Natural history, population ecology, and conservation biology

of Slim-leaf onion (*Allium amplectens*)

by

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We accept this thesis as conforming
to the required standard

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ABSTRACT

Slim-leaf onion (*Allium amplectens* Torr.) is found in western North America from British Columbia to southern California. It is rare in British Columbia and is on the Blue List of the British Columbia Conservation Data Centre. *Allium amplectens* typically occurs on dry rocky bluffs and meadows of Garry oak ecosystems in southwestern British Columbia.

I carried out a field inventory of known and potential population locations of *A. amplectens* in B.C. I relocated eight previously known populations, and (with others) discovered 21 new populations, mainly on the Gulf Islands, and around Nanaimo on Vancouver Island.

I also conducted experiments on the breeding system and reproductive biology of *A. amplectens.* Chromosome counts from 24 British Columbia populations showed them to be triploid ($2n = 3X = 21$) in all cases. Tests for agamospermy resulted in 0 seed set, in contrast to what might be expected in triploid plants. Tests for autogamy and self-compatibility yielded low seed set (about 3%), one-quarter that of control (outcrossed) plants. These findings suggest that *A. amplectens* either has an unbalanced form of meiosis, or is apomictic with a requirement for cross-pollination. Seed germination rates were very low (5%); vegetative propagation via bulb offsets is apparently the major mode of reproduction in these populations.

Populations were monitored at six different sites for total numbers of adult (flowering) plants, and I also mapped plants of all stages within marked plots. All of the monitored sites were moist in spring but dry by midsummer. Data from the marked plots

were used for Lefkovitch matrix (demographic) analyses. Matrix analyses indicated a decreasing growth rate for 3 of the annual transitions at the CFMETR (Nanoose Hill) location, suggesting these populations may be in gradual decline.

Rates of dormancy, as determined from monitoring of individual plants, were very high; 83.7% of the monitored marked plants exhibited dormancy at some point during the study. Dormancy in *A. amplectens* lasted most often for 1 year, but sometimes as long as 3 years. Yearly February-April precipitation levels were positively correlated with total plant numbers and inversely correlated with dormancy rates. Differences among habitats, especially with respect to substrate type, also influenced dormancy rates. Observed (above ground) population numbers of *A. amplectens* fluctuated less in rocky habitats than in those habitats with deeper soils.

However, high densities of nonflowering (vegetative) plants, rapid senescence, high dormancy rates, and bulb offsetting tended to make tracking of individual plants difficult. The monitoring of demographic changes and projecting of future population trajectories is especially challenging in these cases.

Although a number of new populations were discovered during the course of this study, they probably are not recently established, but rather may have existed for quite some time and have persisted because of their relative remoteness. The majority of populations that are no longer extant were located on southern Vancouver Island, where human impacts on habitat are extensive. This suggests that habitat loss is a major factor in the rarity of *A. amplectens* in B.C. Future efforts to conserve *A. amplectens* in B.C. should focus on the protection of known, extant populations.

Examiners:

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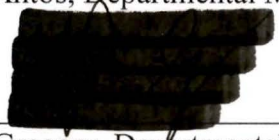

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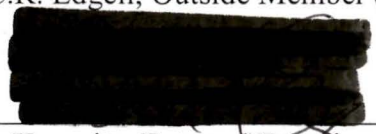

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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DEDICATION

To my parents, who instilled in me a belief in the value of an education from my very early years, and to my wife, Phyllis, and daughters, Allison and Debra, for their patience and suffering through the weekends 'daddy' worked on his thesis.

"The aim of science is not to open the door to
everlasting wisdom, but to set a limit
on everlasting error."
Bertolt Brecht

CHAPTER I. INTRODUCTION

1.0 Concepts of rarity and endangerment

Our planet currently supports approximately 250,000 species of vascular plants (Raven 1987), of which, perhaps as many as 60,000 are considered 'rare'(Primack 2000). The flora of British Columbia includes approximately 2,600 vascular plant species (Douglas et al. 1994). Of these, 271 vascular plant taxa are currently on the Red List, or are candidates for legal designation as endangered or threatened (BCCDC 2002). An additional 346 taxa are on the Blue List, or are considered vulnerable and possible candidates for the Red List. Thus a total of 617 species (almost 24%) is considered rare or potentially so in B.C. (BCCDC 2002).

Rare species are those that are low in total numbers of individuals. They may occur in widely separated small subpopulations, or be restricted to a single population (Drury 1974). Rabinowitz (1981), in her discussion of the nature of plant rarity, suggested three dimensions: geographic range (large or small), habitat specificity (broad or restricted) and local population size (large or small). Rabinowitz et al. (1986) subsequently applied this classification to 31 rare species in the British flora, and found that low numbers were most often associated with restricted geographic range or small population size rather than habitat specificity. The three aspects of rarity appeared to be independent of each other, suggesting that a separate examination of each component may be important in studying rare species.

Although gathering information on distribution and abundance is essential for determining which species are rare, this is only a first step. In order to understand the underlying reasons for the rarity of particular species, work may be needed on their

reproductive biology, genetics, demography, and habitat requirements, and on how these may be impacted by human activity. For example, Pantone et al. (1995) examined the reproductive attributes of an endangered plant as compared to a weedy congener and showed that the rare species had lower seed weight and fewer inflorescences per plant, flowers per inflorescence, and seeds per flower. Menges et al. (1986b) showed that herbivory often reduced seed production in the rare endemic *Pedicularis furbishiae.* Lesica et al. (1988) examined the endangered plant, *Howellia aquatilis* (Gray), and concluded that its lack of genetic diversity and narrow ecological amplitude resulted in its being more prone to extinction. However, Thompson and Hodgson (1996) suggested that abundance of rare plants is largely the product of recent habitat loss. Mehrhoff (1989), examining the dynamics of declining populations of an endangered orchid, noted that performance in one year is probably closely tied to resource accumulation in the previous season. Menges (1986a) considered that in order to predict the future of rare plant populations, a long-term commitment emphasizing matrix projection of stage-structured populations is required.

While rarity is probably a predictor of the long-term survival probability of a species, rarity in the natural habitat is likely not the prime reason for the current rate of species extinctions. For most tropical plant species, the principal factors leading to species endangerment and extinction are land exploitation and clearing, which in recent years have been occurring at an unprecedented rate (Raven 1987). Schemske et al. (1994) indicate that of the 14 categories of causes for endangerment in North American plant species, the six major factors, in decreasing order of significance, are development, grazing, harvesting, oil and gas mining, trampling, and water control. These six

categories account for endangerment in 65.5% of cases; urban development (at 20.4%) is by a factor of 2 the most significant single cause.

2.0 The study species

Slim-leaf onion (*Allium amplectens* Torr., family *Liliaceae*) is one of about 70 species of wild onions in North America (McNeal 1969) and is on the CDC Blue List in British Columbia. This species belongs to the western North American *Allium acuminatum* alliance (Rahman et al. 1966, McNeal 1969) and is most closely related to the California species *A. hickmanii* Eastwood and *A. serra* McNeal & Ownbey.

A single, flowering *A. amplectens* ramet possesses a slender, cylindrical scape bearing a terminal, umbellate inflorescence surrounded by 2 or 3 bracts (Figures 1-2). Flowers have six white to pale pink tepals, and stamens a little shorter than the perianth. The ovary has three carpels, each with two ovules (Hitchcock 1969), thus a single flower can produce up to 6 seeds. Leaves are usually 2-3 in number (occasionally 4) in large vegetative or adult plants; seedlings or first-year plants typically have only one leaf. Bulbs are reddish and ovoid to subspherical, the cross-reticulations of the outer coats forming a characteristic herring-bone pattern unique to this species (Figure 1E).

Allium amplectens is found in western North America from southwestern British Columbia to southern California (Figure 4). The most northerly report is from Mitlenatch Island, British Columbia, and the most southerly report is from near Cuyamaca Lake, San Diego County, California. The farthest inland occurrence is on Steens Mountain in Harney County, Oregon (McNeal 1969). Populations of *A. amplectens* in southwestern

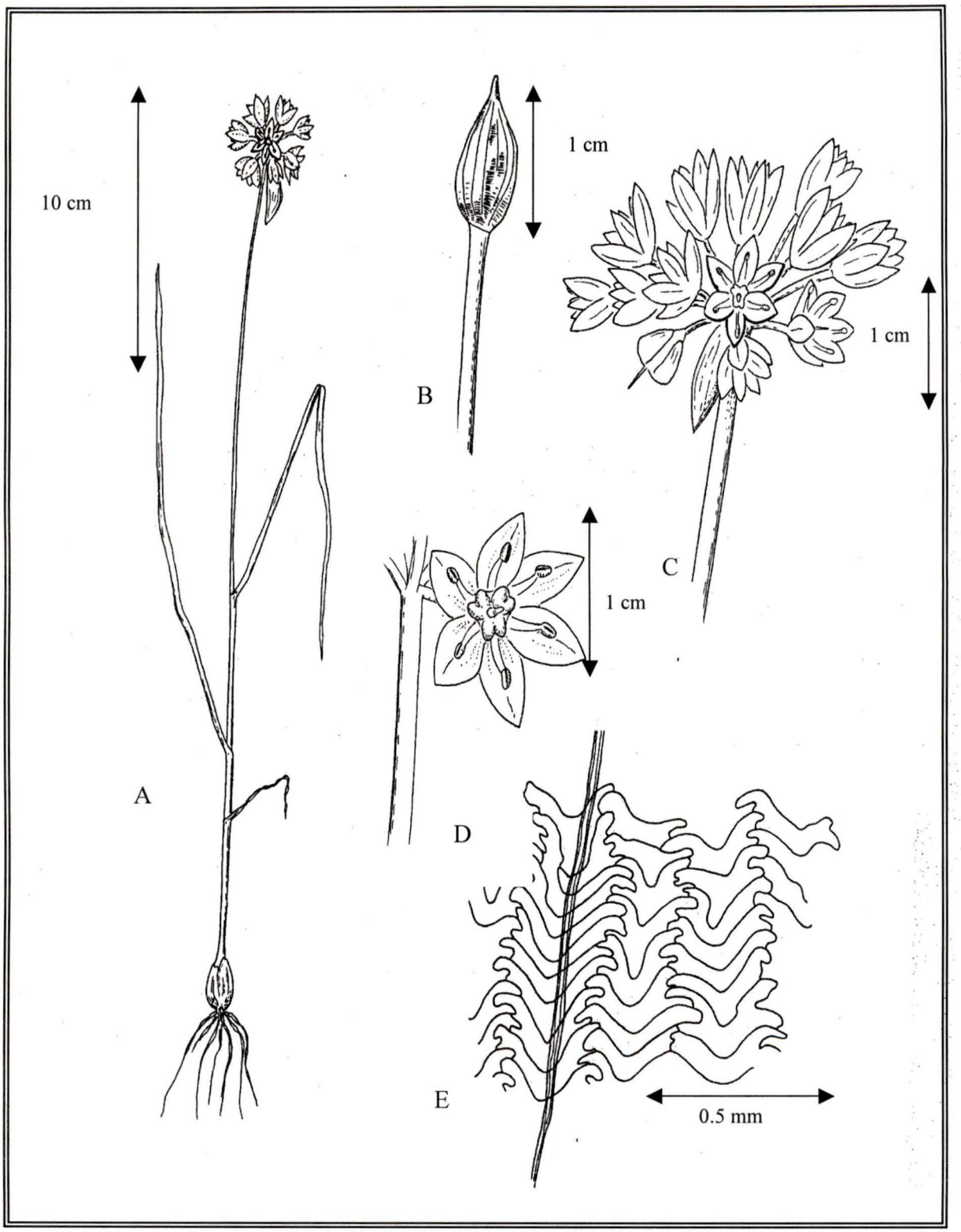


Figure 1. Diagrams of *Allium amplectens*. A. Entire plant. B. Inflorescence bud. C. Inflorescence in flower. D. Individual flower. E. Reticulations on surface of bulb.

Figure 2. Inflorescence buds of *A. amplectens* at Harewood Plains.

Figure 3. Individual inflorescence illustrating a combination of closed floral buds and open flowers at Harewood Plains.

B.C. are disjunct from those further south; no *A. amplectens* populations have been found in the American San Juan Islands or on the Olympic Peninsula.

In British Columbia, *A. amplectens* occurs on the coastal plain of southeast Vancouver Island, the Gulf Islands and the mainland Sunshine Coast. All British Columbia populations are situated within the moist maritime subzone of the Coastal Douglas-fir zone (Nuszdorfer et al. 1991). This region lies in the rainshadow of the Vancouver Island and Olympic mountains, with warm, dry summers and mild, wet winters. Mean annual temperatures range from 9.2 to 10.5°C, and mean annual precipitation varies from 647 to 1263 mm, occurring mostly as rain. Roemer (1993) has classified the Garry oak ecosystem of British Columbia into two major vegetation types or plant associations. In a more recent and detailed habitat study, Erickson (1996) identified 43 different Garry oak plant communities. *Allium amplectens* is found on dry, rocky bluffs and meadows (Douglas et al. 1994). It is a perennial geophyte, well adapted to surviving the dry summers typical of this region. It is in active growth during the period of spring rainfall, and after flowering and fruiting, rapidly dies back. For the rest of the year it is present only as a dormant bulb (Ganders 1987).

The base chromosome number in the *Allium acuminatum* alliance is x = 7. *Allium amplectens* is the only known polyploid species in the group, with diploid (2n = 2x =14), triploid (2n = 3X = 21), and tetraploid (2n = 4X = 28) populations reported (Levan 1940, McNeal 1969, Hickman 1993). In the anthers of *A. amplectens,* meiosis typically produces a tetrad of crescent-shaped pollen grains, although abnormal "asynaptic" pollen (see below) may also be present (Levan 1940). Levan (1940) reported, however, that plants in many populations of *A. amplectens* produce only spherical shaped pollen in

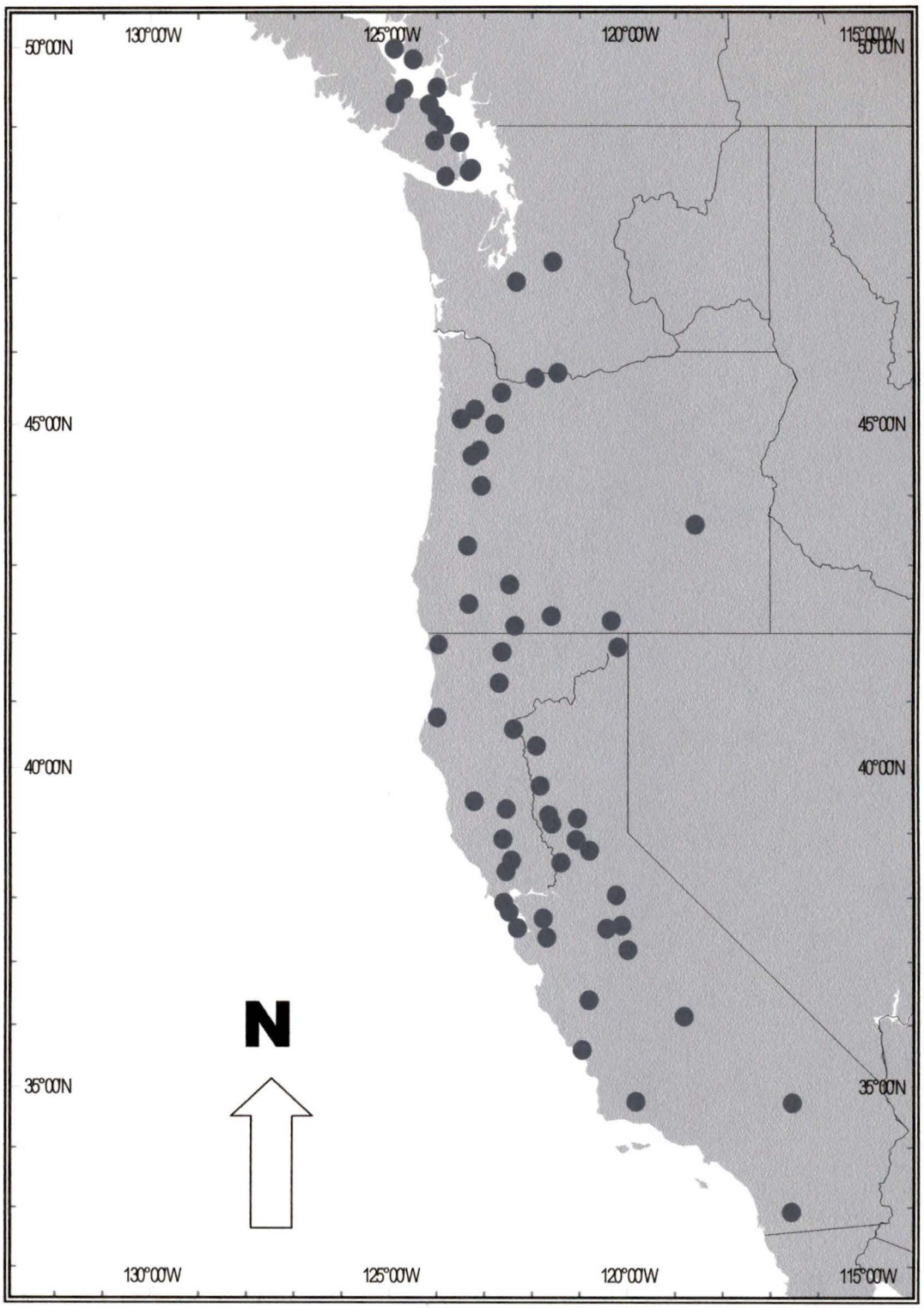


Figure 4. Distribution of *Allium amplectens* in western North America, show both historic and current occurrences from California to British Columbia (Levan 1940).

which the first division of meiosis does not occur, so that only 2 pollen grains are formed from each pollen mother cell. He referred to this pollen type as "asynaptic", and suggested that plants producing this pollen were triploid and probably apomictic. Levan (1940) reported both normal and asynaptic pollen types in populations of central and northern California, whereas populations further north (south and central Oregon), and south (California, San Diego Co.) were asynaptic. Ganders (1987) reported that *A. amplectens* has no need for pollination since it produces its seeds asexually, but this has not been experimentally demonstrated.

Allium amplectens also reproduces vegetatively via bulb division (McNeal and Ownbey 1973). The main or initial bulb is called the renewal bulb, and arises as an axillary bud from the innermost leaf base. As the axis of the renewal bulb develops, one or more additional buds, termed increase bulbs, may appear. In their review of western North American *Allium*, McNeal and Ownbey (1973) reported that plants collected in the field generally had one or two increase bulbs in a given year, but *A. hyalinum* and *A. amplectens* in cultivation could produce as many as eight to twelve increase bulbs per year if given sufficient moisture.

3.0 Demographic analysis

According to Menges and Gordon (1996), monitoring of biological resources ought to have four general goals: detection of significant changes in abundance, understanding of the reasons for the change, determination of the effects of management on the population or community dynamics, and suggestions for key applied research questions. To provide insight into these issues, three levels of monitoring for plant

populations should be conducted (Menges and Gordon 1996). Level I monitoring involves mapping of the distributions of species and determining the occurrence and spatial extent of populations. Level II monitoring provides a quantitative assessment of abundance, thereby providing the basis for an analysis of population trends and hypotheses about demographic mechanisms. Level III, or demographic monitoring of marked individuals, is the most detailed and provides a quantitative assessment of the demographic parameters of survivorship, growth, and fecundity. Level III data can be used for modeling and population viability analysis, as it provides information on the underlying demographic mechanisms and population trends. Schemske et al. (1994) and Owen and Rosentreter (1992) emphasize the importance of type III, or demographic, monitoring for evaluating the status of rare and endangered species. By identifying the life history stages that have the greatest impact on population growth, matrix projection models can be used to suggest future population growth trajectories. With this information, more efficient recovery efforts can be designed.

Population projection or transition matrix models were first introduced to biologists by Leslie (1945) and then by Lefkovitch (1965). Leslie matrices are often used for animal species or where demographic analyses can be based directly on the age of individuals (commonly yearly life stages). Lefkovitch matrices are used when age is not a good indicator of demography, either because individual survival, growth, and reproduction are more directly linked to size, or because the age of individuals is difficult to determine (Cochran & Ellner 1992). This is typically the case for plants.

Matrix models can be employed for a variety of other reasons (Bierzychudek 1999). Byers and Meagher (1997) used this technique to examine the fitness

consequences of alternative life history strategies. Huenneke and Marks (1987) and Horvitz and Schemske (1995) used projection models to examine spatial and temporal variation in the vital rates of species. They can be used for modeling various management strategies in population viability analysis (Doak et al. 1994), or the effects of natural or anthropogenic disturbances such as fire (Silva et al. 1991), grazing (Bullock et al. 1994), or harvesting (Nault and Gagnon 1993). They are commonly used to study rare species (e.g. Menges 1986a, Charron and Gagnon 1991, Oostermeijer et al. 1996, and Lesica 1997), and have been applied to a diverse range of vascular plants, e.g. *Alnus incana* (Huenneke & Marks 1987), *Allium tricoccum* (Nault and Gagnon 1993), *Arisaema triphyllum* (Bierzychudek 1982), and *Erythronium elegans* (Guerrant 1996).

4.0 Objectives of this study

The main objective of this study was to assess the reproductive and life history parameters that influence both local and regional abundance of *Allium amplectens* in British Columbia. In this study, I:

(1) documented the distribution of *A. amplectens*, at both geographic and local landscape levels, and attempted to place it into an ecological context;

(2) investigated the breeding biology of this species, and

(3) carried out population monitoring on several populations to determine how the demographic characters of *A. amplectens* might influence its population and numbers, and to obtain an improved understanding of factors affecting the abundance of this species.

CHAPTER II. MATERIALS AND METHODS

1.0 Range of *A. amplectens*

In 1995 and 1996, I carried out a field inventory of known and previously reported locations for *A. amplectens* on south and central Vancouver Island and the Gulf Islands. Using information provided by various individuals, I also investigated a number of locations of potential new populations. B. C. Conservation Data Centre records and herbarium information from the University of Victoria and University of Washington were used to locate historical sites.

2.0 Breeding system and reproductive biology

Allium amplectens has variation in ploidy level, with unusual asynaptic pollen reported in triploids (Levan 1940). I therefore determined chromosome numbers and examined both breeding system and seed viability in B.C. populations of this species.

I examined root tip material from all of the 8 relocated historic populations (Table 4) and 16 of the 21 newly discovered populations (Table 5). I prepared and examined root tips from a minimum of five plants per populaton. I obtained chromosome squashes, using the procedure outlined by Allen (1984), from root tips taken during May and June from 5 actively growing potted plants collected within each of these 24 populations. I examined the chromosome squashes under a Zeiss compound microscope and photographed individual cells.

I conducted experiments in 1996 and 1997 (Table 1) to determine whether *A. amplectens* was (1) genetically self-compatible, (2) agamospermous (able to set seed by asexual means), or (3) autogamous (able to self-pollinate). To test for self-compatibility I transferred pollen from the stamens to the stigmas of the same flowers with a camel-hair

brush on the first and second days of flower opening, enclosing the inflorescences in insect proof bags. To test for agamospermy I removed the stamens from all open flowers with forceps and enclosed each inflorescence in an insect proof bag. To test for autogamy I simply enclosed each inflorescence in an insect proof bag. I included control plants (with unenclosed inflorescences) in each trial. I made the insect-proof bags of remay fabric (spun polypropylene), which has a very fine mesh that prevents entry of pollinators. I initially conducted the experiments in a greenhouse during the spring of 1996 (using plants transplanted from Harewood Plains site), and repeated them in the spring of 1997, with (1) plants in the field (in situ at Harmac site), and (2) transplants (from Harewood Plains site) grown outdoors in 30 cm square boxes. In all cases I used five replicate plants (inflorescences) for each treatment, and counted all flowers and all seeds produced by each inflorescence at the end of the experiment.

Table 1. Sample sizes for breeding system experiments carried out on *A. amplectens*.

Trials	Plant #	NUMBERS OF FLOWERS PER TREATMENT			
		Control	Autogamy	Agamospermy	Self-compatibility
1996 in pots	1	4	22	2	6
	2	4	10	16	3
	3	6	20	1	3
	4	2	17	3	21
	5	3	6	1	9
All plants		19	75	23	42
1997 in field	1	3	12	1	16
	2	10	8	1	4
	3	12	6	1	5
	4	1	7	2	3
	5	4	20	1	3
All plants		30	53	6	21
1997 in pots	1	5	13	3	6
	2	6	7	1	5
	3	8	13	7	4
	4	9	17	5	7
	5	5	7	7	4
All plants		33	57	23	26

Inflorescences of *A. amplectens* shatter as the seeds mature, and a number of flowers dropped off their inflorescences during the agamospermous treatment. Figures in table 1 reflect numbers of flowers (or ovaries) counted by the end of the experiment. Flowers of *A. amplectens* each contain 6 ovules per ovary (Hitchcock 1969).

To determine seed germination rates, a series of growth chamber experiments were conducted during the fall and winter of 1996-1997, with seeds obtained in 1996 from the population at Harewood Plains near Nanaimo (Table 4). In each set of experiments, five replicates of 20 seeds each were placed into petri dishes and were subjected to 3 different stratification treatments (Table 2).

Table 2. Treatments for seed germination tests (with five replicates of 20 seeds per set).

TREATMENT	LIGHT AND TEMPERATURE REGIME
CONTROL	Maintained for 3 months in a daily regime of 20^0C in light for 15 hours and 15^0C in dark for 9 hours.
STRATIFICATION (1-MONTH)	Held in moist sand at 5^0C for 1 month, then transferred to control conditions for 3 months.
STRATIFICATION (2-MONTH)	Held in moist sand at 5^0C for 2 months, then transferred to control conditions for 3 months.
STRATIFICATION (3-MONTH)	Held in moist sand at 5^0C for 3 months, then transferred to control conditions for 3 months.

3.0 Population monitoring

3.1 Sites used

I made annual counts of the total numbers of flowering plants of *A. amplectens* per population at 6 sites (Table 3). I recorded the numbers of all stages, both vegetative and flowering plants, in permanently marked plots at four of these locations: CFMETR (Nanoose Hill), Mitlenatch Island, Woodley Range and Work Point (Table 3), and in the

plots at CFMETR I recorded the fates of individual marked plants. Numbers of plots at each site and the years each site was monitored are given in Table 3.

I kept records of all plant species observed in the immediate vicinity of the monitored populations and placed these *A. amplectens* populations into communities according to Erickson (1996). I also recorded the slope, drainage, and soil/bedrock composition at each site. Most of the monitored populations occurred in the Rocky, Dogtail Meadow and Orchard Grass communities of Erickson (1996).

Table 3. The six sites chosen for monitoring of *A. amplectens* populations.

LOCATION	# PLOTS (0.5X0.5M)	INVENTORY DATES
(1) Canadian Forces Maritime Experimental Test Range (CFMETR) at Nanoose Hill, north side of Nanoose Bay	23	1995-98, 2000 (15 plots) 1996-98, 2000 (8 plots)
(2) Northwest Bay, Mitlenatch Island	3	1995-98
(3) Woodley Range northeast of Ladysmith	5	1996-98, 2000
(4) Work Point, Esquimalt	1	1996-98, 2000
(5) Eagle Rocks; Denman Island	0	1995-98
(6) Harewood Plains, south of Nanaimo	0	1995-98, 2000

3.2 Data collection

3.2.1 Counts of flowering plants and establishment of marked plots

In order to make flowering plant counts in populations as accurate as possible, I divided each population into a series of belt transects. I proceeded by laying out two transect lines and counting the flowering plants between them, then moving one belt to delineate a new adjacent transect and making a new count between transect lines. I repeated this until I had proceeded through the entire population. Each section was counted at least twice until an entire population was surveyed.

I chose the permanent plot locations for their accessibility, terrain (the slope not too steep for safety), and plant density. Plots of intermediate density were used, because plots with too few plants yielded little data, whereas those with too many plants presented difficulties in differentiating individuals.

I used a wooden 1/2 x 1/2 metre frame, divided into 25 100 cm^2 subunits (Figure 5) to collect the annual census data. The elastic bands subdividing the frame could be removed and then reattached after the frame was correctly positioned, in order to avoid disturbing plants. I placed rebar on both sides of each quadrat to relocate plots, or if the rocky substrate did not permit this, I used paint and/or cement nodes.

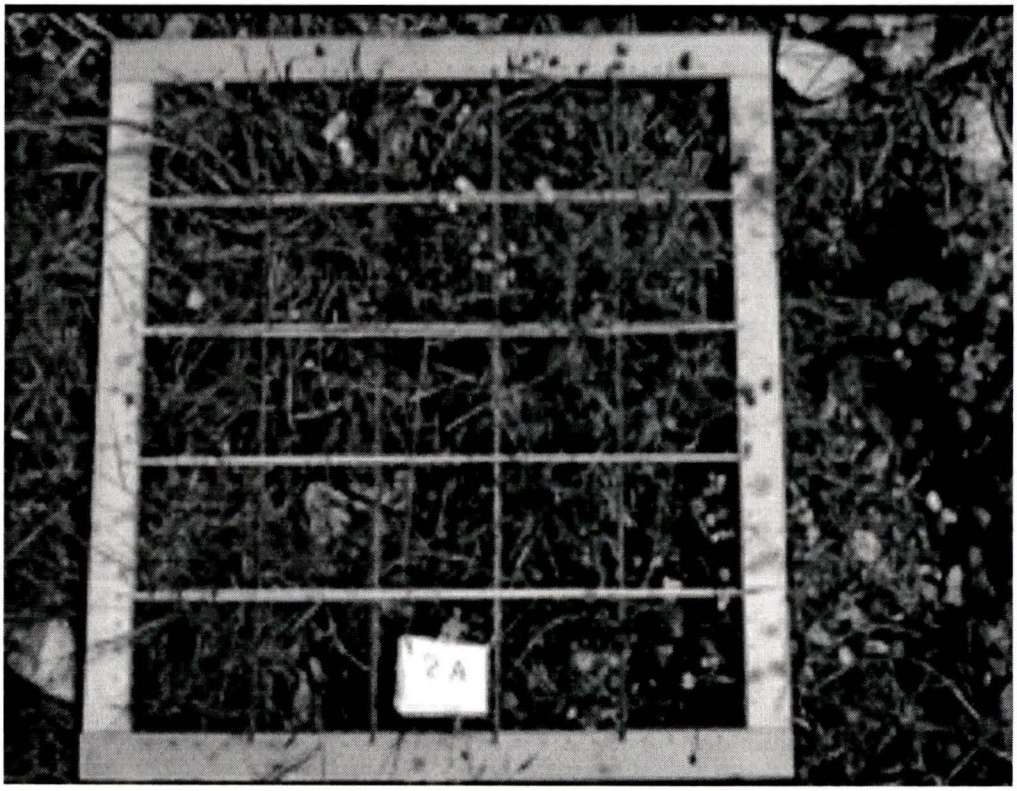


Figure 5. Plot frame used to count plants.

3.2.2 Data collected for individual plants in each plot

I used field data sheets (Appendix 1) to map plants annually at each permanent plot location. For each plant I recorded flowering status, leaf number, longest leaf length (if more than 1 leaf), and (if flowering) scape length and number of flowers. Because leaf dieback (senescence) of vegetative individuals often began to occur before buds on the flowering scapes had fully opened, I made several visits to each population in each year, to avoid missing any nonflowering plants. I did not follow exact yearly census dates, since the phenology of the plants varied from year to year. Inventories usually began in early May of each year and continued until late June.

Initially, in 1995, I segregated plants at the CFMETR site into one vegetative category (no seedlings and/or dense clumps were observed in that year) and four sequential flowering categories based on number of flowers per inflorescence: 1-5, 6-10, 11-15 and > 15. Since flowering categories one and four contained relatively small numbers of plants, I subsequently combined the flowering categories to give two larger categories of 1-10 and > 10 flowers per inflorescence.

In the spring of 1996, when plots were first resampled, I discovered that some grid squares had well-defined clumps of small nonflowering plants, so densely crowded that it was impossible to track the plants individually. In 1996 and subsequent inventory years, I recorded total numbers of nonflowering plants within these clumps. Hence, nonflowering (vegetative) plants were either individually identified and followed ("trackable") or, beginning in 1996, counted as part of a particular clump but not individually identified ("untrackable"). No tracking problems of this sort occurred with the flowering (adult)

plants. Both "untrackable" and "trackable" nonflowering plants were included in the matrix analyses.

3.2.3 Estimation of seedling recruitment and offset rates

In the year 2000 I counted all nontrackable nonflowering plants (i.e. those in large bunches) in the 16 plots in the Dogtail Meadow habitat at CFMETR, and assigned them to one of two groups: (1) seedlings or plants that emerged that year (i.e. with only 1 leaf), and (2) vegetatives (i.e. with > 1 leaf, and assumed to be at least 1 year old). Seedling recruitment rates for 2000 in marked plots were based on the proportion of 1-leafed plants in this sample.

A sample of 39 plant bulbs was excavated at the Harewood Plains site during the same year. These bulbs were individually examined for evidence of offsetting in order to obtain a percentage estimate of plants that exhibited vegetative reproduction.

3.3. Analyses

3.3.1 Population counts

In order to compare numbers of flowering plants with spring precipitation patterns I obtained precipitation records from Environment Canada, and used Nanoose weather station information as a baseline for all localities. February-April precipitation totals were used because this period most closely corresponds with the period of active root and shoot growth in *A. amplectens*. Since not all sites were monitored for the entire 5-year period, I examined the correlation of February-April precipitation totals with total numbers of flowering *A. amplectens* for only three periods: 1995-1998, 1996-1998, and

1996-2000. For each of these intervals, Pearson correlation coefficients were calculated between total February-April rainfall and total numbers of flowering plants.

I calculated average densities of nonflowering and flowering individuals of *A. amplectens* in each sample year for the CFMETR (Nanoose Hill), Mitlenatch Island, Woodley Range, and Work Point sites. Densities were also calculated for sample plots at the CFMETR site according to the following three community types: (*Selaginella/Rhacomitrium* [Rocky], *Cynosurus echinatus* [Dogtail Meadow], and *Dactylis glomerata* [Orchard Grass].

3.3.2 Matrix analyses

3.3.2.1 Introduction to matrix analyses

A projection, or transition matrix, is an array of numbers arranged as a square in a series of columns and rows for a population representing the stage- or age-specific rates of survival and seed production. The matrix N(t) has at most *s* latent roots with *s* representing the number of age or stage classes used. The latent root of the largest absolute value is designated lambda (λ). Since λ indicates the dominant eigenvalue of the matrix (population growth rate per unit of time), a value of 1 indicates no change in the size of the population; less than one indicates a decrease; and more than one indicates a population increase.

In plants, survival and reproduction usually depend on the size of the individual rather than its age. Hence, basing categories on life stage (e.g. seedling vs. vegetative) is preferred in matrix analysis, because it separates organisms into discrete groups assumed to have the same demographic characteristics. Matrices based upon this assumption rather than age are referred to as Lefkovich matrix models. For continuously varying

traits, such as numbers of flowers per inflorescence, this decision is much more difficult. According to Vandermeer (1978), the way in which the categories for continuous variables are chosen may have a significant effect on the transition probability estimates in the matrix due to 'sample errors' and 'errors of distribution'. The only continuous variable I categorized in these matrices was flower number; all other categories clearly fell into different life stages.

A population of a particular structure that changes according to the values in N(t) will, if that matrix is square, nonnegative, and irreducible, approach a vector called the stable stage distribution which corresponds with the dominant eigenvalue (Bierzychudek 1982). In other words each size-class will be increasing by λ during each time interval, i.e. $N(t)v(t) = \lambda v(t)$. Population structure at any future time can then be projected under the assumption of geometric growth. The stable age (stage) distribution is so called because if the population is perturbed from this distribution, it ought to spontaneously return to it over time (Akcakaya et al. 1997a). However, if the population is cycling due to density dependence, or the matrix elements are fluctuating due to environmental stochasticity, the distribution may not tend toward a stable configuration over time. Stage distributions for *A. amplectens* were calculated using Poptools (Hood 2000).

3.3.2.2 Matrix analyses done with *A. amplectens*

For the matrix analysis, I assigned plants to one of five different life stages: seedling (first year nonflowering plant with only 1 leaf), vegetative (nonflowering plant with >1 leaf), flowering 1 (1-10 flowers/inflorescence), flowering 2 (> 10 flowers/inflorescence), and dormant.

Each yearly matrix N (t) summarized three different kinds of information. Most of the cells contained probabilities of transitions from one stage-class to another. The time interval in this study was normally 1 year (t, t + 1) except for the final matrix transition of 1998/2000 which was 2 years (t, t + 2). Some of the cells contained fecundity values during each time interval. Fecundity estimates, where applicable, are contained in the first row of each matrix (cells F_1:S and F_2:S), for offspring from seed, and in the second row (cells V:V, F_1:V and F_2:V) for offsets. Numbers of seedlings were apportioned between F_1 plants (1-10 flowers/scape) and F_2 plants (more than 10 flowers/scape), according to the mean number of flowers produced by each of these stages during the first year of the transition.

The cells in the second row each contain two numbers contributing to the transition probability, the first indicating individually tracked plants, and the second indicating estimated numbers of offsets produced during that transition. Finally, some cells (first column, cell S:V) indicate the probability of seedling survivorship. Since I did not determine seedling survival rates in this study and they can vary substantially (Harper 1977), an arbitrary seedling survivorship rate of 50% was assumed in the first column of the matrix in each transition for which seedlings were counted.

3.3.2.3 Sensitivities, elasticities, and reproductive values

Sensitivity and elasticity analyses were performed on *A. amplectens* and calculated using Poptools (Hood 2000). Demographic prospective perturbation analysis, utilizing the tools of sensitivity and elasticity analysis, explores how population statistics such as population growth rate (λ) respond to changes in vital rates (i.e. survival, growth,

development, reproduction). In other words it can be used to predict how changes in λ would result from any specified change in future vital rates (Caswell 2000a). Hence, sensitivity and elasticity analysis can be used to identify potential management strategies for a species, since positive changes in vital rates with high sensitivity or elasticity will produce much larger positive changes in λ.

Sensitivity analysis measures how population growth would respond to perturbations in any of the transitions (Ferson 1994). Larger sensitivity values indicate the transition element is important in the sense that small changes in it would result in large changes in the overall growth of the population. These values in tandem with a selective manipulation of the matrix elements can provide comprehensive analysis of population responses to changes in life-history parameters. Demographic and temporal stochasticity are not considered. I calculated yearly sensitivity values for *A. amplectens* over the four transitions, including the final 2-year transition.

Elasticity analysis measures the contribution of each element of the matrix to the dominant eigenvalue (Ferson 1994). Since elasticity values are proportional or sum to 1, they are more intuitively interpretable than sensitivities. Elasticity values for *A. amplectens* were calculated for each transition.

Reproductive value is the age-specific measure of the relative contribution of each stage to future generations or the number of offspring an individual in a given stage will produce, including all of its descendants (Akcakaya et al. 1997a). Reproductive values were calculated for each of the transitions using Poptools (Hood 2000).

3.3.3 Population viability analyses

Mean matrices provide an insight into future population trajectories incorporating all of the components within all matrices for the calculation, as opposed to the λ, sensitivity and elasticity averages which average only the matrix outputs in the calculation. I calculated mean matrices by obtaining the arithmetic mean for each corresponding element for all of the cells of the matrices used.

I used mean matrix values, and the standard deviations of the matrix elements (vital rates such as survivorship and fecundities) representing the effect of environmental fluctuations, to construct a population viability simulation for *A. amplectens*. Year 2000 population numbers were used as the starting point for the simulation. RAMAS ECOLAB uses the means and variances of the parameters to predict population abundances in the future by randomly selecting the vital rates for each time step so that the means and variances are the same as those observed in the past. The result, calculated by RAMAS ECOLAB simulation software (Akcakaya et al. 1997b) and producing a population trajectory (abundance curve through time) based on 500 individual variations in growth rates (replications), is called a stochastic simulation. The risk of extinction is equivalent to the probability that the population size will fall to zero at least once during the projected time period, calculated as the percentages of replicates for which this occurs. For example, if there are 500 replicates and 45 of the replicates show an abundance of zero, then the observed probability or risk of extinction is 45/500 or 0.09.

4.0 Dormancy

As the study proceeded, I discovered that a substantial number of individual plants were absent during certain years and subsequently reappeared. I calculated annual dormancy rates, or the percentage of plants dormant during each year, at CFMETR from 1995 to 1998. I added new plants to the dormancy dataset each year (newly observed plants or those dormant in previous years). Any plant absent in a given year but present in the preceding and subsequent years was recorded as dormant in that year. If a flowering plant appeared in a plot but had not been seen in the previous year, it was also assumed to have been dormant in the previous year, since flowering plants would have arisen from vegetative or flowering stages in previous years. No such assumption was made for vegetative plants.

I also examined multiple year dormancy patterns at CFMETR.

Only plants that were tracked for a minimum of 4 years and were still present at the end of this 4-year period as either nonflowering or flowering were used in individual and multiple year dormancy calculations (a total of 241 plants). Dormancy in a given year was calculated as the number of plants inferred to be dormant, divided by the total number (out of 241) of dormant and nondormant plants present in that year. Multiple-year dormancy rates were determined by assigning each plant to one of four categories (0 to 3 years of consecutive dormancy) and calculating the proportion of plants in each category.

The combination of two life history characteristics, dormancy and offset production in *A. amplectens*, presented some problems for the demographic analyses because these traits made individuals difficult to track. In many instances it was difficult

to separate dormancy and mortality, or emergence from dormancy and recruitment through bulb offsets. Decisions about whether plants were the result of offsetting were based on their position relative to other plants. My calculations of dormancy rates were conservative, as I assumed that any plants not reappearing during the study had died.

CHAPTER III. RESULTS

1.0 Range of *A. amplectens*

1.1 Past and present range and new populations found

I examined herbarium specimens and British Columbia Conservation Data Centre records in order to summarize information on both current and historical occurrences of this species. I categorized populations as "historic" if the oldest sighting was prior to 1995. Dates within this group ranged from 1887 to 1993, and a total of 44 sites were classified as historic (Table 4). These sites were then visited if possible to determine their current status. For eleven populations the description of the site was too general (e.g. Maple Bay) to make relocating them feasible. Because of this, some historical localities (especially very old sites from the 1800's and early 1900's) may duplicate extant sites in the same general area. Eight other sites were not visited because of their relative inaccessibility; most of these were located on small islands lacking ferry service. At 17 sites, no populations of *A. amplectens* could be located. Most of these populations probably no longer exist due to habitat loss, especially since many are located within the City of Victoria. Only 8 (18%) of the historical populations were relocated, none of which were in the Victoria area.

Since 1995 when this study was initiated, a total of 21 new *A. amplectens* populations have been found: 13 by me (or by a group including me), and eight by other individuals (Figure 6, Table 5). This has increased the total known number of extant populations to 29. Four of these new sightings are in the Victoria area; the rest are located in the Nanaimo and Gulf Islands areas. The majority of new localities are at isolated locations on the various Gulf Islands, and in the mid-eastern section of Vancouver Island.

Table 4. Historic British Columbia sites for *Allium amplectens* (first located before1995), obtained from herbarium material and Conservation Data Centre records. [1]Herbarium codes are from Index Herbariorum (Holmgren 1990); BCCDC= B. C. Conservation Data Centre. *Locations marked with an asterisk indicate that a chromosome number was determined from the site.

Location	**Habitat**	**Specimen[1] Source, Author Of Sighting & Date**	**Comments**	**Lat. & Long.**
BENTINCK ISLAND Victoria area		V Connell, R. 26/06/1930	Not searched	48° 19' 123° 32'
CHATHAM ISLAND		BCCDC Connell, R. 26/06/1930	Not searched	48° 26' 123° 15'
DEADMAN'S ISLAND (now Hoik Island) near Pt. Alberni, Barkley Sound		GH,V Carter, W.R. 07/1916	Not searched	49° 14' 124° 50'
*DENMAN ISLAND Boyle Point Provincial Park		BCCDC 1992	Found	49° 29' 124° 42'
GALIANO ISLAND Dionisio Point		BCCDC Roemer, H. 26/04/1993	Not found	49° 01' 123° 34'
*GALIANO ISLAND Mount Sutil	On conglomerate rock outcrop with Sedum, moss	RBCPM Janszen, H. 13/07/1976	Found	48° 52' 123° 23'
*MAYNE ISLAND Georgina Point	Rock above sea (Some broom in swales/houses on both sides of light-house property)	V Janszen, H. 17/06/1980	Found	48° 52' 123° 17'
*MITLENATCH ISLAND	North side of Island/on rock face close to sea	V Thomson, D. 17/06/1980	Found	49° 59' 124° 54'

Table 4 continued...

SALTSPRING I. Mount Max-well P. Park	S-facing bluffs and ledges	V Janszen, H. 29/08/1981	Not found	48° 48' 123° 31'
*SAMUEL ISLAND	Rock cliff by the sea	V Janszen, H. 24/06/1980	Found	48° 49' 123°13'
SATURNA ISLAND, On unnamed hill N. of Mt. Fisher		V Janszen, H. 15/06/1986	Not found	48° 48' 123° 12'
THORMANBY ISLAND, S.side, Farm Bay	Dry rocky banks just above high tide	UBC Straley, G.B. 24/05/1992	Not searched	49° 30' 124° 00'
TRIAL ISLANDS Ecological Res. Equisite		BCCDC Roemer, H. 1992	Not searched	48° 24' 123° 18'
VANCOUVER ISLAND				
ALBERNI		WS Anderson 17/06/1919	Too general site descriptor	49° 15' 124° 48'
ALBERNI Somas River		GH Henry & Carter 20/06/1916	Too general site descriptor	49° 14' 124° 49'
ALBERNI Sproat Lake Falls		GH Carter 06/1916	Not found	49° 18' 124° 53'
*LADYSMITH Woodley Range Ecol. Reserve #391		BCCDC Roemer, H. 1992	Found	49° 01' 32.7" 123° 49' 58.7"
LAKE COWICHAN		WS Simpson 07/1916	Too general site descriptor	48° 49' 124° 03'
LANGFORD Mt. Wells, S.W. of Lang-ford Lake	(No suitable sites found/area inaccessible)	V Hardy, G.A. 07/1952	Not found	48° 26' 123° 33'
MAPLE BAY		V Glendenning, R. 06/1918	Too general site descriptor	48° 49' 123° 37'

Table 4 continued...

NANAIMO Near		GH,MO,UC,US Rosendahl 1891	Too general site descriptor	49° 10' 123° 56'
NANAIMO Vancouver Island		BCCDC Macoun 13/06/1887	Too general site descriptor	49° 10' 123° 58'
*NANAIMO Harewood Plains (White Rapids Road)	Growing in dense clumps	V Ceska, A. 23/06/1985	Found	49° 08' 124° 00'
*PARKS-VILLE Nanoose Hill		BCCDC Ceska, A. 1993	Found	49° 17' 124° 10'
N. SAANICH Mt. Newton, south side	Rock outcrop with Rhacomitrium canescens, exp. south, slope 10%; elev. 550 feet	UVIC Roemer, H. 06/1968	Not found	48° 36' 123° 27'
SHAWNIGAN LAKE Old Baldy Mt'n., E. side	Rare in two spots on open, dry, W-facing rocky bluffs (Lots broom)	V Calder, J.A. 22/06/1961	Not found	48° 38' 123° 37'
SOOKE Becher Bay, S.E. of Sooke		V Spier 29/07/1930	Not found	48° 19' 123° 35'
SOOKE Devil's Pot Holes, Sooke		BCCDC Hardy, G.A. 05/06/1926	Not searched	48° 23' 123° 43'
SOOKE Otter Point, bet. Sooke & Jordan River	Occasional in grassy pockets of sea cliffs; flowers pink	WS Calder, J.A. 04/06/1961	Not found	48° 21' 123° 49'
SOOKE Rocky Point	In rocky soil pocket, 5-6 in.soil; with Aira, Plantago & grasses, exp. open, slope-, elev. 33m.	UVIC Keller, R.A. & B.W. Davies 08/06/1965	Not found	48° 19' 123° 34'
SPECTACLE LAKE Lot 130, Malahat Dist., West of Spectacle Cr'k	In Pseudotsuga forest with Zygadenus, Delphinium, Camassia; logged 1945-1955, 900'	UVIC Mitchell, S. 21/6/1977	Not found	48° 34' 123° 33'

Table 4 continued...

S. SAANICH Bedford Rd., Greater Vic.	Rocky area	UVIC Melburn, M.C. 17/06/1956	Not found	48° 27' 123° 16'
S. SAANICH Bedford Road, Ten mile point	Among rocks in deep grass	V Melburn, M.C. 17/06/1956	Not found	48° 27' 123° 16'
S. SAANICH Bedford Road Woods, at Ten Mile Pt		BCCDC Melburn, M.C. 30/06/1962	Not found	48° 27' 123° 16'
S. SAANICH Cadboro Bay		UC Pineo 23/06/1894	Not found	48° 27' 123° 18'
S. SAANICH Cedar Hill		BCCDC Macoun 23/05/1887	Too general site descriptor	48° 27' 123° 21'
S. SAANICH Gordon Head		V Lett, R. 22/06/1936	Too general site descriptor	48° 30' 123° 18'
S. SAANICH Observatory Hill, near Vic.		V Newcombe,C.F. 11/07/1923	Not found	48° 31' 123° 25'
S. SAANICH Telegraph Bay	Above beach, with grasses, mosses & lichens, exp.-e, slope:60, elev. 30'.	UVIC Turner,B. & N. Chapman 30/06/1966	Not found	48° 28' 123° 17'
VICTORIA Foul Bay		V Pemberton, C. 12/06/1927	Too general site descriptor	48° 25' 123° 20'
VICTORIA Gonzales Hill		V Martin, S. 07/06/1924	Not searched	48° 25' 123° 19'
VICTORIA near		MO Macoun,J. 05/05/1908	Too general site descriptor	48° 26' 123° 22'
VICTORIA Victoria Arm, V.I.		GH,NY,US Macoun 10/06/1893	Too general site descriptor	48° 26' 123°22'
CONTINENTAL NORTH AMERICA				
POWELL RIVER S. of Gibson's Beach	Open area on rock bluffs above shore	V Stanley, G. 06/07/1975	Not searched	49° 51' 124° 30'

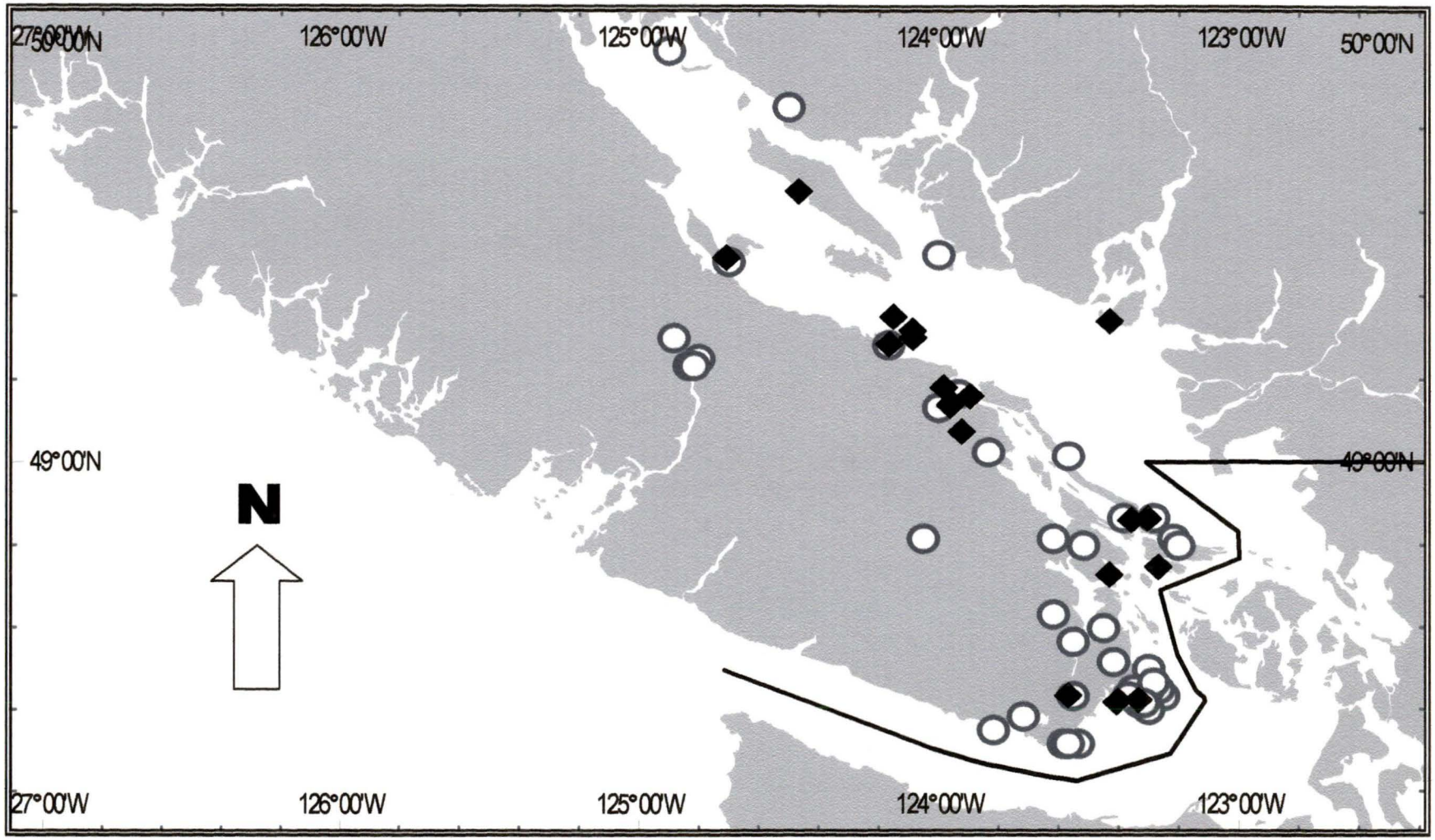


Figure 6. Historic sites (discovered prior to 1995) and new sites (discovered 1995 and subsequently) for *Allium amplectens* in British Columbia. Open circles represent historic sightings and solid diamonds indicate recently located populations.

Table 5. New British Columbia sites for *A. amplectens* (located since 1995); BCCDC=British Columbia Conservation Data Centre.

Location	Source, Author (of report) & Date	Somatic Chromosome Number	Lat. & Long
GULF ISLANDS			
BALLENAS ISLANDS Island closest to Vancouver Island	BCCDC Ceska, A. 02/04/1996		49° 21' 124° 09'
BOWEN ISLAND Cape Roger Curtis	BCCDC Hawryzki, A. & Whitehead, A. 28/06/1997	21	49° 20' 25" 123° 25' 45"
DENMAN ISLAND Between Eaglecrest & Sea Lion roads. Near Hornby ferry terminal	BCCDC Hawryzki, A. 21/06/1996	21	49° 29' 30" 124° 42' 30"
GALIANO ISLAND W. of Collinson Point	BCCDC Hawryzki, A. 31/05/1996	21	48° 51' 36.5" 123° 21' 24.1"
ISABELLA ISLETS	BCCDC Janszen, H. 15/05/1996	21	48° 43' 42.4" 123° 25' 52.1"
MAYNE ISLAND On coast south of Laura Point	BCCDC Hawryzki, A. 31/05/1996	21	48° 51' 49.6" 123° 18' 09.1"
NORTH PENDER ISLAND Oaks Bluff	BCCDC Hawryzki, A. 31/05/1996	21	48° 44' 49" 123° 16' 02.1"
TEXADA ISLAND NE end of Dick Island, off Harwood Point	BCCDC Janszen, H. 19/06/1997		49° 39' 124° 28'
WINCHELSEA ISLANDS Second Island	BCCDC Ceska, A. 24/05/1995		49° 18' 45" 124° 05' 05"
WINCHELSEA ISLANDS Small Winchelsea NWestern	BCCDC Ceska, A. 24/05/1995		49° 18' 30" 124° 05' 10"

Table 5 continued...

VANCOUVER ISLAND			
ESQUIMALT Golf Hill, near Peters St., DND Work Point	BCCDC Penny, J.L. 06/06/1995	21	48° 25' 123° 24'
ESQUIMALT Work Point	BCCDC Hawryzki, A. 14/06/1995	21	48° 25' 12" 123° 24' 2.4"
LANGFORD Mt. McDonald E. of access road	BCCDC Roemer, H. 21/06/1996		48° 26' 123° 34'
NANAIMO East Wellington Road, across from B.C. Hydro	BCCDC Hawryzki, A. 13/06/1999	21	49° 10' 50.1" 123° 58' 56.8"
NANAIMO Empty lot at southeast corner 8th & Howard Sts.	BCCDC Hawryzki, A. 13/08/1996	21	49° 08' 34" 123° 57' 20.2"
NANAIMO Harmac	BCCDC Hawryzki, A. 12/06/1997	21	49° 07' 45.1" 123° 50' 43.4"
NANAIMO Harewood Bluffs	BCCDC Hawryzki, A. 13/08/1996	21	49° 08' 15.4" 123° 57' 36.9"
NANAIMO Jack Point Park	BCCDC Hawryzki, A. 13/06/1996	21	49° 09' 35.7" 123° 53' 38.3"
NANAIMO Nanaimo River	BCCDC Hawryzki, A. 05/06/1997	21	49° 04' 28.2" 123° 55' 20.1"
PARKSVILLE Enos Lake	BCCDC Hawryzki, A. 25/06/1998	21	49° 17' 3.5" 124° 09' 50.1"
VICTORIA Government House	BCCDC Roemer, H. 23/02/1998	21	48° 25' 20" 123° 20' 30"

1.2 Description of habitat

Almost all populations of *A. amplectens* observed in this study were located on south or southwestern exposures (Table 4, Table 5), in plant communities approximating several of Erickson's (1996) community types (see below). As the summer season progressed, direct evidence of moisture often disappeared completely but certain indicator species like *Mimulus alsinoides* were good evidence of moisture earlier in the season. *Allium amplectens* is usually found in areas with evidence of early spring seepage; it most often prefers open sunlight but also can be found in light shade. It often occurs in extremely shallow soil, although also in deep, moist, nutrient rich loamy soils (e.g. in several populations of the Gulf Islands, where it grows on damp ledges on the edges of steep cliffs).

Of the five different populations of *A. amplectens* selected for long-term monitoring at CFMETR (Nanoose Hill), population 2 was located in a bedrock *Selaginella wallacei/Rhacomitrium canescens* community (Rocky), populations three and four were located in a *Cynosurus echinatus* community (Dogtail Meadow), and populations one and five were located in a *Dactylis glomerata* community (Orchard Grass). The *A. amplectens* sites where marked plots were located are shown in Figures 7-14.

Figure 7. CFMETR study area looking north from Nanoose Flats on south side of Nanoose Bay.

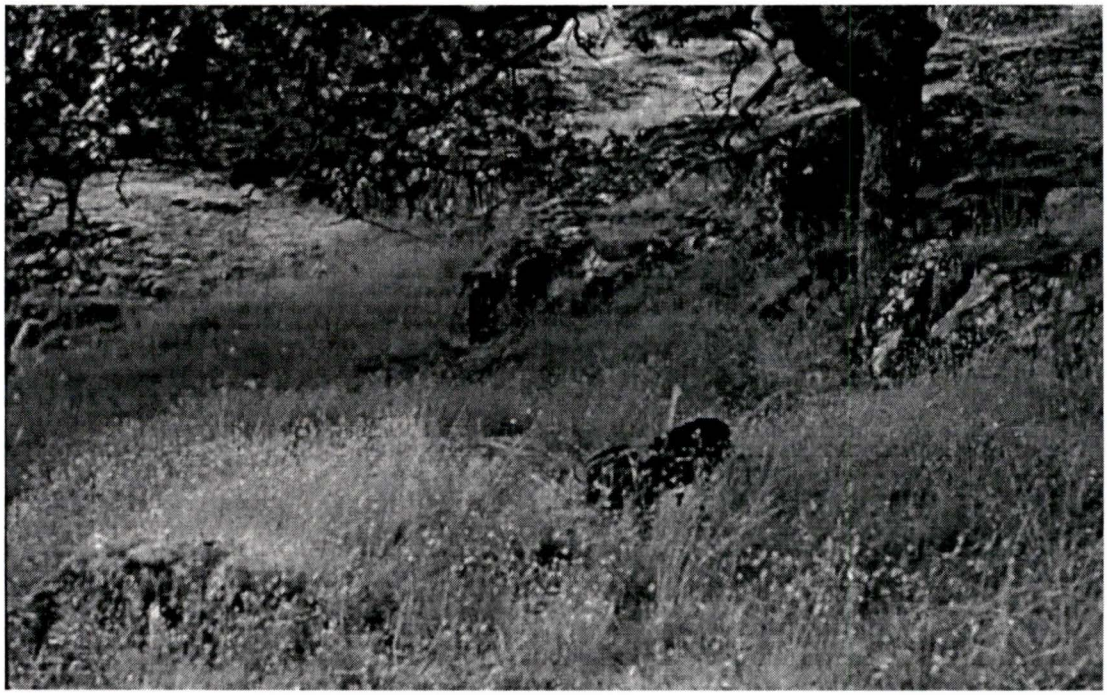


Figure 8. Dogtail Meadow (*Cynosurus echinatus*) community typical of populations 3 and 4 at CFMETR.

Figure 9. Mitlenatch site on western side of Northwest Bay typical of a Rocky (*Selaginella wallacei/Rhacomitrium canescens*) community type.

Figure 10. *A. amplectens* interspersed with the exotic plant *Sedum acre* on Mitlenatch Island site.

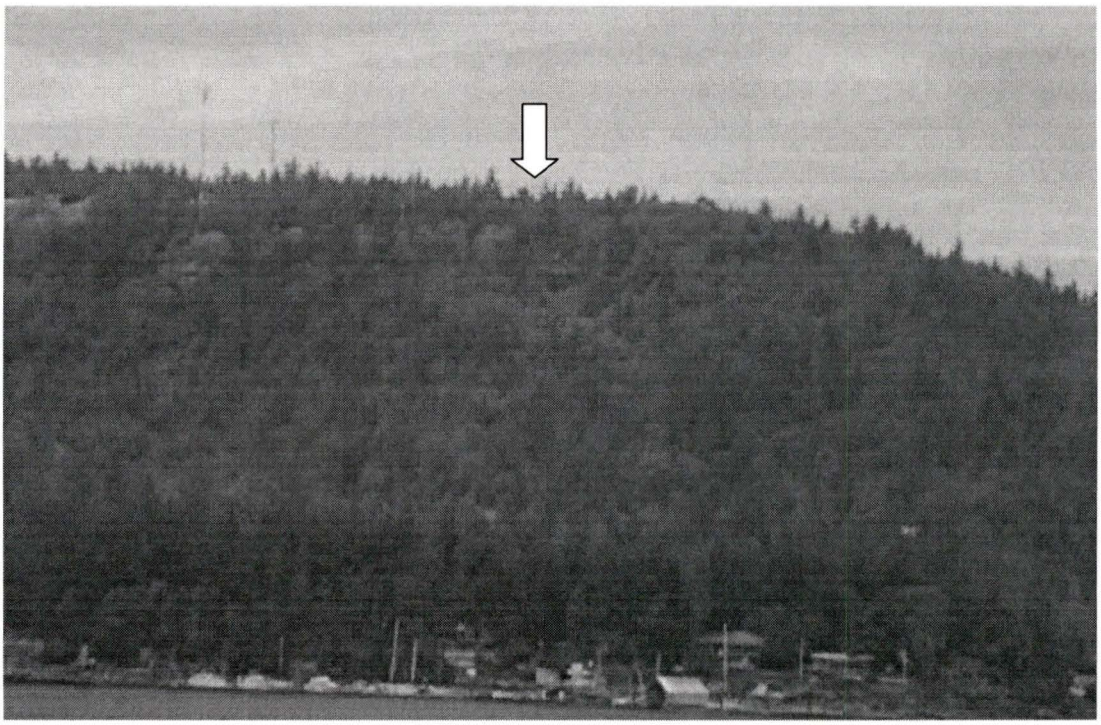


Figure 11. Woodley Range monitoring site looking east from Ladysmith Harbour. Site is located at top of ridge to right (south) of towers.

Figure 12. Damper portion of Woodley Range meadow illustrating presence of *Mimulus guttatus* & *Plectritus congesta.* Extremely thin soil layer on bedrock substrate.

Figure 13. Work Point facing east near plot location.

Figure 14. Work Point plot site located in a grassy pocket between 2 rocky promontories.

2.0 Breeding system and reproductive biology

2.1 Pollination experiments and chromosome determinations

Results of the pollination experiments are summarized in Tables 6 and 7. Each treatment was compared in turn with the self-compatibility treatment (enclosed in bags, hand-pollinated with self pollen). Only the control, in which flowers were exposed to outcross pollen, differed significantly from the self-compatibility treatment in seed set (Table 7). This suggests that outcross pollen is needed for seed set.

In the 24 populations for which chromosome counts were obtained (indicated by asterisks in Table 4 and third column in Table 5), all plants were found to have a somatic chromosome number of 21 (Figure 15), a triploid number for this species.

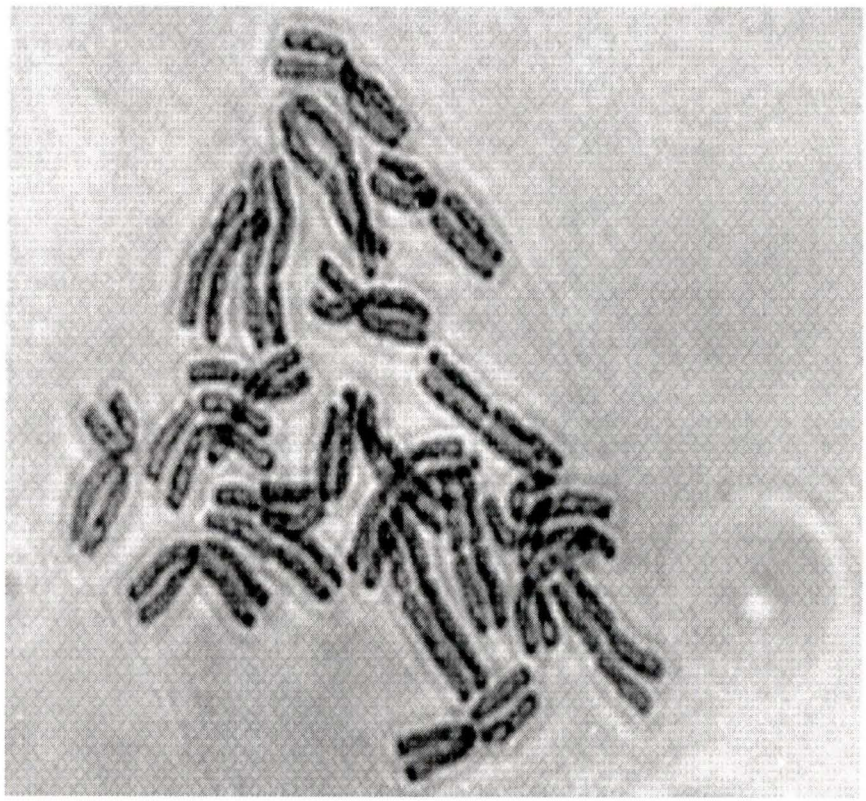


Figure 15. Chromosome squash from root tips of *Allium amplectens* obtained from plants at Work Point, Victoria. A representative triploid chromosome count (2n = 3X = 21) is shown.

Table 6. Results of 1996 and 1997 pollination experiments on *A. amplectens.* Percent seeds produced = (number of seeds per inflorescence)/(number of flowers per inflorescence [from Table 1] x 6 ovules per flower).

Trials	Plant #	TREATMENTS							
		Controls (open-pollinated)		**Autogamy** (enclosed in bags but not selfed)		**Agamospermy** (enclosed in bags, anthers removed)		**Self-compatibility** (enclosed in bags, hand pollinated)	
		Seeds produced		Seeds produced		Seeds produced		Seeds produced	
		#	%	#	%	#	%	#	%
1996 in pots	1	3	12.5	4	3.0	0	0	0	0
	2	4	16.7	0	0	0	0	0	0
	3	7	19.4	0	0	0	0	0	0
	4	1	8.3	11	10.8	0	0	0	0
	5	3	16.7	0	0	0	0	4	7.4
Mean± std dev			**14.7±4.4**		**2.8±4.7**		**0±0**		**1.5±3.3**
1997 in field	1	1	5.5	3	4.2	0	0	5	5.2
	2	11	18.3	1	2.1	0	0	2	8.3
	3	13	18.1	0	0	0	0	1	3.3
	4	1	16.7	4	9.5	0	0	0	0
	5	1	4.2	1	0.8	0	0	0	0
Mean± std dev			**12.6±7.1**		**3.3±3.8**		**0±0**		**3.4±3.6**
1997 in pots	1	0	0	4	5.1	0	0	0	0
	2	3	8.3	0	0	0	0	4	13.3
	3	3	6.3	2	2.6	0	0	0	0
	4	2	3.7	1	1.0	0	0	0	0
	5	1	3.3	1	2.4	0	0	0	0
Mean± std dev			**4.3±3.2**		**2.2±1.9**		**0±0**		**2.7±6.0**
Overall Means± std dev			**10.5±6.6**		**2.8±3.4**		**0±0**		**2.5±4.2**

Table 7. Statistical analysis of results from pollination experiments in 1996 and 1997 on *A. amplectens*. P values for Mann-Whitney U-tests * $p<0.05$ ** $p<0.01$.

Treatments	Trials			
	1996 in pots	**1997 in field**	**1997 in pots**	**Totals**
Controls/ Self-compatibility	0.0069**	0.0465*	0.2204	0.0007**
Autogamy/ Self-compatibility	0.5205	0.9158	0.2204	0.3185
Agamospermy/ Self-compatibility	0.3173	0.0539	0.3173	0.0166

2.2 Seed germinability

To determine seed viability and germination rates *A. amplectens* seeds were subjected to three different stratification treatments (Table 8). Seed germination occurred only after a stratification period of three months. Even after a cold period of this duration, seed germination was very low, only 5% (n = 100 seeds).

Table 8. Results of seed germination tests (with five replicates of 20 seeds per set).

TREATMENTS				
Replicate #	**CONTROL**	**1-MONTH STRATIFICATION**	**2-MONTH STRATIFICATION**	**3-MONTH STRATIFICATION**
	% germination	% germination	% germination	% germination
1	0	0	0	15
2	0	0	0	5
3	0	0	0	5
4	0	0	0	0
5	0	0	0	0
Mean± std dev	0±0	0±0	0±0	5±6.1

2.3 Seedlings and vegetative propagation

Few seedlings of *A. amplectens* were seen during this study. None were seen in marked plots in the years 1995 to 1998. In 2000, of a total of 1735 nontrackable nonflowering plants (i.e. those in large bunches) that I observed in all CFMETR plots, 88 (5.1%) had only 1 leaf (Figure 16 and Table 12), and were treated as seedlings. All individually tracked plants (i.e. total of 174 in 2000) in all years had more than 1 leaf and were considered not to be seedlings.

Vegetative offsetting occurs in both vegetative and flowering plants in this species (Figure 16). An examination of the 39 plants excavated at the Harewood Plains site during the spring of 2000 showed that 18% of these plants were producing an offset. This figure was subsequently used as an estimate of offset rate in the matrix analyses. Plants at the permanent plot sites were left undisturbed during the study to maintain them for subsequent inventories. However, their clumped distribution suggests that this method of asexual reproduction was very common in the populations that I studied. Mother and daughter bulbs were usually indistinguishable in their size and shape. The offsets produced by flowering bulbs were generally, though not always, vegetative during the following year.

3.0 Population monitoring

3.1 Population counts

3.1.1 Numbers of flowering plants and correlations with spring precipitation

Numbers of flowering plants in populations at six different sites on Vancouver and the Gulf Islands are shown in Figure 17. Numbers were generally highest in 1996 and lowest in all populations in 1998. Figure 18 illustrates the relationship between flowering population counts at the six locations and total February to April precipitation. Figure 18 suggests a positive relationship between number of flowering plants and rainfall for each of the six sites, but none of the r values were significant.

Figure 16 *Allium amplectens*, (a) first year seedling; (b) three-leaved vegetative plant; (c) three-leaved flowering plants. Bulb offsets are being formed in (b) and (c).

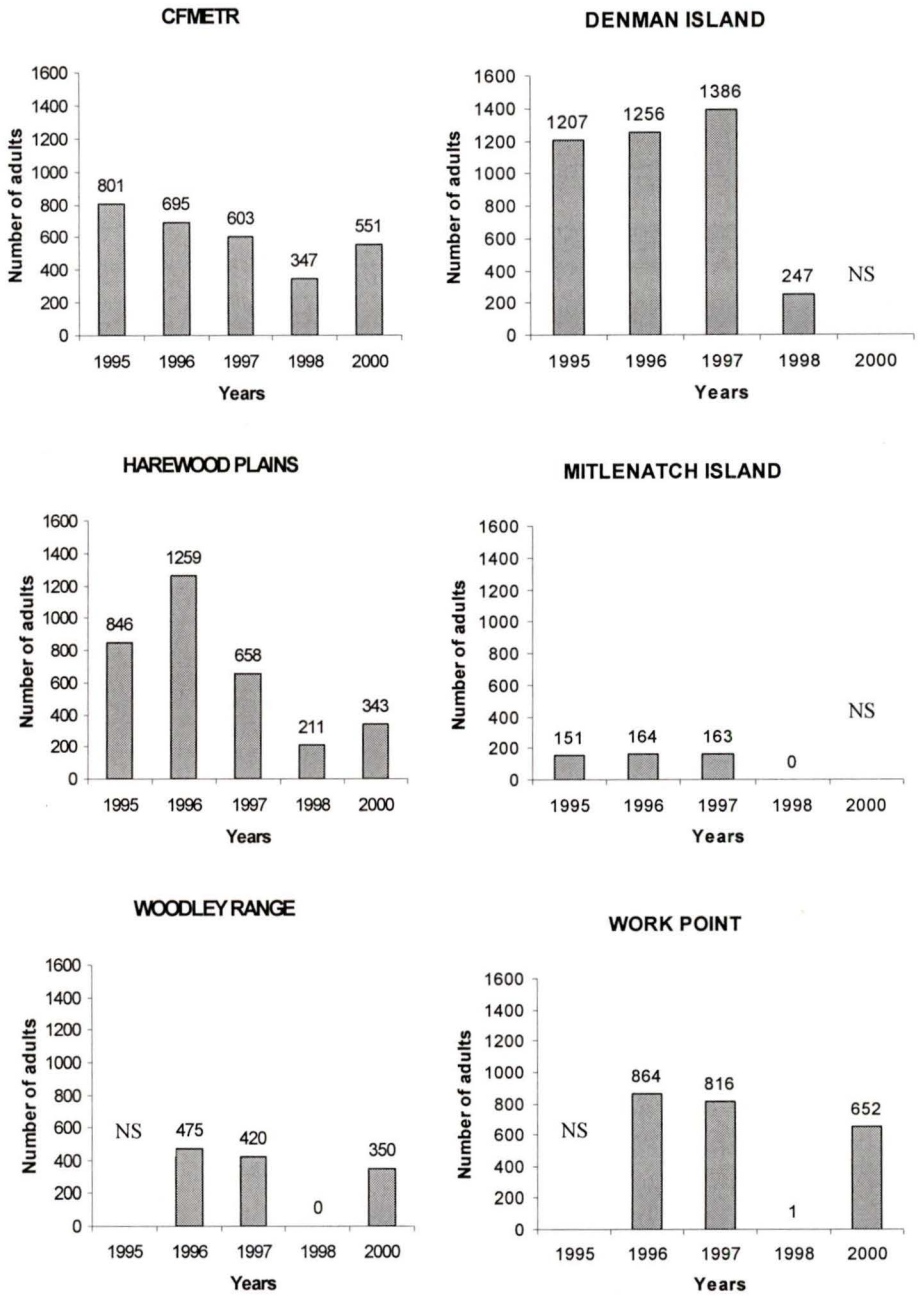


Figure 17. Total numbers of flowering plants at six British Columbia locations: Denman Island (Eagle Rocks), Mitlenatch Island (Northwest Bay), CFMETR (Nanoose Hill), Harewood Plains (Nanaimo), Woodley Range (Ladysmith), & Work Point (Esquimalt). NS = not surveyed. No sites were surveyed in 1999.

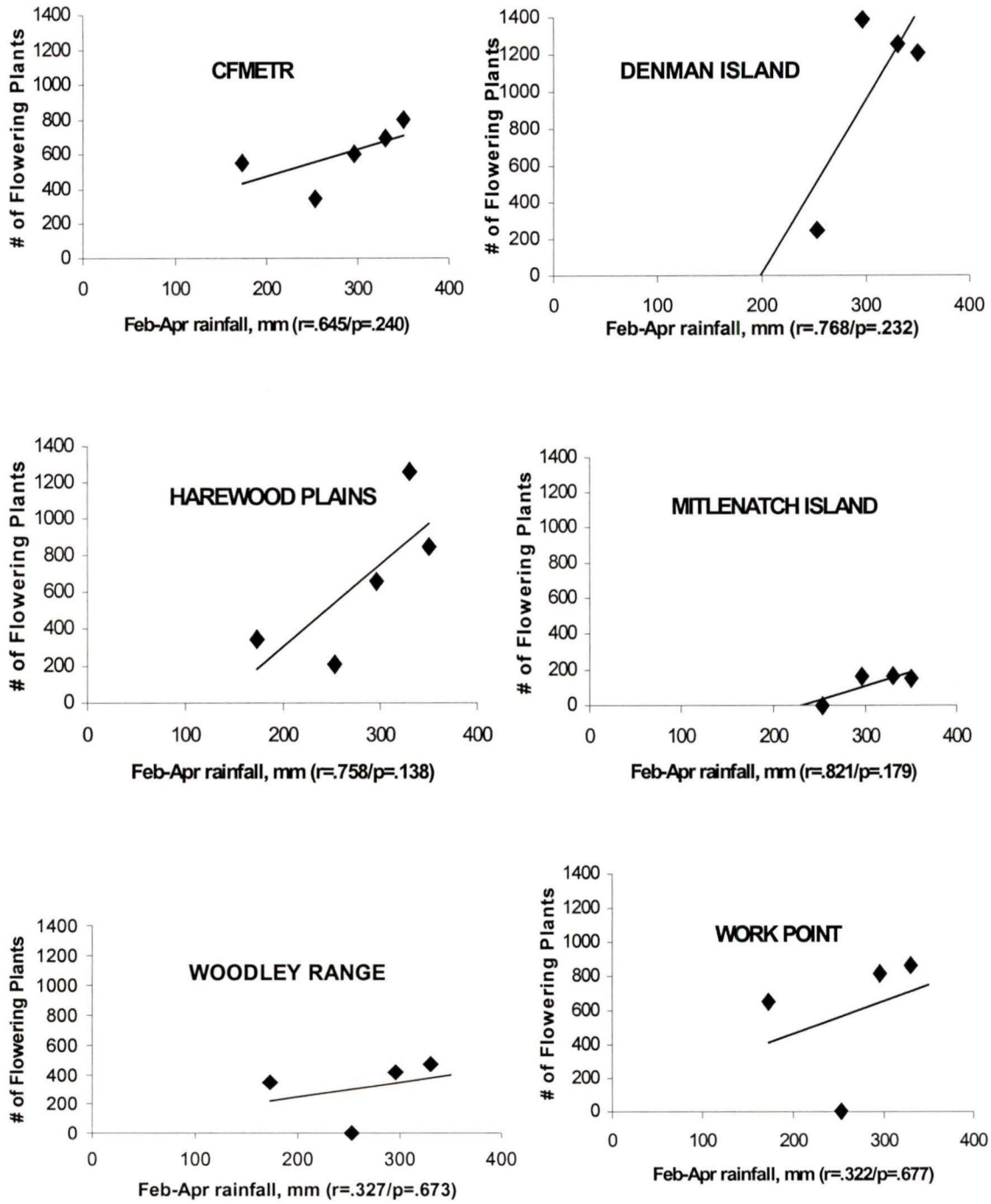


Figure 18. Number of flowering *Allium amplectens* inventoried at six different south-western British Columbia locations in relation to total February-April precipitation (Pearson correlation coefficients (r) & significance (p) values are indicated for each site).

3.1.2 Densities of flowering and nonflowering plants in marked plots

At the four localities that had permanent plots, all stages were counted. All of the sites were censused in 1996, 1997, and 1998 (Figures 19, 20, 21 & 22). Up to 1998, total densities of plants were highest in 1996. During the entire 5-year period of the study, densities of nonflowering plants and all stages of plants were highest in the year 2000 (Figures 19-22) for all populations combined. The lowest numbers were recorded in 1998 for all sites. Few nonflowering plants were found at the Mitlenatch Island site, and no vegetative plants were found at Work Point in any of the three years for which it was inventoried. Proportions of nonflowering individuals were consistently highest at the CFMETR site. Flowering plants tended to be fewer flowered (higher proportions of F_1 plants) at the CFMETR and Woodley Range sites and had more flowers (higher proportions of F_2 plants) in the Mitlenatch and Work Point populations.

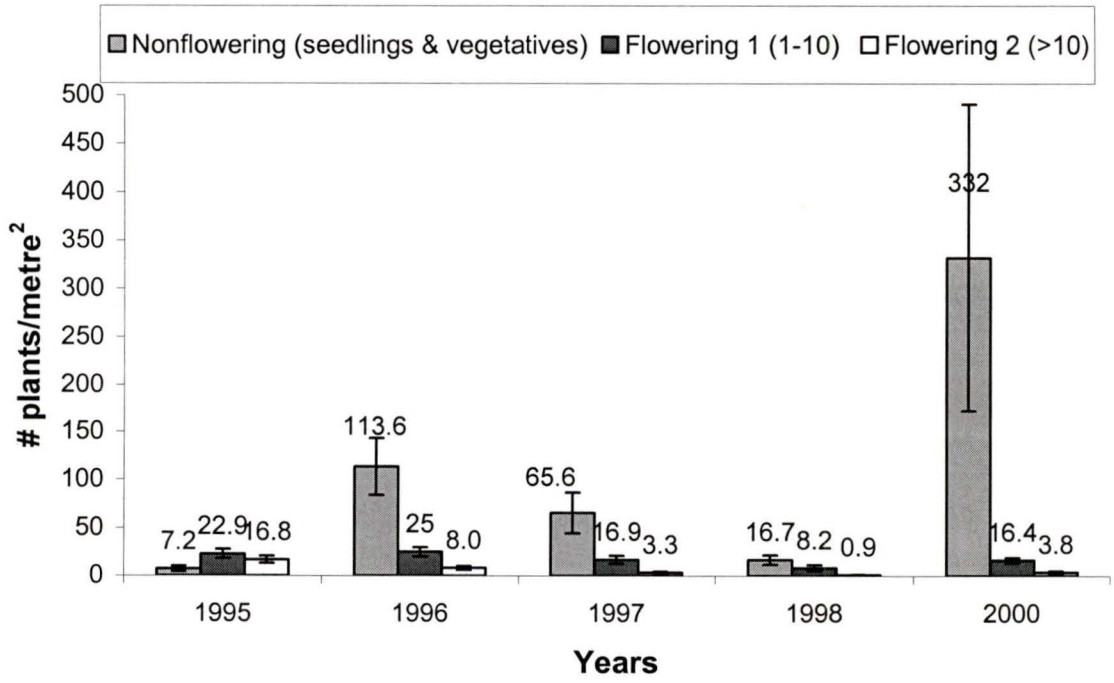


Figure 19. Density (means and std errors) of *Allium amplectens* of different stages in plots at CFMETR (1995-2000). Number of plots = 15 (1995) and 23 (1996-2000).

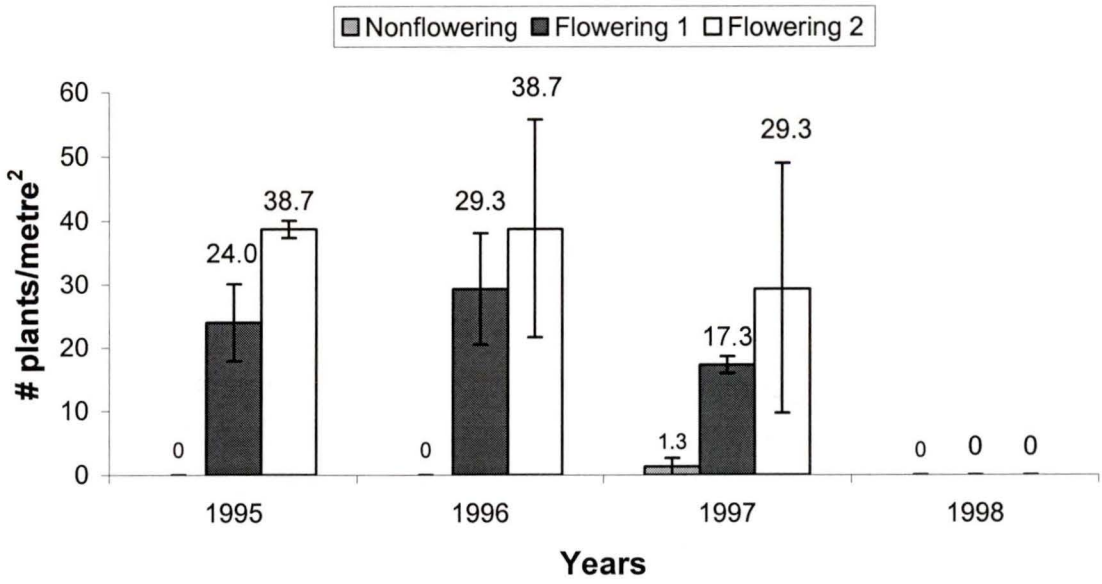


Figure 20. Density (means and std errors) of *Allium amplectens* of different stages in plots at Mitlenatch Island (1995-1998). Number of plots = 3.

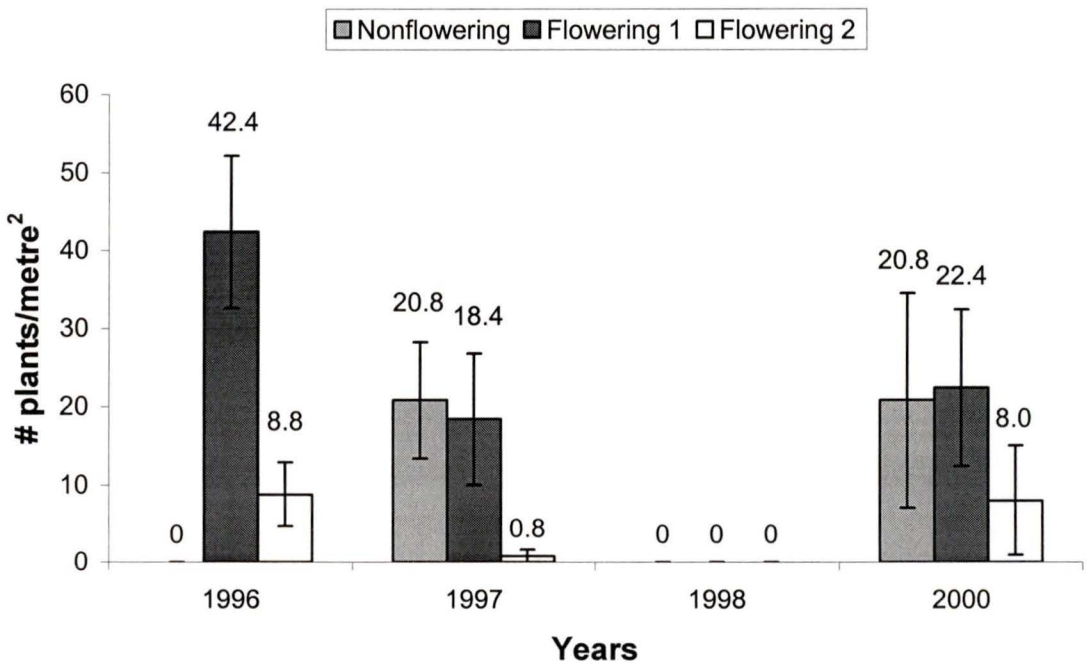


Figure 21. Density (means and std errors) of *Allium amplectens* of different stages in plots at Woodley Range (1996-2000). Number of plots = 5.

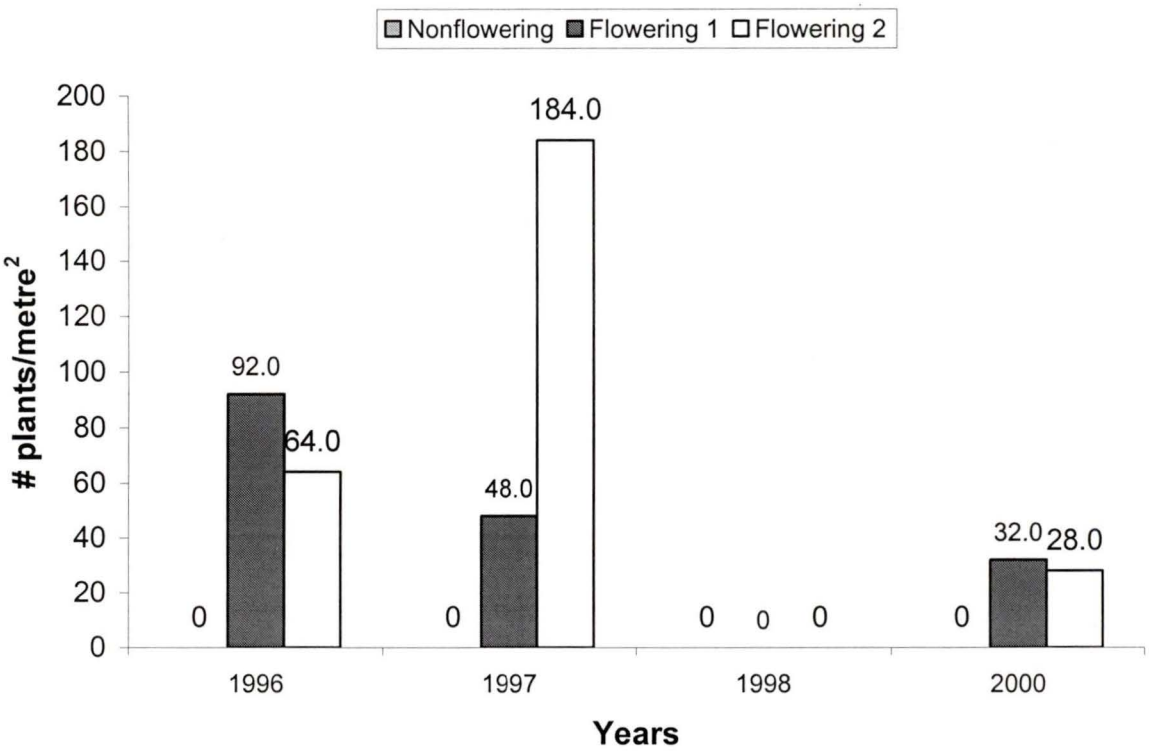


Figure 22. Density of *Allium amplectens* of different stages in plots at Work Point (1996-2000). There was only 1 sample plot at this site.

Figures 23-25 show densities (plants per square metre) of all *A. amplectens* life stages in three different habitats at the CFMETR site only. In 1997 and 2000, plots in the Orchard Grass habitat had the highest densities because of the presence of large numbers of seedlings, offsets, and/or dormant plants, especially during the spring of 2000. Flowering life stages (F_1 and F_2) were relatively more common in Rocky habitats (Figure 23), except in 1998, an extremely dry year. However, densities of vegetative plants were comparatively low at the same locations (Figure 23). In the Dogtail Meadow habitat, there were few consistent patterns among years. For example, densities of nonflowering individuals were higher than in other sites in 1996 and 1998, but intermediate between the other two habitat types in 1997 and 2000 (Figure 24).

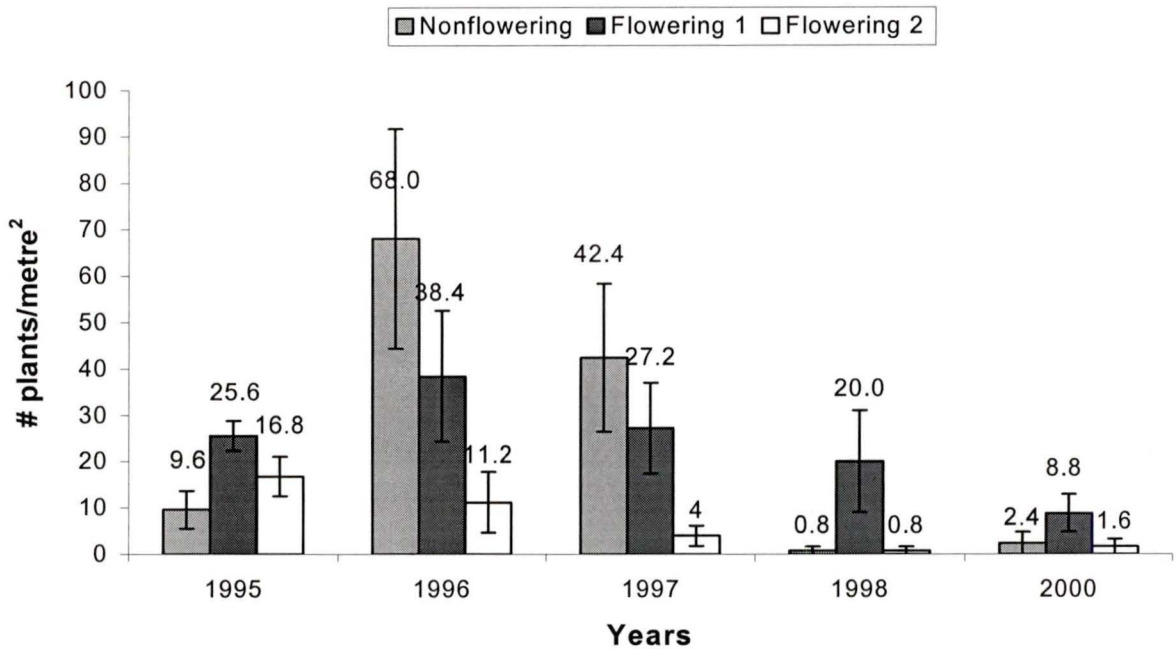


Figure 23. Density (means and std errors) of *Allium amplectens* of different stages in Rocky habitats. Number of plots = 5.

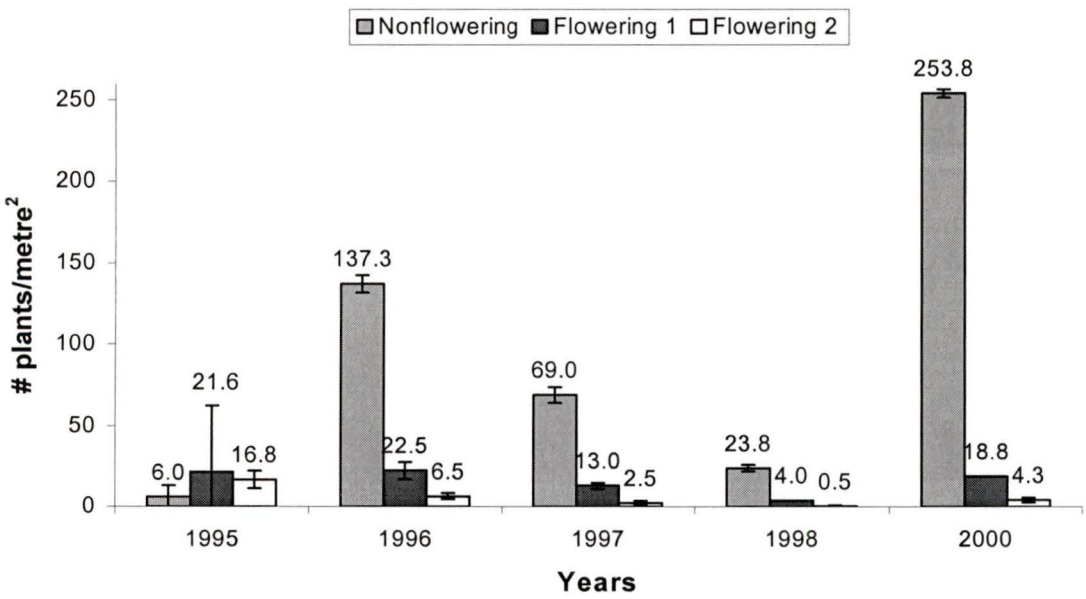


Figure 24. Density (means and std errors) of *Allium amplectens* of different stages in Dogtail Meadow habitats. Number of plots = 10 (1995) and 16 (1996-2000).

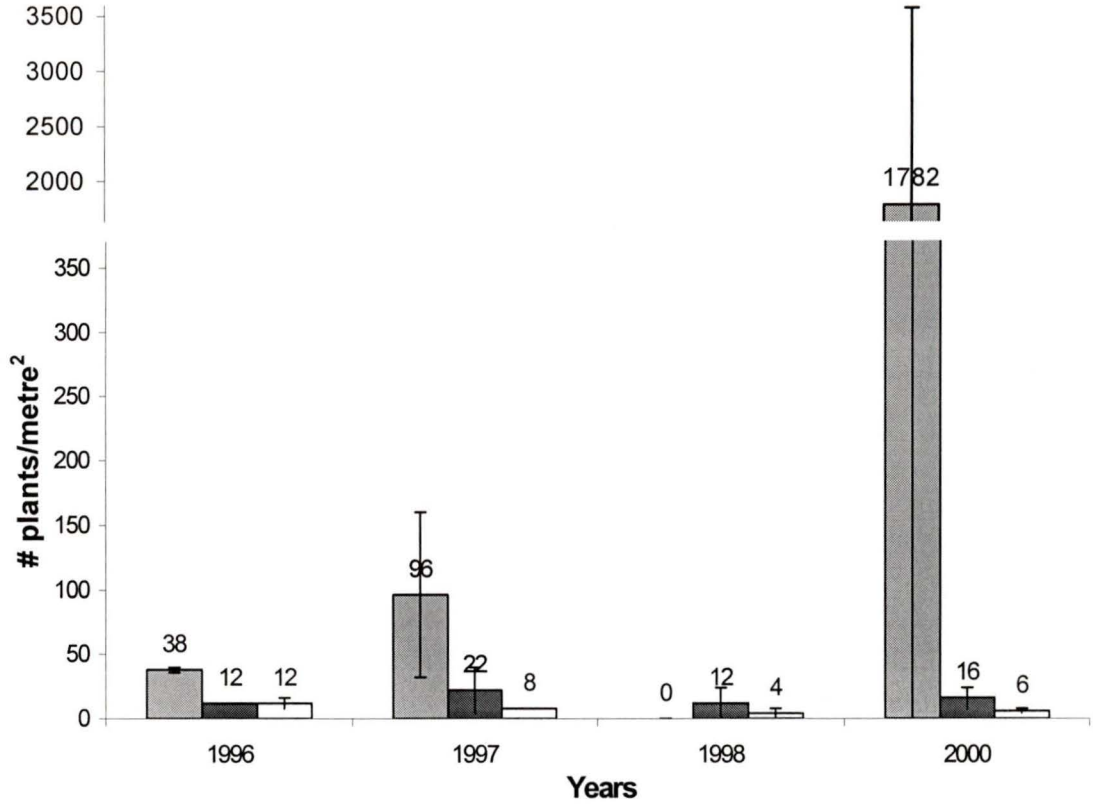


Figure 25. Density (means and std errors) of *Allium amplectens* of different stages in Orchard Grass habitats. Number of plots = 2.

3.2 Matrix analyses at CFMETR

Detailed demographic analyses of the different life stages were conducted on *A. amplectens* at the CFMETR site.

Figure 26 illustrates the life cycle of *A. amplectens*, showing stages used in this analysis. Both the vegetative and the two flowering stages can exhibit one or more seasons of dormancy, before returning to one of the three actively growing stages. Because this is a stage-based rather than age-based model, plants did not necessarily move to the next stage in a subsequent year.

I observed that one or more stages could be bypassed by some plants. All possible transitions between flowering and vegetative stages were also observed (double-ended

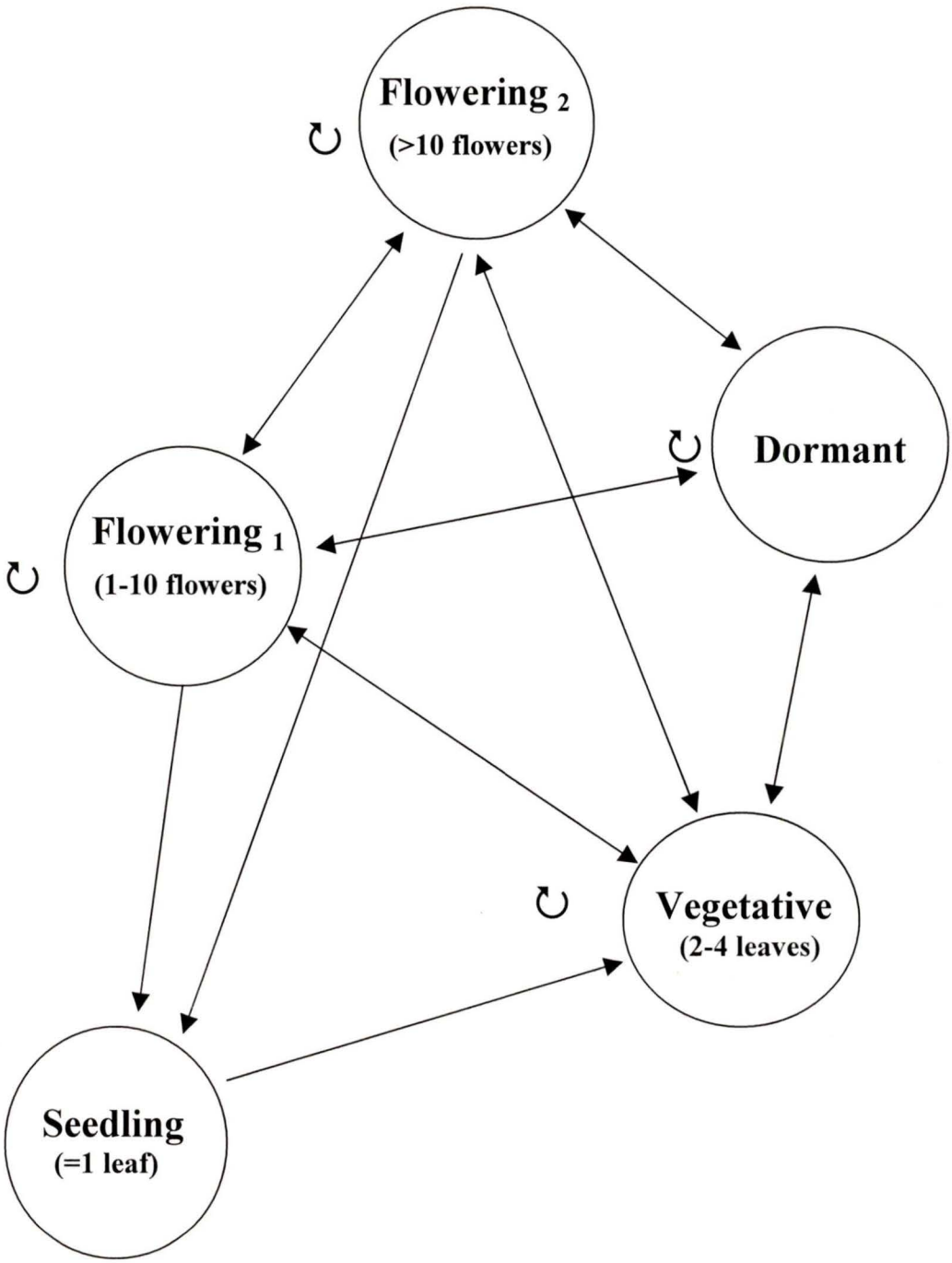


Figure 26. Life cycle diagram of *Allium amplectens*. Double-sided arrow indicates plant can revert to previous stage. ↻indicates that plant can remain in this stage for more than one season.

arrows, Figure 26). Because seedlings result from seed production, they are only produced by flowering plants, not vegetative ones. Yearly variations in lambda values for the populations at CFMETR, given the assumptions made, varied from 0.970 (1997-98 year) to 0.821 (1996-97 year).

All transition probabilities in Tables 9 to 12 are based upon plants observed in the marked plots, except for offset rates in the second row (calculated as 18% based on bulbs sampled at Harewood Plains in 2000), and a 50% probability of dormancy (based upon dormancy statistics compiled during 1995-2000). No seedlings were observed in any of the permanent plots until the 2000 field season, when I observed a total of 88 seedlings (5.1% of all untrackable nonflowering plants in bunches). Thus non-zero fecundity values are only seen for the 1998-2000 transition (Table 12).

The mean matrix, sensitivities, elasticities, predicted stable stage structures, and reproductive values that were calculated from the population transitions for the CFMETR site from 1995-2000 are given in Table 13. Values indicate the highest transition rates of plants occur from F_2's to vegetatives or dormancy, and from dormants to vegetatives.

Elasticities indicate that the most important transitions within a typical plant's life cycle involve vegetative plants and their transitions into or out of dormancy. In the stable stage structure, over 50% of individuals are vegetative plants, with the next most abundant stage being dormants. The least common stage is F_2 plants. Reproductive values of F_2 plants are the highest of any stage category. In addition to its capacity for asexual reproduction, this category has a higher number of flowers per scape than any other life stage, thus could be expected to contribute the most seedlings per plant, when these occur.

Table 9. 1995-1996 transition matrix for *A. amplectens* at CFMETR. (transition based on 15 plots). [1] Seedlings calculated for this transition. [2] Assumed seedling survivorship. [3] Actual numbers of vegetative, F_1 or F_2 plants which appear as vegetative individuals. [4] Number of offsets assumed to arise from vegetative, F_1 or F_2 plants in column. [5] Dormant number plus total number of plants listed in cells $V:V+V:F_1+V:F_2$ equals total number vegetative plants. [6]Highlighted numbers indicate plants counted within each stage. Nonhighlighted numbers indicate plants added to stage that year or dormant/dead plants. S= Seedling V=Vegetative F_1=1-10 flowers F_2=>10 flowers D=Dormant.

λ = **0.944**						
FROM:						
	Nonflowering		Flowering		Dormant	Total in 1996[6]
TO:	S	V	F_1	F_2	D	
S			0.000 (0)[1]	0.000 (0)[1]		
V	0.000 (0)[2]	0.666 (15)[3]+(3)[4]	0.535 (35)[3]+(11)[4]	0.571 (28)[3]+(8)[4]	0.834 (332)[5]	432
F_1		0.037 (1)	0.256 (22)	0.191 (12)	0.126 (50)	85
F_2			0.023 (2)	0.095 (6)	0.040 (16)	24
D		0.222 (6)	0.163 (14)	0.143 (9)		29
Total	0	22	73	55	398	
Dead	0	5	13	8	0	26
Total in 1995[6]	0	27+3	86+11	63+8	398	596

Sensitivities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.000	0.000	0.000
V	0.000	0.713	0.074	0.011	0.182
F_1	0.000	0.762	0.080	0.011	0.195
F_2	0.000	0.000	0.082	0.016	0.199
D	0.000	0.764	0.080	0.011	0.000

Elasticities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.000	0.000	0.000
V	0.000	0.503	0.042	0.006	0.161
F_1	0.000	0.030	0.022	0.002	0.026
F_2	0.000	0.000	0.002	0.001	0.009
D	0.000	0.180	0.014	0.002	0.000

Table 10. 1996-1997 transition matrix for *A. amplectens* at CFMETR. (transition based on 23 plots). [1] Seedlings calculated for this transition. [2] Assumed seedling survivorship. [3] Actual numbers of vegetative, F_1 or F_2 plants which appear as vegetative individuals. [4] Number of offsets assumed to arise from vegetative, F_1 or F_2 plants in column. [5] Dormant number plus total number of plants listed in cells $V:V+V:F_1+V:F_2$ equals total number vegetative plants. [6]Highlighted numbers indicate plants counted within each stage. Nonhighlighted numbers indicate plants added to stage that year or dormant/dead plants. S= Seedling V=Vegetative F_1=1-10 flowers F_2=>10 flowers D=Dormant.

$\lambda = 0.821$						
FROM:						
	Nonflowering		Flowering		Dormant	Total in 1997[6]
TO:	S	V	F_1	F_2	D	
S			0.000 (0)[1]	0.000 (0)[1]		
V	0.000 (0)[2]	0.325 (177)[3]+(35)[4]	0.375 (42)[3]+(12)[4]	0.217 (7)[3]+(3)[4]	0.521 (101)[5]	377
F_1		0.023 (15)	0.174 (25)	0.130 (6)	0.263 (51)	97
F_2		0.003 (2)	0.014 (2)	0.022 (1)	0.072 (14)	19
D		0.352 (230)	0.264 (38)	0.348 (16)	0.144 (28)	312
Total	0	424	107	30	194	
Dead	0	229	37	16	0	282
Total in 1996[6]	0	653+35	144+12	46+3	194	1087

Sensitivities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.000	0.000	0.000
V	0.000	0.424	0.139	0.030	0.291
F_1	0.000	0.485	0.159	0.035	0.332
F_2	0.000	0.439	0.144	0.031	0.301
D	0.000	0.562	0.185	0.041	0.385

Elasticities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.000	0.000	0.000
V	0.000	0.168	0.064	0.008	0.185
F_1	0.000	0.014	0.034	0.005	0.107
F_2	0.000	0.002	0.003	0.001	0.026
D	0.000	0.241	0.059	0.017	0.068

Table 11. 1997-1998 transition matrix for *A. amplectens* at CFMETR. (transition based on 23 plots). [1] Seedlings calculated for this transition. [2] Assumed seedling survivorship. [3] Actual numbers of vegetative, F_1 or F_2 plants which appear as vegetative individuals. [4] Number of offsets assumed to arise from vegetative, F_1 or F_2 plants in column. [5] Dormant number plus total number of plants listed in cells $V:V+V:F_1+V:F_2$ equals total number vegetative plants. [6]Highlighted numbers indicate plants counted within each stage. Nonhighlighted numbers indicate plants added to stage that year or dormant/dead plants. S= Seedling V=Vegetative F_1=1-10 flowers F_2=>10 flowers D=Dormant.

λ = 0.970						
FROM:						
	Nonflowering		Flowering		Dormant	Total in 1998[6]
TO:	S	V	F_1	F_2	D	
S			0.000 (0)[1]	0.000 (0)[1]		
V	0.000 (0)[2]	0.143 (44)[3]+(10)[4]	0.237 (17)[3]+(6)[4]	0.053 (0)[3]+(1)[4]	0.030 (18)[5]	96
F_1		0.024 (9)	0.165 (16)	0.105 (2)	0.034 (20)	47
F_2			0.021 (2)	0.053 (1)	0.003 (2)	5
D		0.430 (162)	0.320 (31)	0.421 (8)	0.933 (556)	757
Total	0	215	66	11	596	
Dead	0	162	31	8	0	201
Total in 1997[6]	0	377+10	97+6	19+1	596	1106

Sensitivities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.000	0.000	0.000
V	0.000	0.025	0.023	0.002	0.509
F_1	0.000	0.027	0.024	0.002	0.541
F_2	0.000	0.000	0.023	0.002	0.527
D	0.000	0.047	0.042	0.004	0.949

Elasticities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.000	0.000	0.000
V	0.000	0.004	0.006	0.000	0.016
F_1	0.000	0.001	0.004	0.000	0.019
F_2	0.000	0.000	0.001	0.000	0.002
D	0.000	0.021	0.014	0.002	0.913

Table 12. 1998-2000 transition matrix for *A. amplectens* at CFMETR. (transition based on 23 plots). [1] Seedlings calculated for this transition. [2] Assumed seedling survivorship. [3] Actual numbers of vegetative, F_1 or F_2 plants which appear as vegetative individuals. [4] Number of offsets assumed to arise from vegetative, F_1 or F_2 plants in column. [5] Dormant number plus total number of plants listed in cells $V:V+V:F_1+V:F_2$ equals total number vegetative plants. [6]Highlighted numbers indicate plants counted within each stage. Nonhighlighted numbers indicate plants added to stage that year or dormant/dead plants. S= Seedling V=Vegetative F_1=1-10 flowers F_2=>10 flowers D=Dormant.

λ = 1.089						
FROM:						
	Nonflowering		Flowering		Dormant	Total in 2000[6]
TO:	S	V	F_1	F_2	D	
S			1.489 (70)[1]	3.600 (18)[1]		88
V	0.500 (0)[2]	0.719 (57)[3]+(12)[4]	0.277 (9)[3]+(4)[4]	0.200 (0)[3]+(1)[4]	0.951 (1738)[5]	1821
F_1		0.063 (6)	0.255 (12)	0.400 (2)	0.041 (74)	94
F_2		0.031 (3)	0.021 (1)	0.400 (2)	0.009 (16)	22
D		0.156 (15)	0.277 (13)	0.200 (1)		29
Total	0	81	35	5	1828	
Dead	0	15	12	0	0	27
Total in 1998[6]	0	96+12	47+70+4	5+18+1	1828	2081

Sensitivities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.030	0.014	0.000
V	0.188	0.593	0.065	0.030	0.107
F_1	0.000	0.931	0.101	0.047	0.168
F_2	0.000	2.302	0.250	0.117	0.415
D	0.000	0.572	0.062	0.029	0.000

Elasticities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.040	0.046	0.000
V	0.086	0.392	0.016	0.006	0.093
F_1	0.000	0.054	0.024	0.017	0.006
F_2	0.000	0.066	0.005	0.043	0.003
D	0.000	0.082	0.016	0.005	0.000

Table 13. Mean matrix, sensitivities, elasticities, stage structure and reproductive values values (1995-2000) at CFMETR (means, sensitivities, and elasticities = or > 0.2 are highlighted in bold).

MEAN MATRIX λ = 0.877					
	S	V	F_1	F_2	D
S	0	0	**0.372**	**0.900**	0
V	0.125	**0.463**	**0.356**	**0.260**	**0.584**
F_1	0	0.037	**0.213**	**0.207**	0.116
F_2	0	0.009	0.020	0.143	0.031
D	0	**0.290**	**0.256**	**0.278**	**0.269**
SENSITIVITIES					
	S	V	F_1	F_2	D
S	0	0	0.012	0.003	0
V	0.057	**0.510**	0.085	0.021	**0.288**
F_1	0	**0.578**	0.097	0.024	**0.327**
F_2	0	**0.672**	0.112	0.027	**0.380**
D	0	**0.634**	0.106	0.026	**0.358**
ELASTICITIES					
	S	V	F_1	F_2	D
S	0	0	0.005	0.003	0
V	0.008	**0.269**	0.035	0.006	0.192
F_1	0	0.024	0.023	0.006	0.043
F_2	0	0.007	0.003	0.005	0.013
D	0	**0.209**	0.031	0.008	0.110

STAGE	**STABLE STAGE STRUCTURE**	**REPRODUCTIVE VALUES**
S	6.0%	2.9%
V	53.0%	20.7%
F_1	8.9%	23.4%
F_2	2.2%	27.3%
D	30.0%	25.7%

Population growth rates (λ's) at the CFMETR site calculated for the 4 different transition intervals are summarized in Table 14. The mean growth rate (λ) of the first three 1-year transitions was 0.912 (std deviation ±0.080), while with the final, two-year, transition included (numbers in parentheses), the mean population growth rate was 0.956 (std deviation ±0.110). The mean of λs for the 1995-1998 (0.912) and 1995-2000 periods (0.956) indicated a slight population decrease. The 1995-2000 mean matrix result, calculated from the arithmetic means for each of the cells from the participating transitional matrices, also indicated a population decrease or λ of 0.877.

Table 14. Lambdas, means and standard deviations of lambdas, and mean matrix lambda for *A. amplectens* at CFMETR for 1995-1996, 1996-1997, 1997-1998 & 1998-20000 transitions.

TRANSITION	**LAMBDAS**
1995-1996	0.944
1996-1997	0.821
1997-1998	0.970
1998-2000	1.089
MEAN OF λs	0.912 for 1995-1998 only (0.956 if all transitions included)
STD DEVIATIONS	0.080 for 1995-1998 only (0.110 if all transitions included)
MEAN MATRIX λ	0.877 for 1995-2000

Figure 27 illustrates the predicted stable stage distributions or percentages of plants at each life stage at CFMETR (Nanoose Hill) for each transition. No consistent

stable age distribution was observed; for example, vegetative plants varied from 72.7% for 1995-1996 to 4.5% for 1997-1998, and dormant plants varied from a high of 91.1% for 1997- 1998 (a dry year) to a low of only 10.9% for 1998-2000 (a relatively wet year).

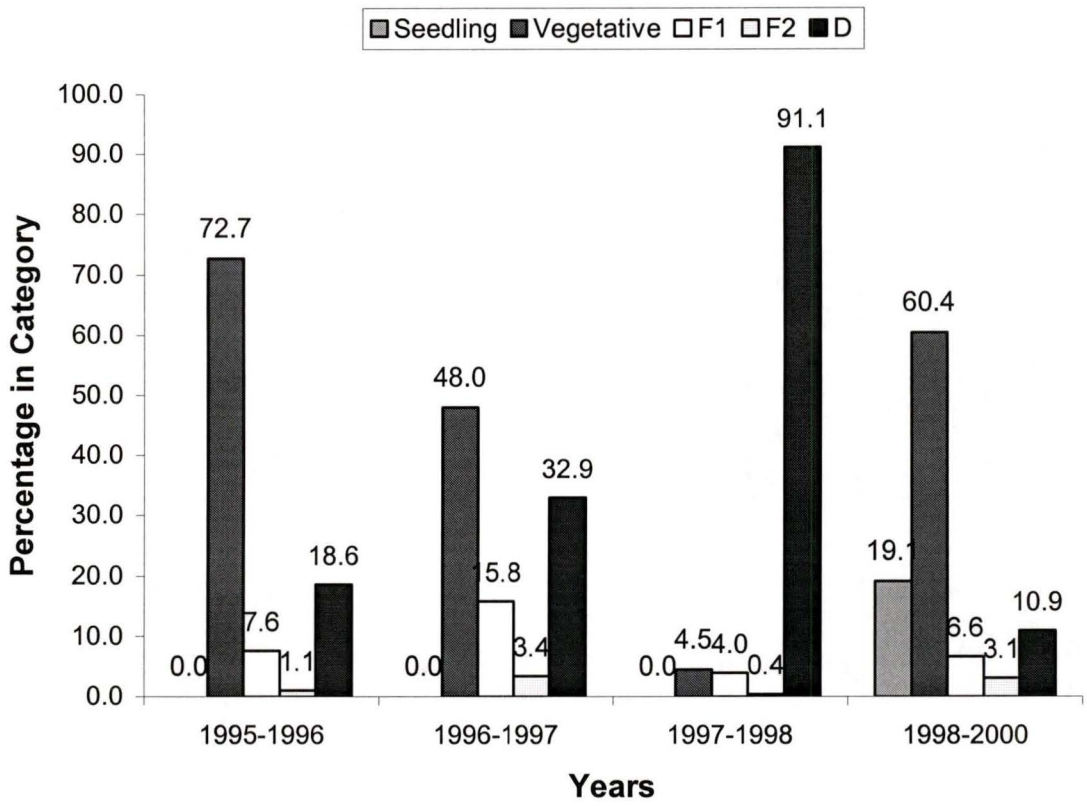


Figure 27. Predicted stable stage structures of *A. amplectens* at CFMETR (growth scenarios) for 1995-1996, 1996-1997, 1997-1998 & 1998-2000 transitions.

Tables 15 and 16 present the means and standard deviations of the sensitivities and elasticities for the growth scenario. The 1995-1996, 1996-1997 and 1997-1998 transitional years are shown. Those elements with the highest sensitivity to change in the population growth rate were D:D, V:D, and V:F_1 (Table 15). Two of these involve dormancy, indicating the large impact of dormancy rates on λ and the importance of the

assumptions made about dormancy. The standard deviations for these elements are also comparatively high.

Table 15. Means and standard deviations of sensitivities of *A. amplectens* at CFMETR for 1995-1996, 1996-1997 & 1997-1998 transitions (mean sensitivity and std values = or > 0.200 are highlighted in bold).

Means of Sensitivities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.000	0.000	0.000
V	0.000	**0.387**	0.081	0.014	**0.327**
F_1	0.000	**0.425**	0.088	0.016	**0.356**
F_2	0.000	0.146	0.083	0.016	**0.342**
D	0.000	**0.458**	0.102	0.019	**0.445**
Standard Deviations of Sensitivities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.000	0.000	0.000
V	0.000	**0.346**	0.058	0.014	0.167
F_1	0.000	**0.371**	0.068	0.017	0.174
F_2	0.000	**0.253**	0.061	0.015	0.168
D	0.000	**0.370**	0.074	0.019	**0.477**

Because elasticities sum to 1 or 100%, they are intuitively more interpretable than sensitivities. The highest elasticities (Table 16) were for the D:D transition of 32.7 %, the second was V:V at 22.5%, and the third was V:D at 14.7%. Elasticities for transitions in and out of dormancy were probably influenced strongly by assumptions about mortality

of dormant plants. Elasticities were also relatively high for those transitions in the second row, illustrating the importance of vegetative offsetting to population growth (Table 16: 22.5%, 3.7%, and 0.5%). Offsetting and dormancy are therefore critical contributors to future population structure and growth rates. The role of seed production is minimal in these analyses. Production of bulb offsets appears to be the major form of reproduction in the populations studied.

Table 16. Means and standard deviations of elasticities of *A. amplectens* at CFMETR for 1995-1996, 1996-1997 & 1997-1998 transitions (mean elasticity and std values = or > 0.200 are highlighted in bold) .

Means of Elasticities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.000	0.000	0.000
V	0.000	**0.225**	0.037	0.005	0.121
F_1	0.000	0.015	0.020	0.002	0.051
F_2	0.000	0.001	0.002	0.001	0.012
D	0.000	0.147	0.029	0.007	**0.327**
Standard Deviations of Elasticities					
	S	V	F_1	F_2	D
S	0.000	0.000	0.000	0.000	0.000
V	0.000	**0.254**	0.029	0.004	0.090
F_1	0.000	0.015	0.015	0.003	0.049
F_2	0.000	0.001	0.001	0.001	0.012
D	0.000	0.114	0.026	0.009	0.509

Reproductive values, or the expected contribution to future generations of individuals within each demographic stage, are illustrated for the CFMETR site in Figure 28. Differences between and within years depended on the percentage of plants that were assumed to have moved into dormancy during that transition. The proportion of dormant individuals during a high growth transition (1998-2000) was much lower than in a low growth year (1997-1998) (see Figure 27). The relatively high numbers illustrated in Figure 28 indicate the significant reproductive value of temporarily dormant plants in future years.

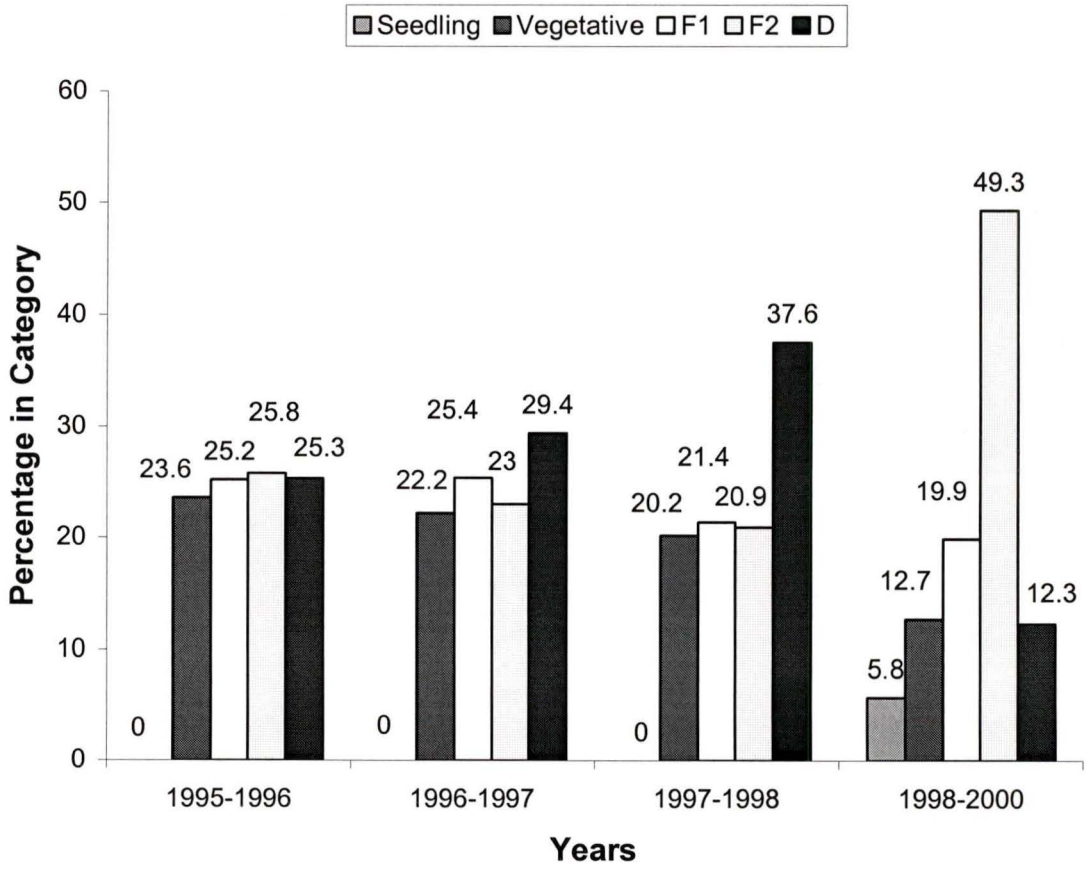
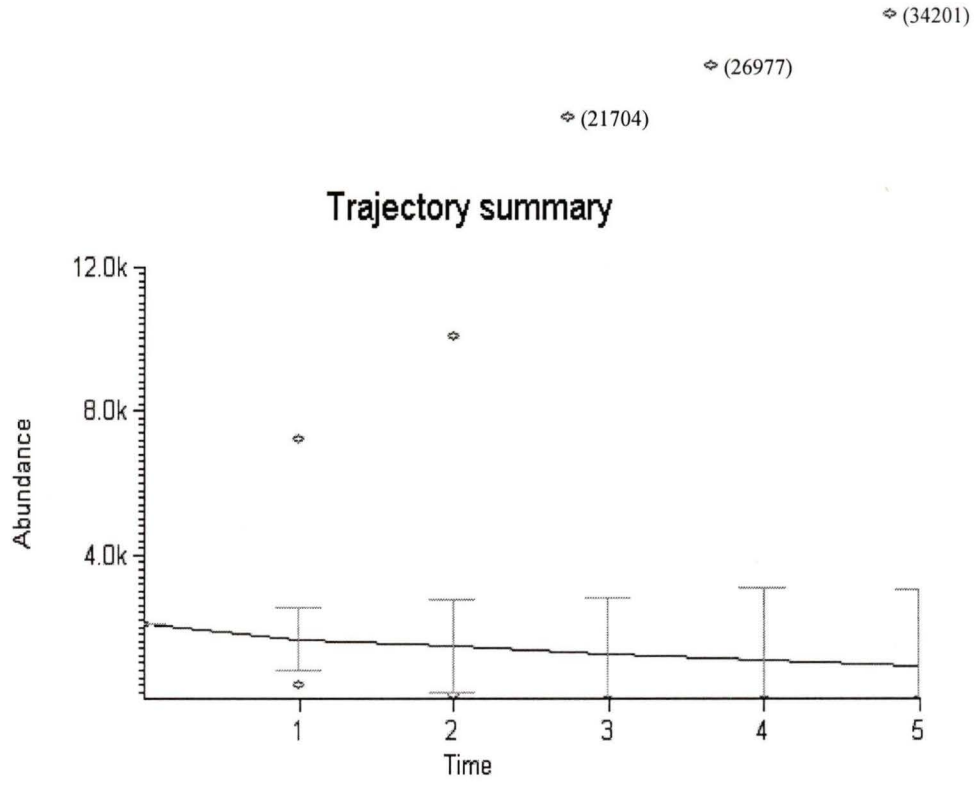


Figure 28. Reproductive values of *A. amplectens* at CFMETR (growth scenarios) for 1995-1996, 1996-1997,1997-1998 & 1998-2000 transitions.

3.3 Population viability scenario for *A. amplectens* at CFMETR

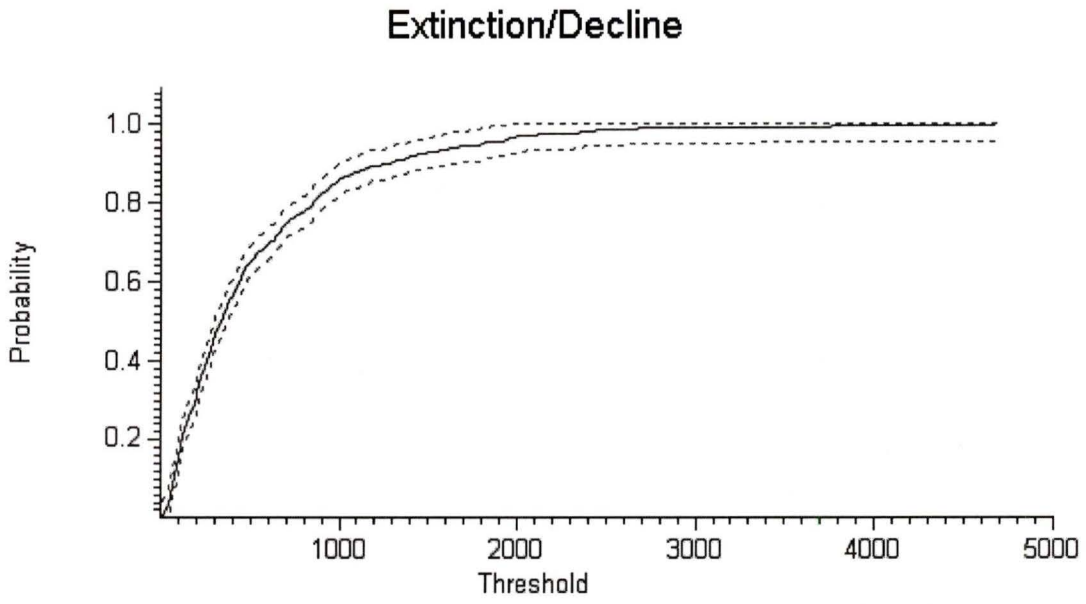
The population viability simulation (Figure 29) extrapolates a steady decline in population numbers, over the five year period, from 2054 plants in the year 2000 down to 916 plants in 2005. It is important to remember that this is a simulation or projection and not a prediction of future population levels. It is based upon a dataset from only one location and also ignores the potential impact of environmental and demographic stochasticity upon *A. amplectens*. Temporal variation (environmental stochasticity) such as rainfall may have an important effect on future population numbers (Figure 18) and the consequent population viability (PVA) that would be calculated.

Concomitant calculation of the quasi-extinction risk curve (Figure 30) is expected to answer the question about what will happen when a population with this current size would fall below some critical threshold within the next time period. Extirpation of populations is generally less likely if the numbers are larger and more dispersed due to increased genetic, demographic, and environmental heterogeneity. The counterbalancing effect of these three parameters is likely to be much greater for this species over its entire range than at any single site. This curve predicts a probability of about 0.34 (34%) that the *A. amplectens* population at CFMETR would decline below 216 plants. For statistical reliability, each simulation was replicated 500 times (Harris, Maguire and Shaffer 1987). With 500 iterations the predicted values of extinction or recovery probability are bounded by a 95% confidence interval of about 8% (Kolmogorov-Smirnov test statistic D). Again, this should be regarded as a projection rather than a prediction of future events.



Time (Years)	Minimum	-1 S.D.	Abundance (Average)	+1 S.D.	Maximum
0	*2054.00	2054.00	2054.00	2054.00	2054.00
1	367.00	767.00	1648.00	2529.00	7212.00
2	110.00	174.00	1460.00	2746.00	10119.00
3	27.00	-359.00	1209.00	2777.00	21704.00
4	18.00	-929.00	1065.00	3059.00	26977.00
5	10.00	-1177.70	916.30	3010.30	34201.00

Figure 29. Trajectory summary of 500 randomly selected growth rates (stochastic) for *A. amplectens* at CFMETR based on *abundances of life stages in year 2000. Note that standard deviations are calculated symmetrically around the mean. Since populations at a given time step often have a skewed distribution resulting in the median being less than the mean, average population sizes should not be interpreted as the expected population size but rather as a summary of the population trend. ⇔ = maximum and minimum values for each year. For last 3 points maximum values off scale.



Extinction/Decline

Threshold	Probability	*95% confidence interval	
10	0.002	0.000	0.042
98	0.154	0.114	0.194
128	0.212	0.172	0.252
216	0.342	0.302	0.382
275	0.432	0.392	0.472
364	0.540	0.500	0.580
452	0.612	0.572	0.652
599	0.700	0.660	0.740
865	0.806	0.766	0.846
1277	0.900	0.860	0.940
3193	0.990	0.950	1.000
4696	1.000	0.960	1.000

Figure 30. Quasi-Extinction risk curve for *A. amplectens* at CFMETR, showing results of simulation using RAMAS ECOLAB/demographic stochasticity option illustrating probability of falling below certain levels (thresholds) anytime during a five year period. *Based on Kolmogorov-Smirnov test statistic D.

4.0 Comparison of population and plot counts with matrix analyses at CFMETR

Table 17 compares different methods of assessing *A. amplectens* population changes over a 5-year period at the CFMETR (Nanoose Hill) site. Sections A-C illustrate R, rates of increase or decrease, over various time periods. Section D shows lambdas calculated for the same intervals. Comparisons of different sections illustrate the effects of sampling the entire flowering plant population (Table 17A), a subset of flowering plants or those within marked plots (Table 17B), all plant stages within marked plots (Table 17C), or carrying out demographic analyses of marked plants (Table 17D).

Lambdas from the matrix analyses (Table 17D) give a picture of less variable population fluctuations than do the rates of increase (Table 17 A-C), because they take into account the probability of dormancy. This was especially notable for the 1997-1998 transition. Over the 5-year period, however, sampling the entire flowering plant population (Table 17A) or a subset of flowering plants (Table 17B) appears to show a similar trend.

In most sections of Table 17, multiple-year calculations suggest a downward trend for these populations, with value of R or λ less than 1. Except for section C the results showed a decrease for the 5-year period of 0.688 (flowering plant population count), 0.779 (flowering plant marked plot count), and 0.877 (mean matrix average).

Table 17. Changes in *Allium amplectens* populations over a 5-year period at the CFMETR site, as assessed by rates of increase ($R=N_{t+1}/N_t$) and λ values.

A. Rates of increase (R) based on total numbers of flowering plants in all populations.

1995	1996	1997	1998	2000	YEAR
801	695	603	347	551	# ADULTS

(R=0.868) (R=0.868) (R=0.575) (R=1.588)

(R=0.753)

(R=0.433)

(R=0.688)

B. Rates of increase (R) based on total numbers of flowering plants in marked plots.

1995	1996	1997	1998	2000	YEAR
149	190	116	52	116	# ADULTS

(R=1.275) (R=0.611) (R=0.448) (R=2.231)

(R=0.779)

(R=0.349)

(R=0.779)

C. Rates of increase (R) based on all vegetative and flowering plants in marked plots.

1995	1996	1997	1998	2000	YEAR
176	843	493	148	2025	# PLANTS

(R=4.790) (R=0.585) (R=0.300) (R=13.682)

(R=2.801)

(R=0.841)

(R=11.506)

D. Lambdas calculated from transition matrices based on mapped individuals.

1995	1996	1997	1998	2000	YEAR

(λ=0.944) (λ=0.822) (λ=0.974) (λ=1.089)

(λ=0.873) (Mean matrix average)

(λ=0.855) (Mean matrix average)

(λ=0.877) (Mean matrix average)

5.0 Dormancy

Table 18 illustrates the resighting histories for all marked plants. Because no dataset exists for 1999, additional unobserved dormancy could have occurred in that year.

Table 18. Complete table of resighting histories for marked plants of *A. amplectens* at CFMETR. (Blank=absent, 1=nonflowering, 2=flowering, 0=dormant, N=545). Only plants present for at least 4 years were used in dormancy rate calculations. [1]Habitat symbols are R (Rocky), D (Dogtail Meadow), and O (Orchard Grass).

[1]Plot Numbers and Habitats	Year					Total number with observed pattern
	1995	1996	1997	1998	2000	
2D/R	2	2	1	2	2	1
4G/D	2	2	1	2	2	1
3A/D	2	1	1	1	2	1
3C/D	2	1	1	1	2	3
3B/D	2	2	1	1	1	1
4A/D	2	2	1	1	1	1
3B/D	2	1	1	1	1	3
3C/D	2	1	1	1	1	4
3C/D	1	1	1	1	1	5
4A/D	2	2	2	1	1	1
4B/D	2	1	1	2	1	1
4G/D	2	1	1	2	1	1
4G/D	2	1	2	2	1	1
4H/D	2	1	2	2	2	1
4H/D	2	2	2	2	1	1
3D/D	-	2	1	1	1	1
4A/D	0	2	1	1	1	2
3G/D	-	2	2	1	1	2
4A/D		1	1	1	1	2
4I/D	-	2	2	1	2	1
5A/O	-	2	2	2	2	1

Table 18 continued…

4H/D	2	0	2	1	1	4
2D/R	2	1	0	2	2	1
3C/D	1	1	0	1	1	4
3A/D	2	1	1	0	1	5
4A/D	2	1	1	0	1	1
4C/D	2	1	1	0	1	1
4H/D	2	1	1	0	1	8
4A/D	2	2	1	0	1	1
4G/D	2	2	1	0	1	3
4B/D	2	2	2	0	1	1
4H/D	2	1	2	0	1	6
4H/D	2	1	1	0	2	1
2A/R	2	2	2	2		2
2D/R	1	1	1	2		1
2D/R	1	1	1	1		1
2D/R	2	1	1	2		1
2E/R	2	2	1	2		1
4C/R	2	1	1	1		1
2E/R		0	2	2	2	1
3G/D		0	2	2	2	1
4G/D		0	2	2	2	1
5A/O		0	2	2	2	2
3D/D		0	2	1	2	1
3G/D		0	2	1	1	1
4H/D		0	2	1	1	1
4H/D		0	2	2	1	5
3E/D	-	2	0	2	2	1
3E/D	-	2	0	1	1	1
3G/D	-	2	0	1	1	1
3G/D	-	2	0	1	2	1
2C/R	0	2	2	0	2	1
3E/D	-	2	2	0	2	1
4J/D	-	2	2	0	2	1
3A/D	0	2	1	0	1	2
3E/D	-	2	1	0	1	1
4A/D	0	2	1	0	1	1
4G/D	0	2	1	0	1	6
3D/D	-	2	1	0	2	1

Table 18 continued…

4E/D	0	2	1	0	2	1
3D/D	-	2	2	0	1	1
4B/D	0	2	2	0	1	1
4D/D	0	2	2	0	1	1
4A/D		1	1	0	1	7
4G/D		1	1	0	1	1
4H/D		1	1	0	1	1
4H/D		1	2	0	1	1
2C/R	2	0	1	0	2	1
4G/D	2	0	1	0	2	1
2C/R	2	0	2	0	1	1
2C/R	2	0	2	0	2	1
3A/D	2	0	1	0	1	1
4G/D	2	0	1	0	1	2
2E/R	0	2	1	2		2
4J/D	-	2	2	1		1
4J/D		1	2	1		3
3B/D	2	1	0	0	2	1
4G/D	2	1	0	0	2	1
4H/D	2	1	0	0	2	1
3B/D	2	1	0	0	1	1
4B/D	2	1	0	0	1	1
4D/D	2	1	0	0	1	3
4G/D	2	1	0	0	1	2
4H/D	2	1	0	0	1	4
3C/D	1	1	0	0	1	1
4D/D	1	1	0	0	1	1
4D/D	2	2	0	0	1	1
4G/D	2	2	0	0	1	2
4H/D	2	2	0	0	1	1
4H/D	2	2	0	0	2	1
2A/R	2	0	2	2		1
2E/R	2	0	2	2		1
2A/R	2	2	2			5
2B/R	2	2	2			2
2C/R	2	2	2			1
2E/R	2	2	2			4

Table 18 continued…

2B/R	2	2	1			3
2C/R	2	2	1			1
2D/R	2	2	1			1
2E/R	2	2	1			2
4E/D	2	2	1			1
2B/R	2	1	1			2
4C/D	2	1	1			1
2B/R	2	1	2			1
2C/R	2	1	2			1
2D/R	1	2	1			1
2D/R	1	1	1			1
3E/D				1	1	1
4A/D				1	1	1
3G/D				1	2	2
4C/D			0	2	2	2
4G/D			0	2	2	1
5A/O			0	2	2	3
3A/D			1	0	2	1
5A/O			1	0	2	1
3D/D			1	0	1	1
3E/D			1	0	1	1
4A/D			1	0	1	3
4G/D			1	0	1	1
5A/O			1	0	1	1
3F/D		0	2	0	2	3
4A/D		0	2	0	2	1
4I/D		0	2	0	2	2
5A/O		0	2	0	2	1
3F/D		0	2	0	1	3
4G/D		0	2	0	1	2
5A/O		0	2	0	1	1
2A/R		0	2	2		1
5A/O		0	2	2		2
4C/D			1	1		1
4I/D			1	1		1
4I/D		0	2	1		2
1A/O	-	2	0	0	2	3

Table 18 continued…

2C/R	0	2	0	0	2	1
2E/R	0	2	0	0	2	1
3D/D	-	2	0	0	2	5
3E/D	-	2	0	0	2	2
3F/D	-	2	0	0	2	2
3G/D	-	2	0	0	2	2
4D/D	0	2	0	0	2	1
4H/D	0	2	0	0	2	1
2C/R	0	2	0	0	1	1
3D/D	-	2	0	0	1	10
3E/D	-	2	0	0	1	4
3G/D	-	2	0	0	1	1
4H/D	0	2	0	0	1	1
4J/D	-	2	0	0	1	1
4B/D		1	0	0	1	2
4G/D		1	0	0	1	2
4H/D		1	0	0	1	4
4D/D		1	0	0	2	2
4E/D		1	0	0	2	1
4J/D		1	0	0	2	1
2A/R	0	2	0	2		1
2E/R	0	2	0	2		5
2A/R		1	0	2		1
4D/D		1	0	1		2
3A/D	2	0	0	0	1	1
4D/D	1	0	0	0	1	1
4B/D	2	0	0	1		1
1A/O	-	2	1			2
2B/R	0	2	1			1
2E/R	0	2	1			2
4E/D	0	2	1			2
4G/D	0	2	1			1
4H/D	0	2	1			2
4I/D	-	2	1			3
4J/D	-	2	1			2
2A/R	0	2	2			1

Table 18 continued…

2E/R	0	2	2			2
4H/D	0	2	2			1
4J/D	-	2	2			2
2D/R		1	1			5
4G/D		1	1			1
4I/D		1	1			2
2E/R		1	2			1
4J/D		1	2			2
2A/R	2	0	2			5
2C/R	2	0	2			1
2E/R	2	0	2			1
4H/D	2	0	2			1
2B/R	1	0	1			3
2C/R	1	0	1			1
2C/R	2	0	1			2
2D/R	2	0	1			1
2E/R	2	2				1
4G/D	2	2				2
2E/R	2	1				3
4G/D	2	1				1
4E/D	1	1				1
2B/R	2					2
2D/R	2					2
2E/R	2					1
3A/D	2					2
4D/D	2					1
4E/D	2					6
4G/D	2					1
4H/D	2					3
2C/R	1					3
2D/R	1					1
4E/D	1					2
1A/O		1				2
2A/R		1				3
2B/R		1				3
2E/R		1				6

Table 18 continued...

4D/D		1				5
4E/D		1				1
4G/D		1				2
4I/D		1				2
4J/D		1				4
1A/0	-	2				2
5A/O	-	2				4
2A/R	0	2				7
2D/R	0	2				1
2E/R	0	2				11
3D/D	-	2				2
3E/D	-	2				5
4D/D	0	2				1
4E/D	0	2				3
4G/D	0	2				2
4I/D	-	2				7
4J/D	-	2				7
1A/0			1			5
4H/D			1			1
4J/D			1			2
5A/O			1			3
1A/0		0	2			3
5A/0		0	2			5
2C/R		0	2			4
2E/R		0	2			1
4E/D		0	2			1
4H/D		0	2			1
4I/D		0	2			3
4J/D		0	2			1
2D/R			0	2		1
2E/R			0	2		5
4D/D			0	2		1
2A/R				0	2	1
2C/R				0	2	4
3A/D				0	2	1
3D/D				0	2	7

Table 18 continued...

3E/D				0	2	6
4A/D				0	2	2
4C/D				0	2	8
4D/D				0	2	1
4E/D				0	2	6
4G/D				0	2	2
4H/D				0	2	4
4I/D				0	2	1
4J/D				0	2	2
2C/R					1	1
3D/D					1	5
3E/D					1	2
3F/D					1	5
4B/D					1	2
4D/D					1	2
4G/D					1	1
4H/D					1	1

5.1 Variation in dormancy rates among years

Figures 31 and 32 illustrate percentages of plants dormant at CFMETR in each year from 1995 to 1998 (results for 241 tracked plants). The dormancy rate for *A. amplectens* plants was highest in 1998 at 61.2% (Figure 31), the driest spring since inventories were first taken. Figure 32 illustrates differences in dormancy rates between the Rocky and Dogtail Meadow habitats during the same 4-year time period. Plants in the Orchard Grass habitat were not included for 1995 since they were not first censused until 1996. Dormancy rates were the highest during the spring of 1998 for the Dogtail Meadow habitat, but not for plants in the other two habitats.

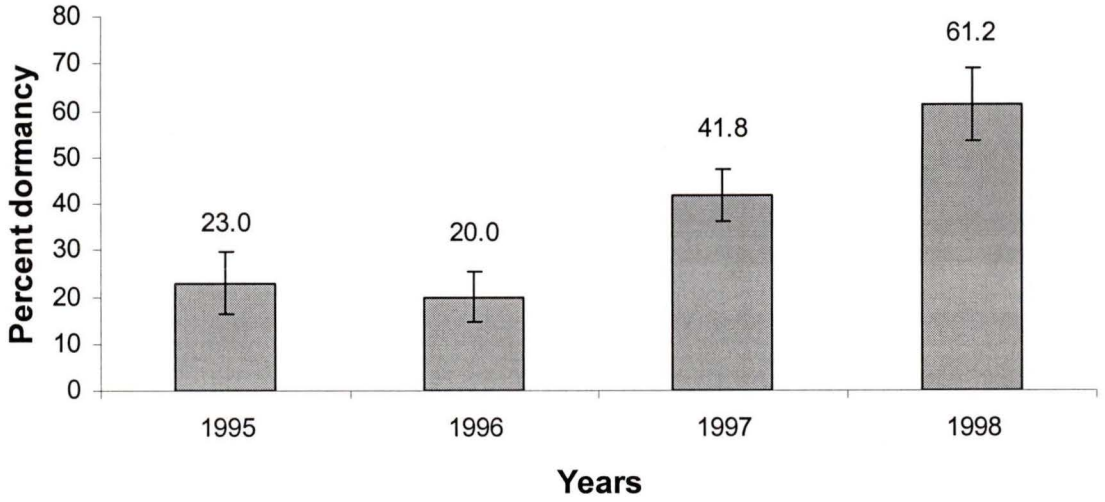


Figure 31. Percentages (means and std errors of individual plots) of plants tracked showing dormancy at CFMETR for the years 1995-1998. Numbers of plots were 15 in 1995 and 23 in 1996-1998.

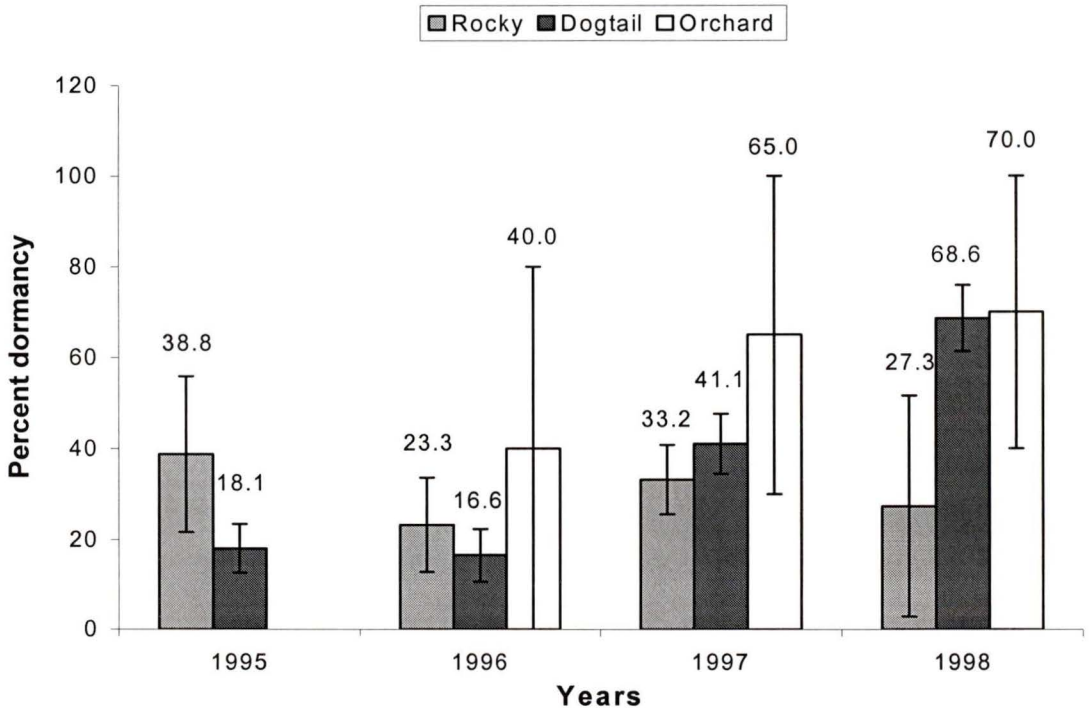


Figure 32. Percentages (means and std errors of individual plots) of plants tracked showing dormancy at CFMETR for the years 1995-1998. Numbers of plots were: 5 (1995-1998) for the Rocky habitat, 10 (1995) and 16 (1996-1998) for the Dogtail Meadow habitat, and 2 (1996-1998) for the Orchard Grass habitat.

5.2 Dormancy patterns of individual plants

Using plants at CFMETR (Nanoose Hill) that could be tracked for a minimum of 4 years and which were still present at the end of the study, I found that 134 plants were dormant for only 1 year, 70 for 2 continuous years, and 2 for 3 continuous years. In total, 85.5% of these plants exhibited dormancy at some point during the study (Figure 33). Dormancy for a single year was the most common pattern. However, this may reflect the difficulty of detecting dormancy for longer periods. Dormancy varied among years; thus the multiple-year dormancy rates I observed may reflect the particular weather patterns over the period of this study.

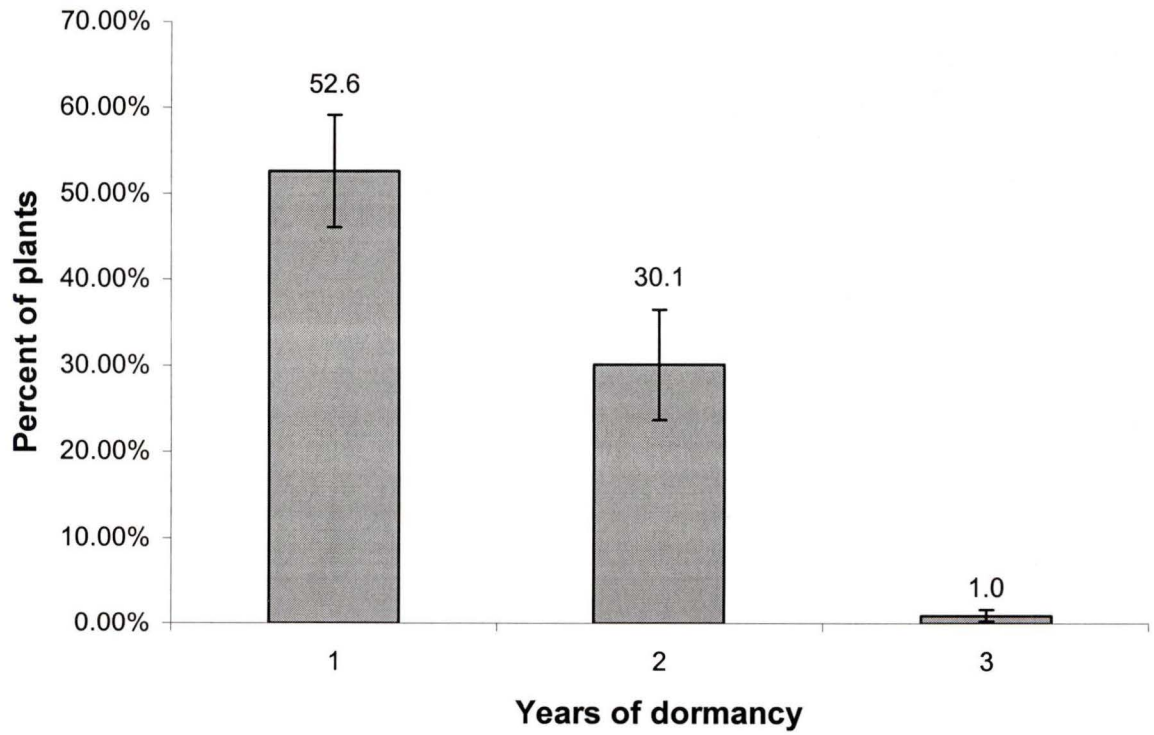


Figure 33. Percentages (means and std errors of individual plots) of plants tracked showing dormancy for one, two and three years during the study at CFMETR. These calculations were based on 23 plots and 241 plants.

CHAPTER IV. DISCUSSION

1.0 Abundance, range, and habitat

As Rabinowitz (1981) suggested, there are many sorts of rare species. Because species become rare by several pathways, rarity has a variety of causes, and the ecological consequences of rarity may be equally diverse. Rabinowitz's categories of rare species are based upon three characteristics: geographic range, habitat specificity, and local population size, resulting in eight classes, of which seven represent kinds of rarity (Table 19). The best fit for *Allium amplectens* is "locally abundant", in dense but small populations over a large range, and occurring within a specific habitat (type 1 rarity).

Table 19. Categories of rarity according to Rabinowitz (1981).

Category	**Geographic Range**	**Habitat Specificity**	**Population Size**
Common	Large	Broad	High somewhere
Rare 1	Large	Restricted	High somewhere
Rare 2	Large	Broad	Low everywhere
Rare 3	Small	Restricted	Low everywhere
Rare 4	Small	Broad	High somewhere
Rare 5	Small	Restricted	High somewhere
Rare 6	Small	Broad	Low everywhere
Rare 7	Small	Restricted	Low everywhere

My surveys of known and suspected localities in British Columbia for this study (Figure 6, Tables 4 & 5) indicate that *A. amplectens* has been disappearing from its region of highest historical record on southernmost Vancouver Island. At the same time, new records of populations have been found in the central Vancouver Island (i.e. Nanaimo)

region. *Allium amplectens* is a spring ephemeral species, present only as a dormant bulb for much of the year. Also, plants often remain dormant through the entire growing season, especially in years with very low rainfall. It seems likely that newly recorded populations from the central Vancouver Island region are not of recent establishment, but have existed undetected for a considerable period of time. *Allium amplectens* has now been inventoried more thoroughly than most rare species in B.C. and most extant populations have probably been found. Much of its habitat in B.C. and elsewhere also supports agriculture and urban development, and has undergone much disturbance and alteration. Thus it is likely that some populations have been extirpated in recent decades.

Allium amplectens in B.C. is restricted to the Garry oak ecosystem, which occurs in a relatively small region of southwestern British Columbia that has some of the highest densities of human populations in the province. Most of the extant populations of *A. amplectens* (both relocated historical sites and newly discovered ones) on Vancouver and the Gulf Islands (Tables 4 & 5) tend to be remote from humans and therefore less susceptible to human interference.

Introduced plant species may also be a factor in the disappearance of some populations. Two exotic plant species encountered in my study populations, *Cynosurus echinatus* at CFMETR (Nanoose Hill), and *Sedum acre* at Mitlenatch Island, were very abundant in some plots and seemed likely to be adversely affecting *A. amplectens*. Other introduced species such as *Rubus discolor* may also have an impact. However, I did not explore these factors in this study.

Spring rainfall patterns appeared to influence the numbers of plants observed in the populations I studied (Figure 18). Whether this is indicative of variation in mortality

or dormancy rates at these locations remains to be seen, but in years of exceptionally low spring rainfall such as 1998, no plants were visible at some sites (Figure 18). This may be most important in habitats with shallow soil such as the Rocky community type (Erickson 1996) seen extensively at the Mitlenatch Island, Woodley Range, and Work Point sites (Figures 20-22).

In different habitats, the various life stages of *A. amplectens* tended to be present in different densities and proportions. In dry or rocky habitats, very low densities of vegetative plants but higher proportions of flowering plants were often found (Figure 23). Although mature (flowering) plants survived to larger sizes in these Rocky habitats than in other habitats, they were also more likely to disappear due to dormancy or death in the dry year of 1998 (Figure 23). Densities of nonflowering ramets were higher in the Dogtail and Orchard Grass habitats (Figures 24 & 25), which had deeper, more loamy soil. Thus, although vegetative ramets tended to be sparser in rocky substrates, those individuals that did survive tended to grow to larger life stages. This may indicate that rocky habitats are less favourable for recruitment, but more favourable to large plants, because of decreased competition with grass and forb species.

2.0 Reproductive biology

Ploidy level. All sampled *A. amplectens* populations from B.C. were found to be triploid, although diploid and tetraploid populations are known to occur farther south (Levan 1940). This is consistent with the general tendency for polyploidy to be more frequent at higher latitudes (Ramsey and Schemske 1998). It also has implications for the reproductive biology of these populations.

Breeding system. My pollination experiments indicated that average seed set is low, though not 0, when only self pollen is available (autogamy and self-compatiblity treatments, Table 6). Comparison of these two treatments with the control suggest that this species requires outcrossing for good seed set. However, even the controls had relatively low seed production (Table 6). Ganders (1987) stated that *A. amplectens* has no need for pollination since it produces its seeds asexually. Also, apomixis often occurs in plants that are polyploid (Ramsey and Schemske 1998) and are found on the edges of their geographic distribution, while their sexual relatives are in the center (Czapik 1994). However, no seed production resulted (Table 6) with the agamospermy treatment, contrary to expectations of high seed set in agamospermous species (Jones and Luchsinger 1986). *Allium amplectens* may require pollen as a physical trigger (pseudogamy) for seed development although the pollen parent's genome is not utilized, as occurs in some apomicts such as certain *Rubus* species (Kollmann et al. 2000). The grass *Paspalum notatum* is a pseudogamous species (Quarin 1999), with endosperm development and seed production occurring independently of the species or the ploidy level of the pollen donor. Alternatively, *A. amplectens* may have unbalanced meiosis, as occurs in certain members of *Rosa* section Caninae (Werlemark 2000).

Seed germination. I obtained a maximum seed germination rate of 5% for *A. amplectens* after a cold stratification period of 3 months at 5° C. Under shorter stratification periods, no seed germination occurred. These are very low germination rates, in comparison with reports for other *Allium* species (Sorensen & Holden 1974) that germinated at rates of 35-40%. This may reflect the test conditions I used. It is possible that *A. amplectens* has a seed bank, and that seeds require more than one season for

germination. Alternatively, *A. amplectens* populations (at least those tested) may have low seed viability under all conditions, and this may be related to the fact that these populations are triploid.

Vegetative reproduction. A sampling of bulbs at CFMETR in 2000 recorded an offset rate of 18%. Although this undoubtedly varies, I did not observe the large numbers of yearly daughter bulbs observed by McNeal and Ownbey (1973), either in the field or in potted plants observed over a 5-year period. All of the bulb offset production that I observed resulted in only 2 daughter bulbs. Nevertheless, offsets appear to be an important means of propagation in these populations.

These data on seed germination, reproductive biology, and offset rates of *A. amplectens* are consistent with conclusions of Cook (1985), who indicated that clonal plant species often establish vegetative offspring 3-30 times more often than they produce offspring from seed. Similarly Silvertown et al. (1993) concluded that clonal growth is about ten times as important for population growth rate as seedling recruitment for species of eleven genera, including *Agropyron*, *Allium*, *Clintonia*, *Disporum*, *Erythronium*, *Fritillaria*, *Potentilla*, and *Ranunculus*. Caswell (1985) argued that "both intuition and evidence" supports a trade-off between sexual and asexual (clonal) reproduction, with the production of clonal offspring favoured under conditions when genet survival is high and a large increase in reproductive value is gained by clonal growth. Ericksson (1997) also reiterates this by concluding that plant life cycles with successful clonal propagation and a long life span would be expected to only utilize alternative reproductive pathways (seeds) to a limited extent.

3.0 Demography

Components of the demographic dataset from CFMETR indicate a downward population trend for the 1995-2000 period. Although the mean matrix lambda value of 0.878 is more encouraging than the rates of increase calculated from total flowering plant populations (λ=0.688) and adults within permanent plots only (λ=0.779), it still indicates a negative trajectory. However, this pessimistic population viability analysis is restricted only to this site and does not necessarily apply to other extant populations.

The great advantage of tracking individual plants over a number of years is that it allows us to follow, and therefore better understand, their various life stages and the ultimate contributions of each life stage to the fate of the entire population. A significant discovery of this work was the considerable role that dormancy plays in the life cycle of *A. amplectens*. About 84% of the tracked plants in the CFMETR (Nanoose Hill) population exhibited at least one year of dormancy, while about 30% were dormant for two continuous years (Figure 33). In all populations monitored in this study, a major decrease in numbers occurred in 1998 (Tables 11 & 17), and a major increase occurred in 2000 (Table 12). Almost all of these changes in numbers were the result of individuals moving into and out of dormancy, probably as a consequence of late winter, early spring rainfall patterns (Figure 18). This makes short-term monitoring of this species quite problematic, because misleading information about its demographic status could easily result from only one or two years of sampling data. Lesica and Steele (1994) also pointed out that prolonged dormancy requires that longer periods of time be spent to obtain useful information, which can complicate monitoring work on endangered species. Guerrant (1996) reported dormancy in the bulbous perennial *Erythronium elegans* Hammond &

Chambers lasting up to five years, but usually no more than one or two years. Schemske et al.'s (1994) initial assumption that a relatively short time period (2-3 years) of matrix monitoring studies could reveal significant demographic changes is not practicable for many species, including *A. amplectens*. For example, because of complications imposed by the combination of dormancy and bulb offsetting and the consequent problems in tracking some individuals, the transition matrices could not be as resolved as desired.

In this study, seedlings were rare; thus variations in seed production did not affect overall population growth rates and seedling survivorship very dramatically. Although offsetting and dormancy rates undoubtedly also differ from site to site and year to year, the 18% offset rate, based upon a sample taken in 2000, and 50% dormancy rate over a 5 year period for CFMETR (Figure 33), are probably reasonable approximations. Means of the sensitivities and elasticities (Tables 15 and 16) for CFMETR indicate that the magnitude of dormancy and clonal (offset) reproduction are major factors in predicting growth rates of these populations. The contribution of seed reproduction is relatively low, although seeds may be important in founding new populations in spatially distinct locations, as opposed to adding new genets within existing ones.

The mean matrix results (Table 13), based upon 1995-2000 information for CFMETR were used as the starting point for a population simulation, which projected a decreasing population at this site (Figure 29). The Quasi-Extinction Risk Curve, generated concomitantly (Figure 30), is also not encouraging. However, it is important to keep in mind: (1) the transition matrices on which the projections are based incorporate many assumptions (see discussion above); (2) this is a projection, and it extrapolates from conditions observed only over the period previously sampled; (3) this projection is for the

entire CFMETR site, which incorporates at least three different community types that may be responding in different ways; and (4) other populations of *A. amplectens* in southwestern British Columbia may have different demographic characteristics.

Caswell (2000b, p.648) notes that models are intended to be simplifications, and hence to varying degrees are always wrong. He states, "It is trivial and inappropriate to test a model by listing factors that it fails to include, just as it is inappropriate to criticize an experiment because it doesn't manipulate all possible factors.....many uses of matrix population models are a form of data analysis, not hypothesis construction". Therefore, the value of developing these matrix models is, amongst other things, to enhance our knowledge about the vital rates which contribute to the demographics of species being studied and to assist conservation biologists in evaluation of the future population viability of these species, especially for those threatened or endangered. Population viability analysis is a projection technique, and therefore describes what would happen given certain assumptions; it is not a forecast or prediction of what will happen (Caswell 2000b).

Bierzychudek (1999) stated, "the enthusiasm with which these models are currently being embraced, however is sometimes insufficiently tempered by a recognition of their limitations". In evaluating their usefulness she examined projections made in 1982 (Bierzychudek 1982) for two different populations of *Arisaema triphyllum.* One of the projections was quite accurate, while the other was not. Her conclusions were that inaccurate projections were probably the result of: (1) too few years of sampling to capture adequately the complete range of environmental stochasticity; (2) sampling of too few plants to provide accurate transition probabilities; and (3) failure to consider the

significance of density dependence in affecting vital rates. Although these conclusions are probably quite correct for many demographic analyses, the precarious status of many rare and endangered species is such that time constraints, low population numbers and limiting information about density dependence make robust, long-term information difficult to obtain. With respect to *A. amplectens,* for example, high density levels within many populations make tracking of individual ramets extremely difficult, but even with this constraint a number of critical life history features previously unknown have been identified. As a consequence of environmental and demographic stochasticity, the vital rates of most organisms will vary spatially and temporally. Although the population trajectory for *A. amplectens* at the CFMETR site does not appear favourable from these findings, this could substantially change if rainfall patterns during the next decade were to change. Also, disturbances such as trampling, insect predation or disease, none of which were evaluated in this study, could have a substantial effect.

The *A. amplectens* populations that I monitored at CFMETR (Nanoose Hill), and other sites had relatively low population densities, and as a consequence relatively low overall population numbers, facilitating the process of tracking individual plants. However, insights from this work indicate that these may not be the best populations for projecting long-term species viability. Decreased rainfall patterns during the past decade may have effects on long-term population vulnerability. According to Kutner and Morse (1996) global warming models suggest that temperature and precipitation changes may be responsible for the loss of 1-10% of our region's flora in the near future. Many of the other remaining extant populations of *A. amplectens* are found in damper, nutrient rich habitats, often as a consequence of spring seepages, resulting in much higher densities

with total population sizes an order of magnitude larger than the ones I studied (i.e. 5,000-10,000 adult plants). These higher density populations are more difficult subjects for demographic study, but may be more likely to persist in the long term.

4.0 Dormancy

Strictly speaking, dormancy implies a state of inactivity without growth; however, complete inactivity is rarely found, since bulbs often grow and divide during the "normally dormant part of the year" (Lesica and Steele 1994). For the purpose of this study, "dormancy" refers to the absence of above-ground activity and growth during the growing season. Many species of perennial geophytes, or plants that survive their dormant season underground as bulbs or corms, are found in southwestern British Columbia (Ganders 1987) and elsewhere (Keeler 1991, Oostermeijer et al. 1992). This ability is viewed by Ganders (1987) as an adaptation to summer drought. *Allium amplectens*, however, also has the ability for "prolonged dormancy" (Lesica and Steele 1994) or the continuation of late summer and winter dormancy through one or more growing seasons. In this study, about 50% of tracked plants were able to remain dormant through at least one growing season, and about 30% were dormant for two consecutive growing seasons (Figure 33). The proportions of plants dormant in any given year are unusually high in *A. amplectens,* with most species having 25% or less of a population dormant at any one time (Lesica and Steele 1994). The length of dormancy in *A. amplectens* is similar to that found by Guerrant (1996) for *Erythronium elegans,* by Shefferson et al. (2000) for *Cypripedium calceolus,* and by Hutchings (1987) for *Ophrys sphegodes*. Lesica and Steele (1994) list certain unusual cases of dormancy as lasting up

to 20 years in some species of wild orchids. In some years and habitats, up to 70% of the tracked *A. amplectens* plants were dormant (Figure 32). Dormancy is biologically advantageous in enabling plants to survive periods of reduced rainfall, temperature, and sunlight. In *Cypripedium*, Shefferson et al. (1982) found a strong relationship between dormancy and spring frost days, although effects of precipitation and mean spring temperature were almost equally strong. Vaughton and Ramsey (2001) conclude that dormancy is a form of phenotypic plasticity that favours a phenotype that responds to environmental cues correlated to future dry conditions. By minimizing exposure to seasonally stressful conditions, dormancy is especially advantageous in habitats with variable summer conditions (Vaughton and Ramsey 2001). In addition to environmental variables, Primack and Stacy (1998) conclude that the length of the dormancy period was a significant and inverse function of plant size just prior to dormancy. This relationship was not examined during the course of this study.

Dormancy presents increased challenges for monitoring studies, because misleadingly low population sizes may be obtained during years of high dormancy. In order to increase the accuracy of information from which future population trends might be inferred, longer-term studies are needed for species exhibiting dormancy.

5.0 Life history strategy of *A. amplectens*

According to Grime (1979), plants basically fall into three life history strategies: competitive, stress-tolerant, and ruderal or weedy. Competitive plants tend to occupy stable habitats with abundant resources, stress-tolerant species tend to occupy habitats with very limited resources, and ruderal or weedy species occupy resource-abundant

temporary habitats. Taking into account the taxonomic position of a species and its life history pattern may yield insights into the relationship of life history strategies and ecological factors affecting the persistence of closely related species and their future plant management strategies.

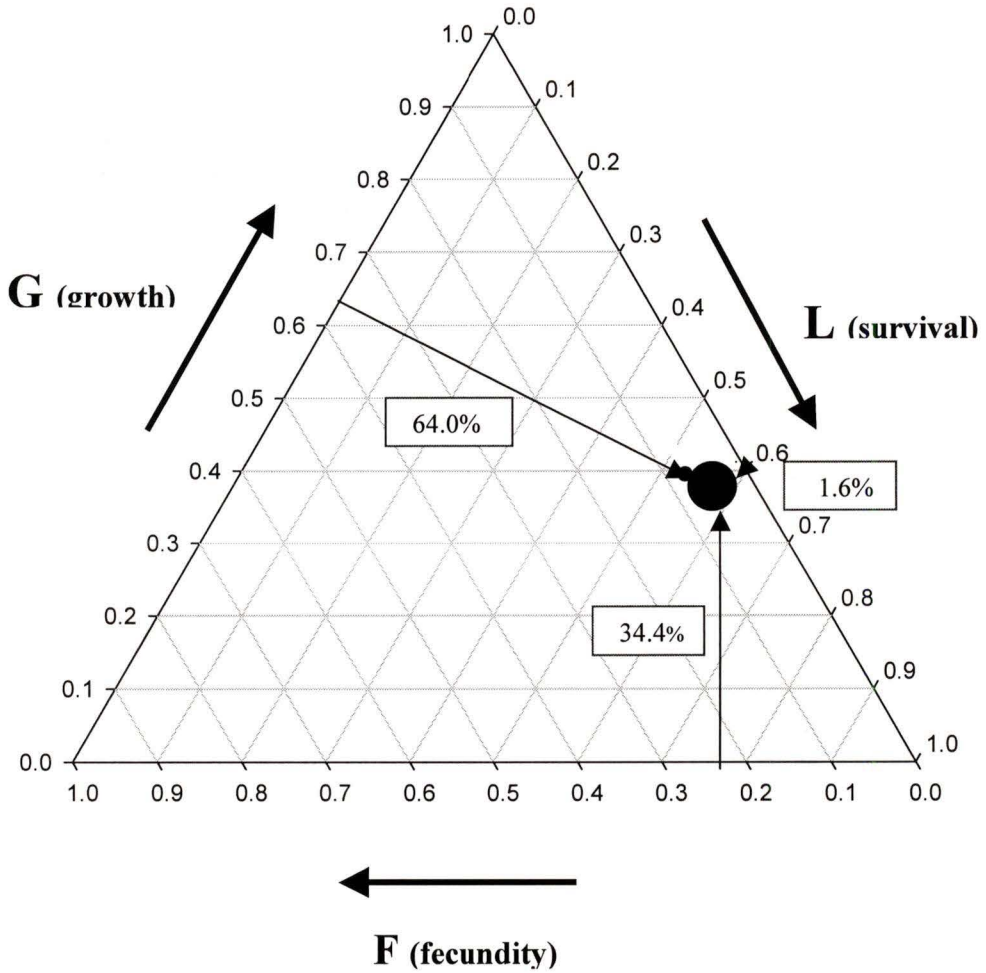
Silvertown et al. (1992) compared 18 herbaceous plant species, and proposed that competitive plants have high growth rates and low to moderate fertility, stress-tolerant species both grow and reproduce more slowly, and weedy plants have high fertility and growth. Their results showed no significant correlations between these factors. In subsequent work with an expanded number of species, Silvertown et al. (1996) and Franco and Silvertown (1996) concluded that species with different life histories tended to cluster in different parts of elasticity space or region of Grime's triangle. The resulting triangular ordinations plot plants onto the growth (G) axis, measuring effects on λ of growth and clonal growth, the survival (L) axis, measuring the combined effects of changes to stasis (individuals remaining in the same size class) and regression (individuals shrinking), and the fecundity (F) axis, measuring the combined effect of recruitment from dormant and nondormant seeds. Caswell (2000b) disputes this conclusion, since work by other researchers indicates that characterizing a species by a single elasticity pattern is an oversimplification. However, this approach may yet provide insight regarding appropriate plant management strategies as a result of the potential correlation between the known taxonomic position of species and their congruent position within Grime's triangle. Plotting of mean matrix elasticity information on Grime's triangle (Figure 34) indicates that *A. amplectens* has the life history strategy of stress tolerant species, or iteroparous herbs of open and forest habitats (Silvertown et al. 1996),

because the contribution of survival elasticity towards λ, at 64.0% was much higher than the remaining contributions of growth at 34.4%, and fecundity at 1.6%. Although the analysis of the significance of different species within Grime's triangle is still at a relatively formative stage, and has several caveats that need to be considered (Silvertown et al. 1996), these relationships could be useful as rules of thumb, indicating the likely demographic characteristics of species similar to those for which we have data.

6.0 Conservation biology of *A. amplectens*

In order to determine the likely fate of populations of this species, individual plant monitoring should ideally be continued at the CFMETR site for at least a half decade more, in addition to total counts or permanent plot population counts at other locations. We could then answer questions such as: how do population growth rates estimated from lambdas based upon individually monitored plants compare with rates of increase determined from flowering plant population counts? Are they still similar? At least two high-density populations should also be sampled for total numbers of flowering individuals. Comparison of moisture regimes between populations, and their relation to demographic features or manipulation of moisture regimes in greenhouse populations would also be valuable. This would indicate whether the offset rate increases with greater moisture levels, thus contributing to higher densities of plants and also whether there is an effect on seedling growth.

Much remains to be learned about the reproductive biology of *A. amplectens*. If the seed is indeed a result of apomixes, does it require some trigger from the male pollen grain to ultimately complete its development? What are the demographic



LEGEND

S = Seedling V = Vegetative F_1 = Flowering (1-10 flowers/inflorescence)
F_2 = Flowering 2 (>10 flowers/inflorescence) D = Dormant

ELASTICITIES

	S	V	F_1	F_2	D
S	0	0.000	0.005	0.003	0
V	0.008	**0.269**	**0.035**	**0.006**	0.192
F_1	0	**0.024**	0.023	0.006	0.043
F_2	0	**0.007**	**0.003**	0.005	0.013
D	0	0.209	0.031	0.008	0.110

Figure 34. Position in elasticity space within Grime's triangle for *A. amplectens* at CFMETR. Fecundity elasticity (seeds to seed bank & seeds to seedlings equals 1.6 %, growth elasticity (clonal growth & progression/**bold**) equals 34.4 %, and survival elasticity (regression & stasis/underlined) equals 64.0%.

consequences of this and how important is seed production for the continuance of *A. amplectens* populations?

Also of interest in this species are patterns of morphological and genetic variation. What is the basis for morphological differences of the various North American populations (Levan 1940)? Are these related to genetic differences or different microsite characteristics? How do all of these characteristics influence the demographic features of populations?

A number of different protected sites, of various ecological conditions, already exist that contain populations of *A. amplectens*. According to an ecological assessment of Department of National Defense Properties (Radcliffe et al.1994), the CFMETR (Nanoose Hill) location contains 32 rare and vulnerable plant species, of which *A. amplectens* is one. The Garry oak grassland ecosystem at this site is considered to be outstanding and the largest one of three relatively large protected locations found on Vancouver Island. Other populations, such as various recently discovered Gulf Islands sites (see Table 6), are located in relatively remote locations and probably much less vulnerable to human interference. Although the initial steps toward conservation (i.e. identification of locations and protected status) have already been taken for a number of locations, it would be desirable if some sort of protected status were also, in the long term, given to many of these recently discovered populations. Because microhabitat moisture regimes may also affect *A. amplectens* it may also be important to monitor extant populations for changes in hydrology that may be a consequence of human activity outside the boundaries of protected areas. Reintroductions of *A. amplectens* may ultimately need to be considered in some areas, with particular attention paid to the type

of microhabitats into which propagules are introduced. Because seed viability may be poor, transfer of bulbs from more vulnerable populations would probably be a more successful alternative.

One problem arising from imprecise historical records and the lack of frequent recensuses is that additional, new populations may cause this species to appear much more common than it currently is. Continued dissemination of information by the British Columbia Conservation Data Centre and similar organizations can be valuable resources to encourage amateur naturalist groups to monitor populations of *A. amplectens* and other rare species.

It is apparent from this study that *Allium amplectens* is not a model species for obtaining robust or easily obtained demographic projections. Its breeding behavior is unusual, its spring ephemeral habit makes populations often difficult to locate and count, and high population densities, dormancy, and vegetative offsetting make individual tracking and enumeration methods difficult, if not impossible, at certain sites. Nevertheless, many rare species for which conservation biologists have concerns may have such features. In our efforts to apply methods of predicting population-growth trajectories, we may not always learn what we hoped. In the case of *A. amplectens*, other approaches, such as investigations of the relationship between abundance and habitat characteristics, or detailed studies of the factors influencing different modes of reproduction, might be more valuable. Each one of these approaches can tell us something new about a species which we did not know before, if we will only be observant and receptive to new conclusions.

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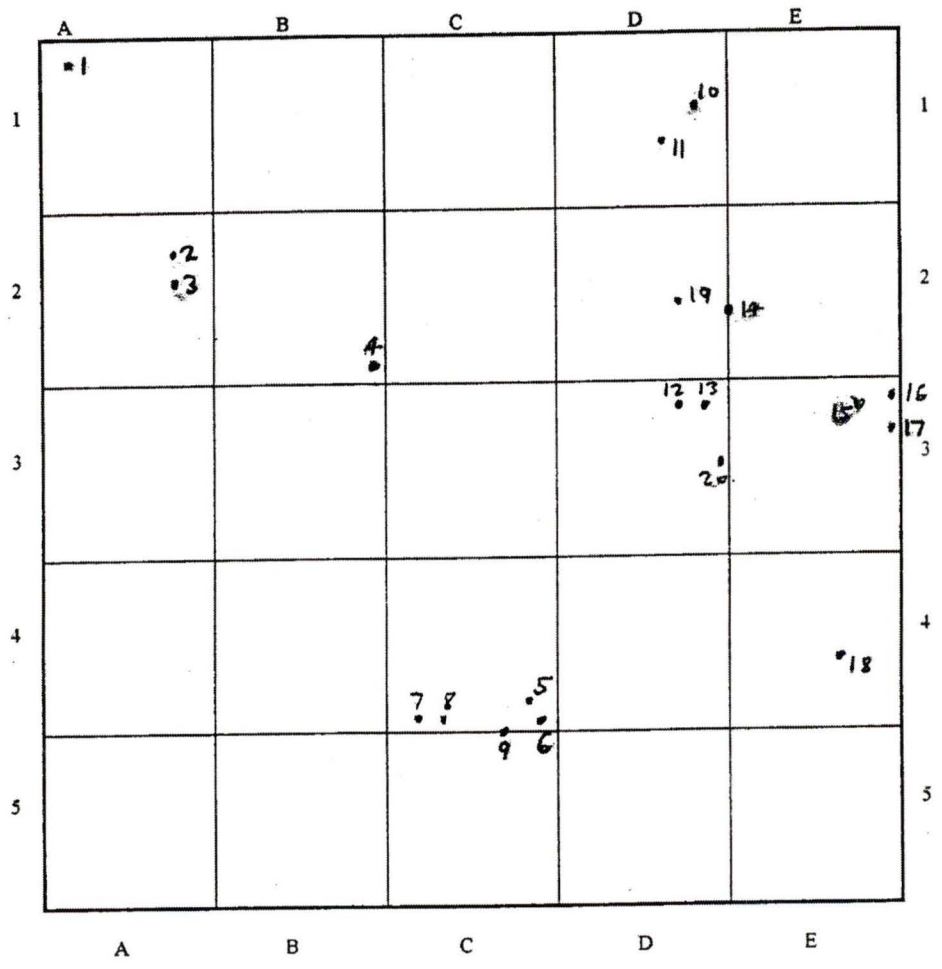
APPENDIX 1: Example of field plot data sheet.

Sheet indicates presence of plants within a plot within population #3 at CFMETR site in 1996.

1. PLOT NO.: 3 D DATE: 96

24. PLOT DIAGRAM:



APPENDIX 2: Plant species associated with *A. amplectens* at sites used in this study.

INSIDE PLOTS	WITHIN GENERAL AREA
Achillea millefolium L.	*Achillea millefolium* L.
	Allium acuminatum Hook.
Allium cernuum Roth in Roem.	*Allium cernuum* Roth in Roem.
	Amelanchier alnifolia (Nutt.)Nutt.
	Anthoxanthum odoratum L.
	Arbutus menziesii Pursh.
	Barbarea orthoceras Ledeb.
	Bromus spp.
	Bromus pacificus Shear
	Bromus rigidus Roth
Bryum miniatum Lesq.	
Camassia quamash (Pursh)Greene	*Camassia quamash* (Pursh)Greene
	Cerastium arvense L.
	Clarkia amoena (Lehm.)Nels.&Macbr.
	Collinsia grandiflora Dougl. ex Lindl.
	Cryptogramma crispa (L.)R.Br. ex Hook.
Cynosurus echinatus L.	*Cynosurus echinatus* L.
	Cytisus scoparius (L.)Link
Dactylis glomerata L.	*Dactylis glomerata* L.
Delphinium menziesii DC. *ssp. menziesii*	*Delphinium menziesii* DC. *ssp. menziesii*
Dicranum scoparium Hedw.	*Dicranum scoparium* Hedw.
	Grindelia integrifolia DC.
	Holodiscus discolor (Pursh)Maxim.
	Hypochaeris spp.
	Kindbergia oregana (Sull.)Ochyra
	Leucanthemum vulgare Lam.
	Lomatium utriculatum (Nutt.)Coult.&Rose
	Lonicera hispidula (Lindl.)Dougl.in T.&G.
	Mahonia aquifolium (Pursh)Nutt.
Mimulus alsinoides Dougl. ex Benth.	
	Opuntia fragilis (Nutt.)Haw.
Plantago lanceolata L.	
	Plectritis congesta (Lindl.)DC.

APPENDIX 2 CONTINUED....

INSIDE PLOTS	WITHIN GENERAL AREA
Poa spp.	
	Quercus garryana Dougl.
	Prunella vulgaris L.
Rhacomitrium canescens (Hedw.)Brid.	
	Rosa nutkana Presl
	Sedum lanceolatum Torr.
	Sedum spathulifolium Hook.
	Selaginella wallacei Hieron.
	Sonchus spp.
	Symphorycarpos albus (L.)Blake
	Taraxacum officinale Weber in Wiggers
Triteleia hyacinthina (Lindl.)Greene	
Zygadenus venenosus S. Wats. *Var. venenosus*	*Zygadenus venenosus* S. Wats. *var. venenosus*

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Title of Thesis:

Natural history, population ecology, and conservation biology

of Slim-leaf onion (*Allium amplectens*)

Author 

Allan Ronald Hawryzki
December 18, 2002