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THE REPRODUCTIVE BIOLOGY AND EDAPHIC CHARACTERISTICS OF A
RARE, GYNODIOECIOUS SAXIFAGE: *SAXIFRAGA BRYOPHORA*
VAR. *TOBIASIAE* (SAXIFRAGACEAE)

by

Kimberly Pierson

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

In

Biology Ecology

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1999

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ABSTRACT

The Reproductive Biology and Edaphic Characteristics of a Rare, Gynodioecous
Saxifrage: *Saxifraga bryophora* var. *tobiasiae*
(Saxifragaceae)

by

Kimberly Pierson, Master of Science

Utah State University, 1999

Major Professor: Dr. Mary Barkworth
Department: Biology

I examined the reproductive biology and general ecology of *Saxifraga bryophora* var. *tobiasiae*, a rare saxifrage endemic to the West Salmon River Mountains of central Idaho. *Saxifraga bryophora* var. *tobiasiae* combines asexual reproduction via bulbils with a sexual mixed-mating system. Flower production occurred in 1996 only, whereas bulbil production occurred in 1995, 1996, and 1997. Bulbil production precedes floral bud formation and is the dominant form of reproduction. When flowering occurs, outcrossing is promoted by protandry and the gynodioecious mating system found in all populations. No autogamous or agamospermous seed set was observed in either female or hermaphrodite flowers, indicating that a pollen vector is required for reproduction. Hermaphrodites were self-compatible but none automatically self-pollinated. Pollinator visitation was extremely low, but this did not significantly affect fruit set. Flower visitors

were infrequent and consisted mostly of syrphids (Diptera: Syrphidae) and empidids (Diptera: Empididae). Female plants produced significantly more bulbils than hermaphrodites. Females may be maintained in the population for this reason.

The populations of *Saxifraga bryophora* var. *tobiasiae* were thoroughly surveyed to identify actual and potential habitat. Twenty-eight soil pits in actual and potential *S. bryophora* var. *tobiasiae* habitat were described. Soils were classified as Lithic Cryoborolls, Lithic Cryochrepts, and Lithic Cryorthents. The physical characteristics of these soils were very similar among habitat and non-habitat sites, but higher rock fragments were found in soils with *S. bryophora* var. *tobiasiae*. The shallow soils and natural disturbance from runoff influence the narrow distribution and rarity of this taxon. Classification tree analysis was used to determine which ecological factors were useful in predicting *S. bryophora* var. *tobiasiae* presence. Bare soil, *Lewisia triphylla*, *Erythronium grandiflorum*, *Vaccinium scoparium*, and *Polytrichum juniperinum* were significant predictors of *S. bryophora* var. *tobiasiae*. The findings of this study provide biological and ecological information about *S. bryophora* var. *tobiasiae* that may be useful to managers in attempting to conserve this rare taxon and the habitat in which it exists.

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CONTENTS

	Page
ABSTRACT	iii
ACKNOWLEDGMENTS	v
LIST OF TABLES	viii
LIST OF FIGURES	x
CHAPTER	
1. INTRODUCTION	1
LITERATURE CITED	6
2. THE REPRODUCTIVE BIOLOGY OF A RARE, GYNODIOECIOUS SAXIFRAGE: <i>SAXIFRAGA BRYOPHORA</i> VAR. <i>TOBIASIAE</i> (SAXIFRAGACEAE)	12
ABSTRACT	12
INTRODUCTION	13
MATERIALS AND METHODS	18
RESULTS	26
DISCUSSION	46
LITERATURE CITED	65
3. THE ECOLOGY OF A RARE, GRANITIC OUTCROP ENDEMIC SAXIFRAGE: <i>SAXIFRAGA BRYOPHORA</i> VAR. <i>TOBAISIAE</i> (SAXIFRAGACEAE)	73
ABSTRACT	73
INTRODUCTION	74
MATERIALS AND METHODS	79
RESULTS	85
DISCUSSION	96
LITERATURE CITED	104
4. CONCLUSION	110
APPENDICES	114

APPENDIX A. TABLES: CLASSIFICATION TREE	
MODELS	115
APPENDIX B. FIGURES: SOIL DESCRIPTION	
SHEETS	117

LIST OF TABLES

Table	Page
2.1 Locations and population information for all populations of <i>Saxifraga bryophora</i> var. <i>tobiasiae</i>	20
2.2 Breeding system treatments of <i>S. bryophora</i> var. <i>tobiasiae</i> . Gender is indicated for each treatment	25
2.3 Comparison of sizes of floral characters and bulbil number between female and hermaphrodite plants in 1996	28
2.4 Comparison of sizes of reproductive characters and bulbil number between plants differing in aspect (FCSE, FCSW) in 1996	28
2.5 Comparison of sizes of floral characters and bulbil number for the gender* aspect (FCSE, FCSW) interaction in 1996	29
2.6 Comparison of proportion of hermaphrodites, females, and functional females in 2 X 2 m ² plots (2FCSE, 2FCSW, 1SB) in 1996	31
2.7 Two-way factorial in a split plot design comparing panicle height between genders, aspect, and interactions	32
2.8 Two-way factorial in a split plot design comparing rosette volume between genders, aspects, and interactions	32
2.9 Comparison of number of panicle-producing adults without flowers, number of females and hermaphrodites, ratio of females to hermaphrodites, and the average number of flowers between FCSE and FCSW and between years	33
2.10 Two-way factorial in a split plot design comparison for number of adult plants without flowers between FCSE and FCSW for 1995, 1996, and 1997	35
2.11 Two-way factorial in a split plot design comparing bulbil number between genders, aspects, and interactions	36
2.12 Average bulbil weight and volume for top five bulbils and bottom five bulbils for females and hermaphrodites of <i>Saxifraga bryophora</i> var. <i>tobiasiae</i>	37

2.13	Three-way factorial in a split plot design comparing average bulbil weight between positions, genders, aspects, and interactions	38
2.14	Three-way factorial in a split-plot design comparing average bulbil volume between positions, genders, aspects, and interactions	40
2.15	Survival, panicle production, and bulbil production in 1996 by rosettes and panicle-producing plants marked in 1995	40
2.16	Survival and reproduction by fall bulbils planted in 1995	44
2.17	Comparison of <i>S. bryophora</i> var. <i>tobiasiae</i> fruit set among xenogamy (X), geitonogamy (G), autogamy (AU), agamopsermy (AG), control (C), emasculated control (EC) for breeding system treatments for 1996	45
2.18	Comparison of <i>Saxifraga bryophora</i> var. <i>tobiasiae</i> seed set among xenogamy (X), control (C), and geitonogamy (G) treatments from Fisher Creek Saddle populations in 1996	47
2.19	Comparison of <i>Saxifraga bryophora</i> var. <i>tobiasiae</i> seed size among xenogamy (X), control (C), and geitonogamy (G) treatments from Fisher Creek Saddle populations in 1996	47
2.20	Insect visitors of <i>Saxifraga bryophora</i> var. <i>tobiasiae</i>	48
3.1	Average occurrence levels of ecological components in plots with <i>S bryophora</i> var. <i>tobiasiae</i> and plots without <i>S. bryophora</i> var. <i>tobiasiae</i>	88
3.2	Selected soil properties summarized by aspect (FCSE, FCSW) and between plots (present and not present)	89
3.3	Summary of family classification of soil pedons	90
3.4	Summary of <i>Saxifraga bryophora</i> var. <i>tobiasiae</i> classification trees	94
A.1.	Classification tree model for 1995 data	116
A.2.	Classification tree model for 1996 data	116

LIST OF FIGURES

Figure	Page
2.1 Distributions of <i>S. bryophora</i> var. <i>tobiasiae</i> in west central Idaho	19
2.2 Floral development in <i>Saxifraga bryophora</i> var. <i>tobiasiae</i>	30
2.3 Regression of bulbil number on rosette volume	42
2.4 Regression of bulbil number on panicle height	42
2.5 Regression of panicle height on rosette volume	42
2.6 Diagrammatic life table for <i>Saxifraga bryophora</i> var. <i>tobiasiae</i>	43
3.1 Layout of a permanent plot	81
3.2 Illustrated cross section of a granitic outcrop island community with <i>Saxifraga bryophora</i> var. <i>tobiasiae</i>	86
3.3 The classification tree generated from 1995 percent coverage data	92
3.4 The classification tree generated from 1996 percent coverage data	95
B.1 Field description sheet for east side soil pedon #1	118
B.2 Field description sheet for east side soil pedon #2	119
B.3 Field description sheet for east side soil pedon #3	120
B.4 Field description sheet for east side soil pedon #4	121
B.5 Field description sheet for east side soil pedon #5	122
B.6 Field description sheet for east side soil pedon #6	123
B.7 Field description sheet for east side soil pedon #7	124
B.8 Field description sheet for east side soil pedon #8	125
B.9 Field description sheet for east side soil pedon #9	126

B.10	Field description sheet for east side soil pedon #10	127
B.11	Field description sheet for east side soil pedon #11	128
B.12	Field description sheet for east side soil pedon #12	129
B.13	Field description sheet for east side soil pedon #13	130
B.14	Field description sheet for east side soil pedon #14	131
B.15	Field description sheet for west side soil pedon #15	132
B.16	Field description sheet for west side soil pedon #16	133
B.17	Field description sheet for west side soil pedon #17	134
B.18	Field description sheet for west side soil pedon #18	135
B.19	Field description sheet for west side soil pedon #19	136
B.20	Field description sheet for west side soil pedon #20	137
B.21	Field description sheet for west side soil pedon #21	138
B.22	Field description sheet for west side soil pedon #22	139
B.23	Field description sheet for west side soil pedon #23	140
B.24	Field description sheet for west side soil pedon #24	141
B.25	Field description sheet for west side soil pedon #25	142
B.26	Field description sheet for west side soil pedon #26	143
B.27	Field description sheet for west side soil pedon #27	144
B.28	Field description sheet for west side soil pedon #28	145

CHAPTER 1

INTRODUCTION

The focus of many species-oriented conservation studies is to determine the factors that limit the distribution or abundance of a species (Kruckeberg and Rabinowitz, 1985; Fiedler, 1986; Soule, 1986; Schmeske et al., 1991; Fiedler and Ahouse, 1992; Falk, 1992; Gaston, 1994). Species may be intrinsically rare or rare as a result of anthropogenic interference (Drury, 1980; Kruckeberg and Rabinowitz, 1985; Gaston, 1994). Rare species are often at greater risk of extinction than are common ones because small populations are more susceptible to stochastic events (Gaston, 1994).

Determination of the causes contributing to the rarity or narrow distribution of species may enable conservationists and managers to effectively design strategies that may reduce the risks of extinction and promote preservation of such species.

Elucidating the factors that contribute to the narrow distribution and rarity of species is one of the central goals of conservation biology. The search for definitive causes of rarity has been the source of wide speculation (Stebbins, 1942, 1980; Kruckeberg and Rabinowitz, 1985; Rabinowitz et al., 1986). In early studies, genetic constraints (Stebbins, 1942; Wright, 1956; Huxley, 1963) and competitive incompetency (Griggs, 1940) were proposed as the basic causes of rarity. Later, Stebbins (1980) proposed the gene pool-niche interaction theory in which rarity is explained by the interaction of a unique, localized environment, a specific genetic structure, and a specific evolutionary history.

Rarity and endemism occur at many scales and result from the interplay of

multiple factors such as evolutionary history, environmental conditions, biological requirements, and geomorphological processes (Cain, 1940; Kruckeberg, 1954; Stebbins and Major, 1965; Stebbins, 1980; Kruckeberg and Rabinowitz, 1985; Soule, 1986; Gaston, 1994). The causes of limited distribution or abundance for a species can differ both spatially and temporally. Understanding the biological and ecological factors that influence the abundance and distribution of each species is essential for successful biological conservation. Information obtained for rare individuals can then be utilized to understand ecological and biological patterns that influence rarity and endemism in intrinsically rare species and rare communities (Izco, 1998).

Examination of the reproductive biology, life history characteristics, population dynamics, and population demography is essential to understand the factors that may perpetuate rarity in a species (Soule, 1986; Schmeske et al. 1991; Fiedler and Jain, 1992; Falk, 1992). Studies of reproductive biology have provided evidence that rarity may be due to such factors as poor dispersal ability (Rabinowitz, 1978; Gawler et al., 1987; Menges, 1990), lack of pollinators, or lack of mates (Karron, 1987; Tepedino, 1979), low seed production, or establishment (Harper, 1967; Menges, 1990; Fiedler and Ahouse, 1992). Life history characteristics (Wyatt, 1984; Fiedler, 1986), population dynamics (Synge, 1981; Gaston, 1994), population demography (Meagher et al., 1978; Gawler et al. 1987; Menges, 1990), and population genetics (Stebbins, 1980; Wyatt, 1984; Gaston, 1994) have also been documented as major contributors to the rarity of plant species.

Edaphic characteristics (Kruckeberg, 1954; Kruckeberg and Rabinowitz, 1985; Shaw, 1987), geomorphological processes (Wild and Bradshaw, 1977; Walck et al., 1996), and ecological associations (Drury, 1980; Stebbins, 1980; Gentry, 1986) have

been shown to influence the distribution and abundance of plant species. Of these, edaphic factors and their effects have been most commonly examined. Edaphic endemism may be related to the physical or chemical characteristics of soils (Kruckeberg and Rabinowitz, 1985; Sharitz and McCormick, 1973; Burbanck and Platt, 1964; Walck et al., 1996; Baskin and Baskin, 1988; Moore et al., 1998) as well as the chemical properties of soils (Kruckeberg, 1954; Stebbins and Major, 1965; Wild and Bradshaw, 1977; Baker et al., 1985; Boyd et al., 1994).

Kruckeberg and Rabinowitz (1985) theorized that the ultimate cause of local rarity and narrow endemism is most likely explained by the discontinuities created by geological processes. Geological processes can be responsible for the creation of unique microhabitats in which only a few taxa can persist. Isolated batholiths, unique mountain ranges, emergent volcanoes, and rock outcrop communities are hosts to many endemic taxa throughout the world (Stebbins and Major, 1965; Wild and Bradshaw, 1977; Kruckeberg and Rabinowitz, 1985; Gentry, 1986; Moore et al., 1998). Topographic, pedological, and lithological discontinuities can provide unique habitats that allow for the ecological separation of species (Kruckeberg, 1954; Denton, 1979; Baskin and Baskin, 1988).

The focus of this study is *Saxifraga bryophora* var. *tobiasiae* Grimes and Packard, a rare sub-alpine taxon endemic to the West Salmon River Mountains of Central Idaho. Currently, only five populations of this taxon are known. Its rarity appears to be a function of its environment and natural history. In this study, I examined the role of ecological and biological characteristics contributing to the natural rarity and narrow distribution of *S. bryophora* var. *tobiasiae*.

The unpredictable environmental conditions such as temperature, growing season length, and moisture availability (Callaghan, 1988) associated with arctic, alpine, and sub-alpine environments exert strong selective pressures upon the life history characteristics, reproductive strategies, and physiological traits of resident plants (Bliss, 1962, 1971; Billings and Mooney, 1968; Grime, 1979; Chambers, 1995). The life history strategies and reproductive traits of organisms within these regions are restricted by the constraints of their ever-changing environments and may contribute to the rarity of species within such habitats (Werner, 1976; Pickett and White, 1985).

Asexual reproduction in higher plants is a successful life history strategy in high altitude, high latitude, and boreal environments (Salisbury, 1942; Williams, 1975; Abrahamson, 1980; Law et al., 1983; Callaghan, 1988). Members of the Saxifragaceae, particularly species of *Saxifraga* L., that persist in sub-alpine, alpine, and arctic environments exhibit to a mix of vegetative and sexual reproduction. Asexual offspring are produced through the formation of disarticulating bulbils, aestivating basal bulbils, and/or stoloniferous runners (Olesen and Warncke, 1989a, 1989b, 1990; Molau, 1992; Molau and Prentice, 1992; Anderson, 1995; Nilsson, 1995; Holderdegger, 1996). Additionally, several of these species have protandrous flowers and are gynodioecious, a population characteristic thought to promote the production of outcrossed sexual offspring (Stevens and Richards, 1985; Stevens, 1988; Stevens and Van Damme, 1988; Anderson, 1995).

Saxifraga bryophora var. *tobiasiae* is characterized by a paniculate inflorescence with a single terminal flower, all other flower primordia being replaced with asexual bulbils (Grimes and Packard, 1981). Little research has been conducted on its

reproductive biology and the factors that promote its combination of asexual and sexual reproduction. My examination of the breeding system, pollination ecology, and factors influencing the balance between the modes of reproduction may provide greater insight into understanding the role of reproductive biology in both rare and common plant species. Additionally, examination of the life history characteristics, population biology, and demography of this rare sub-alpine taxon may further elucidate factors that contribute to the intrinsic rarity of species.

All populations of *Saxifraga bryophora* var. *tobiasiae* occur in the Idaho Batholith and are found in soil-filled depressions surrounded by granitic outcrops. Granite outcrop ecosystems have long been recognized as geologically distinctive habitats that host many endemic, although not rare, plant species in the southeastern United States (Harper, 1939; McVaugh, 1943; McCormick and Platt, 1962; Burbanck and Platt, 1964; Murdy, 1968; Sharitz and McCormick, 1973; Burbanck and Phillips, 1983; Wiser, 1994, 1998). Little research has been conducted on granitic outcrop ecosystems within the western U.S. Thus, this study of the ecological composition and soil morphology associated with *S. bryophora* var. *tobiasiae* depression communities will provide information that, when compared with data from geologically similar areas in the southeast, will aid in identifying and understanding the aspects of such areas that contribute to endemism within rock outcrop ecosystems.

The main objectives for this study are to describe the reproductive biology, life history, population demography, and ecological factors of *Saxifraga bryophora* var. *tobiasiae* and to determine the role that these factors play in its rarity and narrow distribution. This study will provide much needed information for the successful

management and conservation of *S. bryophora* var. *tobiasiae* and the unique habitat in which it exists. Additionally, information gained in this study will further elucidate the role that such factors play in the rarity and endemism of other plant species.

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CHAPTER 2

THE REPRODUCTIVE BIOLOGY OF A RARE, GYNODIOECIOUS SAXIFRAGE:

SAXIFRAGA BRYOPHORA VAR. *TOBIASIAE*

(SAXIFRAGACEAE)

ABSTRACT

I examined the reproductive biology, life history, demographic characteristics, and pollination ecology of *Saxifraga bryophora* var. *tobiasiae*, a rare saxifrage endemic to the West Salmon River Mountains of central Idaho. *Saxifraga bryophora* var. *tobiasiae* combines asexual reproduction via bulbils with a sexual mixed-mating system. Bulbil production precedes floral bud formation and is the dominant form of reproduction. When flowering occurs, outcrossing is promoted by protandrous floral development and the gynodioecious mating system found in all populations. Hermaphrodite flowers were self-compatible but none automatically self-pollinated. No agamospermous fruit set was observed in either gender. No difference in seed number, seed size, bulbil volume, or bulbil weight was observed between genders. Fruit and seed production was both intermittent and infrequent. Females produced significantly more bulbils than did hermaphrodites and may be maintained in the population due to this advantage. A pollen vector is required for fruit production. Flower visitors were infrequent and consisted mostly of syrphids (Diptera: Syrphidae) and empidids (Diptera: Empididae).

INTRODUCTION

To be successful in any environment, an individual must produce viable, fertile offspring (Darwin, 1877; Hartl and Clark, 1989). The reproductive strategies, life history characteristics, and physiological traits of alpine, arctic, and sub-alpine plants are shaped by strong selective pressures exerted by unpredictable climatic conditions (Bliss, 1962, 1971; Billings and Mooney, 1968; Grime, 1979; Chambers, 1995). Wide and unexpected daily and seasonal temperature fluctuations, unpredictable growing season length, and uncertain moisture availability limit the number of successful life history strategies for species of these habitats (Salisbury, 1942; Werner, 1976; Abrahamson, 1980; Pickett and White, 1985; Callaghan, 1988).

Alpine and sub-alpine species persist in harsh environments through the employment of a combination of asexual and sexual modes of reproduction (Salisbury 1942; Harper, 1977; Abrahamson, 1980; Stevens and Van Damme, 1988; Molau 1992; Chambers, 1995; Holderdegger, 1996). Except in unusual cases (Leblanc et al., 1995), asexual reproduction ensures production of offspring genetically identical to the parent and therefore well adapted to the current local habitat. Asexual reproduction also diminishes the need for costly investments to attract pollen vectors (Stebbins, 1950; Williams, 1975; Abrahamson, 1980). In contrast, sexual reproduction produces more genetically diverse offspring (Crow and Kimura, 1965), thus enhancing the species chances for survival, growth, and reproduction in novel or changing habitats under unpredictable conditions (Williams, 1975; Abrahamson, 1980).

Williams (1975) and Abrahamson (1980) theorized that a plant could achieve

optimal fitness through the combination of sexual and asexual reproduction, if the costs of investment provide equal returns. If costs exceed benefits for one mode of reproduction, selection would favor decreased investment in that mode to a level at which the cost/benefit ratio of the modes was equal. If the two modes provide equal returns on investment, both reproductive modes would be maintained. However, because of spatiotemporal changes in abiotic and biotic factors, fluctuations in the importance of each reproductive contribution are expected.

Many investigators have argued that there is trade-off between asexual and sexual reproduction. This trade-off, in which an increase in investment in one reproductive mode results in a direct decrease in investment in the other reproductive mode, has been shown in several species (Sarukhan, 1976; Law et al., 1983; Arizaga and Ezcura, 1995; Chambers, 1995). Many scientists (Sarukhan, 1976; Whigham, 1974; Law et al., 1983; Arizaga and Ezcura, 1995) have investigated the hypothesis that the amount of energy and nutrients invested in sexual reproduction is inversely proportional to the amount invested in asexual reproduction and that environmental factors (e.g., soil moisture, texture, and nutrient content, light, temperature) determine the relative investments made in either mode. The role of various biotic factors (e.g., pollinator limitations, population density, intraspecific and interspecific competition, and species succession) in determining the reproductive mode has also been widely investigated (Salisbury, 1942; Mooney and Billings, 1961; Ogden, 1974; Whigham, 1974; Thomas and Dale, 1975; Williams, 1975; Allen and Forman, 1976; Sarukhan, 1976; Abrahamson, 1980; Law et al., 1983). Despite the intensity of research efforts, no consensus has been reached on

why certain modes are favored under particular environmental regimes.

Members of the Saxifragaceae, particularly those in *Saxifraga* L., persist in sub-alpine, alpine, and arctic environments, partly due to a mix of vegetative and sexual reproduction (Stevens, 1988; Molau, 1992; Holderdegger, 1996). Many *Saxifraga* species are also gynodioecious, a characteristic that promotes the production of outcrossed seeds by females. Heterosis may increase the fitness of outcrossed seeds compared to seeds of hermaphrodites, which may sometimes be the product of self-fertilization and exhibit inbreeding depression (Lewis, 1941; Lloyd, 1974a, 1974c; Charlesworth and Charlesworth, 1978; Stevens and Richards, 1985; Stevens, 1988; Stevens and Van Damme, 1988; Oleson and Warncke, 1989a, 1989b, 1989c, 1990; Molau, 1992; Molau and Prentice, 1992; Anderson, 1995; Holderdegger, 1996).

Gynodioecy has received appreciable interest from evolutionary biologists since Darwin (1877) first introduced the concept. Two fundamental types have been defined: unstable gynodioecy, an intermediate stage in the evolution of dioecy from hermaphroditism (Lloyd, 1974a, 1974b, 1980; Charlesworth and Charlesworth 1978), and stable gynodioecy, a system in which females and hermaphrodites are both maintained within a population due to counterbalancing selection (Lewis, 1941; Lloyd 1974a, 1974b, 1974c, 1975; Charlesworth and Charlesworth 1978; Stevens and Richards, 1985).

Most studies of gynodioecy have been concerned with the maintenance of the sexual polymorphism within a population given that females may be disadvantaged by the absence of male function (Lewis, 1941; Lloyd, 1974a, 1974b, 1975, 1976; Charlesworth and Charlesworth, 1978; Charlesworth and Ganders, 1979). Females can only reproduce

sexually by producing seeds, whereas hermaphrodites can achieve fitness through both pollen donation and seed production. Under nuclear inheritance, female plants must therefore produce, on average, twice the number of seeds a hermaphrodite produces in order to be reproductively equal (Lewis, 1941; Lloyd, 1974b, 1975; Charlesworth and Charlesworth, 1978; Willson, 1983). However, under cytoplasmic or nuclear-cytoplasmic inheritance, only a slight advantage in females is necessary for their maintenance in a population (Lewis, 1941; Lloyd, 1974a, 1974b; Charlesworth and Charlesworth, 1978).

Superior fecundity of females relative to hermaphrodites can result from differences afforded by outbreeding advantages (Lloyd, 1974a, 1975; Charlesworth and Charlesworth, 1978) and sex-specific allocation of resources (Darwin, 1877; Horovitz and Beiles, 1980; Eckhart, 1992; Petterson, 1992). Outbreeding avoids potential reductions in vigor, survival (Kesseli and Jain, 1984; Kohn and Biardi, 1995), and offspring size due to inbreeding depression by hermaphrodites relative to females (Connor, 1973; Lloyd, 1974a, 1975; Assouad et al., 1978; Charlesworth and Charlesworth, 1978; Stevens, 1988). Sex-specific allocation has been hypothesized because females typically have smaller, less costly flowers (reduced male parts) than hermaphrodites (Lloyd, 1974a, 1975, 1976; Charlesworth and Charlesworth, 1978; Delph, 1996), and therefore have more resources to allocate to seed production which can result in more or larger seeds (Darwin, 1877; Kohn, 1988; Delph 1996). Determining the immediate cause of hermaphrodite offspring inferiority is often difficult due to the similar results observed in these processes. Female advantages afforded by these processes can

allow for maintenance of females within gynodioecious populations (Lewis, 1941; Lloyd, 1974a, 1974b, 1975; Charlesworth and Charlesworth, 1978; Stevens, 1988; Puterbaugh et al., 1997).

Saxifraga bryophora var. *tobiasiae* Grimes and Packard is a rare sub-alpine taxon that is endemic to the West Salmon River Mountains of Central Idaho. It is a Federal Species of Concern (USDI Fish and Wildlife Service, 1996) and an Idaho State Sensitive Species. It was described as annual in habit, but very little is known about its sexual reproduction, life cycle, or demography (Grimes and Packard, 1981). My study of the key life history components and reproduction of *S. bryophora* var. *tobiasiae* was designed to develop a greater understanding of its population dynamics and to suggest strategies for its conservation.

In this chapter, I describe my research on the reproductive ecology, demography, and life history characteristics of *S. bryophora* var. *tobiasiae*. The breeding system, flowering phenology, vegetative and floral characteristics, bulbil production, seed set, and pollinator composition are compared between females and hermaphrodites. The following questions are addressed: (1) What is the incidence of female and hermaphrodite plants within populations of *S. bryophora* var. *tobiasiae*? (2) How do female and hermaphrodites differ in floral size, floral structure, and vegetative characteristics? (3) What stages comprise the life cycle of *S. bryophora* var. *tobiasiae*? (4) Is *S. bryophora* var. *tobiasiae* self-compatible, self-fertilizing, or agamospermic? (5) Are there any fitness differences between females and hermaphrodites in seed and bulbil production? (6) What are the important pollinators of *S. bryophora* var. *tobiasiae*?

MATERIALS AND METHODS

The taxon—*Saxifraga bryophora* var. *tobiasiae* is a diminutive taxon, 4 to 20 cm tall, with a basal rosette of leaves each up to 15 mm long. Plants, either female or hermaphrodite, usually produce one panicle (< 5% produce more than 1) that is terminated by a single flower; all remaining flowers are replaced by asexual bulbils. The flowers are 0.6 to 1.2 cm in diameter and composed of separate petals. Petals are sagittate and marked with two small, yellow dots each that may serve as nectar guides. Flowers have 10 to 12 stamens that bear red anthers, 0.1 to 0.9 mm in length. The fruit is a red septicidal capsule, 2.2 to 3.4 mm long, with 10 to 20 small brown seeds (Grimes and Packard, 1981; personal observation).

All five known populations of *S. bryophora* var. *tobiasiae* occur in the Payette National Forest, in Valley, Adams, and Idaho Counties, Idaho, at 2255 to 2600 m elevation (Figure 2.1; Table 2.1). They occur in habitats characterized by exposed bare soil and unstable substrate caused by meltwater runoff and bioturbation. The two largest and most accessible populations, Fisher Creek Saddle East (FCSE) and Fisher Creek Saddle West (FCSW), were used for most experiments.

Gender and flowering morphology—In 1995, twelve permanent plots were established, seven at FCSW and five at FCSE, to follow flowering phenology and record the life stages of *S. bryophora* var. *tobiasiae* individuals. I used more plots at FCSW than at FCSE because the plants there are distributed over a more varied range of microhabitats and are more abundant than those at FCSE. Each permanent plot contained twelve 0.5 m 0.5 m quadrats. The 144 quadrats were sampled monthly from June through

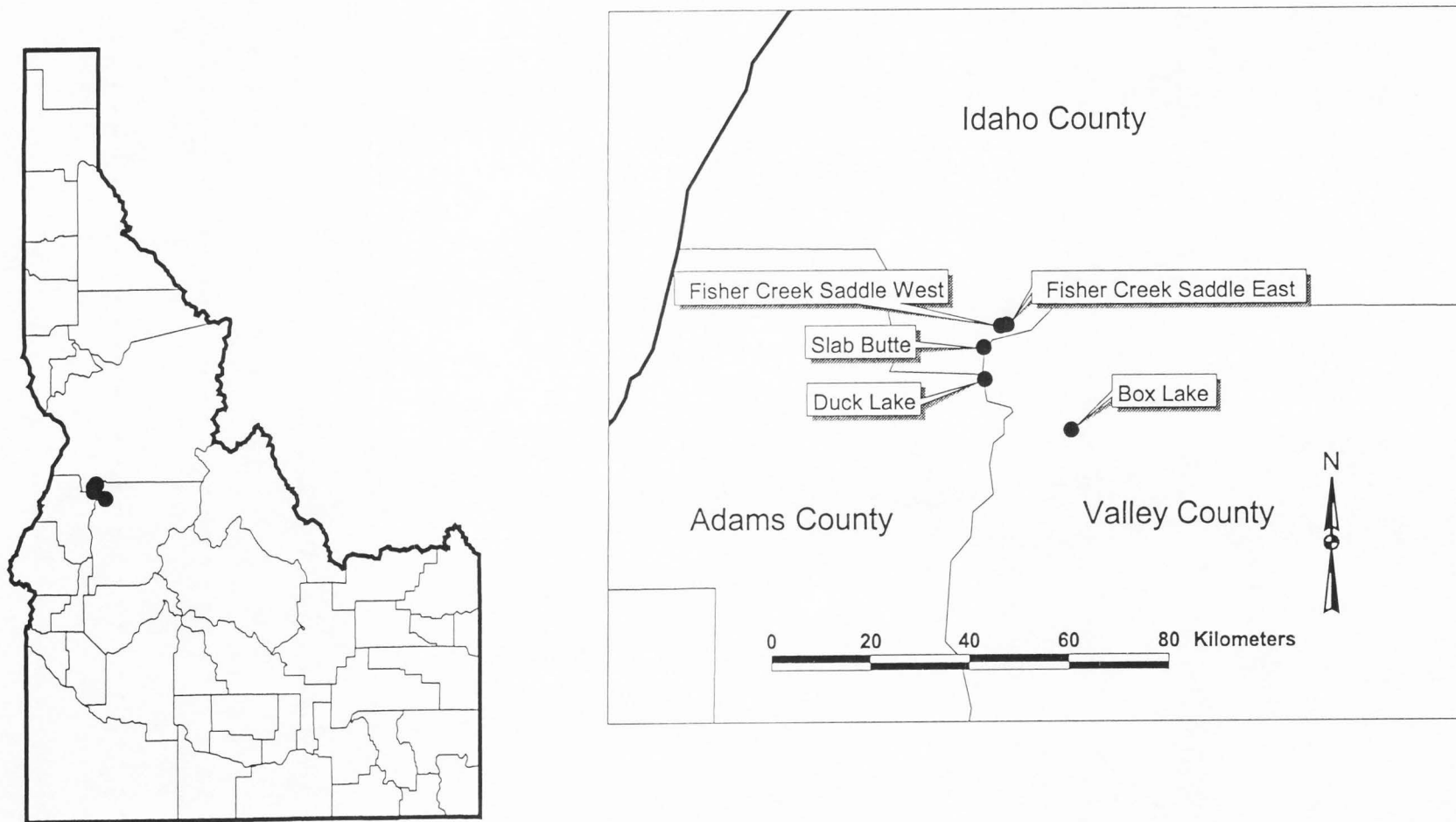


Fig. 2.1. Distribution of *Saxifraga bryophora* var. *tobiasiae* in west central Idaho.

TABLE 2.1. Locations and population information for all populations of *Saxifraga bryophora* var. *tobiasiae*.^a

Population name	Lat./Lon.	Elevation range (m)	Est. number of plants
Fisher Creek Saddle East (FCSE)*	45°09' N, 116°05' W	2255-2500	> 5,000
Fisher Creek Saddle West (FCSW)*	45°09' N, 116°06' W	2255-2600	> 5,000
Beaverdam South (BS)	45°02' N, 115°58' W	2375-2470	1500
Slab Butte (SB)	45°05' N, 116°08' W	2317-2450	> 1,000
Duck Lake (DL)	45°08' N, 116°08' W	2255-2375	250

^a * = Populations selected for study plots.

September in 1995, 1996, and 1997.

Flowering at FCSE and FCSW was studied from late July through August while vegetative data were collected from June through September of each year. The number of flowering individuals in the 12 established permanent plots was counted and their development from flower through fruit maturation was recorded. The development and phenology of the reproductive parts of the flowers was described by following marked flowers through anthesis. Pollen viability was assessed by staining with aniline blue (Alexander, 1980).

In 1996, a banner year for flowering, five additional 2 m X 2 m plots (2 FCSE, 2 FCSW, 1 SB; Table 2.1) were established to further examine the incidence of gynodioecy

in the populations. Flower gender (female, hermaphrodite, or functional female, i.e., individuals whose anthers were filled with white, nonviable pollen) was identified for all individuals within each plot. The number of females (females and functional females) and hermaphrodites were compared between plots (FCSE, FCSW) using a 2 x 2 contingency table. A wet period during flowering suggested that the pollen of some functional females may have been rendered inviable by excessive moisture. To test this, water droplets were applied to dehiscing anthers of fresh flowers of hermaphrodites and pollen from these flowers was compared with that of functional females located in the same field.

To determine if size differences existed for flowers of different genders or aspects, six floral characteristics and bulbil number were measured on 135 randomly selected, panicle-producing plants from FCSE and FCSW in 1996. (These 135 plants were also used in the breeding system experiments.) Stamen number, mean anther size, mean filament length, mean pistil length, flower width, petal number, and bulbil total were measured on 90 hermaphrodites and 45 females. Bulbil number was log transformed due to its nonnormal distribution. A two-factor ANOVA for unbalanced data was used to compare each of these characters by aspect (FCSE, FCSW), gender, and an aspect*gender interaction. Computations were made using PROC GLM in SAS release 6.12 (SAS Institute, 1996).

The 135 randomly selected, panicle-producing plants from FCSE and FCSW were also used to examine asexual reproduction. Asexual reproduction was assessed by collecting and pressing all bulbils from each plant. Bulbils were collected while still

attached to the parent plant. Five each of the uppermost and lowermost bulbils were selected to estimate volume and average weight. Volume was calculated by measuring the lengths and widths of the cone-shaped bulbils to the nearest 0.5 mm and using the equation for the volume of a cone, $v = (1/3)r^2h$ where r = the radius and h = the height. The average dry weight of the 10 bulbils was measured to the nearest mg. The volume and average weight of the bulbils were analyzed using analysis of variance of a three-way factorial in a split plot design comparing between gender, position, aspect, and their interactions. Computations were made using PROC MIXED in SAS release 6.12 (SAS Institute, 1996). For volume, the analysis was partitioned to examine the variation among plants, among locations, and among bulbils. Because weight was averaged, the analysis could only be partitioned to examine the variation among plants and locations. Due to the nonnormal distribution of the data, bulbil volumes were transformed by taking the quarter root and average bulbil weights were log transformed.

To examine the effect of aspect, four 1-m² plots (2 FCSE, 2 FCSW) were established in 1996. Thirty-six randomly selected plants were measured in each plot. Rosette volume (using the formula $v = \pi r^2 h$ where r = the radius and h = the height), panicle height, bulbil number, and flower gender were recorded. For each variable, a two-way factorial in a split plot design was used to compare between genders, between aspects (FCSE, FCSW) and interactions. Computations were made using PROC MIXED in SAS release 6.12 (SAS Institute, 1996) and a slice procedure was used to examine the significance of the interactions.

Demography—The 12 plots at FCSE and FCSW were also used to describe the

demography of *Saxifraga bryophora* var. *tobiasiae*. Individuals from the 144 quadrats were classified as rosettes, adults with a panicle but no flowers (no flower produced), or as adults with panicle and a flower. Flowering individuals were further classified as female or hermaphrodite. The number of individuals in each life stage was averaged per plot and then averaged for FCSE and FCSW. Standard t-tests were used to compare flower genders, and gender ratios between sites (FCSE, FCSW). A two-way factorial in a split plot design (SAS Institute, 1996) was used to compare the average number of adult plants producing panicles without a flower between FCSE and FCSW, between years (1995, 1996, 1997), and interactions. Computations were made using PROC GLM in SAS release 6.12 and a slice procedure was used to examine the significance of the interactions (SAS Institute, 1996).

Life history—The life history of *S. bryophora* var. *tobiasiae* was examined by marking 25 vegetative rosettes and 15 panicle-producing plants in each of four 1 m X 1m plots (2 FCSW, 2 FCSE). Individuals were marked by tying string at the base of each rosette. The plots were established in 1995. Marked individuals were then measured for rosette height and width and the volume of each rosette was calculated. Those individuals producing panicles were also measured for panicle height and total number of bulbils produced. In 1996 and 1997, these marked individuals were relocated and remeasured. One of the FCSW populations was eliminated by extreme run-off in 1996. The mean number of bulbils produced per plant was compared between years for each gender using a paired t-test. Gender was determined for those individuals that produced a flower. Regression analysis was used to examine the relationships between: (1) rosette

volume and bulbil number, (2) panicle height and bulbil number, and (3) rosette volume and panicle height.

To determine the fate of asexually produced bulbils, thirty-six bulbils were planted in each of four 0.5 m x 0.5 m plots (2 FCSE, 2 FCSW). Bulbils were planted 1 cm below the soil to lessen their loss in the spring run-off. A plexi-glass planting board with holes at 5-cm intervals was used to plant the bulbils and to aid in their relocation. In 1996 and 1997, these plots were relocated and the fate of the individuals was recorded. A chi-square test was used to compare the survival into 1997 of plants that in 1996 produced a panicle with no flower with those producing a flower. Standard t-tests were used to compare the mean number of bulbils produced (1) in 1996 by panicle producing plants with a flower and panicle producing plants without a flower, and (2) in 1997 by plants that had been rosettes in 1996 and plants that had been panicle plants in 1996.

Sexual reproduction—The 135 plants from FCSE and FCSW were also used for breeding system experiments. Experimental hand pollination treatments are summarized in Table 2.2. Fifteen plants were assigned randomly to each treatment. All plants were bagged prior to treatment to exclude pollinators and herbivory, and remained so throughout the study. For the xenogamy treatment, the pollen was collected from donor plants greater than 20 m but less than 40 m from recipients to reduce the risk of inbreeding and outbreeding depression (Waser and Price, 1994). To test for self-compatibility, flowers were emasculated immediately prior to anthesis and the anthers stored at 7°C until the respective stigmata became receptive (3 to 4 days). At that time, anthers were removed from storage, allowed to dehisce, and used to pollinate their

TABLE 2.2. Breeding system treatments of *S. bryophora* var. *tobiasiae*. Gender is indicated for each treatment.

Treatment	Gender	Manipulation	Tests for
Agamospermy	Female	Unmanipulated	Asexual seed set
	Herm	Emasculated in bud	
Autogamy	Herm	Unmanipulated	Automatic selfing
Self-pollination	Herm	Pollinated with self-pollen stored at 7°C until pistils receptive	Selfing with vector
Xenogamy	Female	Crossed with plant >20 m away	Outcrossing
	Herm	Emasculated, crossed with plant >20 m away	
Emas.-Control	Herm	Emasculated, unbagged	Emasculated control
Control	Female	Unmanipulated, unbagged	Control
	Herm		

respective flowers. Viability of this refrigerated pollen was not tested prior to transfer.

Fruits were collected as they matured.

Fruit set among treatments was analyzed using contingency tables. To determine if a pollen vector was necessary for pollination of hermaphrodites, the contingency table was partitioned to test the planned comparison of xenogamy and geitonogamy (vector required) versus autogamy and agamospermy (vector not necessary). The table was then partitioned to test for self-compatibility (xenogamy vs. geitonogamy) and the necessity of pollen deposition (agamospermy vs. autogamy). For female plants, only the agamospermy and xenogamy treatments were possible. To determine if seed set was pollinator-limited, xenogamy treatments for both hermaphrodites and females were compared with their respective open-pollinated controls.

The number of seeds was counted for the flowers of the 135 individuals used in the breeding system treatments. Seeds were too light to weigh individually, so the lengths

and widths of 10 randomly selected seeds were measured to the nearest 0.05 mm under a dissecting microscope. The volume of each seed was then estimated from its linear dimensions using the volume of an ellipse, $(4/3)\pi lw^2$ where l = length and w = width. To normalize the distribution, the average seed number was squared. Seed number and seed volume data were analyzed using analysis of variance of a two-way factorial in a completely randomized design between genders and treatments (control and xenogamy). A one-way analysis of variance in a completely randomized design was used to compare hermaphrodite seed number and seed volume between treatments (control, xenogamy, and geitonogamy). Computations were made using PROC GLM in SAS release 6.12 (SAS Institute, 1996).

Insect collection and observation—Observations of floral visitors to individual plants were made during peak flowering (July 26-Aug. 21) in 1996 at the FCSE and FCSW populations. Plants were observed during 1-hour observation blocks at each of the following times: 0800-0900, 1100-1200, 1400-1500, and 1700-1800 on 5 days during the height of flowering. A total of 20 hours was spent observing and collecting insect visitors. All floral visitors to *Saxifraga bryophora* var. *tobiasiae* were collected and identified.

RESULTS

Gender and flowering morphology—All populations of *S. bryophora* var. *tobiasiae* sampled at the three sites (FCSE, FCSW, SB) were gynodioecious. There were no differences in petal number or flower width between genders (Table 2.3), aspects

(Table 2.4), or a gender*aspect interaction (Table 2.5).

Female flowers have anthers but they are either devoid of pollen or contain aborted pollen. Development of both female and hermaphrodite flowers is identical until the male stage of flowering is initiated (Figure 2.2). In bud, both genders produce red anthers (0.1 – 0.3 mm long) that are held adjacent to the small, white, undifferentiated pistils. Female and hermaphrodite flower types are not distinguishable at this point. Anthesis begins as flowers enter an initial male stage. The filaments in hermaphrodite flowers elongate and all anthers dehisce simultaneously, releasing red pollen. Females have anthers that are devoid of pollen, and functional females have anthers filled with white nonviable pollen. When spent, anthers of the hermaphrodites disarticulate, but the filaments remain attached. In contrast, anthers of females turn black as the locules collapse but remain on the filaments throughout the life of the flower. Stamen number did not differ between genders, aspects, or interactions (Tables 2.3, 2.4, 2.5). Anthers and filaments were significantly longer in hermaphrodites than in females when measured just prior to anthesis (Table 2.3) but did not differ due to aspect (Table 2.4) or gender*aspect interaction (Table 2.5).

In female and hermaphrodite flowers, the pistillate stage of flowering is initiated 2 to 3 days after the staminate stage is completed. The small white pistils, two per flower, begin to elongate and the styles and stigmata become distinguishable. No significant difference in pistil size existed between genders ($P = 0.735$) (Table 2.3), aspect (Table 2.4), or interaction (Table 2.5). The flat stigmatic surface becomes sticky and remains receptive for approximately 24 hours. After pollen is deposited on the stigmatic surface,

TABLE 2.3. Comparison of sizes of floral characters and bulbil number between female and hermaphrodite plants in 1996.

Character	Females (N = 45) Mean (range and stderr)	Hermaphrodite (N =90) Mean (range and stderr)	F	P
Stamen number	10.13 (7-13 ± 0.157)	10.08 (8-13 ± 0.109)	0.06	0.801
Anther size (mm)	0.19 (0.1-0.3 ± 0.014)	0.28 (0.1-0.5 ± 0.011)	30.66	< 0.001*
Filament length (mm)	1.53 (0.5-3.0 ± 0.106)	2.30 (1.0-4.0 ± 0.076)	34.57	< 0.001
Pistil size	2.27 (1.5-3.0 ± 0.073)	2.23 (1.5-3.0 ± 0.103)	0.11	0.735
Flower width (mm)	7.02 (4.0 - 10.0 ± 0.303)	7.17 (2.0 - 12.0 ± 0.214)	0.17	0.680
Petal number	5.84 (4 - 8 ± 0.119)	5.71 (4 - 7 ± 0.080)	0.83	0.364
Bulbil number	56.93 (1 - 130 ± 3.97)	49.56 (1 - 176 ± 2.18)	4.95	0.027*

^a Significance levels : * = $P < 0.05$.

TABLE 2.4. Comparison of sizes of reproductive characters and bulbil number between plants differing in aspect (FCSE, FCSW) in 1996.

Character	FCSE (N=68) Mean (stderr)	FCSW (N=67) Mean (stderr)	F	P
Stamen number	10.14 (± 0.134)	10.07 (± 0.132)	0.14	0.712
Anther size (mm)	0.239 (± 0.011)	0.235 (± 0.012)	0.06	0.801
Filament length (mm)	1.89 (± 0.091)	1.93 (± 0.093)	0.12	0.732
Pistil size (mm)	2.18 (± 0.090)	2.32 (± 0.088)	1.39	0.245
Flower width (mm)	7.16 (± 0.263)	7.05 (± 0.260)	0.09	0.763
Petal number	5.85 (± 0.104)	5.70 (± 0.084)	1.07	0.302
Bulbil number	52.69 (± 3.47)	53.81 (± 3.42)	0.05	0.818

^a Significance levels : * = $P < 0.05$.

TABLE 2.5. Comparison of sizes of floral characters and bulbil number for the gender*aspect (FCSE, FCSW) interaction in 1996.

Character	FCSE (N = 68) Mean (stderr)	FCSW (N = 67) Mean (stderr)	F	P
Stamen number			1.16	0.283
Female	10.27 (± 0.218)	10.00 (± 0.215)		
Herm	10.02 (± 0.022)	10.15 (± 0.154)		
Anther size (mm)			0.06	0.801
Female	0.19 (± 0.019)	0.18 (± 0.019)		
Herm	0.28 (± 0.013)	0.28 (± 0.013)		
Filament length (mm)			0.70	0.405
Female	1.45 (± 0.152)	1.60 (± 0.149)		
Herm	2.33 (± 0.107)	2.27 (± 0.107)		
Pistil size (mm)			0.00	0.961
Female	2.20 (± 0.147)	2.34 (± 0.144)		
Herm	2.15 (± 0.103)	2.31 (± 0.103)		
Flower width (mm)			0.09	0.763
Female	7.13 (± 0.433)	6.91 (± 0.423)		
Herm	7.17 (± 0.302)	7.17 (± 0.302)		
Petal number			0.61	0.437
Female	5.86 (± 0.120)	5.82 (± 0.167)		
Herm	5.84 (± 0.302)	5.57 (± 0.120)		
Bulbil Number			2.44	0.121
Female	60.18 (± 5.69)	53.69 (± 3.98)		
Herm	45.20 (± 3.98)	53.93 (± 5.56)		

^a Significance levels : * = $P < 0.05$.

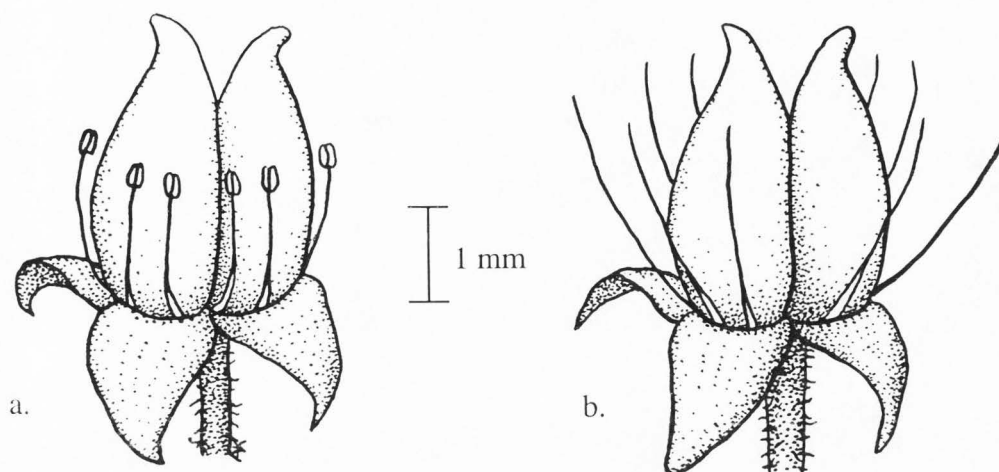


Fig. 2.2. Floral development in *Saxifraga bryophora* var. *tobiasiae*. a) Females have persistent anthers held close to the pistils; b) Hermaphrodites have elongated filaments and anthers that disarticulate after anthesis.

the pistils turn pink and eventually become red. Unpollinated pistils remain white. The fruit becomes swollen, red, and shiny. The septicidal fruits dehisce 3 to 4 weeks after fertilization, releasing 15 to 30 small (0.05 – 2.0 mm) seeds.

The gender for all flowering individuals found in five 2 m x 2 m plots (2 FCSW, 2FCSE, 1 SB) in 1996 was recorded (Table 2.6). The proportions of females and hermaphrodites were significantly different between aspects ($df = 1$; $X^2 = 20.45$, $P = < 0.001$). Eastern (FCSE) plots had significantly more females while western plots had more hermaphrodites. Of the 500 individuals examined, hermaphrodites ranged between 39.5- 56.0 %, and females ranged between 25.0 – 34.1%. The anthers of the remaining individuals (16.0 – 24.0 %) contained white inviable pollen and were classified as functional females. Placing drops of water on fresh anthers of hermaphrodites did not lead to the formation of the white masses of sterile pollen observed in functional females.

TABLE 2.6. Comparison of proportion of hermaphrodites, females, and functional females in 2 X 2 m² plots (2FCSE, 2FCSW, 1SB) in 1996.^a

Gender	FCSE1	FCSE2	FCSW1	FCSW2	SB
Hermaphrodites	45.0 %	39.5 %	56.6 %	52.8 %	51.8 %
Females	33.8 %	34.1 %	27.2 %	25.0 %	28.6 %
Functional females	21.2 %	26.4 %	16.2 %	22.2 %	19.6 %

^a $N = 500$ individuals.

It is not likely, therefore, that potential hermaphrodites were converted to functional females by raindrops or increased moisture. Functional females may represent a transition state between hermaphrodites and females (Stevens, 1988). When functional females were coupled with other females, the functional gender ratio became about 1:1.

I found no significant differences in plant size (panicle height and rosette volume) between genders (Tables 2.7, 2.8). However, significant differences in both variables were observed for aspect. Plants at FCSE were larger than those at FCSW.

Demography—The average number of individuals observed at each life stage per population is summarized in Table 2.9. The proportion of panicle-producing plants varies greatly from year to year. Significantly more plants produced flowerless panicles ($P < 0.001$) in 1996 than in 1995 or 1997 (Table 2.10). The FCSE population had more panicle-producing plants than FCSW in 1995 and 1996, but in 1997 the FCSW population had more panicle-producing individuals. Only in 1996, when FCSE had twice as many panicle-producing plants as FCSW, was the difference significant ($P < 0.001$).

A significant interaction of year and location was also found due to the reversal of

TABLE 2.7. Two-way factorial in a split plot design comparing panicle height between genders, aspect, and interactions.^a

Tests of Fixed Effects				
Source	num df	denom df	F ratio	Prob
Gender	1	135	2.19	0.141
Aspect	1	2	22.10	0.042*
Gender*Aspect	1	135	1.30	0.255
Covariance Parameter Estimates				
Parameter	df	Estimate		
Plant(slope)	2	0.754		
Residual	135	5.582		

^a $N = 78$ for females; $N = 63$ for hermaphrodites. Significance levels : * = $P < 0.05$.

TABLE 2.8. Two-way factorial in a split plot design comparing rosette volume between genders, aspects, and interactions.^a

Tests of Fixed Effects				
Source	num df	denom df	F ratio	Prob
Gender	1	135	0.68	0.410
Aspect	1	2	44.18	0.022*
Gender*Aspect	1	135	1.49	0.224
Covariance Parameter Estimates				
Parameter	df	Estimate		
Plot(aspect)	2	0.8223		
Residual	135	0.0001		

^a $N = 78$ for females; $N = 63$ for hermaphrodites. Significance levels : * = $P < 0.05$.

TABLE 2.9. Comparison of number of panicle-producing adults without flowers, number of females and hermaphrodites, ratio of females to hermaphrodites, and the average number of flowers between FCSE and FCSW and between years. ^a

Character	1995		1996		1997	
	FCSE	FCSW	FCSE	FCSW	FCSE	FCSW
Mean # of adults w/out flowers/plot	3.75 (1.62)	2.64 (2.18)	15.41 (7.23)	7.62 (2.44)	3.56 (1.22)	5.56 (2.78)
% adults with flowers	0.04%	0	13.1 %	18.5%	0.25%	0
Mean # of females/plot	0	0	0.64 (0.30)	0.33 (0.28)	0	0
Mean # of herms/plot	0	0	1.69 (0.79)	1.08 (0.45)	0	0
% herms of all flowering plants	---	---	72.5%	76.6%	---	---
Mean # of flowers/plot	0.08 (0.27)	0	----	-----	0.5 (1.65)	0

^a $N = 5$ plots in FCSE and $N = 7$ in FCSW. Standard deviation is indicated below the mean for each population.

abundances between the FCSW and FCSE sites in 1997 ($P = 0.03$).

Mature bulbil production always precedes flower production on all panicles. Bulbils disarticulate during fall rainstorms and appear to be dispersed in subsequent run-off. The bulbils trap an air bubble in their leafy rosette of leaves and sink in small pools of water after several minutes or become trapped in flow barriers. By late October, the bulbils have formed roots, thus establishing the ramet before the winter snowfalls.

Females, from the 135 plants in 1996, produced slightly more bulbils than did hermaphrodites ($p = 0.027$; Table 2.3) but there was no difference between aspects (Table 2.4) or for the interaction (Table 2.5). However, in the 1 m X 1 m plots, bulbil number was uninfluenced by gender or aspect. A trend of increased bulbil production due to a gender*aspect interaction was observed for plants within FCSE plots but was not significant at a 0.05 level ($P = 0.055$; Table 2.11). Eastern females produced more bulbils (24.78 ± 3.79) than did eastern hermaphrodites (19.11 ± 3.72). Bulbil number only slightly differed between western females (24.78 ± 3.79) and western hermaphrodites (27.21 ± 3.74).

No significant differences in the 135 plants were found between genders or aspects in bulbil volume and bulbil weight. A positional difference, however, for both volume and weight was found. Upper bulbils (Table 2.12) within a panicle were significantly larger than lower bulbils for both weight (Table 2.13) and volume (Table 2.14). No interactions between gender or position were significant.

Flower production per population was extremely low in all years sampled (Table 2.9). In 1995, only one of the 2445 plants sampled produced a flower. Similar

TABLE 2.10. Two-way factorial in a split plot design comparison for number of adult plants without flowers between FCSE and FCSW for 1995, 1996, and 1997. ^a

Tests of fixed effects						
source		num df	denom df		F ratio	Prob
Location (FCSE, FCSW)		1	30		4.13	0.051
Year ('95,'96,'97)		2	30		20.68	< 0.001***
Location*Year		2	30		6.50	0.005**
Covariance parameter estimates						
Parameter		df	Estimate			
Residual		30	11.23			
Tests of effect slices						
	Location	Year	NDF	DDF	F	P
Locate*year		95	1	30	0.32	0.57
Locate*year		96	1	30	15.78	< 0.001***
Locate*year		97	1	30	1.03	0.317
Locate*year	East		2	30	20.51	< 0.001***
Locate*year	West		2	30	3.90	0.031

^a N = 5 plots for FCSE and N = 7 plots for FCSW. Significance levels : * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

TABLE 2.11 Two-way factorial in a split plot design comparing bulbil number between genders, aspects, and interactions. ^a

Tests of fixed effects						
source	num df	denom df	F ratio	Prob		
Gender	1	135	1.87	0.174		
Aspect	1	2	0.77	0.473		
Gender*Aspect	1	135	3.73	0.055		
Covariance parameter estimates						
Parameter	df	Estimate				
Plot(aspect)	2	23.84				
Residual	135	78.36				
Tests of effect slices	Aspect	Gender	NDF	DDF	F	P
Aspect*gender		Female	1	135	0.09	0.768
Aspect*gender		Herm.	1	135	1.95	0.164
Aspect*gender	East		1	135	5.61	0.019*
Aspect*gender	West		1	135	0.15	0.694

^a $N = 78$ for females; $N = 63$ for hermaphrodites. Significance levels : * = $P < 0.05$.

TABLE 2.12. Average bulbil weight and volume for top five bulbils and bottom five bulbils for females and hermaphrodites of *Saxifraga bryophora* var. *tobiasiae*.^a

Gender (position)	Mean weight (mg) (stderr)		Mean volume (mm ³) (stderr)	
Female(top)	4.80	(0.40)	23.87	(1.55)
Herm. (top)	4.10	(0..30)	21.24	(1.09)
Female(bottom)	2.40	(0.09)	6.81	(0.40)
Herm. (bottom)	2.50	(0.13)	6.11	(0.29)
Position				
Top	4.32	(3.21)	22.11	(10.41)
Bottom	2.46	(0.89)	6.34	(2.72)
Gender				
Female	3.65	(3.64)	15.34	(11.24)
Herm.	3.27	(1.43)	13.67	(10.80)
Aspect				
FCSE	3.30	(0.14)	14.32	(10.67)
FCSW	3.26	(0.13)	14.28	(10.12)

^a *N* = 45 for females; *N* = 90 for hermaphrodites.

TABLE 2.13. Three-way factorial in a split plot design comparing average bulbil weight between positions, genders, aspects, and interactions.

Tests of fixed effects				
source	num df	denom df	F ratio	Prob
Gender	1	131	0.02	0.889
Position	1	131	315.34	< 0.001***
Aspect	1	131	0.06	0.814
Gender*Position	1	131	0.02	0.900
Gender*Aspect	1	131	0.29	0.591
Position*Aspect	1	131	0.62	0.434
Gender*Position*Aspect	1	131	1.27	0.262
Covariance parameter estimates				
Parameter	df	Estimate		
Plant(gender*aspect)		<0.0001		
Residual	1212	<0.0001		

^a $N = 45$ for females; $N = 90$ for hermaphrodites. Significance levels : *** = $P < 0.001$.

results were found in 1997 when only six of 2319 plants produced a flower.

Consequently, flower morphology and phenology could only be measured in 1996 when 7.4% (242 of 3273 plants sampled) of the population produced flowers. The percentage of flowering adults was similar between sites and very low in all years studied ($\leq 15\%$). The percentage of females (Table 2.9) was much lower in the permanent plots than in the 2 m X 2 m plots (Table 2.6). Fewer functional females were found in the permanent plots, but fewer flowers of either gender were found within these permanent plots.

Life history—Seventy-three of the 120 plants marked at the end of the 1995 field season were relocated in 1996 (Table 2.15). Most of the relocated individuals produced panicles with bulbils in 1996 regardless of whether they had produced panicles or rosettes in 1995. No individuals reverted to rosette producing plants after they had produced panicles. No individuals survived into the 1997 growing season.

In 1996, bulbil production of rosettes (39.6 ± 11.23) and panicles (44.7 ± 9.87) marked in 1995 did not differ significantly ($t = 1.13$; $df = 73$, $P = 0.25$). Average bulbil production for all panicle producing plants in 1996 (42.2 ± 10.41 bulbils per plant), however, was significantly higher ($t = 11.75$, $df = 123$, $P < 0.001$) than in 1995 (12.83 ± 4.95 bulbils per plant). No flowers were produced in 1995. Only three plants produced a flower in 1996. All three plants had produced a panicle in 1995. No fruit or seed production occurred in any of the marked individuals.

Bulbil number was positively related to rosette volume ($r^2 = 0.44$; $P < 0.001$; Figure 2.3) but not to panicle height ($r^2 = 0.317$; $P = 0.157$; Figure 2.4). Regression of panicle height on rosette volume was significant ($r^2 = 0.12$, $P < 0.01$; Figure 2.5).

TABLE 2.14. Three-way factorial in a split-plot design comparing average bulbil volume between positions, genders, aspects, and interactions. ^a

Tests of fixed effects				
source	num df	denom df	F ratio	Prob
Gender	1	131	3.21	0.075
Position	1	131	728.06	< 0.001***
Aspect	1	131	0.11	0.734
Gender*Position	1	133	0.97	0.327
Gender*Aspect	1	131	0.37	0.546
Position*Aspect	1	131	0.04	0.841
Gender*Position*Aspect	1	131	0.68	0.410

Covariance parameter estimates

Parameter	df	Estimate
Plant(gender*aspect)	131	0.117
Pos*plant(gender*aspect)	131	0.123
Residual	1081	0.141

^a $N = 45$ for females; $N = 90$ for hermaphrodites. Significance levels : *** = $P < 0.001$.

TABLE 2.15. Survival, panicle production, and bulbil production in 1996 by rosettes and panicle-producing plants marked in 1995. ^a

Plot	1995→1996		1995	1996	1996
	# surviving rosettes (%)	# surviving panicles (%)	Mean # of bulbils ^b	Mean # of bulbils ^c	Mean # bulbils ^b
1	19 (77.7)	10 (66.7)	11 (± 1.7)	38.7 (± 1.2)	41.3 (± 2.2)
2	6 (22.5)	12 (80.0)	13 (± 2.1)	43.9 (± 1.9)	39.6 (± 1.8)
3	16 (67.5)	10 (66.7)	14.5 (± 1.8)	49.3 (± 2.3)	52.1 (± 1.7)

^a $N = 25$ vegetative rosettes and $N = 15$ panicle producing plants for each plot.

^b bulbils produced by panicle producing plants from 1995 (stderr).

^c bulbils produced by rosette plants from 1995 (stderr).

The fate of all planted bulbils from emergence to death and the probability of surviving to each life stage from the initial planting is summarized in a diagrammatic life table (Figure 2.6). Seventy-nine of the 144 fall planted bulbils (Table 2.16) emerged in 1996. Forty-three of the emergents remained rosettes in 1996, while 36 emergents produced a panicle and bulbils. Of the latter, 16 also produced flowers though none produced a fruit. Thus, of the 79 emergent bulbils, 43 did not reproduce at all, while the remaining 36 reproduced only by bulbils. Thirty-two of the 1996 emergents (28 panicle producing, 4 rosettes) survived until 1997. There was no significant difference in survival between panicles with bulbils and flowers and panicles with bulbils only ($df=1$; $\chi^2 = 2.4$; $P > 0.10$). All individuals in 1997 produced panicles and bulbils. The number of bulbils produced in 1996 (8.7 ± 3.76) was significantly greater ($t = 1.94$, $df = 57$, $P = 0.05$) than the number produced in 1997 (7.2 ± 4.65). The number of bulbils produced in 1996 by panicles with flowers (7.75 ± 1.25) did not differ significantly ($t = 2.03$; $df = 34$; $P = 0.34$) from those panicle plants without flowers (8.35 ± 1.16). No significant differences ($t = 0.35$, $df = 30$, $P = 0.72$) in bulbil number in 1997 were found between panicle-producing plants from 1996 (7.2 ± 1.67) and rosette plants from 1996 (7.5 ± 4.58). Sixteen flowers were produced in 1996 and three floral buds were produced in 1997. These floral buds were killed, probably by the freezing temperatures that occurred shortly after their development. Thus, reproduction for all emerging plants was asexual in 1997. All individuals were dead by the end of the 1997 growing season. It is extremely important to note that 104 of 144 plants did not reproduce at all. Of those individuals that did reproduce, 28 produced panicles and bulbils for 2 years and 12 only reproduced in 1

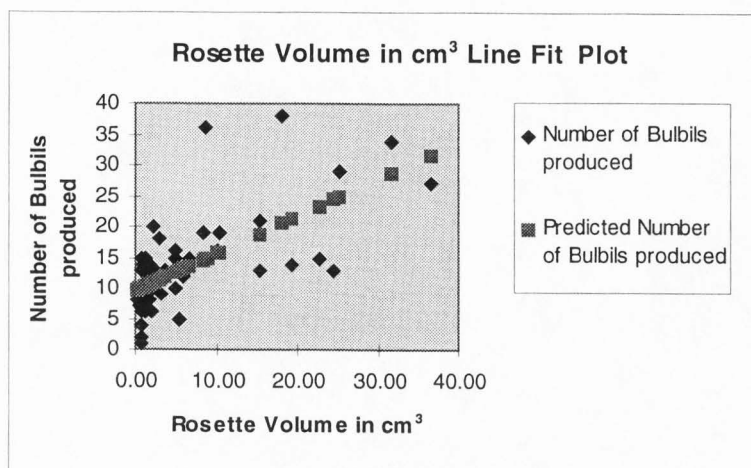


Fig. 2.3. Regression of bulbil number on rosette volume ($r^2=0.44$, $P < 0.01$).

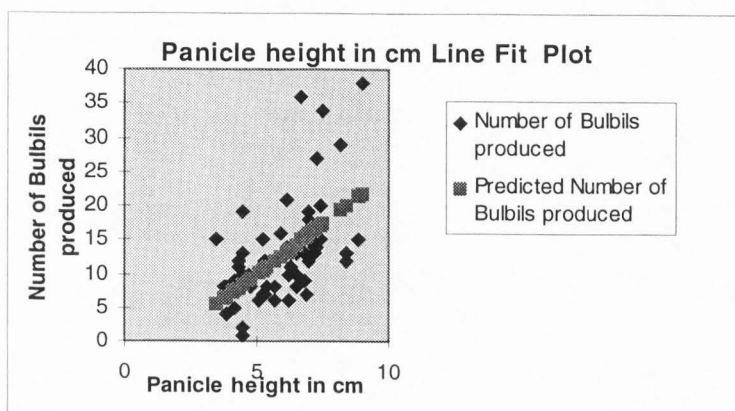


Fig. 2.4. Regression of bulbil number on panicle height ($r^2=0.317$, $P = 0.157$).

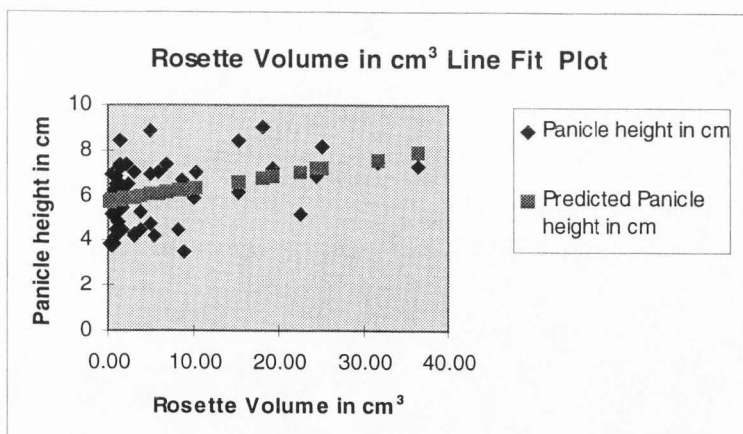


Fig. 2.5. Regression of panicle height on rosette volume ($r^2=0.12$, $P < 0.01$).

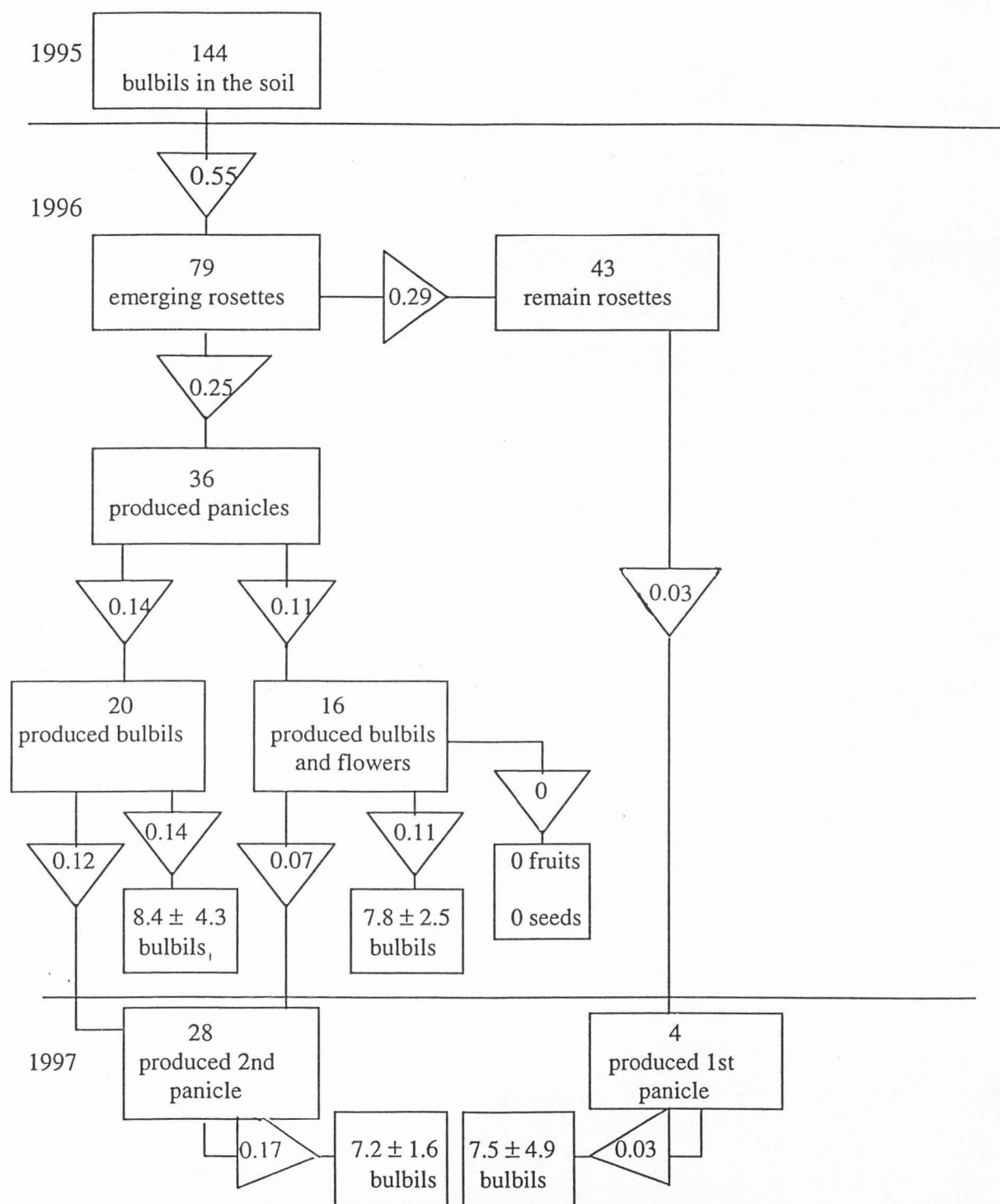


Fig 2.6. Diagrammatic life table for *Saxifraga bryophora* var. *tobiasiae*. By convention, rectangles represent stages of the life cycle, triangles represent transition probabilities to stage from initial, and rectangles represent bulbils and/or seed production.

TABLE 2.16. Survival and reproduction by fall bulbils planted in 1995. All plots were sampled in 1996 and 1997.^a

Plot	1996				1997			
	# EM	# PN	# BB (stderr)	# FW	# EM	# PN	# BB (stderr)	# FW
1	15	8	6.2 (± 2.6)	0	6	6	6.7 (± 1.3)	0
2	22	9	8.9 (± 2.4)	4	3	3	6 (± 1.2)	1
3	17	9	13.1 (± 1.9)	11	11	11	7.6 (± 2.1)	0
4	25	10	6.6 (± 3.8)	1	12	12	8.3 (± 1.8)	2

^a $N=36$ for each of four planted plots. # EM = number of emerging rosettes, # PN = number of rosettes producing panicles, # BB = average number of bulbils produced per panicle, # FW = number of flowers produced.

year. All were very short lived.

Sexual reproduction—In 1996, I found significant differences in fruit production among the breeding system treatments for both hermaphrodites and females. Fruit production for hermaphrodites was significantly lower for autogamy and agamospermy treatments (no pollen vector) than for xenogamy and geitonogamy treatments (vector required). Fruit production in females was also significantly lower for agamospermy (no pollen vector) than for xenogamy (vector required). Indeed, *Saxifraga bryophora* var. *tobiasiae* produced no fruits or seeds by either autogamy or agamospermy (Table 2.17). Fruits and seeds were, however, produced in the hand self-pollination treatment, demonstrating that hermaphrodites are self-compatible but a pollen vector is required to affect pollination.

Comparisons of other reproductive treatments suggest that fruit production is usually not pollen limited (Table 2.17). There were no significant differences between

TABLE 2.17. Comparison of *S. bryophora* var. *tobiasiae* fruit set among xenogamy (X), geitonogamy (G), autogamy (AU), agamospermy (AG), control (C), emasculated control (EC) for breeding system treatments for 1996. ^a

Treatment	Gender	Fruit	No fruit	Comparisons	Gender	DF	χ^2	P
Xenogamy (X)	Herm.	8	7	X*G*A*AG	Herm	3	23.80	< 0.001*
Geitonogamy (G)	Herm.	9	6	(X, G) vs. (A, AG)	Herm.	1	23.68	< 0.001*
Autogamy (AU)	Herm.	0	15	(X) vs. (G)	Herm	1	0.16	> 0.50
Agamospermy (AG)	Herm.	0	15	(C) vs. (EC)	Herm	1	3.58	> 0.05
Control (C)	Herm.	12	3	(C) vs. (X and G pooled)	Herm	1	2.67	> 0.05
Emas.Control (EC)	Herm.	7	8					
Xenogamy (X)	Female	8	7	X*AG*C	Female	2	13.78	> 0.005*
Agamospermy (AG)	Female	0	15	(X) vs. (AG)	Female	1	10.92	< 0.01*
Control (C)	Female	9	6	(C) vs. (X)	Female	1	0.277	> 0.25

^a N=15; Significance levels : * = $P < 0.05$.

open pollination and hand pollination treatments (X and G pooled since there was no significant difference for hermaphrodites) for either females or hermaphrodites.

Fruit production is but one measure of reproductive success. A second measure of fitness is the number of seed produced per fruit for those flowers that produce fruit. I found no significant difference in seed number for gender, treatment, or gender*treatment interaction (Table 2.18). Nor did seed size differ between genders or treatments. Seed number and seed size did not differ significantly between xenogamy, open control and self-fertilization for hermaphrodites (Table 2.19).

Insect collection and observation—Flowers of *Saxifraga bryophora* var. *tobiasiae* were seldom visited by insects (Table 2.20). In 20 hours of observation, only four insects were captured. Most of these are unlikely to be pollinators. The most frequent visitors during the day were the floral beetles, Malachididae that fed upon the base of pistils, eating completely through the pistil walls. One bee, *Andrena*, was observed. Syphids and empidids were also occasionally observed. Flies are the most likely pollinators but they were not observed visiting *S. bryophora* var. *tobiasiae* flowers successively. Although I determined in 1997 that flowers remain open at night, there were too few flowers to test for night pollination. Thus, moth pollination remains a possibility.

DISCUSSION

Gynodioecy—In 1996, the only year of three when flowering was abundant enough to estimate the gender ratio, all populations of *Saxifraga bryophora* var. *tobiasiae*

TABLE 2.18. Comparison of *Saxifraga bryophora* var. *tobiasiae* seed set among xenogamy (X), control (C), and geitonogamy (G) treatments from Fisher Creek Saddle populations in 1996. ^a

Treatment	N	Gender	Mean (stderr)	Source	F	P
X	8	Herm	22.50 (1.89)	Sex	0.27	0.61
	8	female	21.31 (1.74)	Treatment	0.81	0.37
				Sex*trt	0.86	0.36
C	12	Herm	18.87 (1.57)			
	9	female	21.67 (1.78)			
X	8	Herm	22.5 (1.89)	Treatment	1.44	0.25
C	12	Herm	18.87 (1.54)			
G	9	Herm	22.11 (1.78)			

^a Initial N for all treatments was 15; not all fruits produced seeds.

TABLE 2.19. Comparison of *Saxifraga bryophora* var. *tobiasiae* seed size among xenogamy (X), control (C), and geitonogamy (G) treatments from Fisher Creek Saddle populations in 1996. ^a

Trt	N	character	Gender	Mean (μ m)(stderr)	Source	F	P
X	8	seed	Herm	25.32 (1.83)	Sex	0.17	0.68
	8		Female	25.96 (1.89)	Treatment	1.49	0.24
					Sex*trt	2.75	0.11
C	12	seed	Herm	26.01 (1.50)			
	9		Female	22.51 (1.51)			
X	8	seed	Herm	25.32 (1.83)	Treatment	1.95	0.16
C	12		Herm	26.01 (1.50)			
G	9		Herm	29.82 (1.73)			

^a Initial N for all treatments was 15; not all fruits produced seeds.

TABLE 2.20. Insect visitors of *Saxifraga bryophora* var. *tobiasiae*.

Order	Family	Species	Number of observations
Hymenoptera	Andrenidae	<i>Andrena</i>	1
	Formicidae		1
	Vespidae		1
Diptera	Syrphidae	<i>Chrysotoxum fasciatum</i> Mulleo	3
	Anthomyidae		1
	Empididae	<i>Empis</i> sp.	2
		<i>Rhamphomyia</i> sp.	2
	Tipulidae		1
Coleoptera	Malachididae		12
Hemiptera	Aphididae	<i>Aphis</i> sp.	

examined were found to be gynodioecious. The selective forces that introduce and/or maintain females within gynodioecious populations and the mode of inheritance for these male-sterile individuals have been the subject of much discussion. Several models seek to explain the maintenance of females given different modes of inheritance (Lewis, 1941; Lloyd, 1974a, 1974b, 1974c, 1975; Charlesworth and Charlesworth, 1978; Charlesworth, 1981). Unless inbreeding depression (Kohn and Biardi, 1995; Schultz and Ganders, 1996) and the incidence of selfing (Ross and Shaw, 1971; Ross and Weir, 1974) are high, nuclear control of male-sterility requires female ovule production to be at least twice that of hermaphrodites for females to be maintained in the population. The resulting equilibrium frequency of females is expected to be less than 0.50 (Lewis, 1941; Lloyd, 1974b, 1975; Charlesworth and Charlesworth, 1978).

Alternatively, if male-sterility is cytoplasmic or nuclear-cytoplasmic, then females

need only a slight advantage in fitness (e.g., ovule production, ovule survival, ramet survival) to be maintained within the population (Lewis, 1941; Lloyd, 1976; Stevens and Van Damme, 1988). The mode of inheritance of male-sterility in *S. bryophora* var. *tobiasiae* is not known, but it seems probable that, like several other species of *Saxifraga*, it is cytoplasmic or nuclear-cytoplasmic (Stevens and Richards, 1985; Stevens, 1988). Thus, male-sterile plants need exhibit only a small advantage over hermaphrodites to be maintained in the population.

One way in which females may gain the requisite advantage is by redistribution of reproductive resources (Darwin, 1877; Lloyd, 1975, 1976; Charlesworth and Charlesworth, 1978; Agren and Willson, 1991). Resources normally used to produce pollen may be diverted instead to ovule, seed, and/or bulbil production (Darwin, 1877; Lloyd, 1974b; Stevens and Richards, 1985; Eckhart, 1992). In *Saxifraga bryophora* var. *tobiasiae*, however, the amount of resources available for reallocation by females is negligible given that only one flower is produced and it even has nonfunctional anthers and filaments. Functional female flowers have even fewer reallocatable resources because their anthers contain pollen, though it is inviable. Therefore, it is unlikely that reallocation of resources plays much of a role in maintaining gynodioecy.

Females may also be maintained by an outbreeding advantage if self-fertilization by hermaphrodites results in reduced progeny fitness via inbreeding depression (Lewis, 1941; Lloyd, 1976; Charlesworth and Charlesworth, 1978; Webb, 1981; Puterbaugh et al., 1997). However, inbreeding in *Saxifraga bryophora* var. *tobiasiae* is unlikely because extreme protandry in the single flower per year produced by most plants prevents

self-fertilization. Selfing can only occur in the $< 5\%$ of plants that produce more than one panicle. Even when forced self-fertilizations were performed artificially, no evidence of inbreeding depression was observed for seed production. Seed number and seed size did not differ for self-fertilized (geitonogamous) individuals in comparison with xenogamous and open control hermaphrodites (Table 2.18). Seeds were slightly larger in selfed crosses, thus providing further evidence for the lack of inbreeding depression (Table 2.17). Unless seeds from self-crossed treatments suffer decreased survival due to inbreeding (not examined) or retarded germination, females do not appear to benefit from any outbreeding advantage within these populations.

Comparisons of actual sexual fitness components between females and hermaphrodites did not provide compelling evidence that females were superior to hermaphrodites in fitness. Although the sample sizes were small and limited to one year, seed number and seed size did not differ significantly between females and hermaphrodites for any breeding system treatment (Tables 2.17, 2.18). With no significant difference in seed set or seed size, and no male function to contribute genes to the population *Saxifraga bryophora* var. *tobiasiae* females appear to be at a selective disadvantage based on sexual reproduction alone.

Several recent studies of *Saxifraga* species (Stevens and Richards, 1985; Stevens and Van Damme, 1988; Stevens, 1988) have examined the possibility of superior female fitness due to increased vegetative production over that of hermaphrodites (Lloyd, 1973; Webb, 1981). Stevens (1988) provided evidence for asexual female advantage in *Saxifraga granulata* L., in which females produced fewer but larger bulbils than did

hermaphrodites. Female bulbils were more successful in establishment and had increased survivorship over bulbils produced by hermaphrodites. Females of *S. bryophora* var. *tobiasiae* produced significantly more bulbils than did hermaphrodites (Table 2.3). A trend, though not significant (Table 2.11), due to a gender*aspect interaction was observed for FCSE, in which eastern females produced more bulbils than did hermaphrodites and western females. The weight and volume of bulbils did not differ significantly between genders (Table 2.7, 2.8). Thus, if female *S. bryophora* var. *tobiasiae* plants maintain a reproductive advantage over hermaphrodites, it is due to superior asexual reproduction of bulbils.

The frequency of females and hermaphrodites within gynodioecious populations is directly affected by the relative fecundity of each gender (hermaphrodite/female), the differential survival of the sexes (zygote formation through reproductive maturity of hermaphrodites divided by the survival of females), and the precise levels of pollination (Lewis, 1941; Lloyd, 1974a, 1975). Under cytoplasmic inheritance, because all offspring are the same sex as their parent, the proportions of females and hermaphrodites are stable only if fecundity, mortality, and the probability of ovule fertilization are equal for both genders (Lloyd, 1974a, 1974c, 1975). In *Saxifraga bryophora* var. *tobiasiae* the fecundity of females and hermaphrodites is equal (Table 2.17), as is the differential mortality (Table 2.15). However, because *S. bryophora* var. *tobiasiae* plants are self-incompatible, the probability of hermaphrodites fertilizing female ovules is greater than the proportion of females within the population, assuming flowers of the two genders are equally attractive. Thus, the proportions of females and hermaphrodites are not stable

under Lloyd's hypothesis for cytoplasmic inheritance (Lloyd, 1974a, 1974b, 1975).

Under such conditions, it is predicted (Lloyd, 1974a) that the frequency of females will gradually increase, thus leading to the eventual extinction of the population or increased dependence on asexual reproduction (Lloyd, 1974a, 1975, 1976). It is therefore possible that in *S. bryophora* var. *tobiasiae* populations, hermaphrodites and sexual reproduction are at a risk of becoming extinct.

More recent models, however, have predicted that cytoplasmic inheritance in self-incompatible species is not possible (Charlesworth and Gander, 1979; Couvet et al., 1986) and a growing body of evidence supports the maintenance of gynodioecy under nuclear-cytoplasmic inheritance (Horovitz and Beiles, 1980; Belhassen et al., 1991; Koelewijn and Van Damme, 1995; Dinnetz and Jerling, 1998; Gigord et al., 1998). Females, under nuclear-cytoplasmic inheritance, are capable of producing hermaphrodite offspring due to nuclear "restorer" genes which counteract male-sterile cytoplasm. Pollen and seeds can disperse nuclear restorer genes, while cytoplasmic genes can only be spread by seeds and/or bulbils due to maternal inheritance. Because of this mechanism, hermaphrodites can be restored and maintained within populations (Charlesworth, 1981; Couvet et al., 1986; Koelewijn and Van Damme, 1995).

Nuclear-cytoplasmic inheritance has been shown for many species, i.e., *Nemophila menziesii* (Ganders, 1978), *Hirschfeldia incana* (Horovitz and Beiles, 1980), *Origanum vulgare* L. (Kheyr-Pour, 1980), *Vicia faba* L. (Thiellement, 1982), *Thymus vulgaris* (Belhassen et al., 1991), and *Plantago maritima* (Dinnetz and Jerling, 1988). Stevens and Richards (1985) ruled out simple one or two locus control of male-sterility in

Saxifraga granulata and suggest that nuclear-cytoplasmic inheritance is indeed responsible for the presence of male-sterile plants. It is therefore likely that in *S. bryophora* var. *tobiasiae*, male-sterility is under nuclear-cytoplasmic control. If confirmed, the risk of the extinction of hermaphrodites and sexual reproduction would be eliminated.

Additional information on the type of inheritance of male-sterility, demography, pollinator activity, and gender dynamics is needed to resolve the question of equilibrium maintenance of gynodioecy within these populations. In addition, one needs to incorporate the production of bulbils by gender and the biases toward female production when attempting to understand maintenance of gynodioecy.

Higher rates of male-fertility restoration (higher proportions of hermaphrodites) are predicted in more stable populations under nuclear-cytoplasmic inheritance, while higher proportions of females are predicted in new or less stable habitats (Couvét et al., 1986). Cytoplasms are thought to differ between populations, and hermaphrodites from one population may not have the restorer genes for the cytoplasm of another population. Crosses between individuals from different populations most likely occur when populations are founded or disturbed, resulting in high frequencies of females (Couvét et al., 1986; Belhassen et al., 1991; Dinnetz and Jerling, 1998). When these new cytoplasms are introduced as a result of migration or mutation, selection pressures for specific nuclear restorers increase. Local adaptation is then predicted for specific nuclear genes capable of restoring male-fertility for each type of cytoplasm (Couvét et al., 1986). High frequencies of females have been observed in some young and/or disturbed populations

(Baker and Dalby, 1981; Belhassen et al., 1991; Jerling, 1988; Dinnetz and Jerling, 1998) but other studies, e.g., *Thymus vulgaris* (Gigord et al., 1998), found no support for local adaptation hypothesis proposed by Couvet et al. (1986).

My data for *Saxifraga bryophora* var. *tobiasiae* do not seem to support the hypothesis of Couvet et al. (1986). I found the highest frequencies of females (44 – 60%) in stable, highly vegetated regions (2 m X 2 m plots) while the more unstable, sparsely populated microdrainages (permanent plots) had much lower frequencies of females (23 – 27%). Although it is conceivable that the dense, stable regions are newer populations and the high frequencies of females observed there are a result of this founder effect (Couvet et al., 1986), the lower frequencies of females in more disturbed regions does not support this hypothesis. Disturbance (Chapter 3) is more likely to create new patches for establishment, thus it seems unlikely that the more stable patches (2 m X 2 m plots) are new.

Fewer flowers of either gender, however, were found in the microdrainages, possibly due to increased disturbance. It has been shown that in stressful microhabitats, reproductive allocation can become more costly for one gender than the other and that gender may suffer a higher mortality, thus creating a spatial segregation of genders (Lloyd and Webb, 1977; Bierzychudek and Eckhart, 1988). In this case the increased disturbance may cause the reproductive allocation cost for females to be higher than that of hermaphrodites, and females may be less frequent as a result. Further examination of the microhabitats, plant demography, and the influence of nuclear-cytoplasmic inheritance is needed to determine if females could be maintained at such high

frequencies within these populations.

It is quite apparent that this snap-shot of sex expression in a single year does not provide the complete story of gynodioecy within *S. bryophora* var. *tobiasiae* populations. Confirmation of nuclear-cytoplasmic inheritance of male-sterility for *S. bryophora* var. *tobiasiae* is needed to replace speculation on the maintenance of hermaphrodites and sexual reproduction with scientific evidence. It appears female advantage is afforded by increased vegetative reproduction (Table 2.3) and this advantage is likely responsible for the long-term maintenance of females within these populations. Also, females could be benefitted by other factors; for example, females might produce more nectar at night and attract more moth pollinators. Further research of seed and bulbil fate by gender, demographic data, and survival information is needed to estimate the fate of female maintenance within these populations.

Asexual and sexual reproduction—Evolutionary pressures appear to have directed the almost total replacement of the flower primordia on *Saxifraga bryophora* var. *tobiasiae* with asexual bulbils; only a small fraction of resources is still being allocated to flower production. Sexual reproduction, though less assured and intermittent, is apparently maintained because some seedlings are successfully recruited to natural and novel habitats.

The considerable amount of resources devoted to asexual reproduction by *S. bryophora* var. *tobiasiae* is likely due to several factors: environment (Stevens and Van Damme, 1988; Chambers, 1995), flowers unappealing to insect visitors (Abrahamson, 1980), phylogeny (Stevens, 1988; Molau, 1992; Holderdegger, 1996), and rarity. The

unpredictable environmental conditions associated with sub-alpine habitats can include wide variation in temperature, moisture availability, and growing season length. All of these factors may direct the evolutionary responses of life history characters (Bliss, 1962, 1971; Billings and Mooney, 1968; Chambers, 1995) and may affect the balance between modes of reproduction (Abrahamson, 1980; Nault and Gagnon, 1993; Chambers, 1995).

Small flowered sub-alpine plants often rely upon asexual reproduction (Stevens, 1988; Chambers, 1995; Holderdegger, 1996). Presumably asexual reproduction ensures that offspring will be produced despite changing resource levels and extreme fluctuations in environmental conditions (Billings and Mooney, 1968; Williams, 1975; Abrahamson, 1980; Chambers, 1995). Significant flowering of *Saxifraga bryophora* var. *tobiasiae* occurred only in 1996, the only year of three in which temperature was higher than normal and precipitation was lower than normal. The average temperatures for the region between June and September in 1995 (12.7 °C) and 1997 (13.8 °C) were lower than average (14.2 °C, 1930 – 1998; WRCC, 1999), while in 1996 temperatures were almost a full degree higher (15.1°C). The average precipitation levels for June through September in 1995 (5.96 cm/month) and in 1997 (5.56 cm/month) were much higher than average (3.28 cm/month); in 1996 precipitation was much lower (1.24 cm/month; WRCC, 1999). These striking temperature and precipitation differences may be responsible for curtailing sexual reproductive success throughout the populations for 2 of the 3 years in which *S. bryophora* var. *tobiasiae* was investigated. Disturbance due to meltwater runoff (Chapter 3) may be influencing this flowering pattern as well. In the drier years, disturbance may be less, thus allowing for increased flowering. However, despite the fluctuations in

environmental conditions, asexual reproduction was still possible and ensured the production of offspring in all years examined.

Another factor that may be contributing to the predominance of asexual reproduction within *Saxifraga bryophora* var. *tobiasiae* is that these small flowered individuals appear to be less appealing to insect visitors than larger-flowered co-blooming species (Abrahamson, 1980). Flowers of *S. bryophora* var. *tobiasiae* had few insect visitors and fewer pollinators (Table 2.19). Extremes in weather, especially cold temperatures and increased precipitation, curtail the activity of pollinators (Harper, 1977; Waser and Real, 1979). This apparent lack of insect visitors, along with the extremes in temperature and precipitation in this region, may serve as additional pressures for vegetative reproduction (Williams, 1975; Abrahamson, 1980). Vegetative reproduction frees the plant from investing excess energy in pollinator attractants and rewards (Williams, 1975; Harper, 1977; Abrahamson, 1980).

The balance of vegetative versus sexual reproduction in *Saxifraga bryophora* var. *tobiasiae* may also be influenced by its rarity. The increased expenditure in energy and/or resources to produce bulbils may be rewarded by the sure production of offspring with genotypes well adapted to the parental habitat (Williams, 1975; Abrahamson, 1980). Maintenance of local populations due to increased vegetative reproduction has been documented for several species, e.g., *Oxyria diglyna* (L.) Hill (Mooney and Billings, 1961), *Uvalaria perfoliata* L. (Whigham, 1974), and *Allium tricoccum* Ait (Nault and Gagnon, 1993). In *S. bryophora* var. *tobiasiae* populations, plants that produce many bulbils and few flowers on average probably give rise to many more ramets than those

plants producing few bulbils and more flowers. Vegetative reproduction may afford progeny several additional advantages over seedlings for establishing within the parental population including: (1) increased nutrient composition of bulbils, although costly to the parent because of prolonged attachment (Harmer and Lee, 1978; Stevens and Van Damme, 1988) may increase the chances of establishment (developing bulbils or plantlets may contribute to their own costs through photosynthesis), (2) increased survival due to larger size at time of detachment, e.g., *Festuca vivipara*, *Dentaria bulberifa* (Williams, 1975; Harmer and Lee, 1978), and (3) rapid development to the reproductive portion of the life-cycle, e.g., *Uvularia perfoliata* (Whigham, 1974; Harmer and Lee, 1978).

Given the advantages of asexual reproduction, the question "What use is sex?" raised by Bonner (1958), has been addressed by many authors (Maynard Smith, 1968, 1971, 1976; Williams, 1975; Harper, 1977; Abrahamson, 1980). Sex is thought to be an adaptation to the probability of progeny having to face changed or uncertain conditions relative to the parental environment (Williams, 1975). Sexual offspring have the advantage of greater genetic diversity through recombination (Crow and Kimura, 1965; Maynard Smith, 1971; Williams, 1975; Abrahamson, 1980), may possess the means for wide dispersal to new and potentially favorable habitats (Harper, 1977; Chambers and MacMahon, 1994), and have the ability to remain dormant until favorable germination conditions are met (Harper, 1977; Bradbeer, 1988; Schupp, 1995). Increased genetic diversity may also benefit these offspring by the phenomenon of heterosis or hybrid vigor (Hartl and Clark, 1989). Sexual reproduction, however, may be declining in *S. bryophora* var. *tobiasiae*. This hypothesis is supported by the short life span of these individuals, the

success of ramets which produce only bulbils, and the increased production of bulbils in years in which flowering potential is high. Detailed demographic studies over several years are necessary to further examine this hypothesis.

The strategy of asexual reproduction via bulbils and less frequent sexual reproduction with protandrous flowers and gynodioecious populations observed in *Saxifraga bryophora* var. *tobiasiae* is prevalent in several congeners found in similarly harsh environments (Stevens and Richards, 1985; Stevens, 1988; Molau 1992). In *Saxifraga granulata*, females are maintained through the production of larger and heavier bulbils and gynodioecy is maintained in all populations (Stevens and Richards, 1985; Stevens, 1988). It is likely that females are maintained in *S. bryophora* var. *tobiasiae* by increased female bulbil production as well.

Many studies have shown a trade-off exists between asexual and sexual modes of reproduction (Whigham, 1974; Sarukhan, 1976; Law et al., 1983; Arizaga and Ezcura, 1995). The trade-off hypothesis proposed in these studies is perhaps oversimplified and only applies when resources are significantly limited. Sexual and asexual reproduction are dependent upon the same limited resources that must be allocated in a way to maximize fitness (Abrahamson, 1980). When resources become extremely limited, these modes of reproduction are thought to become competitive, thus creating a trade-off in which an increase in the output of one mode results in the decreased output of the other (Salisbury, 1942). However, increases in moisture, temperature, or resource availability would most likely increase the reproductive output of both modes of reproduction.

My data support a hypothesis that an increase in resource availability or more

favorable environmental conditions results in increased output from both reproductive modes. An increase in floral production does not automatically ensure a decrease of bulbil production. Asexual reproduction was observed in all three years, with a significant increase in bulbil production in 1996 in comparison with 1995 (Table 2.12). Flowering was also significantly higher in 1996. It is therefore curious to note that bulbil production increased significantly prior to the increase in floral production. If a trade-off of reproductive efforts was occurring, as shown in many other studies (Sarukhan, 1976; Whigham, 1974; Law et al., 1983, Arizaga and Ezcura, 1995), a decrease in bulbil production would be predicted to co-occur with an increase in flower production. In this system, bulbil production increased significantly prior to, and was maintained during, an increase in floral production. A reproductive trade-off is not supported.

Life history—Although originally described as annual, my results prove that *Saxifraga bryophora* var. *tobiasiae* is a short-lived perennial that is monocarpic, but capable of vegetative reproduction in more than one year. No plants flowered in more than one year. All panicle-producing plants produced significantly more bulbils in 1996 than in 1995. The increases in bulbil production, as well as increased floral production, seemed directly influenced by more favorable environmental conditions.

The majority of congeners are also perennial. Indeed, annual sub-alpine saxifrages and sub-alpine annuals in general are extremely rare (Chambers, 1995), probably because of the extreme unpredictability of environmental conditions within these high-elevation habitats (Nilsson, 1995). Perennial species are at a selective advantage due to their ability to delay or repeat reproduction until environmental

conditions are conducive to the production and establishment of offspring (Harper, 1977; Chambers, 1995).

Bulbil number is also influenced by the volume of the rosette (Figure 2.3) and possibly by aspect (Table 2.11). Rosette volumes were larger in the eastern FCSE populations and female plants subsequently had more bulbils ($p = 0.055$; Table 2.11). The FCSE populations have greater vegetation cover and a denser cover than the FCSW populations. This increase in shade may prevent stress from direct afternoon insolation and may allow for increased plant growth. More organic material (Chapter 3) appears to accumulate in the FCSE populations along with increased moisture availability due to shading by the overstory. Soils in the FCSE may have more nutrients available for uptake as a result. These factors are most likely responsible for the increased plant size and vegetative success at FCSE.

Although *Saxifraga bryophora* var. *tobiasiae* is not autogamous, it is self-compatible. Self-pollen stored at 7°C for several days remained viable and was successful in producing fruits. There is probably little selective pressure for adaptations leading to self-incompatibility. First, due to extreme protandry, it is not currently possible to self except in the rare occasions when more than one flower is produced. Second, fruit set, seed set, and seed size did not differ significantly between geitonogamy and xenogamy treatments. Thus, inbreeding depression does not appear to be limiting seed production or selecting for self-incompatibility. The deleterious recessive alleles responsible for inbreeding depression are quickly purged in many sexual or partially sexual organisms (Hartl and Clark, 1989).

It is not surprising that few pollinators visit the flowers of *Saxifraga bryophora* var. *tobiasiae* based upon its diminutive floral display and low nectar/pollen reward. All attempts to extract nectar with a small syringe were unsuccessful. It is likely that abundant co-blooming species such as *Aster alpinus* L., *Aster conspicuous* Lindl., *Arnica fulgens* Pursh, *Polygonum bistortoides* Pursh, and *Ligusticum canbyi* J.M. Coult. & Rose, which have larger floral displays and greater pollen/nectar rewards, are more attractive to pollinators and are the subject of more frequent and consistent visitation. As a result, it appears that the small *S. bryophora* var. *tobiasiae* flowers are outcompeted for floral visitors. Facilitation (Waser and Real, 1979) does not appear to be occurring for these diminutive flowers because the co-occurring flowering species are much taller (generally 2 times as tall), their flowers are much larger (3 – 4 times larger) and more attractive to the visitors that frequent these habitats. Although visitors to *S. bryophora* var. *tobiasiae* were rare, the observed syrphids and emphidids (Table 2.19) are common visitors of congeners such as *S. granulata* L. (Stevens, 1988), *S. hirculus* L (Oleson and Warncke, 1989a, 1989b), *S. mutata* L (Holderdegger, 1996) and *S. osloensis* Knaben (Nilsson, 1995) and are probable pollinators.

Salisbury (1942) hypothesized that pollination, or the lack thereof, may be among the most influential factors affecting the balance between sexual and asexual reproduction. Harsh environmental conditions may limit or alter the composition of successful pollinators that occur within these regions. Flies may be more prevalent than other pollinators such as bumblebees, when flowers are few and the abundance of nectar and pollen is low (Heinrich, 1979). Perhaps, the historical lack of pollinator visitors for

this taxon provided selective pressures that forced the shift in the balance of reproductive modes from a mostly sexual taxon to a more efficient and insured asexual system.

Conservation implications—The mode of inheritance of male-sterility within *Saxifraga bryophora* var. *tobiasiae* populations must be determined to understand not only the fate of gynodioecy, but more importantly the fate of sexual reproduction for this rare taxon. Given the higher asexual reproductive success of females, and the greater likelihood of female ovules being fertilized than hermaphrodite ovules, hermaphrodites are at risk within these populations if inheritance is strictly cytoplasmic. If hermaphrodites vanish from the populations, then so will sexual reproduction. However, if male-sterility in *S. bryophora* var. *tobiasiae* is under nuclear-cytoplasmic control, the risk to hermaphrodites and sexual reproduction is eliminated because females may be capable of producing hermaphrodite offspring through the influence of nuclear “restorer” genes. Detailed information on this genetic system of reproduction is vital in understanding the population dynamics and fate of *S. bryophora* var. *tobiasiae*.

Saxifraga bryophora var. *tobiasiae* populations are found in extremely small, unique granitic regions (Chapter 3) characterized by small-scale disturbance. Any management strategy must include a habitat-based preservation plan to allow for the persistence of these dynamic habitats. Vegetatively produced offspring require these melt-regions for their transport and establishment. Microdrainages and runoff regions must be protected from large-scale direct disturbances such as sheep and cattle grazing or logging. Indirect disturbances from historic grazing by sheep and cattle are responsible for the introduction of exotic species such as *Polygonum phytolactifolium*. These introduced

species readily establish in the microdrainages and destroy potential habitat by desiccating the moist environments in which *S. bryophora* var. *tobiasiae* thrives (personal observation).

Bulbil transplantation from parent plants in surrounding habitat has successfully been used to expand *Saxifraga bryophora* var. *tobiasiae* populations. The majority of emerging bulbils reproduced vegetatively within the first year (Figure 2.6). Flowers were initiated but no fruits or seeds were successfully produced (Figure 2.6). Additionally, many of these plants were capable of reproduction for a second year. Although these individuals are short lived, they are capable of establishing and reproducing in new habitats. Because I found that eastern aspects supported larger plants with more bulbils, I recommend that restoration initiation and augmentation efforts be conducted on slopes with eastern aspects to improve their chances for establishment and increase their likelihood for survival and reproduction.

Many areas in the West Salmon River Mountains appear to be ideal habitat for *Saxifraga bryophora* var. *tobiasiae*. However, the apparent absence of long-distance dispersal mechanisms (except water) has limited its colonization of these sites. One previously known population of *S. bryophora* var. *tobiasiae* was destroyed by fire in 1994 (Moseley, 1996). Restoration and expansion efforts could be benefited by transplanting bulbils into these currently uninhabited regions.

Although a major consistent pollinator or pollinators were not identified in this study, pollinators are necessary for the production of fruit and seed set. Further research is needed to explore the possibility of moth pollination and the requirements needed to

sustain such a pollinator. Further examination of other possible pollinators could benefit the understanding of the biology of *Saxifraga bryophora* var. *tobiasiae*.

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CHAPTER 3

THE ECOLOGY OF A RARE, GRANITIC OUTCROP ENDEMIC SAXIFRAGE,
SAXIFRAGA BRYOPHORA VAR. *TOBIASIAE* GRIMES & PACKARD

ABSTRACT

Saxifraga bryophora var. *tobiasiae* is a rare, gynodioecious saxifrage with only five known populations, all in the West Salmon River Mountains of central Idaho. I examined the vegetative composition, edaphic characteristics, and habitat dimensions of the unique granitic outcrops on which *S. bryophora* var. *tobiasiae* is endemic. Using percent coverage vegetation sampling, 38 ecological components were found to occur with *S. bryophora* var. *tobiasiae*. Classification tree analysis was used to determine which ecological factors were useful in predicting the presence of *S. bryophora* var. *tobiasiae*. In 1995, bare soil (> 2.5%) and *Lewisia triphylla* (> 1.5%) were significant factors in predicting *S. bryophora* var. *tobiasiae* presence. In 1996, *Lewisia triphylla* (< 3.5%), bare soil (> 2.5%), and (< 1 %) *Erythronium grandiflorum* were predictors of *S. bryophora* var. *tobiasiae* presence, as were *Lewisia triphylla* (> 3.5%), *Vaccinium scoparium* (< 2.5%), and the presence of *Polytrichum juniperinum*. Twenty-eight soil pits in actual and potential *S. bryophora* var. *tobiasiae* habitat were described. Soils were classified as Lithic Cryoborolls, Lithic Cryochrepts, and Lithic Cryorthents. The physical characteristics of these soils were very similar among habitat and non-habitat sites. The shallow soils and natural disturbance from runoff greatly influence the endemic distribution and rarity of this taxon.

INTRODUCTION

To adequately design an effective conservation strategy for any rare taxon, the ecological factors contributing to its rarity, endemism, and population biology must be examined (Kruckeberg and Rabinowitz, 1985; Soule, 1986; Schmeske et al., 1991).

Rarity and endemism, common themes in conservation biology, occur at many scales and are the result of multiple factors such as environmental conditions, evolutionary history, and geomorphological processes (Cain, 1940; Kruckeberg, 1954; Stebbins and Major, 1965; Stebbins, 1980; Kruckeberg and Rabinowitz, 1985).

The causes of rarity have been the subject of wide speculation. Early theoretical work speculated on genetic causes of rarity (Stebbins, 1942; Wright, 1956; Huxley, 1963) and competitive incompetency (Griggs, 1940). Later, Stebbins (1980) provided one of the first definitive theories of rarity. In his gene pool-niche interaction theory, rarity is explained by the interaction of a unique, localized environment, a specific genetic structure, and a specific evolutionary history. Most recently and perhaps most comprehensively, the classification of rarity in vascular plants proposed by Rabinowitz et al. (1986) defined seven forms of rarity based upon habitat specificity (narrow or wide), abundance (large-dominant or small-nondominant), and geographic distribution (large or small). This categorization ties a species to its habitat but does not clarify whether these classes are consequences or causes of rarity.

The distributions of rare plant taxa can range from a few individuals with a wide habitat specificity scattered over a large geographic region to many individuals with narrow habitat specificity restricted to small geographic isolates (Rabinowitz, 1981;

Rabinowitz et al., 1986; Fiedler and Ahouse, 1992). Species with narrow habitat requirements, isolated distributions, and low population abundances are often considered the most critically imperiled and are thus the focus of most conservation efforts (Soule, 1986; Schmeske et al., 1991; Fiedler and Ahouse, 1992). Narrowly distributed taxa are often endemic to ecological or environmental factors provided by the habitat in which they persist. Endemism does not, however, imply rarity or small range (Gentry, 1986; Kruckeberg and Rabinowitz, 1985); many species are endemic to entire continents or regions while others are endemic to only a few square kilometers. The scale of observation must be defined when attempting to understand both endemism and rarity.

Narrowly endemic taxa are defined as those occurring in a few small populations that are confined to a single domain or few geographic locations (Drury, 1980; Kruckeberg and Rabinowitz, 1985). Two fundamental forms of endemism have been defined: *neoendemism* – species of recent origin that are likely capable of expansion (Cain, 1940; Kruckeberg, 1954; Stebbins and Major, 1965), and *paleoendemism* – species of once widespread distribution that have become restricted to relictual populations due to increased specialization and habitat constriction (Cain, 1940; Stebbins and Major, 1965; Gentry, 1986).

As with rarity, there are many causes of endemism that can shape the distributions of plant taxa (Cain, 1940; Stebbins, 1942; Stebbins and Major, 1965). These causes may include population genetics (Stebbins, 1980; Wyatt, 1984), life history characteristics (Wyatt, 1983), edaphic characteristics (Kruckeberg, 1954; Kruckeberg and Rabinowitz, 1985; Shaw, 1987) geomorphological processes (Wild and Bradshaw, 1977; Walck et al.,

1996), and ecological associations (Drury, 1980; Stebbins, 1980; Gentry, 1986). Of these, the edaphic factors and their effect on endemism are most commonly examined.

Edaphic endemism can involve both the physical and chemical properties of soil (Kruckeberg and Rabinowitz, 1985). Endemic taxa can be narrowly restricted due to physical characteristics of soils such as depth to bedrock (Burbanck and Platt, 1964; Baskin and Baskin, 1988; Moore et al., 1998), moisture holding capacity (Sharitz and McCormick, 1973; Walck et al., 1996), texture (Kruckeberg and Rabinowitz, 1985), and topography. Chemical properties of soils are also widely known to restrict plant distributions of endemic species as well (Kruckeberg, 1954; Stebbins and Major, 1965; Wild and Bradshaw, 1977). Many endemics are persistent in inhospitable soils, e.g., serpentine soils or heavy metal soils, and have evolved metabolic mechanisms that allow for the avoidance or tolerance of such chemicals (Kruckeberg, 1954; Baker et al., 1985; Boyd et al., 1994).

Kruckeberg and Rabinowitz (1985) theorized that the ultimate cause of local rarity and narrow endemism is most likely explained by the discontinuities created by geological processes. Geological processes can create microhabitats that support only a few distinct taxa. Isolated batholiths, emergent volcanoes, unique mountain ranges, and rock outcrop communities host many endemic taxa throughout the world (Stebbins and Major, 1965; Wild and Bradshaw, 1977; Kruckeberg and Rabinowitz, 1985; Gentry, 1986; Moore et al., 1998). Topographic, pedological, and lithological discontinuities can provide unique habitats that allow for the ecological separation of species (Kruckeberg, 1954; Denton, 1979; Baskin and Baskin, 1988).

Granite outcrop ecosystems have long been recognized as geologically unique habitats that host many endemic, although not rare, plant species in the southeastern United States (Harper, 1939; McVaugh, 1943; McCormick and Platt, 1962; Burbanck and Platt, 1964; Sharitz and McCormick, 1973; Burbanck and Phillips, 1983). Soil-filled depressions within exposed granitic outcrops form unique habitats for vegetation establishment. These depression communities are similar across the landscape but are geographically separated, thus forming a series of "island communities" (Burbanck and Platt, 1964) or habitat islands. Endemic species within these islands have adapted to the severe environmental conditions provided by these habitats such as extreme fluctuations in moisture and temperature, low soil pH, high light intensity, and shallow sandy soils (McCormick and Platt, 1962; Burbanck and Platt, 1964; Murdy, 1968; Sharitz and McCormick, 1973; Baskin and Baskin, 1988).

Burbanck and Platt (1964) completed an extensive study of succession within granite outcrop island communities and correlated the composition of seral stages with edaphic factors. Island communities are composed of concentric zones of seral stages. Pioneer species are restricted to the periphery where the soils are shallowest and biotic competition prevents their expansion (Burbanck and Platt, 1964; Sharitz and McCormick, 1973). As the soil deepens from the periphery, more competitive, deeper-rooted species invade the center of the island. The increased capacity for water retention and increased soil depth at the center of the habitat island are considered the two major edaphic factors responsible for this successional pattern. Other descriptive studies of succession in outcrop substrates correlate the formation of seral states with soil accumulation and water retention (Oosting and Anderson, 1939; Quarterman, 1950; Wyatt and Fowler, 1977).

Saxifraga bryophora var. *tobiasiae* Grimes and Packard is a rare sub-alpine taxa that is endemic to the West Salmon River Mountains of central Idaho. It is currently designated as a Federal Species of Concern (USDI Fish and Wildlife Service, 1996) and an Idaho State Sensitive Species (Idaho Conservation Data Center, 1998). The reproductive biology, life history, and demography of this taxon are described in Chapter 2. Little is known, however, about the factors that contribute to its endemic distribution and the ecological factors associated with its habitat. *Saxifraga bryophora* var. *tobiasiae* populations occur in granitic outcrop communities similar to those found in the southeastern U.S. (McVaugh, 1943; McCormick and Platt, 1962; Burbank and Platt, 1964; Sharitz and McCormick, 1973; Wiser, 1994, 1998). A study of the ecological components, namely, vegetation composition and soil morphology, associated with *S. bryophora* var. *tobiasiae* habitats is needed. This information, when compared to other granitic outcrop ecosystems, may help explain the population dynamics of this taxon and provide habitat-based information for its conservation.

This study of the ecological and edaphic characteristics associated with *Saxifraga bryophora* var. *tobiasiae* is useful in elucidating factors that contribute to the endemism of rock outcrop species. In this chapter, I document ecological components of granitic outcrop communities associated with *Saxifraga bryophora* var. *tobiasiae* and the soil properties of actual and potential habitat islands for this taxon. I propose that shallow soils and natural disturbance created by runoff greatly influence the distribution and rarity of *S. bryophora* var. *tobiasiae*.

MATERIALS AND METHODS

The taxon—*Saxifraga bryophora* var. *tobiasiae* is a diminutive taxon, 4 to 20 cm tall, characterized by a small basal rosette of leaves. Both female and hermaphrodite plants usually produce one panicle (< 5% produce more than 1) that is terminated by a single terminal flower with all remaining flower primordia being replaced by asexual bulbils. The terminal flower, 0.6 to 1.2 mm in diameter, is composed of separate, sagittate, white petals each marked with two small, yellow dots that probably serve as nectar guides. Flowers have 10 to 12 stamens that bear 0.04- to 0.09-mm red anthers. The fruit is a red septicidal capsule, 2.2 to 3.4 mm long, with 10 to 20 small brown seeds (Grimes and Packard, 1981; personal observation).

The study area—Only five populations of *Saxifraga bryophora* var. *tobiasiae* are known. All populations occur in the Payette National Forest in the West Salmon River Mountains of central Idaho (Table 2.1; Fig. 2.1). Records (1930 to present) from the nearest climate station in McCall, ID, show that the mean annual temperature is 4.85 °C. The mean annual maximum temperature is 12.5 °C and the mean annual minimum temperature is -2.6 °C. The mean annual precipitation is 0.69 meters. The mean annual snowfall totals 3.5 meters (WRCC, 1999). The growing season for this area is very short, from late June to mid September.

Soils that support these populations have a cryic temperature regime, as mean annual soil temperature was estimated from climatic data to be between 0 °C and 8 °C, with cool mean summer soil temperatures (Soil Survey Staff, 1994). The soils have a udic moisture regime, as the soil moisture control section was observed not to be dry for

as long as 90 cumulative days per year (Soil Survey Staff, 1994). The two largest and most accessible populations, Fisher Creek Saddle East (FCSE) and Fisher Creek Saddle West (FCSW), were used for most experiments.

Habitat description and vegetation sampling—To determine the size of the granitic outcrop microhabitats and to classify the vegetation composition of these island regions, 12 permanent plots were established in 1995. Seven plots were established at FCSW and five plots at FCSE because the plants there are distributed over a more varied range of microhabitats and are more abundant than those at FCSW. Each permanent plot was centered on a sub-population within each primary population (Fig. 3.1).

Microdrainages were observed running through the center of the habitat islands.

These microdrainages were often parallel with the slope and were characterized as the main path of surface flow. The first transect (T1) was aligned with the microdrainage, extending from 1 m above to 1 m below the length of the subpopulation to include surrounding vegetation. A second, third, and fourth transect (T2, T3, T4, respectively) were placed perpendicular to T1 at three equal intervals down slope from T1 and extended 1 m in each direction beyond the last plant in the sub-population. The lengths of T2, T3, and T4 also varied depending upon the distribution of *S. bryophora* var. *tobiasiae* plants. Each permanent plot contained 12 0.5-m X 0.5-m quadrats. Four equidistant quadrats were located on T1 (one quadrat above T2, one quadrat below T4, and two between T2 and T4). On T2 and T4, one quadrat was located at each terminal end of the transect and one was centered between the terminal quadrats. Two quadrats were located on T3, each centered equidistantly from T1. A total of 144 quadrats was established.

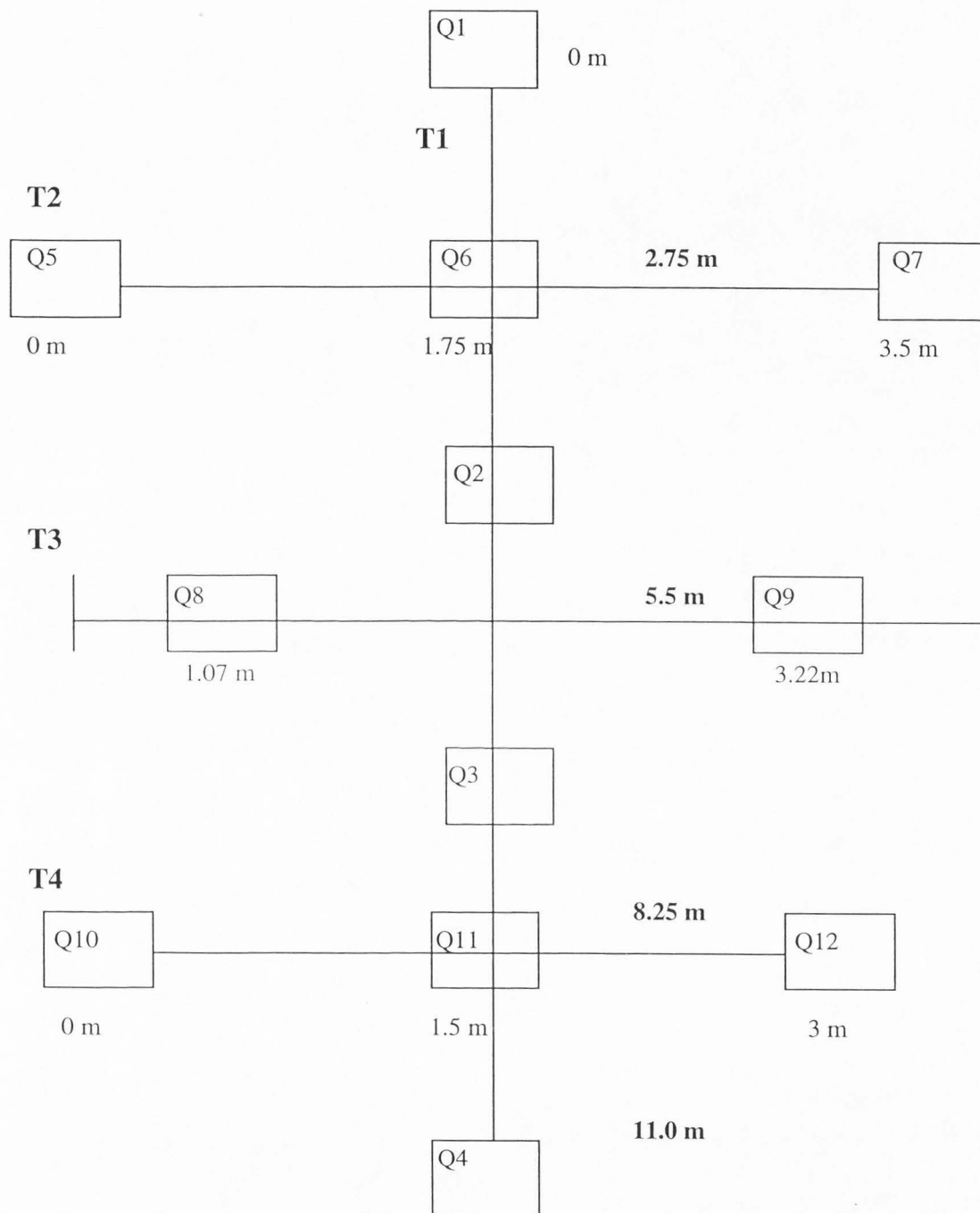


Fig. 3.1. Layout of a permanent plot. Dimensions of the transect are specific to the distribution of *Saxifraga bryophora* var. *tobiasiae* populations.

The vegetation composition within *Saxifraga bryophora* var. *tobiasiae* habitat islands was examined during two summer field seasons (1995, 1996). Each year, the 144 quadrats were sampled monthly from June to September. In each quadrat, the percent cover of all biotic and abiotic components was estimated visually using a Daubenmire frame. Because the habitat islands are often covered by mosses and lichens, counts of individuals or stem counts were not possible.

Soil characterization—*Saxifraga bryophora* var. *tobiasiae* populations were thoroughly surveyed to identify actual and potential habitat in 1995 and 1996. Potential habitat sites were classified as open granitic islands with bare soil pockets and sufficient moisture availability to support *S. bryophora* var. *tobiasiae* individuals. All populations of *S. bryophora* var. *tobiasiae* occur in soils formed in granodiorite colluvium derived from the Idaho Batholith. In 1996, soil habitat pits and five potential habitat pits were established in each of the FCSE and FCSW populations. Pits were located in the center of microdrainages.

Soil pits were manually excavated to the contact with the granodiorite bedrock (lithic contact). The genetic horizons were identified for each soil pedon. Horizon depth, boundary distinctness, color, texture, structure, consistence, pH, presence of roots, effervescence, and rock fragments were described and recorded for each genetic horizon. All classifications of the soils sampled were made by using the *Keys to Soil Taxonomy* (Soil Survey Staff, 1994).

Data analysis—Classification tree analysis is a relatively new nonparametric method (Breiman et al., 1984; Verbyla, 1987; Moore et al., 1991) that attempts to identify the exact conditions (rather than the range of environmental conditions as in parametric

models) associated with an organism. Recent studies have used classification tree analysis to predict rare plant habitat in the Great Basin Desert (Aitken, 1998) and to predict habitat conditions important in nest locations of smallmouth bass (Rejwan et al., 1999). There are many advantages afforded by classification tree analysis: (1) linear relationships between variables and homoscedasticity of variances are not required (Breiman et al., 1984) and interactions among environmental variables are automatically detected (Clark and Pregibon, 1992); (2) categorical and continuous variables can be used in any combination within the model (Breiman et al., 1984); (3) classification trees are robust with respect to outliers because each observation carries the same weight (Breiman et al., 1984; Verbyla, 1987; Moore et al., 1991); and (4) tree based models are often easier to interpret and discuss than linear models (Clark and Pregibon, 1992). Because of these advantages, classification tree analysis was used to examine the relationships between the ecological components associated with *Saxifraga bryophora* var. *tobiasiae* habitats.

Classification tree analysis and regression tree analysis sort data by binary recursive partitioning of plots (presence and absence of *Saxifraga bryophora* var. *tobiasiae*), which splits the dataset into increasingly homogeneous subsets. The allocation of quadrats with *S. bryophora* var. *tobiasiae* into homogenous subsets was determined by sequential examination of each ecological variable within the data set. Separate classification trees were created for percent cover data collected in 1995 and 1996. Percent cover data were selected for these analyses because they are more representative of the scale of the associations between *S. bryophora* var. *tobiasiae* and the ecological factors than presence or absence. Soil data were not collected in the

permanent plots because monitoring and sampling will continue these plots.

Tree growth consists of the dataset being repeatedly divided into two groups using every possible combination of variables and calculating the variability for each binary split (within-group sum of squares). The split point or node that results in the lowest variance or deviance between two groups is then used to divide the data set in the classification tree. Binary recursive partitioning of the data set then continues for each of the newly formed groups, which results in the decrease in the number of data points to include with each subsequent split. Partitioning continues until there is no more variation between the groups, or it is infeasible to continue because all predictor variables have been used or groups have fewer than five unclassified observations remaining (Breiman et al., 1984; Verbyla, 1987; Moore et al., 1991; Clark and Pregibon, 1992).

The classification tree that is produced by this analysis can be interpreted much like a dichotomous key. Each classification tree has hierarchical structure that is followed from the top node called the root (the initial undivided data set), through branches (binary splits), to the bottom terminal nodes called leaves (undivided groups). The vertical length of each branch is determined by the proportion of variance explained by each split (Breiman et al., 1984). The early partitions of a tree are likely to represent the true relationships between the ecological variables and the presence of *Saxifraga bryophora* var. *tobiasiae*. However, the precision diminishes as subsequent splits occur because the sample sizes grow smaller and smaller. A technique termed cross-validation is then needed to determine the appropriate tree size to quantify the relationships between measured variables and *S. bryophora* var. *tobiasiae* (Clark and Pregibon, 1992).

Cross-validation analysis divides the original data set into mutually exclusive

subsets. Each subset then serves as an independent test that is compared with trees generated from the remaining subsets (Clark and Pregibon, 1992). Thus, each data point is used in one independent test set by the end of this process. The deviance of the cross-validated trees can then be used to predict the optimal tree size (the optimal tree size is the tree with the lowest deviance). The true error rate of the classification was estimated using ten-fold cross-validation (Clark and Pregibon, 1992). The classification tree can then be pruned at the point of minimum deviance. Classification accuracy estimates for the tree are produced for each pruning step. Large trees with many predictor variables often have high misclassification values while small trees with few variables have low misclassification values. Therefore, the tree produced in cross-validation is the tree with the lowest misclassification value.

RESULTS

Habitat description and vegetation sampling—Saxifraga bryophora var.

tobiasiae plants were found in relatively isolated pockets or islands of shallow soils surrounded by exposed granitic outcrops and perennial vegetation (Figure 3.2). These islands were irregular elliptical to sub-circular regions with an average length of 9.84 m (ranging from 8.00 – 12.25 m) and width of 4.85 (2.75 – 8.00 m). Large exposed outcrops have pockets or depressions in which sediment and soils form from weathering granite and decomposing organic material. Outcrops rise above the soil surface 20 to 50 cm on average, but can extend > 1 m in some islands observed throughout the study area.

All ecological factors found co-occurring with *Saxifraga bryophora* var. *tobiasiae* are summarized in Table 3.1. The average occurrence level for each factor was

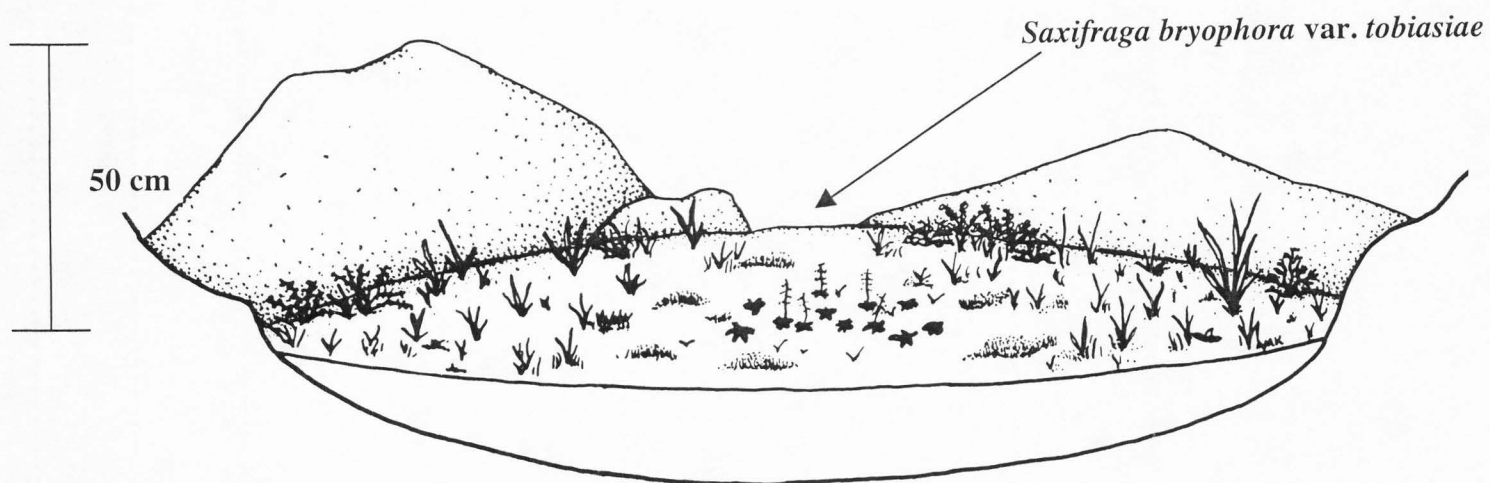


Fig. 3.2. Illustrated cross section of a granitic outcrop island community with *Saxifraga bryophora* var. *tobiasiae*.

calculated by determining the percentage of quadrats in which each factor was present or absent based upon presence or absence of *S. bryophora* var. *tobiasiae*. Occurrence levels were averaged over the two years (1995, 1996) sampled. The average occurrence levels are indicated in Table 3.1.

Saxifraga bryophora var. *tobiasiae* plants are found in the center of the granitic islands in microdrainages and pools formed by runoff meltwater and seasonal precipitation. Surrounding these centers of *S. bryophora* var. *tobiasiae* plants are moss-mats composed of *Polytrichum juniperinum*. *Lewisia triphylla*, a small annual species, and *Antennaria lanata*, a small perennial species are often found interspersed within the moss-mats. *Carex rostrata* and *Juncus paryii* are found in clumps surrounding these mats. Interspersed along the periphery of the moss-mat regions are perennial sub-shrubs species such as *Xerophyllum tenax*, *Vaccinium scoparium*, and *Phyllodoce empetriformis*, which appear to stabilize the edges of the habitat islands.

Soil characterization—The morphological characteristics of the soils in habitat and non-habitat sites were very similar (Appendix B.1 – B.28) with the exception of the average rock fragment (% volume). Rock fragments were higher (Table 3.2) in soils with *Saxifraga bryophora* var. *tobiasiae*. The soil depth to bedrock was very shallow in all soils ranging between 6 and 39 cm (Table 3.2). A thin litter layer ranging from 0.5 to 3.5 cm was measured in all soils (Table 3.2). Sandy or coarse textures were generally found for all soils (Table 3.2).

Additional similarities were found for soils in habitat and non-habitat sites (Appendix B.1 – B.28). Colors ranged from 10YR 4/2 to 5 YR 3/2 for moist soils. The average moist consistence was friable, ranging from very friable to firm. The

TABLE 3.1. Average occurrence levels of ecological components in plots with *S. bryophora* var. *tobiasiae* and plots without *S. bryophora* var. *tobiasiae*.^a

Character ^b	Occurrence Level	
	Present	Absent
* Bare Soil	1	1
* Litter	2	1
* Rock (solid and fragments	1	4
<i>Abies lasiocarpa</i> (Hook.) Nutt.	8	8
<i>Achillea millefolium</i> L.	8	8
Moss	7	7
<i>Antennaria alpina</i> (L.) Gaertn.	6	6
* <i>Antennaria lanata</i> (Hook.) Greene	3	4
<i>Arnica latifolia</i> Bong.	8	8
<i>Aster alpigenus</i> (T. & G.) Gray	7	7
* <i>Carex rostrata</i> Stokes	7	7
<i>Chinophila tweedyi</i> (Canby & Rose) Hend.	8	8
<i>Claytonia lanceolata</i> Pursh	7	8
<i>Cryptogramma crispa</i> (L.) R. Br.	8	8
* <i>Dodecatheon jeffreyi</i> van Houtte	7	7
* <i>Erythronium grandiflorum</i> Pursh	6	7
<i>Gentiana calycosa</i> Griseb.	7	7
* <i>Hypericum formosum</i> H.B.K.	7	7
* <i>Juncus parryi</i> Englem.	4	4
* <i>Lewisia triphylla</i> (S.Wats) Gray	1	5
Lichens	8	8
* <i>Ligusticum canbyi</i> Coult. & Rose	7	7
* <i>Luzula hitchcockii</i> Hamet-Ahti	8	7
<i>Muhlenbergia richardsonis</i> (Trin.) Rydb.	8	8
<i>Pedicularis bracteosa</i> Benth.	8	8
<i>Penstemon procerus</i> Dougl.	8	8
<i>Penstemon globosus</i> (Piper) Pennell & Keck	8	8
<i>Phlox multiflora</i> A. Nels.	8	8
* <i>Phyllodoce empetrifomis</i> (Sw.) D. Don	7	6
<i>Pinus albicaulis</i> Engelm.	8	8
<i>Polemonium pulcherrimum</i> Hook.	8	8
<i>Polygonum aviculare</i> L.	8	8
* <i>Polygonum bistortoides</i> Pursh	6	7
<i>Polygonum phytolaccaefolium</i> Mesin.	8	8
* <i>Polytrichum juniperum</i> Hedw.	1	4
<i>Sedum lanceolatum</i> Torr.	8	8
<i>Senecio resedifolius</i> Less.	8	8
<i>Suksdorfia ranunculifolia</i> (Hook.) Engl.	8	8
<i>Vaccinium membranaceum</i> Dougl.	8	8
* <i>Vaccinium scoparium</i> Leiberg	7	4
<i>Xerophyllum tenax</i> Michx.	8	6

^a 1 = >90%, 2 = 90 - 75 %, 3 = 75 - 60%, 4 = 60 - 45 %, 5 = 45 - 30% 6 = 30 - 15%, 7 = 15 - 5 %, 8 = <5%;

^b * = factors used in classification tree analysis.

TABLE 3.2. Selected soil properties summarized by aspect (FCSE, FCSW) and between plots (present and not present).

Character	FCSE		FCSW	
	P ^a range (mean)	NP ^b range (mean)	P range (mean)	NP range (mean)
Depth to bedrock (cm)	11 - 27 (19.5)	6 - 39 (21)	7.8 - 25 (20.7)	14 - 20.1 (18.5)
Texture (fine earth fraction) ^c	vfsl-s (sl)	fsl - s (fsl)	vfsl - cosl (sl)	fsl - cosl (sl)
Rock fragments (% volume)	15 - 78 (30.4)	8 - 30 (22)	15 - 77 (38.5)	11 - 45 (20.6)
Litter depth (cm)	1.5 - 3.1 2.28	0.5 - 3.1 2.24	2.1 - 3.4 2.73	2.2 - 3.5 2.76

^a P = *Saxifraga bryophora* var. *tobiasiae* present

^b NP = *Saxifraga bryophora* var. *tobiasiae* not present

^c Abbreviations: Texture: v = very; f = fine; s = sandy; l = loam; co = coarse. average

wet consistence was slightly sticky and slightly plastic ranging from non-sticky and non-plastic to sticky and plastic. The average pH was 7.0 and ranged from 6.8 to 7.2. All horizons were non-calcareous. Many pedons had a thin Cr layer of paralithic material lying above the lithic contact, ranging from 1.5 to 6.0 cm.

The family classifications for all pedons are summarized in Table 3.3. Soils with mollic epipedons were identified as Mollisols. Soils with ochric epipedons and cambic horizons were classified as Inceptisols. Soils with ochric epipedons and no diagnostic subsurface horizons were classified as Entisols. All soil pedons had a lithic contact within 50 cm of the mineral soil surface (Appendix B.1 – B.28).

The Mollisols were further classified as belonging to the suborder Borolls, the great group Cryoborolls based on the cryic temperature regime, and the subgroup Lithic

TABLE 3.3. Summary of family classification of soil pedons (Soil Survey Staff, 1994).

Family classification	Number of pedons			
	East		West	
	P ^a	NP ^b	P	NP
Loamy, mixed, semiactive Lithic Cryoboroll	4	2	4	1
Loamy-skeletal, mixed, semiactive Lithic Cryoboroll	1	-	4	1
Loamy, mixed, semiactive Lithic Cryochrept	1	2	-	1
Loamy-skeletal, mixed, semiactive Lithic Cryochrept	1	-	-	-
Loamy, mixed, semiactive, nonacid Lithic Cryorthent	1	1	1	2
Loamy-skeletal, mixed, semiactive, nonacid Lithic Cryorthent	1	-	-	-

^a P= *Saxifraga bryophora* var. *tobiasiae* present

^b NP= *Saxifraga bryophora* var. *tobiasiae* not present

Cryoborolls due to the lithic contact within 50 of the mineral soil surface. Based upon the presence of an ochric epipedon, a cambic horizon, and a cryic temperature regime, the Inceptisols were classified as belonging to the suborder Ochrepts and the great group Cryochrepts. With a lithic contact within 50 cm of the surface, these soils were classified in the subgroup of Lithic Cryochrepts. The Entisols were further classified as belonging to the suborder Orthents and the great group Cryorthents due to the cryic soil temperature regime. With a lithic contact within 50 cm of the surface, these soils in the subgroup of Lithic Cryorthents. Pedons with *Saxifraga bryophora* var. *tobiasiae* were most often Mollisols, thus indicating that more organic material is available for possible uptake by these individuals than in the Entisol or Inceptisols pedons.

The majority of the soils described were characterized as having a loamy particle-size class (>15% sand, <35% clay, < 35% rock fragments). Those with greater than 35% or more by volume rock fragments were classified as loamy-skeletal. Due to the loamy and loamy-skeletal particle classes and the lack of a single mineral being greater than 40% all soils were classified as belonging to the mixed mineralogy class. The cation exchange capacity class for all soils was estimated to be semiactive (J. Boettinger; personal communication) and Entisols were further classified as nonacid due to the neutral pH.

Classification tree analysis and cross validation—In 1995, the classification tree results (Fig. 3.3) predicted the presence of *Saxifraga bryophora* var. *tobiasiae* by including the percent cover levels for bare soil and *Lewisia triphylla*. The classification tree was pruned to three terminal nodes or leaves because subsequent partitions did not improve the prediction of *S. bryophora* var. *tobiasiae* presence in cross-validation. The

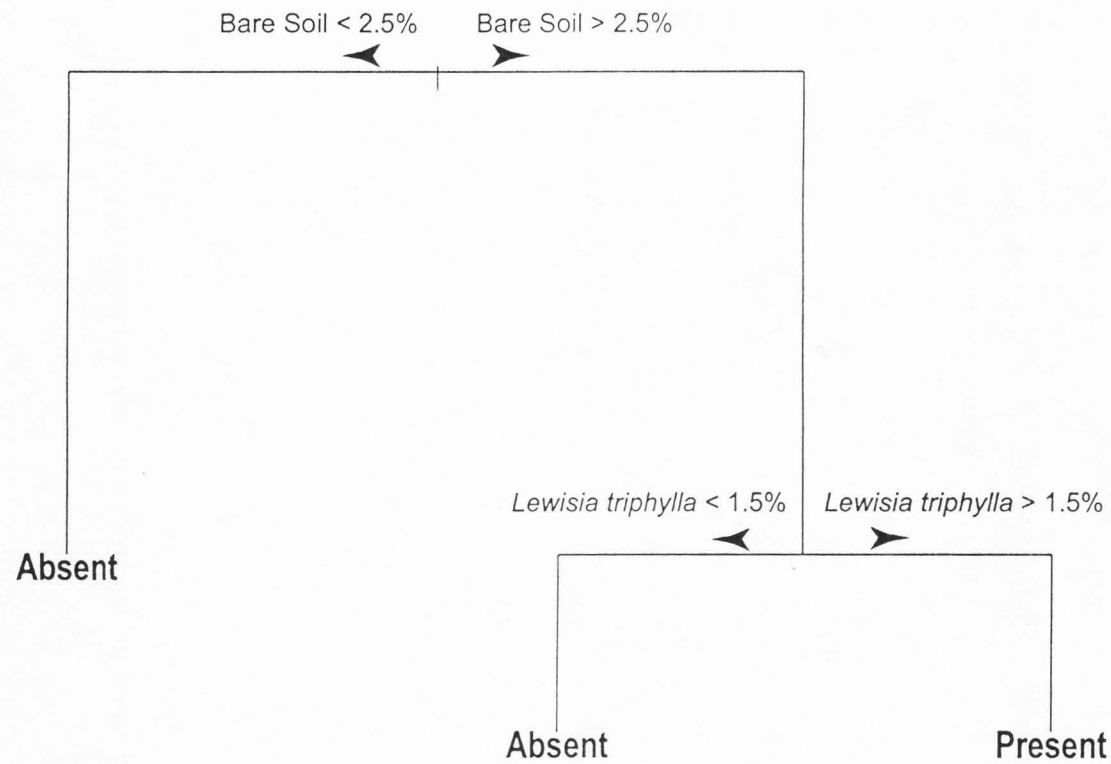


Fig. 3.3. The classification tree generated from 1995 percent coverage data. The tree was pruned to 3 terminal nodes (leaves) and distinguishes between the presence and absence of *Saxifraga bryophora* var. *tobiasiae*. Vertical lines identify the criterion used in binary partitioning of the tree.

ecological factors used in the initial classification and the cross-validated trees for 1995 are summarized in Table 3.4. Based on the classification tree, *S. bryophora* var. *tobiasiae* is present when bare soil coverage is greater than 2.5% and *Lewisia triphylla* coverage is greater than 1.5%. *Saxifraga bryophora* var. *tobiasiae* is not present if soil coverage is less than 2.5% or if soil coverage greater than 2.5% but *Lewisia triphylla* coverage is less than 1.5%. The misclassification error rate for this tree was low (19.2%) and this tree likely identifies important predictors of *S. bryophora* var. *tobiasiae* presence.

In 1996, the classification tree results (Figure 3.4) predicted the presence of *Saxifraga bryophora* var. *tobiasiae* by including the percent cover of *Lewisia triphylla*, bare soil, *Erythronium grandiflorum*, *Vaccinium scoparium*, and *Polytrichum juniperinum*. The classification tree was pruned to six terminal nodes or leaves because subsequent partitions did not improve the prediction of *S. bryophora* var. *tobiasiae* presence. The ecological factors used in the initial classification and cross-validated trees for 1996 are summarized in Table 3.4. Based upon this tree, *S. bryophora* var. *tobiasiae* is present when the percent cover of *Lewisia triphylla* is less than 3.5%, bare soil is greater than 2.5%, and *Erythronium grandiflorum* is less than 1%, or when *Lewisia triphylla* is greater than 3.5%, *Vaccinium scoparium* is less than 2.5%, and *Polytrichum juniperinum* is present. *Saxifraga bryophora* var. *tobiasiae* is not present when (1) *Lewisia triphylla* is less than 3.5% and bare soil is less than 2.5%, (2) *Lewisia triphylla* is less than 3.5%, bare soil is greater than 2.5%, and *Erythronium grandiflorum* is greater than 1%, and (3) *Lewisia triphylla* is greater than 3.5% and *Vaccinium scoparium* is greater than 2.5%. The misclassification error rate was also low (19.1%).

TABLE 3.4. Summary of *Saxifraga bryophora* var. *tobiasiae* classification trees. ^a

Character	1995	1996
Bare Soil	CV	CV
Litter	IT	IT
Rock (solid and fragments)	IT	NU
<i>Antennaria lanata</i>	NU	NU
<i>Carex rostrata</i>	NU	NU
<i>Dodecatheon jeffreyi</i>	NU	NU
<i>Erythronium grandiflorum</i>	NU	CV
<i>Hypericum formosum</i>	NU	NU
<i>Juncus parryi</i>	NU	NU
<i>Lewisia triphylla</i>	CV	CV
<i>Ligusticum canbyi</i>	NU	NU
<i>Luzula hitchcockii</i>	NU	NU
<i>Phyllodoce empetriflorum</i>	NU	NU
<i>Polygonum bistortoides</i>	IT	IT
<i>Polytrichum juniperum</i>	IT	CV
<i>Vaccinium scoparium</i>	IT	CV
<i>Xerophyllum tenax</i>	NU	NU

^a NU = variable was present but not used in any tree; IT = variable used in initial tree classification but not included in the cross-validated tree; **CV** = variable included in cross-validated tree.

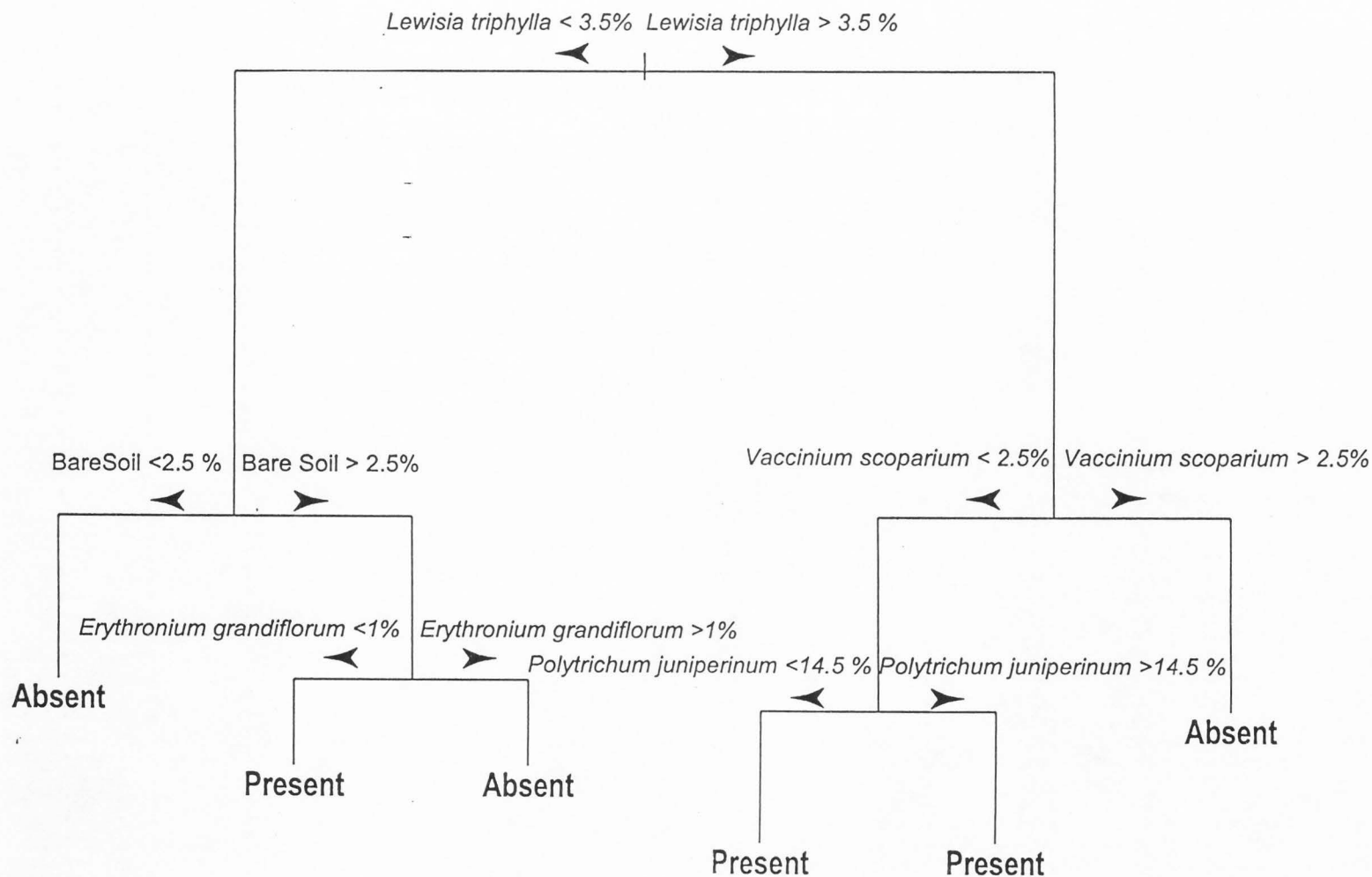


Fig. 3.4. The classification tree generated from 1996 percent coverage data. The tree was pruned to 6 terminal nodes (leaves) and distinguishes between the presence and absence of *Saxifraga bryophora* var. *tobiasiae*. Vertical lines identify the criterion used in binary partitioning of the tree.

DISCUSSION

The granitic outcrop habitat islands of *Saxifraga bryophora* var. *tobiasiae* populations have several unique ecological characteristics and habitat dynamics that appear to contribute to its endemism and rarity. First, the soil physical characteristics of the granitic habitat islands of *Saxifraga bryophora* var. *tobiasiae* are unique and appear to influence its endemic distribution. The depth to bedrock (Table 3.2) in habitat islands are extremely shallow. Shallow soils often have reduced moisture retention in areas of high light intensity and limit the number of species that can successfully establish in such regions (Burbanck and Platt, 1964; Sharitz and McCormick, 1973; Baskin and Baskin, 1988). The shallow soil depth and soil morphological properties of granitic habitat islands may best describe the endemism of many granitic outcrop species throughout the southeastern United States (McVaugh, 1943; McCormick and Platt, 1962; Burbanck and Platt, 1964; Sharitz and McCormick, 1973; Wiser, 1994, 1998). It is therefore likely that the shallow soils associated with *Saxifraga bryophora* var. *tobiasiae* are contributing to its endemic distribution.

Edaphic characteristics do not appear to be responsible for the lack of *S. bryophora* var. *tobiasiae* individuals in potential habitats. The morphological characteristics are very similar in actual and potential habitat soil pedons (Table 3.2). Higher percentages of rock fragments, however, were found in soils with *Saxifraga bryophora* var. *tobiasiae*. This finding is best explained by the frequency of meltwater runoff observed in habitat islands. Finer soil particles are removed from these islands when flow is high, while larger particles and rock fragments persist. *Saxifraga*

bryophora var. *tobiasiae* is dependent upon runoff and seasonal precipitation for dispersal of its propagules (Chapter 2) into new regions. This mechanism of dispersal may limit movement of *S. bryophora* var. *tobiasiae* bulbils into potential habitat islands and most likely explains the lack of individuals in these regions.

Soil chemistry has been shown to limit the distribution of plant taxa in many soil systems (Kruckeberg, 1954; Kruckeberg and Rabinowitz, 1985; Baker et al., 1985). No unique soil chemistry, however, has been shown for the endemic taxa of granitic depression communities in the southeastern United States (McVaugh, 1943; McCormick and Platt, 1962; Burbanck and Platt, 1964; Sharitz and McCormick, 1973; Wisser, 1994, 1998). Thus, it seems equally unlikely that unique chemical properties exist in the soils associated with *Saxifraga bryophora* var. *tobiasiae*.

Endemic plant taxa of granitic outcrop communities in the southeastern United States appear to be restricted to granitic depression communities because of an increased tolerance to low soil pH and high light intensity (Burbanck and Platt, 1964; Sharitz and McCormick, 1973; Burbanck and Phillips, 1983). The soil pH of the habitat islands associated with *Saxifraga bryophora* var. *tobiasiae* are much higher (6.8 – 7.2; Table 3.2) than that in the southeast (4.0 – 4.4; Burbanck and Platt, 1964). Nutritional deficiencies or toxicities are least at a neutral pH (Brady and Weil, 1999). Thus, the neutral soil pH does not appear to influence the endemic distribution of this taxon. *Saxifraga bryophora* var. *tobiasiae* does, however, appear to have increased resistance to high insolation rates because of high levels of anthocyanins (personal observation). High levels of anthocyanins in sub-alpine and alpine species allow for persistence in habitats with high light intensity (Baskin and Baskin, 1988; Moore et al., 1998).

Second, the comparison of the island communities of *Saxifraga bryophora* var. *tobiasiae* with those of the southeastern United States (Oosting and Anderson, 1939; Burbanck and Platt, 1964; Sharitz and McCormick, 1973; Burbanck and Phillips, 1983; Wiser, 1994, 1998) identified several key differences in spatial patterns, ecological processes, and components. These differences may influence the rarity and narrow distribution of this taxon.

The differences in spatial patterns observed between the southeastern granite outcrop communities (Burbanck and Platt, 1964; Sharitz and McCormick, 1973; Burbanck and Phillips, 1983) and those of central Idaho may be explained by several factors. *Saxifraga bryophora* var. *tobiasiae* populations occur in habitat islands between 2300 – 2600 m while southeastern outcrops occur between 600 – 1300 m (Burbanck and Platt, 1964; Wiser, 1994, 1998). The central Idaho habitat islands receive 3.57 m of snow on average, while southeastern outcrops receive far less (less than 0.01 m in Georgia to 1.27 m in North Carolina [Taylor and Daly, 1999]). The dramatic difference in snowfall and accumulation in central Idaho provides for extreme amounts of meltwater runoff in early spring and summer months. The difference in elevation also accounts for the much reduced growing season in central Idaho habitat islands (late June – September) when compared with that of the southeast (February – October; Burbanck and Platt, 1964). Precipitation patterns in the southeastern United States appear to be evenly distributed throughout the year. The majority of moisture for central Idaho can be attributed to snowfall, thus providing for a pulse of extreme runoff in the short summer season. Further examination of granitic habitat islands in both central Idaho and the southeastern United States is needed to elucidate additional factors that may be contributing to the

spatial differences observed between these unique ecosystems.

In an extensive survey of southeastern granitic outcrop succession, Burbanck and Platt (1964) correlated the composition of seral stages with edaphic factors. Island communities are composed of concentric zones of seral stages that are correlated with the depth of soil within the habitat island. Pioneer species are abundant in shallow soils where biotic competition is low (Burbanck and Platt, 1964; Sharitz and McCormick, 1973). These species are often restricted to the periphery of the habitat island where soils are shallowest and biotic competition prevents their expansion. As the soil deepens from the periphery, more competitive, deeper-rooted species (lichen-annual herb and perennial herb communities) are found in intermediate zones of the island. Herb-shrub communities (climax communities) are most abundant in the center of the habitat islands where soils were deepest. As soil depth increases over time due to weathering of granite and the accumulation of organic debris, pioneer species are replaced by more competitive climax species.

The habitat islands associated with *Saxifraga bryophora* var. *tobiasiae* have a strikingly different community composition and successional processes than those of the southeastern United States (Burbanck and Platt, 1964; Sharitz and McCormick, 1973; Burbanck and Phillips, 1983). Although the size and average depth of the soil-filled depressions were similar to those of the southeast (Burbanck and Platt, 1964), the successional patterns and community stages observed were exactly opposite. The herb-shrub communities associated with *S. bryophora* var. *tobiasiae* are located on the periphery of the habitat islands where soils were typically shallowest. Moving concentrically inward from the periphery, the soils deepen and the annual-perennial herb

communities followed by the lichen-annual herb communities establish. Finally, *S. bryophora* var. *tobiasiae* individuals, which are likely pioneer species, are located in the center of the habitat islands.

The successional pattern observed in this study is most likely explained by the natural disturbance pattern observed in these habitat islands. Extreme meltwater runoff appears to scarify the center of these habitat islands and clear patches where pioneer species such as *Saxifraga bryophora* var. *tobiasiae* can readily establish. The magnitude of disturbance decreases outwardly from the center of the habitat island, creating the observed differences in community type establishment. Those species better adapted to some level of disturbance are located closer to the center of the habitat island, while the most competitive species (least adapted to disturbance) are located on the periphery where the effects of disturbance are the lowest.

The frequency and intensity of disturbance have been found to affect the compositional and structural nature of plant communities (White, 1979; Pickett and White, 1985; Sprugel, 1991). High frequency disturbance may provide for the constant presence of a species adapted to that disturbance type. A community may become structurally and compositionally adapted to high disturbance frequencies as well (Gill, 1975; White, 1979; Sprugel, 1991). The community composition under the "intermediate disturbance" hypothesis (Grime, 1973; Connell, 1978; Huston, 1979) is predicted to vary given the level and frequency of disturbance. In low-level or low-frequency disturbance, less competitive species are excluded by competitively superior species. In intermediate levels of disturbance, maximum species diversity is attained due to newly created patches with pioneer species and mature patches of competitive species. In very high levels or

frequencies of disturbance, pioneer species exist because competitively superior species are removed.

High levels of disturbance created by meltwater runoff appear to contribute to the rarity of *Saxifraga bryophora* var. *tobiasiae*. Meltwater runoff creates new patches within the habitat islands. *Saxifraga bryophora* var. *tobiasiae* appears to be a pioneer species that can readily establish within these newly created patches. An extensive study of the reproductive biology and population dynamics (Chapter 2) of *S. bryophora* var. *tobiasiae* provided strong evidence of adaptation to high frequencies of disturbance. Indeed, this taxon is dependent upon meltwater runoff and seasonal precipitation for dispersal of its bulbils (vegetative propagules) to new habitats. Hydrochory (the dispersal of propagules by water) has been shown for many species as a successful mechanism for recolonization in new patches created by disturbed channels (Bernard et al., 1998). The dependence of *Saxifraga bryophora* var. *bryophora* on hydrochory for the dispersal of bulbils is very important because flower production in this taxon appears to be infrequent and limited by extreme fluctuations in temperature and precipitation levels (Chapter 2). The production of seeds and their recruitment into new habitats appears to be low and unpredictable. Thus, *S. bryophora* var. *tobiasiae* is often dependent upon disturbance for expansion into new habitats.

The soils associated with *S. bryophora* var. *tobiasiae* populations also lend support to this disturbance hypothesis. Higher percentages of rock fragments (Table 3.2) were found in soils with *S. bryophora* var. *tobiasiae* than in potential habitat sites. Increased meltwater runoff is responsible for removing finer particles from these soils and creating new patches for establishment. Potential habitat sites may have lower levels

of meltwater runoff and disturbance.

Levels of disturbance may vary across a landscape and over time, thus creating spatiotemporal patterns that may limit the distribution of *Saxifraga bryophora* var. *tobiasiae*. Disturbance may create new patches for establishment in some habitat islands, but may also be responsible for the removal of *S. bryophora* var. *tobiasiae* individuals in others. A detailed study of the life history and population demography of *S. bryophora* var. *tobiasiae* (Chapter 2) provided evidence that plants are somewhat resistant to intense levels of meltwater runoff. Plants were marked within microdrainages in 1995. Most of these marked plants were found again in 1996. Only marked plants from habitat islands with the greatest amount of meltwater runoff and disturbance were lost. There may be balance between recolonization and losses that limits the long-term expansion of *Saxifraga bryophora* var. *tobiasiae* populations.

Intermittent patterns of high disturbance across a landscape can contribute to the rarity of a species. *Pedicularis furbishiae* S. Wats. populations are restricted to riparian flood regions along the St. John River, Maine, which suffer yearly flooding, bank slumping, and ice scouring (Gawler, 1985; Gawler et al., 1987; Menges, 1990). These high levels of disturbance eliminate some pockets of established plants while moving other individuals into new unoccupied regions. Rare prairie grasses (Rabinowitz, 1978) also inhabit rare patches that vary both spatially and temporally due to intermittent levels of disturbance. It is therefore likely that disturbance is also contributing to the rarity of *Saxifraga bryophora* var. *tobiasiae*.

Classification tree analysis—The classification trees produced in this study identify several important ecological factors that can be used to predict the presence of

Saxifraga bryophora var. *tobiasiae* (Figures 3.2, 3.3). Bare soil ($> 2.5\%$) and *Lewisia triphylla* ($> 1.5\%$) were included in both of the 1995 and 1996 classification trees. This requirement for bare soil confirms the previously discussed finding that *Saxifraga bryophora* var. *tobiasiae* individuals readily establish in bare soil regions scarified by meltwater runoff. *Lewisia triphylla*, a diminutive annual, is a pioneer species that is often interspersed with *S. bryophora* var. *tobiasiae*. *Lewisia triphylla* is typically shorter-lived than *S. bryophora* var. *tobiasiae*, but its dried leaves persist throughout the entire growing season and are useful in predicting the presence of this *S. bryophora* var. *tobiasiae*.

In 1996, bare soil and *Lewisia triphylla* were again both included as predictors of *Saxifraga bryophora* var. *tobiasiae* presence along with several additional ecological factors. The presence of *S. bryophora* var. *tobiasiae* is predicted if *Lewisia triphylla* ($< 3.5\%$), bare soil ($> 2.5\%$), and *Erythronium grandiflorum* ($< 1\%$) are present.

Erythronium grandiflorum is a perennial species that may be competitively superior to *S. bryophora* var. *tobiasiae*. Greater than 1% coverage of *E. grandiflorum* may limit the successful establishment of *S. bryophora* var. *tobiasiae*. When *Lewisia triphylla* ($> 3.5\%$), *Vaccinium scoparium* ($< 2.5\%$) and *Polytrichum juniperinum* are present, the presence of *S. bryophora* var. *tobiasiae* is also predicted. *Vaccinium scoparium* is a subshrub species that appears to be competitively superior to *S. bryophora* var. *tobiasiae* and is generally restricted to the periphery of the habitat islands in years with a high frequency of disturbance. If percent coverage of *V. scoparium* exceeds 2.5% or if disturbance frequencies are decreased, this species will likely replace *S. bryophora* var. *tobiasiae*. *Polytrichum juniperinum* is a mat-forming moss found in the lichen-annual communities that surround *S. bryophora* var. *tobiasiae* populations. It is a significant

predictor of *S. bryophora* var. *tobiasiae* at any coverage level if the requirement for *Lewisia triphylla* and *Vaccinium scoparium* is met first.

More variables were included in the classification tree for 1996 than for 1995. This may be explained by increased temperatures and lower moisture levels (Chapter 2) in 1996. There may have been less disturbance due to decreased moisture levels, thus allowing for greater species abundance in the habitat islands. Warmer temperatures may have also promoted increased species abundance.

The initial classification trees were very similar (Table 3.2; Tables A.1 – A.2, Appendix A) for 1995 and 1996. For each analysis, the percent coverage for litter, *Polygonum bistortoides*, *Vaccinium scoparium*, and *Polytrichum juniperinum* was included in the initial classification but not the cross-validated trees for both years. Although not included in the final analysis, these ecological variables may be indicators of proper habitat for *Saxifraga bryophora* var. *tobiasiae* and could be used to predict habitat for this rare taxon.

Overall, bare soil and *Lewisia triphylla* appear to be the most important indicators for the presence of *Saxifraga bryophora* var. *tobiasiae*. This information could be utilized to identify potential habitat for conservation efforts. Bulbils were successfully transplanted (Chapter 2) into potential habitat islands. Identification of areas with bare soil and *Lewisia triphylla* could be useful in augmenting restoration or habitat expansion efforts.

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CHAPTER 4

CONCLUSION

Elucidating the biological and ecological factors that contribute to the rarity and endemic distribution of plant species can provide critical information needed to effectively manage and conserve such species. The examination of the population dynamics, reproductive biology, life history characteristics, demography, and ecology of a species can provide detailed information about the factors that contribute to its narrow distribution or rarity. This information can then be utilized to understand the requirements of a species for persistence, to predict future trends for the population, and to minimize the risks of extinction.

This study of the reproductive biology, life history characteristics, population demography, and ecology of *Saxifraga bryophora* var. *tobiasiae* provided detailed information concerning factors that appear to contribute to its rarity and endemic distribution. This study also provided key information needed to effectively design and implement conservation management strategies for this taxon.

Evolutionary and environmental pressures appear to have directed the almost total replacement of flower primordia with asexual bulbils. The considerable amount of resources devoted to asexual reproduction by this taxon is likely explained by the unpredictable environmental conditions associated with its habitat, the lack of apparent insect visitors, and its phylogeny. Bulbils are dependent upon meltwater runoff and seasonal precipitation for dispersal. Expansion of *S. bryophora* var. *tobiasiae* vegetative propagules into new habitats may be limited by this mechanism.

Sexual reproduction in *Saxifraga bryophora* var. *tobiasiae* appears to be intermittent, occurring only in years in which proper environmental conditions for flowering are met. In the rare years when flowers are produced, seed production and recruitment into new habitats are very low. Evidence of increased bulbil production in years in which flowering potential is high, ramet production of bulbils, and the short life span of these individuals indicate that sexual reproduction in *S. bryophora* var. *tobiasiae* may be declining. The lack of flowering in many years and the low production of seeds also appear to contribute to the narrow distribution of this taxon.

In the rare years in which flowers are produced, outcrossing is promoted by extreme protandry and gynodioecy. An external pollen vector is required for fruit production. A major consistent pollinator or pollinators were not identified in this study, though moth pollination remains an option. Future research efforts should include the examination of such a possibility and the determination of the requirements needed to protect this pollinator as well.

Although *Saxifraga bryophora* var. *tobiasiae* is not autogamous, hermaphrodite flowers are self-compatible. There is apparently little selective pressure for adaptations leading to self-incompatibility because selfing can only occur in the rare occasions when more than one flower is produced. Additionally, inbreeding depression does not appear to be limiting seed production or selecting for self-incompatibility within this taxon.

The gynodioecious populations of *Saxifraga bryophora* var. *tobiasiae* present interesting consequences for conservation. With no resource reallocation, pollen production, or advantages afforded by outbreeding, females appear to be at a selective

disadvantage based upon sexual reproduction alone. Female advantage in *Saxifraga bryophora* var. *tobiasiae* is, however, afforded by increased vegetative reproduction and this advantage is likely responsible for the maintenance of females within these populations. The mode of inheritance of male-sterility in *S. bryophora* var. *tobiasiae* populations must be determined to understand the fate of gynodioecy and more importantly the fate of sexual reproduction for this rare taxon. Hermaphrodites are at risk if inheritance is strictly cytoplasmic due to the increased asexual reproductive success of females and the greater likelihood of females being fertilized. If male-sterility is under nuclear-cytoplasmic control, there is no risk to hermaphrodites and sexual reproduction because females could be capable of producing hermaphrodite offspring due to nuclear "restorer" genes, which offset male-sterile cytoplasm.

The unique granitic habitat islands in which *Saxifraga bryophora* var. *tobiasiae* populations exist greatly influence its distribution and abundance. The soils associated with *S. bryophora* var. *tobiasiae* are extremely shallow. The number of species that can successfully establish in shallow soils is often limited. *Saxifraga bryophora* var. *tobiasiae* appears to be adapted to the shallow soils associated with the granitic habitat islands.

Natural disturbance patterns due to extreme meltwater within these habitat islands shape the narrow distribution and rarity of *Saxifraga bryophora* var. *tobiasiae*. Meltwater runoff creates new patches for establishment and bulbils are moved into these new patches by runoff and seasonal precipitation. Disturbance may also remove individuals from previously established patches. Thus, spatiotemporal fluctuations in the frequency

and intensity of disturbance seem to shape the narrow distribution and rarity of *S.*

bryophora var. *tobiasiae*.

The findings of this study provide several key areas of focus for conservation of *Saxifraga bryophora* var. *tobiasiae*. Habitat-based management is essential for this taxon. *Saxifraga bryophora* var. *tobiasiae* is uniquely adapted to the granitic habitat islands of this region and is dependent upon the natural disturbance patterns associated with these islands. The introduction of exotic species through sheep and cattle grazing threatens the habitat in which *S. bryophora* var. *tobiasiae* populations exist.

Expansion of *Saxifraga bryophora* var. *tobiasiae* populations can be facilitated through bulbil transplantation. These individuals are short lived but are capable of establishing and reproducing in new habitats. Eastern aspects should be utilized in transplantation efforts to improve the chances for establishment and to increase the likelihood for survival and reproduction. Additionally, the ecological factors identified in classification tree analysis and soil characterization should be used to identify suitable habitat for the expansion of *Saxifraga bryophora* var. *tobiasiae* populations.

Monitoring of permanent plots established in this study will also provide long-term demographic information of *Saxifraga bryophora* var. *tobiasiae* populations and may be used to further elucidate factors that contribute to its rarity and endemic distribution.

APPENDICES

APPENDIX A. TABLES: CLASSIFICATION TREE MODELS

TABLE A.1. Classification tree model for 1995 data. ^a

Node	Split	n	deviance	Y value
1) root		144	198.300	yes
2) Soil < 2.5		34	24.630	no*
3) Soil > 2.5		110	122.605	yes
6) Letr < 1.5		27	37.101	no*
7) Letr > 1.5		83	68.593	yes*

^a * = denotes terminal node.

TABLE A.2. Classification tree model for 1996 data. ^a

Node	Split	n	deviance	Y value
1) root		144	198.300	yes
2) Letr < 3.5		77	99.550	no*
4) Soil < 2.5		25	8.397	no
5) Soil > 2.5		52	71.390	no
10) Ergr < 1		41	56.620	yes*
11) Ergr > 1		11	6.702	no*
3) Letr > 3.5		67	62.980	yes
6) Vasc < 2.5		57	33.880	yes
12) Poju < 14.5		40	0.000	yes*
13) Poju > 14.5		17	20.600	yes*
7) Vasc > 2.5		10	12.220	yes*

^a * = denotes terminal node.

APPENDIX B. FIGURES: SOIL DESCRIPTION SHEETS

USU SOIL DESCRIPTION SHEET SOIL # 1 - in habitat DESCRIBED BY: Kim Pierson DATE: 9/16/96

soil series _____ phase _____ location (USGS Quad) Black Tip

parent material grano-diorite elevation 7600' slope 0% aspect N-NW drainage class well drained

landform toeslope climate _____

natural cover Sax. bry. tob / Polytrichum / Lewisiatrichillum

MAP MAT MAST MSST MWST

water table surface stone and rock

HORIZON	DEPTH (mm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr. sl. sh	CONSISTENCE			REACTION		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
						dry	moist	wet	pH	eff			
Oe	0-25	a,s	10YR 4/2	SL	1 wg	FR	ss/po	6.8	eo	F	IVF		
A	25-40	a,s	10YR 3/3	SL	1 w sbk	FR	ss/po	6.8	eo	IVF	IVF		
AB	40-70	c,s	7.5 YR 3/2	VFSL	1 w sbk	FR	ss/po	7.0	eo	IVF	IVF		
B	70-110	g,w	10YR 4/3	VFSL	1 w sbk	FR	ss/ps	7.0	eo	IVF	IVF		
R	110												

REMARKS (Present Landuse) large granite boulders surrounding soil "pools", shallow soil between boulders

DIAGNOSTIC EPEDON, HORIZONS AND OTHER CHARACTERISTICS Ochr

CLASSIFICATION (Family) Loamy, Mixed, Semiactive, Nonacid Lithic Cryorthent

Fig. B.1. Field description sheet for east side soil pedon #1.

USU SOIL DESCRIPTION SHEET SOIL # 2 - in habitat DESCRIBED BY: Kim Pierson DATE: 9/16/96

soil series phase location (USGS Quad) Black Tip

parent material granodiorite elevation 7600' slope 2% aspect N-NW drainage class well drained

landform climate

natural cover Sax. bry. tob / Polytrichum / Lewisia triphylla

HORIZON	DEPTH (mm)	BDY (d.t.)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr. si. sh	CONSISTENCE			REACTION		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
						dry	moist	wet	pH	eff			
O _e	0-15	a, s	7.5 YR 3/2	FSL	3 VF GR	FR	so	po	6.8	eo	IVF	IVF	
O _A	15-40	a, s	10 YR 3/1	VFSL	3 F GR	FR	so	po	6.8	eo	IVF	IVF	
A	40-70	c, s	10 YR 3/2	FSL	3 M GR	FR	ss	po	6.8	eo	IVF	IVF	
AB	70-100	g, w	10 YR 3/3	SL	2 C sbk	FI	ss	po	6.8	eo	IVF	IVF	
BC	100-140	g, w	7.5 YR 3/4	SL	2 W sbk	FI	ss	po	7.0	eo	IVF	IVF	gravelly
CR	140-190	g, w	10 YR 4/3	SL	2 W sbk	VFI	sq	po	7.0	eo	IVF	none	
R	190												

REMARKS (Present Landuse) Saxi plants taller, deep soil pool

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS Mollic

CLASSIFICATION (Family) Loamy, Mixed, Semiactive, Nonacid Lithic Cryoboroll

Fig. B.2. Field description sheet for east side soil pedon #2.

USU SOIL DESCRIPTION SHEET				SOIL # 3 in habitat		DESCRIBED BY: Kim Pierson		DATE: 9/16/96				
soil series			phase			location (USGS Quad)						
parent material			elevation			slope		aspect				
granodiorite			8000'			2%		W				
landform			climate			drainage class						
						well drained						
natural cover					MAP		MAT		MAST			
Sax. bry. tob/ surrounded by Aster, Phyllodoce					water table		MSST		MWST			
					surface stone and rock							
HORIZON	DEPTH (cm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr. sl. sh	CONSISTENCE dry moist wet			REACTION pH eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
O _a	0-20	d, w	10 YR 3/1	CSL	3 sg		VFR	50/po	6.8 eo	2VF	1VF	
A	20-35	a, s	10 YR 3/1	FSL	3 fg		FR	50/po	6.8 eo	2VF	1VF	
AB	35-70	d, s	10 YR 3/2	CSL	3 cg		FR	50/ps	6.8 eo	3VF	1VF	
BA	70-110	a, s	5 YR 3/2	VFSL	3 w sbk		FR	50/ps	7.0 eo	3VF to F	1VF	
BC	110-150	d, w	7.5 YR 3/2	CSL	2 mtsbk		FR	50/po	7.0 eo	1F + L	none	
BC ₂	150-190	a, w	7.5 YR 3/4	gSL	2 mtsbk		FR	50/po	7.0 eo	1L	none	
C	190-240	a, w	5 YR 3/2	VFSL	2C sbk		FR	S/p	7.0 eo	none	none	
CR	240-270	a, s	10 YR 3/4	SiL	2 w sbk		FI	S/po	7.0 eo	none	none	
REMARKS (Present Landuse)												
R 270												
DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS												
Mollic Epipedon												
CLASSIFICATION (Family)												
Loamy, Mixed, Semiactive, Nonacid Lithic Cryoboroll												

Fig. B.3. Field description sheet for east side soil pedon #3.

USU SOIL DESCRIPTION SHEET SOIL # 4 - non habitat DESCRIBED BY: Kim Kierson DATE: 9/16/96

soil series phase location (USGS Quad)

parent material elevation slope aspect drainage class

landform climate

natural cover MAP MAT MAST MSST MWST

JUPA, VASC, LUHF, Lewisia water table surface stone and rock

HORIZON	DEPTH (cm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, sl, sh	CONSISTENCE dry moist wet			REACTION pH eff		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
Oe	0-30	a,s	10 YR 3/2	CSL	3 C gr	VFR	s/p	6.8	eo	1VF	1VF		
Oa	30-60	a,s	10 YR 3/2	SL	3 F Gr	VFR	s/p	6.8	eo	2F	1VF		
A	60-80	a,i	10 YR 3/3	FSL	2 VF Gr	FR	s/p	7.0	eo	2F	1VF		
AB	80-110	a,w	7.5 YR 3/4	VFSL	3 w sbk	FR	s/p	7.0	eo	2F	1VF		
BC	110-150	a,i	10 YR 4/4	SIL	3 c sbk	FR	vs/p	7.2	eo	1L	1VF		
R	150												

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

CLASSIFICATION (Family)

Ochnic Epipedons, cambic ep horizons

Loamy, Mixed, Semiaactive, Nonacid Lithic Cryochrepts

Fig. B.4. Field description sheet for east side soil pedon #4.

USU SOIL DESCRIPTION SHEET SOIL # 5 nonhabitat DESCRIBED BY: Kim Pierson DATE: 9/16/96

soil series location (USGS Quad) Buck Tip

parent material Grand-Diorite elevation 8000' slope flat aspect W drainage class well drained

landform Ridgetop climate

natural cover MAP MAT MAST MSST MWST

ANLA, Polytrichum, JUPA, VASC water table surface stone and rock

HORIZON	DEPTH (cm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, si, sh	CONSISTENCE dry moist wet			REACTION pH eff		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
Oa	0-1A	a,s	5YR 3/2	VCs	3C Gr		VFR	ss/po	7.0	eo	1VF	1VF	
A	1A-6A	d,s	10YR 3/1	Cs	3M Gr		VFR	ss/po	6.8	co	3F to VF	1VF	
AB	6A-82	a,s	10YR 3/1	GCoSL	3C Gr		VFR	ss/po	6.8	eo	2F	1VF	
B	82-109	a,i	10YR 3/2	SL	2wsbk		FR	ss/po	7.0	eo	2F	1VF	
BC	109-160	a,w	5YR 3/2	FSL	1wsbk		FI	ss/po	7.0	eo	1F	1VF	
R													

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

CLASSIFICATION (Family) Mollic Epipedon

Loamy, Mixed, Semiaactive, Nonacid Lithic Cryoborol

Fig. B.5. Field description sheet for east side soil pedon #5.

USU SOIL DESCRIPTION SHEET SOIL # 6 in habitat DESCRIBED BY: Kim Pierson DATE: 9/16/96

soil series phase location (USGS Quad)

parent material elevation slope aspect drainage class

landform climate

ridge top MAP MAT MAST MSST MWST

natural cover water table surface stone and rock

Sax. bry. top / Polytrichum / Ant. lan / Luz. hit / Jun. par

HORIZON	DEPTH (cm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr. si. sh	CONSISTENCE dry moist wet	REACTION pH eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
Da	0-31	a, s	10 YR 3/1	SL	3 S Gr	VFR ss/po	6.8 eo	3VF	1VF	
A	31-60	a, i	10 YR 3/2	FSL	3 mt gr	VFR ss/po	6.8 eo	2VF	1VF	
AB	60-92	a, w	10 YR 3/3	FSL	2 csbk	FR s/p	6.8 eo	3FbL	1VF	
B	92-124	a, w	10 YR 3/4	CSiL	2 mtsbk	FR s/po	7.0 eo	2M	1VF	
BC	124-155	a, s	7.5 YR 3/4	g FSL	1 wsbk	FI ss/po	7.0 eo	1M	1VF	
CR	155-188	a, w	10 YR 3/6	g SL	1 wsbk	FI ss/po	7.2 eo	none	none	
R										

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

CLASSIFICATION (Family)

Ochric Epipedon, Cambic horizon

Loamy, Mixed, Semiactive, Nonacid Lithic Cryochrept

Fig. B.6. Field description sheet for east side soil pedon #6

USU SOIL DESCRIPTION SHEET SOIL # 7 - non habitat DESCRIBED BY: Kim Pierson DATE: 9/17/96

soil series phase location (USGS Quad)

parent material elevation slope aspect drainage class

landform climate

natural cover MAP MAT MAST MSST MWST

JUPA, VASC, LUHI, Mulenbergia

HORIZON	DEPTH (cm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, sl, sh	CONSISTENCE dry, moist, wet	REACTION pH, eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
Oa	0-32	a, s	10YR 2/1	FSL	2 mt gr	VFR ss/p	7.0 eo	3VF	1VF	
A ₁	32-64	a, s	10YR 3/2	FSL	2 c sbk	FR ss/ps	7.0 eo	3VF	1VF	
A ₂	64-90	a, s	10YR 3/3	SL	2 c sbk	FR ss/ps	7.0 eo	2F	1VF	
BA ₁	90-130	a, s	10YR 3/4	FSL	2 w sbk	FR ss/p	7.0 eo	2F	1VF	
BA ₂	130-230	a, s	10YR 3/4	CSL	2 mt gr	FR ss/po	7.0 eo	3F-C	1VF	
B	230-280	a, s	10YR 4/4	GCSL	3 w sbk	VFR ss/po	7.2 eo	1 L	1VF	
BC	280-330	a, s	10YR 4/4	GSL	2 w sbk	VFR ss/po	7.2 eo	1 F	—	
CR	330-390	a, w	5Y 4/4	VFSL	2 w pt	VFR ss/po	7.2 eo	—	—	

REMARKS (Present Landuse)

R

DIAGNOSTIC EPIPEDON, HORIZONS, AND OTHER CHARACTERISTICS

Ochnic Epipedon, Cambic Horizon

CLASSIFICATION (Family)

Loamy, Mixed, Semiactive, Nonacid Loamy Cryochrepts

Fig. B.7. Field description sheet for east side soil pedon #7.

USU SOIL DESCRIPTION SHEET SOIL # 8 - non veg - po. habitat DESCRIBED BY: Kim Pierson DATE: 9/17/96

soil series phase location (USGS Quad) Black Tip

parent material elevation 8200' slope flat aspect W to NW drainage class well drained

landform ridgetop climate

natural cover MAP MAT MAST MSST MWST

Polytrichum / Phyllocladus / VASC / ANLA water table surface stone and rock

HORIZON	DEPTH (cm) mm	BDP (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, si, sh	CONSISTENCE dry moist wet			REACTION pH eff		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
Oa	0-30	a, s	10YR 3/1	gr S	3 st gr	VFR	ss/po	6.8	eo	3 F-VF	IVF		
A	30-55	a, s	10YR 4/2	gr SL	3 mt gr	FR	ss/po	6.8	eo	3 VF	IVF		
AB	55-90	a, w	10YR 3/2	gr FSL	2 w sbk	FR	ss/po	7.0	eo	2 F	IVF		
B	90-150	a, s	10YR 4/3	gr CSL	3 mt gr	VFR	ss/po	7.0	eo	2 F	IVF		
BC	150-170	a, s	10YR 5/3	FSL	2 w sbk	FR	ss/po	6.8	eo	1 F	IVF		
R													

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

CLASSIFICATION (Family) Ochric Epipedon, Loamy, Mixed, Semiactive, Nonacid ~~Loam~~ Lithic Cryorthent

Fig. B.8. Field description sheet for east side soil pedon #8.

USU SOIL DESCRIPTION SHEET SOIL # 9 - in habitat DESCRIBED BY: Kim Pierson DATE: 9/17/96

soil series		phase		location (USGS Quad)	
				Black Tip	
parent material		elevation	slope	aspect	drainage class
Grano-dionite		8200'	2%	NW	well drained
landform		climate			
ridgetop					
natural cover		MAP	MAT	MAST	MSST MWST
Sax. bry. tobo / JUPA / ASKY / Lig. can		water table		surface stone and rock	

HORIZON	DEPTH mm	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr. sl. sh	CONSISTENCE			REACTION	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
						dry	moist	wet	ph eff			
O	0-31	a, s	10 YR 3/1	grcs	3 St gr		VFR	sq/po	7.0 eo	3F	IVF	
A	31-70	a, w	10 YR 3/2	g CSL	3 mt gr		FR	ss/ps	7.2 eo	2F	IVF	
AB	70-100	a, w	10 YR 3/3	g SL	2 w sbk		FR	ss/ps	7.0 eo	1 L	IVF	
B	100-119	a, w	10 YR 4/2	SL	2 c sbk		FR	sq/po	7.0 eo	1 L	IVF	
BC	119-150	a, i	10 YR 4/4	FSL	2 w sbk		FR	ss/po	7.2 eo	-	-	
CR	150-190	g, w	10 YR 4/3	SL	2 w sbk		FI	sq/po	7.0 eo	-	-	
R												

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

CLASSIFICATION (Family)

Mollic

Loamy - skeletal, Mixed, Semiactive, Nonacid Lithic Cryoboroll

Fig. B.9. Field description sheet for east side soil pedon #9.

USU SOIL DESCRIPTION SHEET SOIL # 10 - in habitat DESCRIBED BY: Kim Pierson DATE: 9/17/96

soil series phase location (USGS Quad) Black Tip

parent material Grano - Diorite elevation 8200' slope Flat aspect NW drainage class well drained

landform climate

natural cover MAP MAT MAST MSST MWST

Sax. bry. tob/ JUPA/ Polytrichum/ ANLA/ Phyllocladus water table surface stone and rock

HORIZON	DEPTH (cm)	BDY (d.t.)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr. si. sh	CONSISTENCE dry moist wet	REACTION pH eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
O	0-30	a ₁ s	10YR 3/2	CSL	3 mtgr	VFR ss/p	7.0 eo	2VF	IVF	
A	30-66	d ₁ s	10YR 3/1	SL	2 mtgr	FR ss/ps	7.0 eo	2F	IVF	
AB	66-110	d ₁ s	10YR 3/3	gSL	2 wsbk	FR s/p	7.0 eo	2F	IVF	
BA	110-150	a ₁ w	7.5 YR 3/2	FSL	2 c sbk	FR ss/po	7.0 eo	2L	IVF	
BC	150-190	a ₁ w	10YR 4/3	gFSL	3 wsbk	FR so/po	7.2 eo	1L	-	
CR	190-240	a ₁ i	10YR 5/3	CoSL	3 st gr	VFR ss/po	7.2 eo	-	-	
R										

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

CLASSIFICATION (Family) Mollic Epipedon

Loamy, Mixed, Semiactive, Nonacid Lithic Cryoboroll

Fig. B.10. Field description sheet for east side soil pedon #10.

USU SOIL DESCRIPTION SHEET SOIL # 11 - nonhabitat DESCRIBED BY: Kim Pierson DATE: 9/17/96

soil series location (USGS Quad) phase Black Tip

parent material granodiorite elevation 8000' slope flat aspect W to NW drainage class well drained

landform climate

natural cover JUPA / Polytichum / Lewisia / VASC / LUHI

HORIZON	DEPTH (cm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, si, sh	CONSISTENCE			REACTION pH eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
						dry	moist	wet				
Oa	0-5	a, s	10 YR 3/1	g s	2 st gr		VFR	ss/po	6.8 eo	—	IVF	
A	5-30	a, s	10 YR 3/2	FSL	2 w sbk		FR	ss/po	7.0 eo	1 VF	IVF	
AB	30-44	a, w	10 YR 2/2	FSL	2 c sbk		FR	so/po	6.8 eo	3F	IVF	
CR	44-60	a, w	10 YR 3/1	FSL	2 st sbk		FR	ss/po	6.8 eo	1F	—	
R	60											

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

Ochric Epipedon

CLASSIFICATION (Family)

Loamy, Mixed, Semiactive, Nonacid Lithic Cryorthent

Fig. B.11. Field description sheet for east side soil pedon #11.

USU SOIL DESCRIPTION SHEET SOIL # 12 - in habitat DESCRIBED BY: Kim Pierson DATE: 9/17/96

soil series		phase		location (USGS Quad)								
parent material		elevation	slope	aspect	drainage class							
Orano - diorite		8200'	5%	NW	well drained							
landform		climate										
just below ridgetop												
natural cover		MAP	MAT	MAST	MSST	MWST						
Sax. bry. tob / JUPA / Lig. can / Phyllodoce / ANLA / JUPA		water table		surface stone and rock								
HORIZON	DEPTH (mm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr. sl. sh	CONSISTENCE dry moist wet			REACTION pH eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
Oa	0-25	a1w	10YR 2/1	CSL	3 st gr	VFR	ss/p	7.0 eo	3VF	IVF		
A	25-47	a1s	10YR 3/2	FSL	3 c sbk	FR	ss/p	7.0 eo	3F	IVF		
AB	47-76	a1w	10YR 3/3	FSL	3 mtsbk	FR	s/p	7.0 eo	3F	IVF	> 50% Rock	
BA	76-130	d1w	10YR 3/4	g SL	2 st gr	FR	ss/po	7.0 eo	2F	IVF	> 50% Rock	
BC	130-160	a1w	10YR 4/2	CoSL	2 c sbk	VFR	ss/po	7.2 eo	2F	IVF	> 50% Rock	
CB	160-180	a1w	10YR 4/4	g SL	2 w sbk	FR	ss/po	7.2 eo	2F	—	> 50% Rock	
CR	180-196	a1w	5Y 4/2	FSL	2 w sbk	FR	s/p	7.2 eo	—	—		
R												

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

Ochnic Epipedon, Cambic Horizon

CLASSIFICATION (Family)

Loamy-skeletal, Mixed, Semiactive, Nonacid Lithic Cryochrept

Fig. B.12. Field description sheet for east side soil pedon #12.

USU SOIL DESCRIPTION SHEET SOIL # 13 - non habitat DESCRIBED BY: Kim Pierson DATE: 9/17/96

soil series		phase		location (USGS Quad)						
parent material		elevation	slope	aspect	drainage class					
Grano-diorite		8200'	flat	W	well drained					
landform		climate								
ridgetop-bench										
natural cover		MAP	MAT	MAST	MSST					
Polytrichum/ANLA/VASC/Liq.can/JUPA/		water table		surface stone and rock						
HORIZON	DEPTH (cm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, sl, sh	CONSISTENCE dry moist wet	REACTION pH eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
Oa	0-31	a,s	7.5 YR 3/0	g S	3 stgr	VFR 50/po	7.0 eo	3F	IVF	
A	31-61	g,s	10 YR 3/1	g SL	3 mtgr	VFR 50/po	7.0 eo	1F	IVF	
AB	61-110	a,s	10 YR 3/2	CSL	2 w sbk	FR 50/po	7.0 eo	2F	IVF	
BA	110-155	g,s	10 YR 4/3	g CoSL	3 C sbk	FR 50/po	7.2 eo	2 L	IVF	
B ₁	155-180	a,w	10 YR 4/4	g FSL	2 C sbk	FR 50/po	7.2 eo	2 M	IVF	
B ₂	180-220	a,s	10 YR 5/3	CoSL	2 w sbk	FR 50/po	7.2 eo	1F	-	
BC	220-240	a,w	10 YR 4/4	FSL	2 w sbk	FR 50/po	7.2 eo	-	-	
CR	240-300	a,w	10 YR 4/6	FSL	2 w sbk	FR 5/ps	7.2 eo	-	-	

REMARKS (Present Landuse)
R 300

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS
Mollic

CLASSIFICATION (Family)
Loamy, Mixed, Semiactive, Nonacid Lithic Cryoboroll

Fig. B.13. Field description sheet for east side soil pedon #13.

USU SOIL DESCRIPTION SHEET SOIL # 14-non habitat DESCRIBED BY: Kim Pierson DATE: 9/17/96

soil series phase location (USGS Quad)
 parent material Grano- Diorite elevation 8200' slope flat aspect N drainage class well drained
 landform bench climate

natural cover MAP MAT MAST MSST MWST
 LUH1 Mulenburgia/ANLA/Lewisia water table surface stone and rock

HORIZON	DEPTH (cm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, si, sh	CONSISTENCE dry moist wet			REACTION pH eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
Oa	0-29	a,s	10 YR 2/2	CSL	3 mt gr	VFR	so	po	6.8 eo	IVF	IVF	
A	29-55	g,s	10 YR 3/2	FSL	2 C gr	VFR	ss	po	6.8 eo	2VF	IVF	
A/B	55-82	a,w	10 YR 3/3	g SL	2 mt gr	FR	so	po	7.0 eo	3 L	IVF	
AB	82-110	a,w	10 YR 3/3	g FSL	3 C sbk	VFR	so	po	6.8 eo	2F	IVF	
B	110-150	a,s	10 YR 4/3	FSL	2 mt sbk	FR	ss	ps	7.0 eo	IVF	IVF	
BC	150-180	a,s	10 YR 4/4	SL	2 w sbk	FR	so	po	6.8 eo	—	—	
CR	180-203	a,w	10 YR 4/6	FSL	2 mt sbk	VFR	so	po	6.8 eo	—	—	
R	203											

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS
 Mollic Epipedon

CLASSIFICATION (Family)
 Loamy, Mixed, Semiactive, Nonacid Lithic Cryoboroll

Fig. B.14. Field description sheet for east side soil pedon #14.

USU SOIL DESCRIPTION SHEET SOIL #15 in habitat DESCRIBED BY: Kim Pierson DATE: 9/18/96

soil series phase location (USGS Quad)

parent material Grano-diorite elevation 8000' slope 40% aspect E drainage class well drained

landform on slope climate MAP MAT MAST MSST MWST

natural cover Sax. bry. top / HYFO / ANLU / XETE water table surface stone and rock

HORIZON	DEPTH (cm) mm	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr. si. sh	CONSISTENCE			REACTION		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
						dry	moist	wet	pH	eff			
Oa	0-25	a, s	10 YR 7/2	g FSL	3 st gr		VFR	ss/p	6.8	eo	3VF	1VF	
A	25-80	a, s	10 YR 3/1	Co SL	3 w gr		VFR	ss/p	6.8	eo	3VF	1VF	> 50% Rock
AB	80-120	a, w	10 YR 3/2	FSL	2 w sbk		FR	ss/p	6.8	eo	3F	1VF	> 50% Rock
CR	120-170	a, w	10 YR 4/4	g SL	2 w sbk		FR	ss/p	7.0	eo	1F	1VF	> 50% Rock
R	170												

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

CLASSIFICATION (Family) Mollic Epipedon

Loamy-skeletal, Mixed, Semiactive, Nonacid Lithic Cryoboroll

Fig. B.15. Field description sheet for west side soil pedon #15.

USU SOIL DESCRIPTION SHEET SOIL # 16 - non habitat DESCRIBED BY: Kim Pierson DATE: 9/19/96

soil series phase location (USGS Quad) Black Tip

parent material Grano-diorite elevation 7600' slope flat aspect E drainage class well drained

landform bench climate

natural cover Lig. can / JUPA / POPH

HORIZON	DEPTH (cm)	BDY (d.t.)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, si, sh	CONSISTENCE			REACTION		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
						dry	moist	wet	pH	eff			
Oa	0-25	a, s	10 YR 3/1	g SL	3 st gr		VFR	ss/po	7.0	eo	IVF	IVF	
A	25-112	a, w	10 YR 3/2	Co SL	2 w sbk		FR	ss/ps	7.2	eo	2 F	IVF	
AB	112-165	a, w	10 YR 3/3	Co SL	3 mt gr		FR	ss/po	7.2	eo	-	-	
R	165												

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS Mollic Epipedon

CLASSIFICATION (Family) Loamy, Mixed, Semiactive, Nonacid Lithic Cryoboroll

Fig. B.16. Field description sheet for west side soil pedon #16.

USU SOIL DESCRIPTION SHEET SOIL # 17 - non veg DESCRIBED BY: Kim Pierson DATE: 9/18/96

soil series		phase		location (USGS Quad)	
				Black Tip	
parent material		elevation	slope	aspect	drainage class
Grano-diorite		8200'	flat	E	well drained
landform		climate			
bench					
natural cover		MAP	MAT	MAST	MSST MWST
JUPA/LUHI/POPH/VASC/ANLA		water table		surface stone and rock	

HORIZON	DEPTH (cm) mm	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, sl, sh	CONSISTENCE			REACTION		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
						dry	moist	wet	pH	eff			
O	0-22	a, s	10 YR 3/1	g CoSL	3 st gr		VFR	50/po	6.8	eo	2 VF	1 VF	
A	22-45	a, w	10 YR 2/1	CoSL	2 w gr		VFR	55/po	6.8	eo	2 F	1 VF	
AB	45-80	d, w	10 YR 3/3	SL	2 c sbk		FR	50/po	6.8	eo	3 VF	1 VF	
BA	80-105	a, w	10 YR 3/4	g FSL	2 c sbk		VFR	50/po	6.8	eo	3 F	1 VF	
CR	105-140	a, w	10 YR 4/4	FSL	3 mt sbk		FR	55/po	6.8	eo	1 L	—	
R	140												

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

Ochric Epipedon

CLASSIFICATION (Family)

Loamy, Mixed, Semiactive, Nonacid Lithic Cryorthent

Fig. B.17. Field description sheet for west side soil pedon #17.

USU SOIL DESCRIPTION SHEET SOIL # 18 - in habitat DESCRIBED BY: Kim Pierson DATE: 9/18/96

soil series phase location (USGS Quad) Black Tip

parent material Grano-diorite elevation 8200' slope 2% aspect E drainage class well drained

landform bench climate MAP MAT MAST MSST MWST

natural cover ANLA/Sax.bry.bb/JUPA/Polytrichum/Lewisia/XETE water table surface stone and rock

HORIZON	DEPTH (cm) mm	BØY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr. sl. sh	CONSISTENCE			REACTION		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
						dry	moist	wet	pH	eff			
Oi	0-32	a, s	10YR 3/1	g SL	2 mt gr		VFR	so/ps	6.8	eo	3VF	IVF	
Oa	32-55	a, s	10YR 3/2	CoSL	2 w gr		VFR	so/po	6.8	eo	3F	IVF	
A	55-86	a, s	10YR 3/2	FSL	3 st sbk		FR	ss/ps	6.8	eo	3F	IVF	
AB	86-134	d, w	10YR 3/3	g SL	3 c sbk		VFR	s/ps	6.8	eo	2F	IVF	
BA	134-190	d, w	10YR 3/4	FSL	2 mt gr		FR	ss/ps	6.8	eo	2F	IVF	
CR	190-230	a, w	10YR 3/3	FSL	2 w sbk		FR	ss/ps	6.8	eo	1L	IVF	
R	230												

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

CI ASSIFICATION (Family) Mollic Epipedon

Loamy, Mixed, Semiactive, Nonacid Lithic Cryoboroll

Fig. B.18. Field description sheet for west side soil pedon #18.

USU SOIL DESCRIPTION SHEET SOIL # 19 - in habitat DESCRIBED BY: Kim Kiersorn DATE: 9/18/96

soil series phase location (USGS Quad) Black Tip

parent material Grano-diorite elevation 8200+ slope Flat aspect E drainage class well drained

landform bench climate

natural cover MAP MAT MAST MSST MWST

Sax. bry. tob / VASC / JUFA / ANLA / Aster water table surface stone and rock

HORIZON	DEPTH (cm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr. sl. sh	CONSISTENCE dry moist wet			REACTION pH eff		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
Oi	0-28	a,s	10 YR 2/1	FSL	3 st gr	VFR	s/p	6.8	eo	3VF	IVF		
Oa	28-71	d,s	10 YR 3/2	CoSL	2 st sbk	FR	s/p	6.8	eo	2F	IVF		
A	71-120	d,s	10 YR 3/3	g FSL	2 c sbk	FR	s/p	6.8	eo	1L	IVF		
A ₂	120-165	d,w	10 YR 2/2	FSL	2 w sbk	FR	s/p	6.8	eo	3L	IVF		
AB	165-210	a,w	10 YR 3/3	FSL	2 c sbk	FI	s/p	6.8	eo	2L	IVF		
BA	210-270	a,w	10 YR 3/3	VFSL	2 c sbk	FI	s/p	6.8	eo	2L	IVF		
BC	270-320	a,w	10 YR 3/2	FSL	2 w sbk	FI	ss/p	6.8	eo	1L	—		
CR	320-350	a,w	10 YR 5/3	SL	2 st gr	VFR	ss/p	6.8	eo	2M	—		

REMARKS (Present Landuse)
R 350

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS
Mollic Epipedon

CLASSIFICATION (Family)
Loamy, Mixed, Semiaactive, Nonacid Lithic Cryoboroll

Fig. B.19. Field description sheet for west side soil pedon #19.

USU SOIL DESCRIPTION SHEET SOIL # 20 - in habitat DESCRIBED BY: Kim Pierson DATE: 9/18/96

soil series		phase		location (USGS Quad)	
				Black Tip	
parent material		elevation	slope	aspect	drainage class
Granodiorite		8200+	flat	N to NE	well drained
landform		climate			
bench					
natural cover		MAP	MAT	MAST	MSST MWST
ANLA / Dodonaea / Phyllodoce / Polytrichum		water table		surface stone and rock	

HORIZON	DEPTH (cm) mm	BDY (d.t.)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, sl, sh	CONSISTENCE			REACTION		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
						dry	moist	wet	pH	eff			
Oi	0-21	a.s	10 YR 3/2	g SL	3 st gr		VFR	ss/ps	6.8	eo	3VF	1VF	
Oa	21-35	d.s	10 YR 3/1	FSL	2 c sbk		FR	ss/po	6.8	eo	3VF	1VF	
A	35-60	a.s	10 YR 2/2	FSL	2 w sbk		FR	ss/p	6.8	eo	2F	1VF	
AB	60-78	a.w	10 YR 3/3	FSL	2 mt sbk		FR	ss/p	7.0	eo	1L	-	
R	78												

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

Ochric Epipedon

CLASSIFICATION (Family)

Loamy, Mixed, Semiactive, Nonacid Lithic Cryorthent

Fig. B.20. Field description sheet for west side soil pedon #20.

USU SOIL DESCRIPTION SHEET		SOIL # 21 - non veg		DESCRIBED BY: Kim Pierson		DATE: 9/18/96				
soil series		phase		location (USGS Quad)						
parent material		elevation		slope		aspect				
Grano - diorite		8200'		2%		N				
landform		climate		drainage class						
bench				well drained						
natural cover		MAP		MAT		MAST				
Phyllodoce / Cassiope / Polytrichum / XETE / ANLA				water table		MSST				
						MWST				
						surface stone and rock				
HORIZON	DEPTH (cm) mm	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, si, sh	CONSISTENCE dry, moist, wet	REACTION pH, eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
Oi	0-27	d.s	10 YR 3/2	gFSL	3 stsbk	VFR ss/ps	6.8 eo	3VF	IVF	
Oa	27-56	a.w	10 YR 3/3	FSL	3st sbk	FR ss/p	6.8 eo	3F	IVF	
A	56-107	g.s	10 YR 3/4	FSL	2 w sbk	FR ss/p	6.8 eo	3M	IVF	
AB	107-160	g.s	10 YR 4/4	VFSL	2c sbk	FI ss/p	6.8 eo	2L	IVF	
B	160-210	g.w	10 YR 4/4	CsL	2st sbk	FR ss/ps	6.8 eo	3L	IVF	
CR	210-240	a.w	10 YR 3/4	SL	2 w sbk	FR s/p	6.8 eo	2F	-	
R	240									
REMARKS (Present Landuse)										
DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS										
Ochnic Epipedon, Cambic horizon										
CLASSIFICATION (Family)										
Loamy, Mixed, Semiactive, Nonacid Lithic Cryochrept										

Fig. B.21. Field description sheet for west side soil pedon #21.

USU SOIL DESCRIPTION SHEET SOIL # 22 - in habitat DESCRIBED BY: Kim Pierson DATE: 9/18/96

soil series		phase		location (USGS Quad)						
parent material		elevation	slope	aspect	drainage class					
Grano-diorite		8300'	10%	E	well drained					
landform		climate								
slope										
natural cover		MAP	MAT	MAST	MSST MWST					
Sax. bry. tob / Polytichum / ANLA / VASC / HYFO / Phyll.		water table		surface stone and rock						
HORIZON	DEPTH (cm) mm	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr. si. sh	CONSISTENCE dry moist wet	REACTION pH eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
Oi	0-29	a.1s	10 YR 3/1	g SL	3 st gr	VFR 50/po	6.8 eo	2F	1VF	
Oa	29-59	a.1s	10 YR 2/1	g SL	3 mt gr	VFR 50/po	6.8 eo	2VF	1VF	
A	59-107	a.1w	10 YR 3/2	g FSL	2 c sbk	FR 50/po	6.8 eo	3VF	1VF	
AB	107-158	a.1w	10 YR 3/3	FSL	2 c sbk	FR 50/po	6.8 eo	2VF	1VF	
B	158-191	a.1s	10 YR 4/3	g SL	3 w sbk	FR 50/ps	6.8 eo	2VF	1VF	35% Rock
CR	191-225	a.1w	10 YR 5/3	FSL	3 mt gr	VFR 50/po	7.2 eo	-	-	
R	225									
REMARKS (Present Landuse)										
DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS										
Mollic Epipedon										
CLASSIFICATION (Family)										
Loamy-skeletal, Mixed, Semiactive, Nonacid Lithic Cryoboroll										

Fig. B.22. Field description sheet for west side soil pedon #22.

USU SOIL DESCRIPTION SHEET SOIL # 24 - in habitat DESCRIBED BY: Kim Pierson DATE: 9/18/96

soil series		phase		location (USGS Quad)						
				Black Tip						
parent material		elevation	slope	aspect	drainage class					
Grano - diorite		8400'	5%	E to SE	well drained					
landform		climate								
rock bench										
natural cover		MAP	MAT	MAST	MSST MWST					
Sax. by job / ANLA / Carex / Phlox / ANLA / Aster		water table		surface stone and rock						
HORIZON	DEPTH (cm)	BDY (d.t.)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, si, sh	CONSISTENCE dry moist wet	REACTION pH eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
O _i	0-34	g.s	7.5 YR 3/2	g SL	3 st sbk	VFR 50/po	6.8 eo	3VF	IVF	
O _a	34-62	g.s	10 YR 3/2	g FSL	2 c sbk	VFR 50/ps	6.8 eo	2VF	IVF	
A	62-100	a.s	10 YR 3/1	FSL	3 mt sbk	FR 50/ps	6.8 eo	1L	IVF	
AB	100-148	a ₁ w	10 YR 2/1	g FSL	3 w sbk	FR 50/ps	6.8 eo	1L	IVF	
CR	148-205	a ₁ w	10 YR 3/3	g SL	3 st gr	VFR 50/po	7.0 eo	1F	IVF	
R	205									

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

CLASSIFICATION (Family)

Mollic Epipedon

Loamy-skeletal, Mixed, Semiactive, Nonacid Lithic Cryoboroll

Fig. B.24. Field description sheet for west side soil pedon #24.

USU SOIL DESCRIPTION SHEET SOIL # 25 - nonhabitat DESCRIBED BY: Kim Pierson DATE: 9/18/96

soil series		phase		location (USGS Quad)	
parent material		elevation	slope	aspect	drainage class
landform		climate			
natural cover		MAP	MAT	MAST	MSST MWST
ANLA/Canex/		water table		surface stone and rock	

HORIZON	DEPTH (cm) mm	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, si, sh	CONSISTENCE			REACTION		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
						dry	moist	wet	ph	eff			
Oi	0-35	g.s	10 YR 3/1	g SL	3 st gr		VFR	ss/po	6.8	eo	3VF	IVF	
Oa	35-70	g.s	10 YR 3/2	SL	2 mt gr		FR	ss/po	6.8	eo	3VF	IVF	
A	70-115	a.s	10 YR 3/3	FSL	3 mtsbk		FR	ss/po	7.0	eo	3F	IVF	
AB	115-148	a.s	10 YR 4/2	g SL	2 c sbk		FR	ss/po	7.0	eo	3F	IVF	
BC	148-180	a.w	10 YR 3/3	g c SL	2 w sbk		FR	ss/po	7.0	eo	1L	—	
CR	180-201	a.w	10 YR 4/4	FSL	2 mt gr		VFR	ss/po	7.2	eo	1L	—	
R	201												

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

CLASSIFICATION (Family)

Mollic Epipedon

Loamy, Mixed, Semiactive, Nonacid Lithic Cryorthent

Fig. B.25. Field description sheet for west side soil pedon #25.

USU SOIL DESCRIPTION SHEET SOIL # 27 - in habitat DESCRIBED BY: Kim Pierson DATE: 9/19/96

soil series		phase		location (USGS Quad)	
parent material		elevation		slope	
Grano-diorite		8300'		5% E	
landform		climate		drainage class	
bench-slope				well drained	
natural cover		MAP		MAT	
VASC/Sax.bry.tob/ANLA/JUPA/Phyllo/Aster		water table		MAST	
				MSST	
				MWST	
				surface stone and rock	

HORIZON	DEPTH (cm) mm	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, sl, sh	CONSISTENCE			REACTION pH eff	ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)
						dry	moist	wet				
Oa	0-27	d,w	10YR 3/1	gSL	3mtgr	VFR	ss/po	6.8	eo	1VF	1VF	
Oi	27-57	d,w	10YR 3/2	gSL	3mtgr	VFR	ss/po	6.8	eo	3F	1VF	
A	57-98	a,w	10YR 2/2	CoSL	3wgr	VFR	ss/po	6.8	eo	3F	1VF	
AB	98-160	a,w	10YR 3/2	gSL	2wsbk	FR	ss/po	6.8	eo	3M	1VF	
CR	160-182	a,w	10YR 4/2	gFSL	2csbk	VFR	ss/po	7.0	eo	1L	-	
R	182											

REMARKS (Present Landuse)

DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS

Mollic Epipedon

CLASSIFICATION (Family)

Loamy, skeletal, Mixed, Semiactive, Nonacid, Lithic Cryoboroll

Fig. B.27. Field description sheet for west side soil pedon #27.

USU SOIL DESCRIPTION SHEET										SOIL # 28 - in habitat		DESCRIBED BY: Kim Kiersen		DATE: 9/19/96	
soil series				phase				location (USGS Quad)							
parent material				elevation		slope		aspect		drainage class					
landform				climate		MAP		MAT		MAST					
natural cover				water table		surface stone and rock		MSST		MWST					
Sax. bry. tob / JUPA / ERGR / Polytichum / Phyllodoce															
HORIZON	DEPTH (cm)	BDY (d.t)	COLOR dry/moist	TEXTURE %C	STRUCTURE gr, sl, sh	CONSISTENCE dry, moist, wet			REACTION pH, eff		ROOTS	PORES	MISC (CLAY FILMS, % > 2mm)		
O _i	0-25	a, w	10 YR 3/1	FSL	3 st gr	VFR	ss/ps	6.8	eo	3F	IVF				
O _a	25-40	a, w	10 YR 2/2	FSL	3 st gr	VFR	ss/ps	6.8	eo	2F	IVF				
A	40-110	a, w	10 YR 3/2	SL	2 c sbk	VFR	ss/po	6.8	eo	2L	IVF				
AB	110-160	a, w	10 YR 3/3	FSL	3 m sbk	FR	s/p	6.8	eo	3F	IVF				
B	160-210	a, w	10 YR 4/3	SL	3 w sbk	FR	s/ps	6.8	eo	1L	IVF				
CR	210-250	a, w	10 YR 3/3	FSL	3 w sbk	FR	ss/ps	6.8	eo	3/1F	IVF				
R	250														
REMARKS (Present Landuse)															
DIAGNOSTIC EPIPEDON, HORIZONS AND OTHER CHARACTERISTICS															
Mollic Epipedon															
CLASSIFICATION (Family)															
Loamy, Mixed, Semiactive, Nonacid Lithic Cryoboroll															

Fig. B.28. Field description sheet for west side soil pedon #28.