* and *C. macrocarpus* on Black Mt. for the transition periods 1996-97, 1997-98, 1998-99 and 1999-00, from census data pooled across populations. Stages: Sd = seedling, J1 = small juvenile, J2 = large juvenile, R1 =small reproductive, R2 = large reproductive, V = vegetative adult, DJ = dormant juvenile, DR = dormant reproductive, DV = dormant vegetative. (Bolded entries indicate fecundity terms.)

	Sd	J1	J2	R1	R2	V	DJ	DR	DV
					C. lyallii				
1996-97									
Sd	0.0000	0.0000	0.0000	**0.4989**	**1.3043**	0.0000	0.0000	0.0000	0.0000
J1	0.5209	0.1429	0.0087	0.0000	0.0000	0.0000	0.0972	0.0092	0.0010
J2	0.0000	0.4643	0.4551	0.0806	0.0703	0.0777	0.3174	0.1479	0.2435
R1	0.0000	0.0000	0.0348	0.1774	0.0884	0.0939	0.0010	0.0350	0.0673
R2	0.0000	0.0000	0.1101	0.4032	0.5261	0.4434	0.0010	0.0433	0.0673
V	0.0000	0.0000	0.1971	0.2097	0.1365	0.2201	0.0667	0.1817	0.2508
DJ	0.0000	0.3250	0.1075	0.0000	0.0000	0.0000	0.3908	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0419	0.0637	0.0000	0.0000	0.2331	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0540	0.0000	0.0000	0.1622
1997-98									
Sd	0.0000	0.0000	0.0000	**0.0866**	**0.5796**	0.0000	0.0000	0.0000	0.0000
J1	0.3464	0.3175	0.0251	0.0000	0.0040	0.0038	0.0212	0.0010	0.0010
J2	0.0000	0.4286	0.5363	0.0784	0.0747	0.1174	0.3814	0.1241	0.1198
R1	0.0000	0.0000	0.0028	0.1569	0.1111	0.0644	0.0010	0.0248	0.0010
R2	0.0000	0.0000	0.0335	0.0882	0.2242	0.1818	0.0010	0.0010	0.0010
V	0.0000	0.0000	0.1173	0.4020	0.3232	0.3333	0.0636	0.2730	0.2395
DJ	0.0000	0.1321	0.1266	0.0000	0.0000	0.0000	0.4661	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.1735	0.1427	0.0000	0.0000	0.4218	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.1722	0.0000	0.0000	0.4790
1998-99									
Sd	0.0000	0.0000	0.0000	**0.1296**	**1.1687**	0.0000	0.0000	0.0000	0.0000
J1	0.5690	0.7097	0.0349	0.0000	0.0162	0.0054	0.1495	0.0457	0.0207
J2	0.0000	0.1398	0.6223	0.0549	0.0432	0.1405	0.5435	0.3732	0.4142
R1	0.0000	0.0027	0.0284	0.1429	0.0811	0.1162	0.0272	0.0609	0.0414
R2	0.0000	0.0027	0.1048	0.5604	0.6649	0.4216	0.0010	0.2133	0.1864
V	0.0000	0.0000	0.1026	0.1099	0.1189	0.2135	0.0951	0.1980	0.2278
DJ	0.0000	0.0215	0.0498	0.0000	0.0000	0.0000	0.1416	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0527	0.0181	0.0000	0.0000	0.0729	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0384	0.0000	0.0000	0.0828
1999-00									
Sd	0.0000	0.0000	0.0000	**0.0250**	**0.5951**	0.0000	0.0000	0.0000	0.0000
J1	0.6878	0.5125	0.0051	0.0000	0.0000	0.0000	0.0282	0.0674	0.0640
J2	0.0000	0.2867	0.5816	0.1089	0.1186	0.0822	0.4801	0.2358	0.1920
R1	0.0000	0.0018	0.0170	0.1980	0.1349	0.1644	0.0282	0.0337	0.0010
R2	0.0000	0.0036	0.0799	0.3564	0.4791	0.3288	0.0010	0.1684	0.0640
V	0.0000	0.0000	0.0697	0.1188	0.1093	0.1826	0.0565	0.0674	0.1920
DJ	0.0000	0.1012	0.1234	0.0000	0.0000	0.0000	0.3123	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.1014	0.0631	0.0000	0.0000	0.2905	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.1081	0.0000	0.0000	0.3210

Table A4.3, continued.

Mean matrix									
Sd	0.0000	0.0000	0.0000	**0.1850**	**0.9119**	0.0000	0.0000	0.0000	0.0000
J1	0.5310	0.4206	0.0185	0.0000	0.0051	0.0023	0.0740	0.0308	0.0217
J2	0.0000	0.3298	0.5488	0.0807	0.0767	0.1045	0.4306	0.2202	0.2424
R1	0.0000	0.0011	0.0207	0.1688	0.1039	0.1097	0.0144	0.0386	0.0277
R2	0.0000	0.0016	0.0821	0.3521	0.4736	0.3439	0.0010	0.1065	0.0797
V	0.0000	0.0000	0.1217	0.2101	0.1720	0.2374	0.0705	0.1800	0.2275
DJ	0.0000	0.1449	0.1018	0.0000	0.0000	0.0000	0.3277	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0924	0.0719	0.0000	0.0000	0.2546	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0932	0.0000	0.0000	0.2613
				C. macrocarpus					
1996-97									
Sd	0.0000	0.0000	0.0000	**0.1987**	**0.4258**	0.0000	0.0000	0.0000	0.0000
J1	0.6373	0.5426	0.0010	0.0000	0.0000	0.0073	0.0961	0.0180	0.0157
J2	0.0000	0.2072	0.2564	0.0996	0.0379	0.0584	0.5176	0.2899	0.2880
R1	0.0000	0.0000	0.0010	0.0677	0.0833	0.1168	0.0354	0.0916	0.0646
R2	0.0000	0.0000	0.0256	0.0438	0.1439	0.1241	0.0000	0.0094	0.0000
V	0.0000	0.0078	0.3077	0.4781	0.4848	0.4526	0.0842	0.1950	0.3970
DJ	0.0000	0.0305	0.1897	0.0000	0.0000	0.0000	0.2277	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.1120	0.0652	0.0000	0.0000	0.3579	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.1226	0.0000	0.0000	0.2071
1997-98									
Sd	0.0000	0.0000	0.0000	**0.1612**	**0.6648**	0.0000	0.0000	0.0000	0.0000
J1	0.5795	0.5426	0.0010	0.0000	0.0167	0.0033	0.1176	0.0010	0.0010
J2	0.0000	0.2072	0.4842	0.0962	0.0667	0.1137	0.4706	0.2180	0.2381
R1	0.0000	0.0000	0.0105	0.0769	0.0167	0.0635	0.0010	0.0272	0.0010
R2	0.0000	0.0000	0.0010	0.0010	0.0500	0.0100	0.0000	0.0010	0.0000
V	0.0000	0.0078	0.1053	0.3077	0.4500	0.4548	0.1176	0.2452	0.4167
DJ	0.0000	0.0305	0.2611	0.0000	0.0000	0.0000	0.2353	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.2594	0.2192	0.0000	0.0000	0.4087	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.2348	0.0000	0.0000	0.2976
1998-99									
Sd	0.0000	0.0000	0.0000	**1.1648**	**3.7857**	0.0000	0.0000	0.0000	0.0000
J1	0.6154	0.5938	0.1484	0.0000	0.0000	0.0043	0.0010	0.0521	0.0450
J2	0.0000	0.1094	0.3681	0.1667	0.2500	0.1379	0.7090	0.2606	0.3601
R1	0.0000	0.0000	0.0110	0.0714	0.0833	0.0647	0.0373	0.0521	0.0600
R2	0.0000	0.0000	0.0110	0.0952	0.0833	0.0948	0.0000	0.0261	0.0000
V	0.0000	0.0156	0.2033	0.5000	0.5000	0.5216	0.0010	0.3388	0.4202
DJ	0.0000	0.0406	0.1286	0.0000	0.0000	0.0000	0.2239	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0071	0.0083	0.0000	0.0000	0.3198	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0763	0.0000	0.0000	0.1200

Table A4.3, continued.

1999-00									
Sd	0.0000	0.0000	0.0000	**0.9412**	**1.2605**	0.0000	0.0000	0.0000	0.0000
J1	0.7170	0.4915	0.0200	0.0000	0.0000	0.0000	0.1696	0.0010	0.0010
J2	0.0000	0.3051	0.5400	0.1333	0.0333	0.1078	0.3731	0.3911	0.2657
R1	0.0000	0.0000	0.0550	0.1000	0.1667	0.2888	0.0678	0.1955	0.1328
R2	0.0000	0.0000	0.0010	0.0667	0.0667	0.0345	0.0000	0.0010	0.0000
V	0.0000	0.0000	0.2000	0.5333	0.6000	0.4655	0.1357	0.0010	0.3543
DJ	0.0000	0.0203	0.1181	0.0000	0.0000	0.0000	0.2239	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0571	0.0432	0.0000	0.0000	0.3451	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0682	0.0000	0.0000	0.2036
Mean matrix									
Sd	0.0000	0.0000	0.0000	**0.6165**	**1.5342**	0.0000	0.0000	0.0000	0.0000
J1	0.6373	0.5426	0.0426	0.0000	0.0042	0.0037	0.0961	0.0180	0.0157
J2	0.0000	0.2072	0.4122	0.1239	0.0970	0.1044	0.5176	0.2899	0.2880
R1	0.0000	0.0000	0.0194	0.0790	0.0875	0.1334	0.0354	0.0916	0.0646
R2	0.0000	0.0000	0.0097	0.0517	0.0860	0.0659	0.0000	0.0094	0.0000
V	0.0000	0.0078	0.2041	0.4548	0.5087	0.4736	0.0846	0.1950	0.3970
DJ	0.0000	0.0305	0.1744	0.0000	0.0000	0.0000	0.2277	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.1089	0.0840	0.0000	0.0000	0.3579	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.1255	0.0000	0.0000	0.2071

Appendix 4.4 Left and right eigenvectors

Stable stage distributions varied among years (Table A4.4), reflecting variation in the structure of the matrices. In both species, the stable stage distribution tended to be dominated by small pre-reproductive plants (juveniles); among the adult stages, large reproductive plants were most abundant in *C. lyallii*, whereas vegetative plants dominated in *C. macrocarpus*. In years of projected population increase ($\lambda > 1$), seedlings comprised about 20% of the *C. lyallii* population and about 12 % of the *C. macrocarpus* population. In years of negative growth ($\lambda < 1$), seedling representation in the stable structure dropped to between 5-10% in *C. lyallii* and as low as 0.8% in *C. macrocarpus*. The proportion of the population 'at rest' (i.e., exhibiting extended dormancy) under equilibrium conditions ranged from 2-24% in *C. lyallii* and from 7-27% in *C. macrocarpus*. In contrast to seedlings, the proportion of dormant plants in the two populations tended to decline with increasing λ.

The relative representation ('reproductive values') of the different stage classes in the left eigenvector indicate that large reproductives are most important in contributing to future *C. lyallii* and *C. macrocarpus* populations (Table A7.1). Seedlings have the lowest reproductive values, followed by juveniles and dormant plants. This pattern is consistent between species and also among years.

Table A4.4 Estimated stable stage distributions (w) and stage-specific reproductive values (v), together with 95% bias-corrected bootstrap confidence intervals, for *Calochortus lyallii* and *C. macrocarpus* over four annual transitions at Black Mt. Stages: Sd = seedling, J1 = small juvenile, J2 = large juvenile, R1 =small reproductive, R2 = large reproductive, V = vegetative adult, DJ = dormant juvenile, DR = dormant reproductive, DV = dormant vegetative.

Year	Stage	w	95% bootstrap confidence interval	v	95% bootstrap confidence interval
			Calochortus lyallii		
1996-97					
	Sd	0.2207	0.2053--0.2355	1.0000	--
	J1	0.1411	0.1346--0.1475	2.0042	1.9696--2.0364
	J2	0.2119	0.1944--0.2325	2.5641	2.4401--2.6840
	R1	0.0372	0.0294--0.0451	3.8280	3.3690--4.3443
	R2	0.1624	0.1498--0.1761	4.5909	4.2431--4.9974
	V	0.1007	0.0886--0.1146	3.2985	3.0273--3.5866
	DJ	0.1051	0.0951--0.1166	1.8939	1.8613--1.9269
	DR	0.0147	0.0105--0.0190	1.6399	1.5581--1.7289
	DV	0.0062	0.0038--0.0094	2.2911	2.1763--2.4153
1997-98					
	Sd	0.0547	0.0420--0.0695	1.0000	--
	J1	0.0542	0.0397--0.0756	2.5616	2.3264--2.8429
	J2	0.3293	0.2678--0.3996	2.5257	2.1312--3.0365
	R1	0.0332	0.0234--0.0462	2.9754	2.3883--3.7516
	R2	0.0788	0.0620--0.0980	3.5912	3.0291--4.0324
	V	0.2092	0.1666--0.2554	2.8301	2.2258--3.5664
	DJ	0.1159	0.0756--0.1749	2.8576	2.4116--3.4486
	DR	0.0365	0.0247--0.0580	2.5040	1.9566--3.2470
	DV	0.0882	0.0496--0.1734	2.4230	1.4712--3.3625
1998-99					
	Sd	0.1858	0.1625--0.2086	1.0000	--
	J1	0.3549	0.3158--0.4024	1.8328	1.6694--2.0261
	J2	0.1872	0.1595--0.2204	3.6562	3.1385--4.3200
	R1	0.0296	0.0217--0.0393	5.2021	4.3447--6.2779
	R2	0.1625	0.1409--0.1858	6.4225	5.4200--7.6298
	V	0.0543	0.0429--0.0682	4.8211	4.1214--5.7326
	DJ	0.0188	0.0127--0.0269	3.1815	2.7083--3.7720
	DR	0.0046	0.0018--0.0100	4.2160	3.6060--5.0141
	DV	0.0022	0.0009--0.0042	4.2325	3.5796--5.1372
1999-00					
	Sd	0.0973	0.0845--0.1116	1.0000	--
	J1	0.1632	0.1413--0.1890	1.3996	1.2962--1.5412
	J2	0.3344	0.2949--0.3739	1.6074	1.4438--1.7900
	R1	0.0548	0.0439--0.0696	2.1858	1.8494--2.5735
	R2	0.1552	0.1368--0.1742	2.9342	2.6033--3.3013
	V	0.0714	0.0580--0.0863	2.0802	1.7999--2.3836
	DJ	0.0888	0.0685--0.1125	1.5277	1.3559--1.7303
	DR	0.0228	0.0164--0.0325	1.7574	1.4075--2.1535
	DV	0.0120	0.0073--0.0217	1.5393	1.0498--2.0731

Table A4.4, continued.

		Calochortus macrocarpus			
1996-97					
	Sd	0.0500	0.0366--0.0685	1.0000	--
	J1	0.1208	0.0942--0.1539	1.3916	1.3344--1.4386
	J2	0.1761	0.1361--0.2351	1.9095	1.6067--2.1767
	R1	0.0699	0.0505--0.0953	2.3282	1.9714--2.7812
	R2	0.0716	0.0463--0.0986	2.6860	2.2159--3.2711
	V	0.3656	0.2982--0.4290	2.3635	1.8885--2.9493
	DJ	0.0563	0.0269--0.1046	2.1293	1.9718--2.2608
	DR	0.0236	0.0163--0.0333	2.4162	2.1843--2.6990
	DV	0.0660	0.0398--0.0960	2.4428	2.1381--2.8131
1997-98					
	Sd	0.0075	0.0030--0.0150	1.0000	--
	J1	0.0677	0.0114--0.2040	1.5282	1.2999--1.8650
	J2	0.3615	0.2439--0.5085	2.1158	1.7108--2.6788
	R1	0.0263	0.0121--0.0444	2.0595	1.5436--2.7239
	R2	0.0036	0.0009--0.0091	2.8712	2.3115--3.6022
	V	0.2636	0.1362--0.3773	2.2996	1.8237--3.0291
	DJ	0.1483	0.0861--0.3148	2.2266	1.6974--2.8488
	DR	0.0160	0.0072--0.0342	2.2763	1.8299--2.9141
	DV	0.1053	0.0534--0.1967	2.4922	1.9636--3.2726
1998-99					
	Sd	0.1358	0.0652--0.2324	1.0000	--
	J1	0.3357	0.2331--0.4590	1.5290	1.2365--2.0437
	J2	0.2107	0.1458--0.2786	2.9984	1.9926--4.7883
	R1	0.0232	0.0120--0.0394	5.4807	3.6921--8.2827
	R2	0.0266	0.0166--0.0404	8.4993	2.6933--17.7183
	V	0.1926	0.1197--0.2827	4.5164	2.6542--7.7011
	DJ	0.0568	0.0362--0.0931	3.2581	2.1986--5.2888
	DR	0.0006	0.0001--0.0018	4.6661	2.9167--7.8861
	DV	0.0179	0.0087--0.0348	4.1114	2.6677--6.7307
1999-00					
	Sd	0.1170	0.0872--0.1571	1.0000	--
	J1	0.1866	0.1410--0.2420	1.4079	1.2252--1.6989
	J2	0.2619	0.2192--0.3176	2.2454	1.8224--2.8403
	R1	0.1035	0.0834--0.1266	3.4870	2.6683--4.5206
	R2	0.0164	0.0071--0.0288	3.9683	3.0826--5.1263
	V	0.2402	0.1893--0.2962	2.8711	2.2922--3.6794
	DJ	0.0442	0.0311--0.0647	2.1676	1.7379--2.7753
	DR	0.0100	0.0030--0.0209	2.3607	1.8137--3.1450
	DV	0.0203	0.0123--0.0326	2.5791	2.0424--3.3526

Appendix 4.5 Elasticity matrices

Table A4.5 Elasticity matrices for *Calochortus lyallii* and *C. macrocarpus* on Black Mt. for the transition periods 1996-97, 1997-98, 1998-99 and 1999-00, and for the mean annual matrix, from census data pooled across three populations. Stages: Sd = seedling, J1 = small juvenile, J2 = large juvenile, R1 =small reproductive, R2 = large reproductive, V = vegetative adult, DJ = dormant juvenile, DR = dormant reproductive, DV = dormant vegetative. For each matrix, the two largest elasticity values are bolded.

	Sd	J1	J2	R1	R2	V	DJ	DR	DV
					C. lyallii				
1996-97									
Sd	0.0000	0.0000	0.0000	0.0071	0.0810	0.0000	0.0000	0.0000	0.0000
J1	0.0881	0.0155	0.0014	0.0000	0.0000	0.0000	0.0078	0.0001	0.0000
J2	0.0000	0.0643	**0.0946**	0.0029	0.0112	0.0077	0.0327	0.0021	0.0015
R1	0.0000	0.0000	0.0108	0.0097	0.0210	0.0138	0.0002	0.0008	0.0006
R2	0.0000	0.0000	0.0410	0.0263	**0.1501**	0.0784	0.0002	0.0011	0.0007
V	0.0000	0.0000	0.0527	0.0098	0.0280	0.0280	0.0088	0.0034	0.0020
DJ	0.0000	0.0332	0.0165	0.0000	0.0000	0.0000	0.0298	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0010	0.0065	0.0000	0.0000	0.0021	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0048	0.0000	0.0000	0.0009
1997-98									
Sd	0.0000	0.0000	0.0000	0.0012	0.0195	0.0000	0.0000	0.0000	0.0000
J1	0.0208	0.0189	0.0091	0.0000	0.0003	0.0009	0.0027	0.0000	0.0001
J2	0.0000	0.0251	**0.1907**	0.0028	0.0064	0.0265	0.0477	0.0049	0.0114
R1	0.0000	0.0000	0.0012	0.0066	0.0111	0.0171	0.0001	0.0012	0.0001
R2	0.0000	0.0000	0.0169	0.0045	0.0271	0.0584	0.0002	0.0001	0.0001
V	0.0000	0.0000	0.0467	0.0161	0.0308	**0.0844**	0.0089	0.0121	0.0256
DJ	0.0000	0.0088	0.0509	0.0000	0.0000	0.0000	0.0660	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0062	0.0120	0.0000	0.0000	0.0165	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0373	0.0000	0.0000	0.0438
1998-99									
Sd	0.0000	0.0000	0.0000	0.0012	0.0594	0.0000	0.0000	0.0000	0.0000
J1	0.0606	**0.1442**	0.0037	0.0000	0.0015	0.0002	0.0016	0.0001	0.0000
J2	0.0000	0.0567	0.1331	0.0019	0.0080	0.0087	0.0117	0.0020	0.0010
R1	0.0000	0.0016	0.0086	0.0069	0.0214	0.0102	0.0008	0.0005	0.0001
R2	0.0000	0.0019	0.0394	0.0333	**0.2169**	0.0459	0.0000	0.0020	0.0008
V	0.0000	0.0000	0.0289	0.0049	0.0291	0.0174	0.0027	0.0014	0.0007
DJ	0.0000	0.0076	0.0093	0.0000	0.0000	0.0000	0.0026	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0021	0.0039	0.0000	0.0000	0.0004	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0028	0.0000	0.0000	0.0002

Table A4.5, continued

1999-00									
Sd	0.0000	0.0000	0.0000	0.0008	0.0538	0.0000	0.0000	0.0000	0.0000
J1	0.0546	0.0683	0.0014	0.0000	0.0000	0.0000	0.0020	0.0013	0.0006
J2	0.0000	0.0439	**0.1823**	0.0056	0.0173	0.0055	0.0400	0.0050	0.0022
R1	0.0000	0.0004	0.0072	0.0138	0.0267	0.0150	0.0032	0.0010	0.0000
R2	0.0000	0.0010	0.0457	0.0334	**0.1272**	0.0401	0.0002	0.0066	0.0013
V	0.0000	0.0000	0.0283	0.0079	0.0206	0.0158	0.0061	0.0019	0.0028
DJ	0.0000	0.0147	0.0368	0.0000	0.0000	0.0000	0.0247	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0057	0.0100	0.0000	0.0000	0.0068	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0069	0.0000	0.0000	0.0035
				C. macrocarpus					
1996-97									
Sd	0.0000	0.0000	0.0000	0.0074	0.0163	0.0000	0.0000	0.0000	0.0000
J1	0.0237	0.0487	0.0001	0.0000	0.0000	0.0020	0.0040	0.0003	0.0008
J2	0.0000	0.0255	0.0460	0.0071	0.0028	0.0218	0.0297	0.0070	0.0194
R1	0.0000	0.0000	0.0002	0.0059	0.0074	0.0531	0.0025	0.0027	0.0053
R2	0.0000	0.0000	0.0065	0.0044	0.0148	0.0651	0.0000	0.0003	0.0000
V	0.0000	0.0012	**0.0684**	0.0422	0.0438	**0.2088**	0.0060	0.0058	0.0330
DJ	0.0000	0.0042	0.0380	0.0000	0.0000	0.0000	0.0146	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0101	0.0060	0.0000	0.0000	0.0109	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0585	0.0000	0.0000	0.0178
1997-98									
Sd	0.0000	0.0000	0.0000	0.0022	0.0013	0.0000	0.0000	0.0000	0.0000
J1	0.0035	0.0291	0.0003	0.0000	0.0000	0.0007	0.0138	0.0000	0.0001
J2	0.0000	0.0154	**0.1922**	0.0028	0.0003	0.0329	0.0766	0.0038	0.0275
R1	0.0000	0.0000	0.0041	0.0022	0.0001	0.0179	0.0002	0.0005	0.0001
R2	0.0000	0.0000	0.0005	0.0000	0.0003	0.0039	0.0000	0.0000	0.0000
V	0.0000	0.0006	0.0454	0.0097	0.0020	**0.1431**	0.0208	0.0047	0.0523
DJ	0.0000	0.0024	0.1090	0.0000	0.0000	0.0000	0.0403	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0081	0.0009	0.0000	0.0000	0.0077	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0801	0.0000	0.0000	0.0405
1998-99									
Sd	0.0000	0.0000	0.0000	0.0104	0.0387	0.0000	0.0000	0.0000	0.0000
J1	0.0491	**0.1171**	0.0184	0.0000	0.0000	0.0005	0.0000	0.0000	0.0005
J2	0.0000	0.0423	0.0894	0.0045	0.0077	0.0306	0.0464	0.0002	0.0074
R1	0.0000	0.0000	0.0049	0.0035	0.0047	0.0262	0.0045	0.0001	0.0023
R2	0.0000	0.0000	0.0076	0.0072	0.0072	0.0597	0.0000	0.0001	0.0000
V	0.0000	0.0091	0.0743	0.0202	0.0231	**0.1744**	0.0001	0.0004	0.0131
DJ	0.0000	0.0171	0.0339	0.0000	0.0000	0.0000	0.0159	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0003	0.0004	0.0000	0.0000	0.0004	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0232	0.0000	0.0000	0.0034

Table A4.5, continued

1999-00									
Sd	0.0000	0.0000	0.0000	0.0428	0.0091	0.0000	0.0000	0.0000	0.0000
J1	0.0519	0.0567	0.0032	0.0000	0.0000	0.0000	0.0046	0.0000	0.0000
J2	0.0000	0.0562	**0.1395**	0.0136	0.0005	0.0255	0.0163	0.0038	0.0053
R1	0.0000	0.0000	0.0221	0.0159	0.0042	0.1062	0.0046	0.0030	0.0041
R2	0.0000	0.0000	0.0005	0.0120	0.0019	0.0144	0.0000	0.0000	0.0000
V	0.0000	0.0000	0.0661	0.0696	0.0124	**0.1410**	0.0076	0.0000	0.0091
DJ	0.0000	0.0036	0.0294	0.0000	0.0000	0.0000	0.0094	0.0000	0.0000
DR	0.0000	0.0000	0.0000	0.0061	0.0007	0.0000	0.0000	0.0036	0.0000
DV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0185	0.0000	0.0000	0.0047

Appendix 4.6 LTRE analysis

Figures A4.6a and b are surfaces plots showing the covariances of the matrix elements a_{ij} among years, and the resulting matrix of contributions of those covariances to the intraspecific variance in growth rate, $V_t(\lambda)$. For *C. lyallii*, the largest covariance occurs at peak C, corresponding to the variance in a_{15} (fecundity of large reproductives) (Fig. A4.6a). Peaks A and B represent the variance in a_{22} (J1 stasis) and the covariance between a_{16} and a_{15} (R2 and R1 fecundity), respectively. None of these elements except A makes a significant contribution to $V_t(\lambda)$. Most of the variance in λ is due instead to variance in a_{55} (stasis of large reproductives).

The covariance matrix of *C. macrocarpus* has a single large peak, corresponding to fecundity of large reproductives (Fig. A4.6b). However, the largest contribution to $V_t(\lambda)$ in this case is from variance in a_{46} (growth from vegetative to small reproductive), followed by the contribution from variance in a_{33} (stasis of large juveniles).

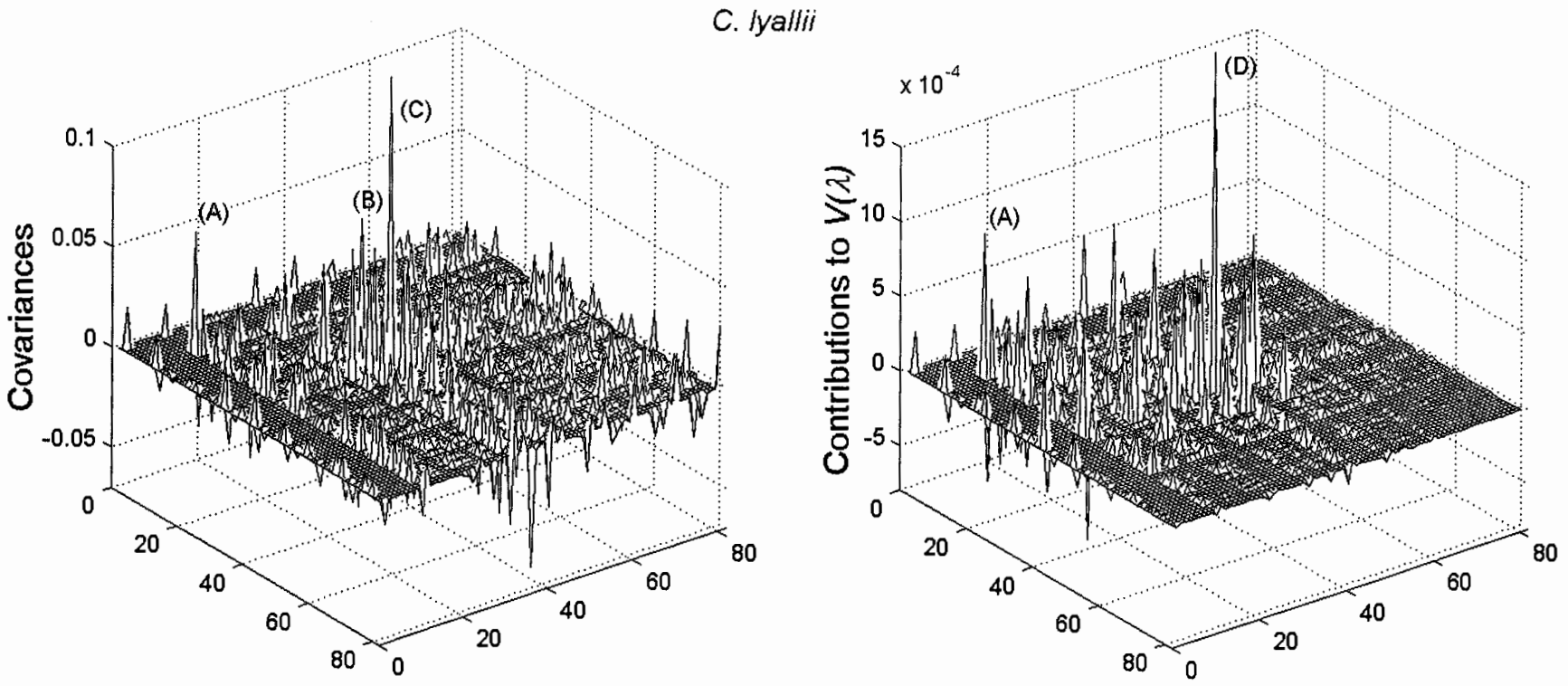

Figure A4.6a *Left:* Surface plot of the inter-year covariances of the matrix elements a_{ij} and a_{kl} for *Calochortus lyallii*, for the period 1996-2000. Variances appear on the diagonal; off-diagonal entries are covariances. Important peaks are identified by letter. A = the variance in J1 stasis; B = the covariance of R1 and R2 fecundity; C = the variance in R2 fecundity; G = the variance in R2 fecundity. *Right:* The contributions of the covariances to $V(\lambda)$. D = the variance in R2 stasis; E = the variance in J2 stasis; F = the variance in growth from V to R1. The 81 entries of the 9 x 9 matrix are arranged in column order: columns 1-9 = fates of seedlings ($a_{11},\ldots, a_{19}$), columns 10-18 = fates of small juveniles ($a_{12},\ldots, a_{92}$), etc.

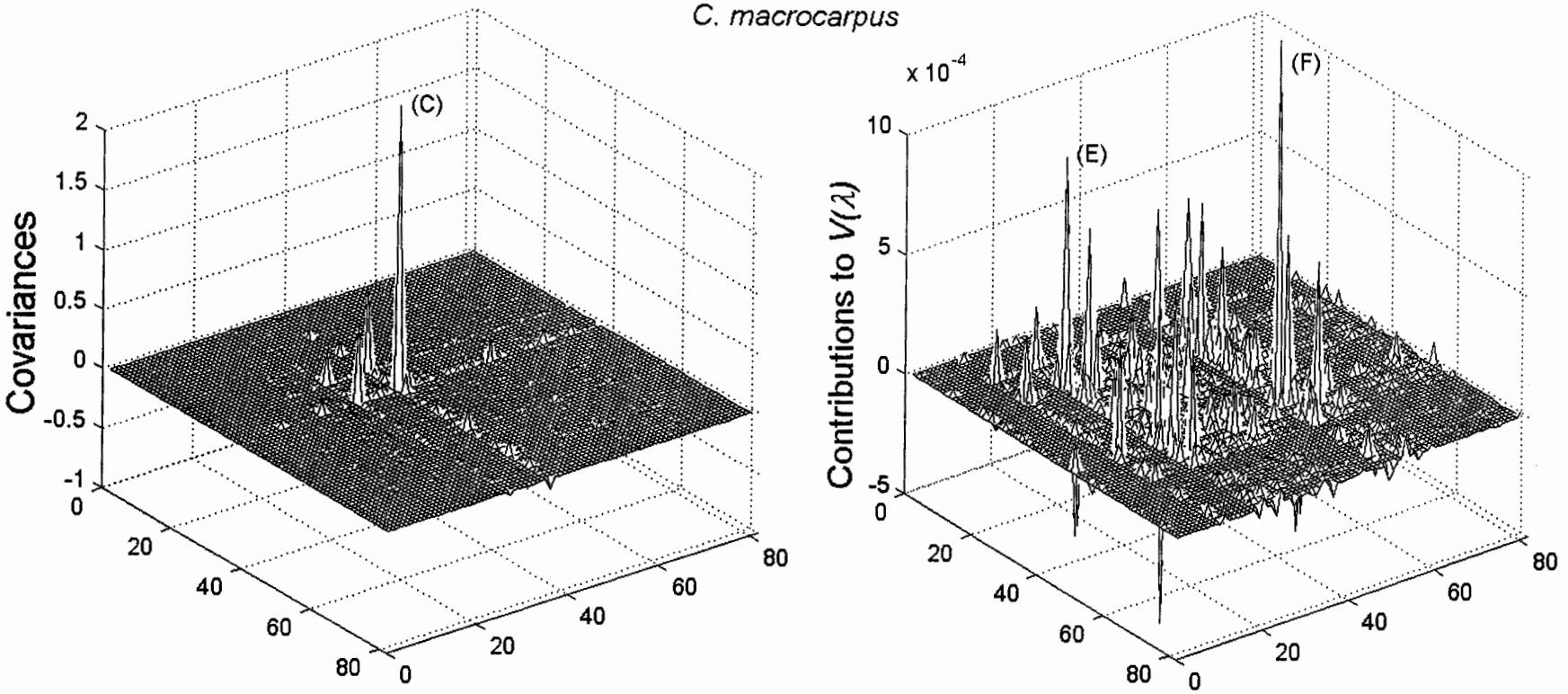

Figure A4.6b *Left:* Surface plot of the inter-year covariances of the matrix elements a_{ij} and a_{kl} for *Calochortus macrocarpus*, for the period 1996-2000. Variances appear on the diagonal; off-diagonal entries are covariances. Important peaks are identified by letter. A = the variance in J1 stasis; B = the covariance of R1 and R2 fecundity; C = the variance in R2 fecundity; G = the variance in R2 fecundity. *Right:* The contributions of the covariances to $V(\lambda)$. D = the variance in R2 stasis; E = the variance in J2 stasis; F = the variance in growth from V to R1. The 81 entries of the 9 x 9 matrix are arranged in column order: columns 1-9 = fates of seedlings ($a_{11},\ldots, a_{19}$), columns 10-18 = fates of small juveniles ($a_{12},\ldots, a_{92}$), etc.