

THE UNIVERSITY OF CALGARY

Life History Trade-offs and Resource Allocation in the Common Butterwort,
Pinguicula vulgaris L. (Lentibulariaceae)

by

Anne C. Worley

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGICAL SCIENCES

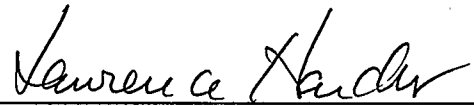
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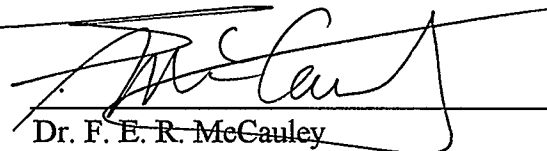
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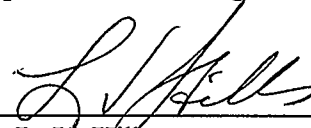
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ABSTRACT

Perennial plants allocate resources to sexual reproduction, vegetative propagation, and growth. Patterns of resource allocation evolve to maximize lifetime reproduction and reflect effects of growth and propagation on survival and fertility, and trade-offs between functions. I examined effects of resource availability, size, growth form, developmental phenology and pollen availability on trade-offs and allocation options in *Pinguicula vulgaris*. Sexual reproduction varied positively with plant size and growth varied negatively. Trade-offs occurred between reproduction and vegetative functions, but growth and vegetative propagation varied positively. These relations reflect phenology and developmental ties between perennating structures and vegetative propagules. Supplementing resources increased plant size and therefore indirectly increased vegetative propagation. Although autonomous self-pollination indicates resource limitation of reproduction, resource supplementation did not increase reproduction. Preformation of floral primordia prevents *P. vulgaris* from adjusting current reproduction to short-term changes in resource availability. Consequently, extra resources are allocated to vegetative functions which promote future reproduction.

ACKNOWLEDGEMENTS

Many people contributed to the successful completion of my thesis. In particular, I thank my supervisor, Lawrence Harder, who stimulated my original interest in the project. Lawrence was generous with enthusiasm and endless patience, as well as logistical and financial support. The other members of my committee, Ed McCauley, C.C. Chinnappa, Mary Reid, and Len Hills provided valuable feedback which improved the final version of the thesis considerably.

I could not have completed my data collection without considerable help. Lara Grinivitch and Debbie Macey's company, hard work and willingness to tolerate cold, wet weather made the field work much easier and more enjoyable. Ed Yeung provided much appreciated photography equipment, supplies, and advice. Finally, C.C. Chinnappa supplied growth-chamber space, and Ken Girard and Bonnie Smith gave helpful advice on *Pinguicula* horticulture.

Fellow graduate students also provided support and encouragement. I particularly appreciated long, philosophical discussions and afternoon trips to the cookie vendors with Sal Rasheed. Lunchtime conversations with Bea Beisner were very enjoyable. Lisa Wilkinson and Steve Bradbury supplied support and the occasional diversion during a harrowing last six weeks.

My family's support and encouragement were also very important. I thank my parents, Ray and Elizabeth Worley, for encouragement throughout my academic career, and for numerous hikes which stimulated my interest in nature. My parents-in-law, Bogdan and Jaga Czaykowski, were also supportive. Last, but certainly not least, I thank my husband, back-up field assistant, and chief photographer, Piotr Czaykowski, for his love and support throughout my time here.

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1 RESOURCE ALLOCATION BY PLANTS

1.1 Life History Evolution

Natural selection favours traits that allow organisms to make greater than average genetic contributions to future generations. An individual's fitness reflects reproduction over its lifetime and reproduction by its offspring. Lifetime reproduction depends on three demographic traits which, together, comprise the life histories of organisms: (1) age at first reproduction; (2) survival between reproductive episodes, which determines the number of reproductive episodes; and (3) fertility patterns, or the number and size of offspring produced per reproductive episode (Stearns 1976, Wilson 1983, Stearns 1992). Age at first reproduction, survival, and fertility reflect resource allocation to maintenance, growth, and reproduction. Allocation of resources to growth and maintenance influences size at first reproduction and survival, whereas allocation to reproduction determines offspring size and number. Thus, demographic life-history traits result from the cumulative effects of resource allocation to physiological functions over an organisms's lifetime (Stearns 1992).

Ideally, lifetime reproduction is maximized by reproducing early and rearing many offspring during each of an infinite number of reproductive episodes (Law 1979). However, in reality, survival often varies negatively with fertility, due to biological or environmental constraints that prevent organisms from simultaneously maximizing all factors contributing to lifetime reproduction (Law 1979, Partridge and Sibly 1991). Resource limitation is probably the most important and universal constraint on life history evolution. If reproduction and other functions draw from the same finite resource pool, increased allocation to current reproduction can only occur at the expense of growth, and therefore survival and future reproduction (Williams 1966a, b). Consequently, the ideal distribution of resources depends on the gains in fitness associated with current reproduction relative to potential gains in fitness resulting from future reproduction (Williams 1966a). Therefore, the life histories that evolve reflect the

magnitude of trade-offs as well as parent and offspring survival and fertility probabilities (Williams 1966a, b, Gadgil and Bossert 1970, Schaffer 1974, Caswell 1982).

As a group, angiosperms share a number of features that influence trade-offs and survival probabilities and therefore affect the distribution of resources between growth, survival and propagation. I discuss these factors below.

1.2 Factors Influencing Trade-offs and Resource Allocation by Plants

1.2.1 Vegetative Propagation

For many species, the ability to propagate vegetatively introduces an allocation option in addition to growth and sexual reproduction (review in Abrahamson 1980). Although both clonal and sexual propagation produce physiologically independent individuals, sexual reproduction introduces new genetic individuals (genets) to the population, whereas vegetative propagation produces genetically identical clones (ramets) that contribute to the survival and reproductive success of the parental genet (Abrahamson 1980). Production of physiologically independent ramets decreases the risk of genet mortality (Cook 1979, de Steven 1988). Vegetative spread also allows the genet to exploit larger areas and new locations, if vegetative propagules are widely dispersed (Janzen 1977, Louvett-Doust 1981). Thus, vegetative propagation is distinct from both sexual reproduction and growth, so that the ability to propagate vegetatively introduces the potential for additional trade-offs.

Allocation of resources to vegetative propagation should depend on factors similar to those governing allocation to sexual reproduction and growth, i.e. the costs and benefits of clonal growth relative to those associated with investment in other functions (Loehle 1987). Thus, the balance between clonal propagation and sexual reproduction will reflect the survival probability of each propagule type, the potential contribution of each type to future generations, and the magnitude of trade-offs between the two functions (Sackville-Hamilton et al. 1986, Loehle 1987). Most consideration of vegetative propagation focusses on relative allocation to sexual and vegetative “reproduction” in relation to environmental factors and ignores allocation to growth

(e.g., Williams 1975, Abrahamson 1975, 1980, Sackville-Hamilton et al. 1986, Loehle 1987). Allocation to each means of propagation may also depend on trade-offs with growth (Reekie 1991, Reekie and Bazzaz 1992) and the relative benefits of continued growth and reproduction by the parental genet.

Given the diversity of options, complete analysis of resource allocation strategies requires examination of all resource sinks (Rameau and Gouyon 1991). Apparently only four studies have simultaneously examined allocation to sexual reproduction, vegetative propagation, and growth. Three of these studies involved corm- or tuber-producing species and they found that sexual reproduction varied negatively with growth and vegetative propagation, but did not investigate the relation between growth and vegetative propagation (Snow and Whigham 1989, Rameau and Gouyon 1991, Mendez and Obeso 1992). The fourth study, of a rhizomatous grass, demonstrated negative genetic correlations between sexual reproduction and growth and between vegetative propagation and growth, but never between the two modes of propagation (Reekie 1991). These studies reveal that trade-offs vary between species and suggest that patterns of resource allocation may depend on growth form. No study has considered the independent effects of each of the other two functions on allocation to sexual reproduction, vegetative propagation and growth.

1.2.2 Plant Size and Resource Availability

The size of individual ramets often reflects overall resource availability. Large plants generally have both greater resource garnering abilities (large leaf areas and root volumes) and more reserves in storage organs than smaller plants. The positive association between resource availability and plant size is reflected in relations between size and reproductive allocation. In many species, only plants above a threshold size have sufficient energy to sustain flower and fruit formation (Werner 1975, Harper 1977, review in Mendez and Obeso 1992) and above the threshold size, reproductive output often increases with size (reviews in Pitelka et al. 1985, Samson and Werk 1986, Weiner 1988). Similarly, allocation to other functions may vary positively with size (review in

Pitelka et al. 1985). Variation in plant size / resource availability that exceeds variation in resource allocation may obscure trade-offs by introducing positive relations between functions which are negatively related in plants at the same resource level (van Noordwijk and de Jong 1986, also see Venable 1992).

Implicit recognition of the association between size and resource availability underlies the use of percentage or relative allocation in comparisons of resource allocation between habitats (cf. Harper 1967, Harper and Ogden 1970). Constant relative allocation implies that allocation patterns vary isometrically with plant size. However, resource allocation to reproduction often varies allometrically (Samson and Werk 1986, Weiner 1988, Ohlson 1988, Peters et al. 1988). For example, if there is a threshold size for reproduction and reproduction increases linearly with size beyond the threshold, relative allocation to reproduction asymptotically approaches a constant. Non-linear relations between reproduction and plant size will lead to more complex relations between relative allocation and plant size (Klinkhamer et al. 1992). Relative allocation to growth and vegetative propagation may also be allometric (Mendez and Obeso 1992), although the possibility has received little consideration.

Allometric patterns of resource allocation imply that variation in relative allocation may reflect differences in plant size. The same factors that influence trade-offs and survival probabilities (e.g. plant density and competition, light levels, temperature) also affect overall resource availability and plant size. Consequently, differences in allocation which have been interpreted as direct responses to environmental differences (e.g. Ogden 1974, Abrahamson 1975, Holler and Abrahamson 1977, Bostock 1980, Pitelka et al. 1980, Douglas 1981, Ashmun et al. 1985, reviews in Samson and Werk 1986, Weiner 1988) may also reflect allometric relations between resource allocation and plant size (Samson and Werk 1986, Weiner 1988, Coleman et al. 1994). Environmental changes may still affect resource allocation strategies by altering threshold sizes or the slopes of relations between reproduction and plant size (Ohlson 1988, de Ridder and Dhondt 1992, Schmid and Weiner 1993). Because size differences can confound the isolation of environmental effects on relative allocation, it is best to examine absolute

allocation as a function of plant size (Klinkhamer et al. 1990, 1992). That environmental variation in relative allocation to reproduction may result primarily from allometry is well established (see above). However, the possibility that similar relations may govern allocation to vegetative propagation or growth has not been considered.

Resource availability may also vary independently from plant size. For example, reproductive individuals may limit reproductive costs by acquiring more resources than non-reproductive individuals (Tuomi et al. 1983). The reproductive structures of many plants photosynthesize and supply some of their own resources (Reekie and Bazzaz 1987a, Willson 1983, Gilman and Crawley 1990, Galen et al. 1993). Furthermore, flowers and fruits are powerful carbon and nutrient sinks which stimulate increased photosynthesis in leaf tissue (Reekie and Bazzaz, 1987a). Because of such compensatory mechanisms, measures of carbon or nutrient content of flowers and fruit may overestimate reproductive costs, so that costs of reproduction should be measured in terms of growth and/or survival of parent plants (Hirshfield and Tinkle 1975, Reekie and Bazzaz 1987b, Snow and Whigham, 1989).

1.2.3 Growth Form and Developmental Phenology

In this thesis, “growth form” refers to both the general appearance or habit of plants (e.g., bulbous species, rhizomatous herbs, trees) and patterns of meristem commitment (e.g., determinate versus indeterminate inflorescences). Below, I describe how growth form and developmental phenology affect allocation options and opportunities for trade-offs.

The physiological and functional distinction between vegetative propagation and growth depends largely on growth form. Vegetative propagules include diverse structures, ranging from interdependent ramets in rhizomatous and stoloniferous species to bulbils, which disperse from inflorescences in a manner similar to seeds (review in Abrahamson 1980, Law et al. 1983). Growth and vegetative propagation are almost indistinguishable in rhizomatous or stoloniferous species with interdependent ramets. Consequently, trade-offs between growth and vegetative propagation or independent

reproductive costs to growth and vegetative propagation seem unlikely. Because most consideration of vegetative propagation has been concerned with rhizomatous and stoloniferous species (e.g., Williams 1975, Abrahamson 1975, Armstrong 1982, 1984, Sackville-Hamilton et al. 1986), relations between vegetative propagation and plant growth have received little attention. The potential for trade-offs in species with completely independent vegetative propagules (e.g., adventitious buds, bulbils, gemmae, cauline rosettes, cormels) may be greater. However, even in species with independent propagules, the potential for trade-offs between clonal propagation and growth may depend on the timing of propagule formation. If the perennating organ and vegetative propagules are structurally related and form simultaneously, as in bulbous, tuberous and corm-forming species, they are more likely to vary positively than if vegetative propagules form separately (e.g., adventitious buds, cauline rosettes).

Meristem commitment can also affect patterns of resource allocation. Once meristems are committed to reproduction, they can no longer contribute to vegetative functions. Thus, early commitment of meristems to reproduction reduces the number available for growth or vegetative propagation and therefore limits final size and reproductive output by the plant (Watson 1984, Geber 1990, but see Bishop and Davy 1985). For example, in *Potentilla anserina*, and probably several other *Potentilla* species, an initial investment to clonal growth is required to increase the number of reproductive meristems (Eriksson 1985). Similarly, species with determinate inflorescences may be unable to increase current flower number in response to increased resources, even when reproduction is resource limited (Casper and Neisenbaum 1993).

The current reproductive potential of many spring-flowering species is wholly or partially determined during the previous growing season. Such preformation of floral primordia probably increases reproductive success by allowing plants to flower during short growing seasons or early in the growing season (reviews in Sørensen 1941, Billings and Mooney 1968, Mark 1970, Dafni et al. 1981). However, preformation may place further restrictions on reproductive flexibility. For some species, both vegetative and reproductive potential are pre-determined (Boeken and Gutterman, 1989). In such

species, reproduction and leaf production during one season often correspond to resource levels during the previous season (Mark 1965, Billings and Mooney 1968, Mark 1968, 1970, Boeken 1989, Svensson et al. 1993). Because flower number often depends on plant size (section 1.2.2), the effects of resource availability on future reproduction are probably mediated through their effects on the size of the perennating organ (Boeken 1989).

That the reproductive and growth potential of some species may be pre-determined raises questions about their ability to respond to short-term changes in resource availability. Such species can probably respond to adverse environmental conditions (e.g., low resource levels) by reducing leaf expansion, or the numbers of flowers and fruit matured. However, species with meristem limitation, preformation, or pollen limitation of reproduction (section 1.2.4, below) may be less able to respond to good conditions, at least in terms of current size attained and/or reproductive effort. However, flexibility may be maintained by production of surplus floral primordia or flowers, that can be matured if resource availability permits. Similarly, if pollination is assured (section 1.2.4, below), seed set may increase in response to extra resources. Alternatively, plants may increase future reproduction through increased allocation to perennating organs and vegetative propagules. The possibility that plants whose reproductive output is limited by factors other than resource availability may invest surplus resources in activities contributing to future reproduction has received little attention.

Phenological events may be canalized (i.e. follow each other after fixed time intervals) or independently controlled by different environmental conditions (Rathcke and Lacey, 1985). Canalized phenology may restrict storage options as well as current growth and reproduction. For example, if formation of perennating structures does not begin until after flowering, then nutrients attained before flowering cannot be stored for subsequent years and would have to be used to increase flower number or to accelerate leaf expansion. Conversely, if these structures begin forming near the start of the growing season, resource storage for next year can begin immediately. The ability to

adjust the timing of the formation of the perennating organ and floral buds according to resource levels may allow some species to take greater advantage of extra resources.

1.2.4 Pollen Limitation

Reproductive effort in plants can be limited by the quantity and quality of pollen received, rather than by resource availability (reviews in Bierzychudek 1981, Zimmerman and Pyke 1988, Ayre and Whelan 1989). The consequences of pollen limitation are most severe in obligate outcrossers that rely on animal vectors (review in Karoly 1992). Ultimately, pollen-limited outcrossers should increase resource allocation to pollinator attraction (or shift flowering phenology [Ackerman and Montalvo 1990]) until an optimal allocation of resources to pollinator attraction and seed maturation is attained (Haig and Westoby 1988). If this evolutionary optimum is reached, seed set will be limited simultaneously by pollen and resources, so that increasing seed set decreases resource availability for other functions (Haig and Westoby 1988). Numerous studies of orchids supported Haig and Westoby's hypothesis (reviews in Snow and Whigham 1989, Ackerman and Montalvo 1990, Calvo 1993), indicating that studies of pollen limitation must consider the effects of increased reproduction on subsequent growth and reproduction (Zimmerman and Pyke, 1988).

In self-compatible plants, autonomous self-fertilization can assure reproductive success despite low pollinator abundance (Jain 1976, Richards 1986). Facultative or delayed autogamy allows self-compatible plants to receive the potential benefits of outcrossing (e.g., increased genetic variability, hybrid vigour) while avoiding the drawback of pollen limitation (Lloyd 1979, 1992). In animal-pollinated species, autonomous selfing can compensate for infrequent pollinator visits (Sih and Baltus 1987, Jennerston 1988, Vaughton 1988, Karoly 1992) or poor conditions for pollination (Schoen and Brown 1991).

1.3 Objectives

In this thesis, I present the results of studies on resource allocation in the common butterwort, *Pinguicula vulgaris* L. (Lentibulariaceae), a carnivorous perennial. My primary objectives are (1) to assess the effects of trade-offs and plant size on resource allocation to growth, vegetative propagation and sexual reproduction, and (2) to determine how increased resource availability affects allocation to current and future activities.

To facilitate interpretation of trade-offs and patterns of resource allocation, I provide natural history information on growth form, pollination syndrome, and phenology in Chapter 2. Observations described in this chapter reveal that the perennating organ and vegetative propagules are physically distinct, so that the potential for trade-offs between vegetative propagation and growth exists. In addition, preformation of leaf and flower primordia may restrict *Pinguicula vulgaris*' responses to increased resource availability.

In Chapter 3, I consider resource allocation in unmanipulated plants. I measure allocation to reproduction, vegetative propagation and growth. I statistically separate the effects of plant size and of trade-offs between reproduction, vegetative propagation, and growth on allocation to each of the three functions. The study includes plants at two sites so that I can assess whether between-site differences in relative allocation result from size effects or other differences between sites.

In Chapter 4, I assess responses by *Pinguicula vulgaris* to increases in overall resource availability. In particular, I compare allocation to current reproduction with allocation to growth and vegetative propagation (both indices of potential future reproduction) in control plants and resource supplemented plants. My interpretation of the results emphasizes the restrictions placed on current reproduction by preformation and the implications of increased allocation to growth and vegetative reproduction for future reproductive potential.

Finally, in chapter 5, I discuss my results from chapters 2, 3 and 4 in the context of general strategies of resource allocation by plants and consider the demographic implications of the patterns of resource allocation observed in earlier chapters.

2 NATURAL HISTORY OF *Pinguicula vulgaris* POPULATIONS ALONG THE SHEEP RIVER

Factors such as plant size, growth form, developmental phenology, and pollination intensity can have important influences on trade-offs and resource allocation in plants. Consequently, interpretation of resource allocation requires detailed information on such factors (Chapter 1). Because much of the previous work on *Pinguicula vulgaris* focussed on carnivory (although Karlsson [1986] and Karlsson et al. [1990] investigated biomass and nutrient allocation to reproduction and other functions, and Svensson et al. [1993] investigated demography) I needed to gather information on other aspects of the species' biology. In this chapter, I describe the Sheep River study sites and my observations on the morphology and phenology of *Pinguicula vulgaris* plants in the field and growth chamber. I also review literature documenting the importance of insects as a nutrient source and report experiments assessing the mode of self-fertilization.

2.1 Habitat and Study Sites

Pinguicula vulgaris has a circumpolar distribution and grows in bogs and on damp rocks and ledges (Moss, 1983). The plants grow on a wide range of soil types, from acidic, nutrient-poor mires to calcareous soils (Karlsson 1988). The study populations for this thesis grow on beaches and former side channels along the Sheep River, in the Sheep River Wildlife Sanctuary, 85 km southwest of Calgary (50°36'N, 114°47'W). All sites were bordered by spruce (*Picea glauca* (Moench) Voss) and buffalo berry (*Shepherdia canadensis* (L.) Nutt.). Moss was the main ground cover, although some plants grew on coarse sandy soil or among grass. The Sheep River floods occasionally and the ground at all sites was wet for much of the 1992 and 1993 growing seasons.

Four sites were used for my studies and they are numbered according to their order of appearance in the text. Site 1 was a 3 x 20 m stretch along a steep river bank which faced north-west. Site 2 was in a former side channel on the east side of the river, 350 m downstream from Site 1, and was approximately 4 x 50 m. Most plants at Sites 1 and 2 grew among moss and were at or just above the flood line. Site 3 was a 20 x 30 m beach

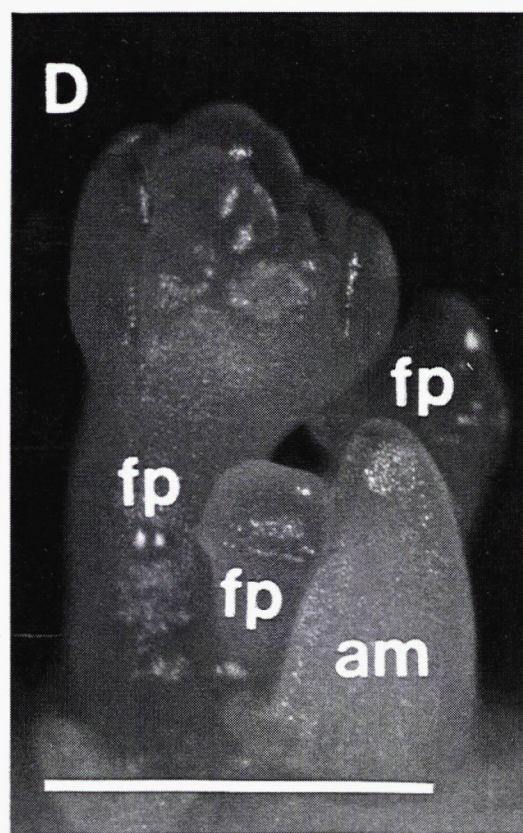
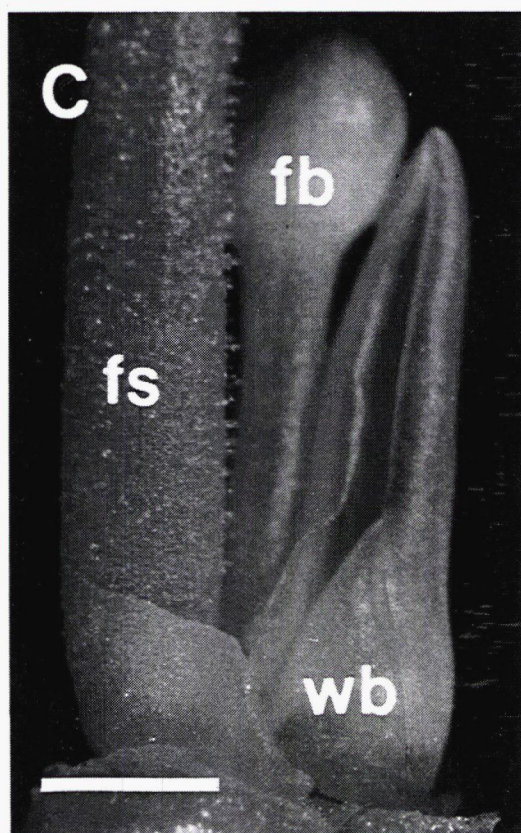
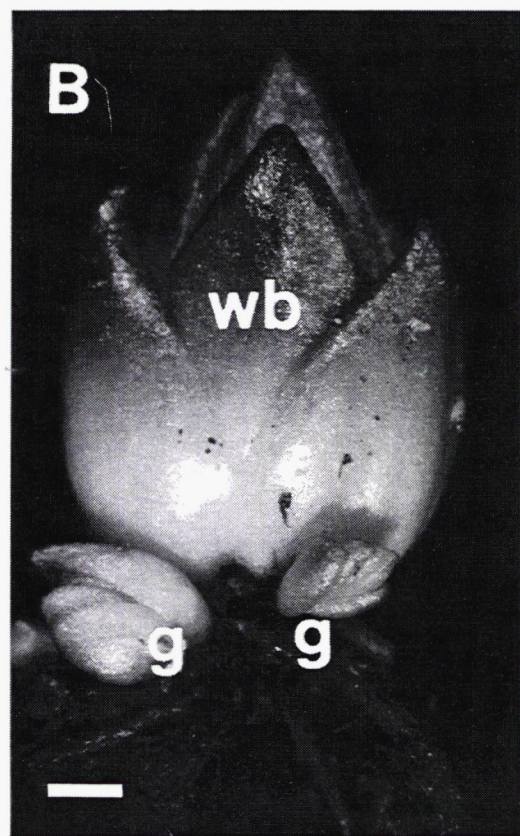
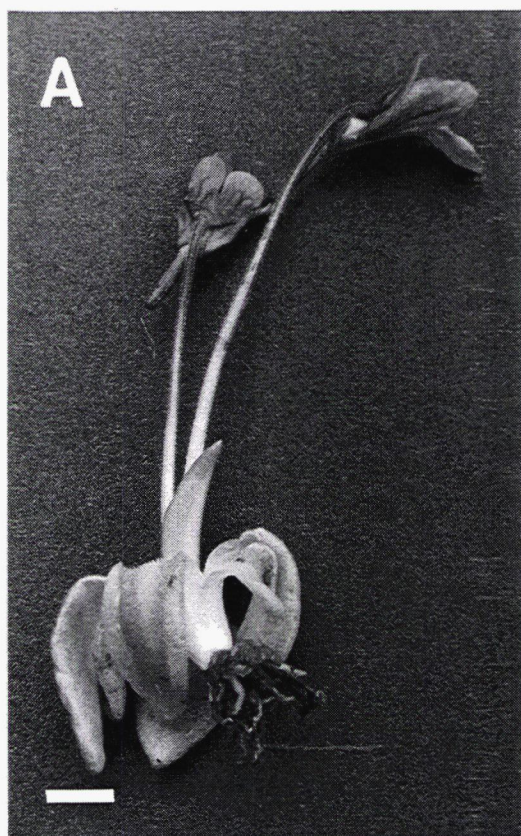
with large rocks, surrounded by moss or sand and was approximately 500 m upstream from Site 1. Most plants grew in mossy pockets adjacent to rocks, although several groups of plants occupied areas silted over by floods. Finally, Site 4 was a long, narrow, east-facing beach across the river from Site 1, approximately 4 x 200 m. Although Site 4 flooded most often, many plants were less vulnerable to silting than plants at Site 3 because they grew in grassy areas close to the highest floodline. At all sites, I marked study plants by placing galvanized roofing nails beside them. The nail heads were painted so that plant identifications could be written on them.

2.2 Morphology and Phenology

Pinguicula vulgaris plants produce a flat basal rosette of oblanceolate leaves (Fig. 2.1a). The leaves are glandular and secrete a sticky mucopolysaccharide which traps small insects and other arthropods (Heslop-Harrison and Knox 1971). The perennating organ is a winter bud, situated just beneath the soil surface (Fig 2.1b, Schnell 1976), which forms during the growing season (Fig. 2.1c). The winter bud contains leaf and flower primordia (Fig. 2.1d), which mature during the following season. Plants reproduce vegetatively by producing subsidiary buds (gemmae) in the outer leaf axils of the winter bud (Fig 2.1b). These become independent from the parent plant and form leaves during the following season. The chances of gemmae establishment are probably highest when they are dispersed by animals or floods which disturb the soil, because gemmae surrounding the parent plant often become covered by the parent's leaves (Pietropaolo and Pietropaolo 1986). The flowers are purple, violet-like, and are borne singly on leafless 10-15 cm scapes (Fig. 2.1a). Plants may produce up to six flowers, with one to two being most common in the Sheep River populations. The ovary of each flower matures into a two-lobed capsule containing 110-140, 24 μ g seeds (Karlsson 1986).

Plants along the Sheep River differ from Swedish populations studied by Karlsson and colleagues (Aldenius et al. 1983, Karlsson and Carlsson 1984, Karlsson 1986, Karlsson 1988, Karlsson et al 1990, Karlsson et al. 1991, Svensson et al. 1993) in size

Figure 2.1. Developmental stages of *Pinguicula vulgaris*. **A.** Flowering plant. In situ, the portion of the leaves that are curled back in the photograph hug the ground to form a flat rosette. Note the developing leaf furled at the center of the rosette and the poorly developed root system. The apical meristem and developing winter bud are at the center of the leaf bases. The scale bar indicates 1 cm. **B.** Dormant winter bud (wb) and gemmae (g). The dead roots are still attached to the base of the winter bud. **C.** Close-up of the developing winter bud (wb). The apical meristem is at the center of the bud. A flower stalk (fs) and developing flower bud (fb) are also present. **D.** Center of a fully developed winter bud. Three flower primordia (fp) at varying stages of development are visible. The apical meristem (am) is sheathed by a leaf primordium. Scale bars for **B** through **D** indicate 1 mm.



and production of vegetative propagules. Swedish plants have a maximum leaf length of 21 mm (Svensson et al. 1993), whereas the longest leaf length of my plants was approximately 60 mm. Gemmae are not mentioned in any studies of *Pinguicula vulgaris* by Karlsson and colleagues. Because many of these studies involved excavation of winter buds, it seems that vegetative propagation does not occur in Swedish populations.

Phenology may significantly influence resource allocation by *P. vulgaris* because preformation means that growth and reproduction are determined so early during the growing season (section 1.2.3). Whether phenology is canalized or responsive to environmental conditions also has important implications for resource allocation (section 1.2.3). Therefore, in the summer and fall of 1992, I examined the development and phenology of *Pinguicula vulgaris* to characterize the timing of developmental events and to determine whether phenology responds to altered environmental stimuli.

In May 1992, I randomly selected 120 plants at Site 1. Every week for 18 weeks (May 23 - Sept. 20), eight plants were chosen at random, excavated, and dissected under a Wild-M5 dissecting microscope. The number of leaves, gemmae, flowers and fruit as well as the presence of incipient winter buds and the number of leaf and floral primordia in the winter bud were recorded. Structures were categorized as “developing,” “mature” or “senescing”.

During autumn 1992, a similar procedure was followed using plants from Site 4 grown in a growth chamber. Each plant had been established in a square pot (10 cm height and width) in a 2:1:1 mixture of peat moss, vermiculite, and sand. These plants were followed for 17 weeks (Sept. 22- Jan. 13). The plants had broken dormancy and begun to develop by Sept. 17, despite being in cold storage (5°C). On September 17, the plants were placed in a growth chamber with a 9-h photoperiod and 10°C day / 5°C night. The photoperiod and temperatures were increased to 10 h, 13°C day / 8°C night and 12 h, 18°C day / 12°C night on October 6 and 17, respectively. After October 17, temperatures and day length were held constant to determine whether the plants entered dormancy in the absence of environmental stimuli. Each week, three plants were dissected as described above and photographed under a Wild TYP 355110 dissecting

microscope using Ilford FP4 plus, 125 ASA black and white film. Table 2.1 summarizes the phenology of major developments in field and growth-chamber plants.

In the field, the 1992 growing season ran from mid May to late September. When observations began on May 23, bud scales on the outer portion of the winter bud were still present, four to five leaves were fully expanded, and four to five leaves remained furled at the center of the plant. The number of functional leaves remained relatively constant (three to six) throughout the growing season as new leaves unfurled and older leaves senesced. Flower primordia formed during the previous season were already developing when observations began on May 23, although the buds did not become visible in intact plants until early June (Table 2.1). The first flowers matured in late June and their ovaries began to swell by early July (Table 2.1). The capsules continued to mature until late August when they split and the seeds dispersed. Almost all plants had at least one undeveloped flower primordium after flowering was complete. These primordia were outside the developing winter bud (see below) so that they had no protection over the winter and eventually senesced and were sloughed off.

Formation of the winter bud and associated structures continued throughout the growing season. A plant's leaf petioles and apical meristem remained approximately 5 mm below the soil surface year-round. Leaf primordia for the incipient winter bud began differentiating from the apical meristem by early June. By mid-August the full complement of leaves for the next season had differentiated (Table 2.1), although winter bud mass continued increasing until the end of September. Gemmae were evident by the middle of July (Table 2.1) when the incipient winter bud had seven to ten leaf primordia; gemmae increased in size and number until the end of the season. Flower primordia were first evident by late August (Table 2.1) and by late September most plants had two to three flower primordia at varying stages of development, with sepals visible in the oldest primordia (Fig. 2.1d).

Although the sequence of developmental events was consistent in growth chamber and field plants (Table 2.1), the growing season was considerably shorter in the growth chamber (13 weeks compared to 18 in the field: Table 2.1). In addition, plants in the

Table 2.1. Developmental phenology of *Pinguicula vulgaris* plants grown in the field and in a growth chamber. Observations on field plants began after dormancy had been broken. To facilitate comparisons between growth chamber and field plants, I set week 1 as the week during which all plants had a rosette of three to five leaves. Some developments may have been noted earlier in plants grown in the growth-chamber because I was using a more powerful microscope. The date of fruiting is missing for plants in the growth chamber because I picked their flowers to observe autonomous selfing (section 2.4).

	FIELD		GROWTH CHAMBER	
	week	date	week	date
VEGETATIVE GROWTH				
dormancy broken	-	-	-2	Sept. 22
leaves fully expanded	1	May 23	1	Oct. 20
onset of dormancy	18	Sept. 20	13	Jan. 13
REPRODUCTION				
flower buds visible	3	June 6	2	Oct. 28
mature flowers	6	June 26	4	Nov. 11
first fruit set	7	July 3	-	-
mature fruit	12	Aug. 20	-	-
WINTER BUD FORMATION				
winter bud meristem evident	2	May 30	2	Oct. 27
leaf differentiation begins	2	May 30	2	Oct. 27
gemmae formation begins	9	July 17	6	Nov. 24
leaf formation complete	13	Aug. 14	10	Dec. 22
flower primordia develop	14	Aug. 20	10	Dec. 22

growth chamber started and finished their seasonal cycle in the absence of external stimuli. Thus, it seems that developmental patterns in *P. vulgaris* may be fairly fixed. Differences in the duration of the growing season between field and growth chamber plants probably reflect accelerated growth and development in response to the consistently warm, high-light conditions experienced by plants in the growth chamber. Although growth chamber plants began growing in the absence of environmental cues, it seems unlikely that plants in the field would do the same. The lowest possible temperature in the growth chamber was 5° C. Clearly, winter temperatures in the field can be much lower. However, growing seasons did vary in the field. Plants at Site 4, which faced south-west, emerged earlier in spring and entered dormancy earlier in autumn than plants at east-facing sites. Thus, it seems that once development begins, it continues until the formation of next year's winter bud is complete and then plants enter winter dormancy, even when summery conditions continue.

The set growing pattern coupled with the fact that flower and leaf primordia form during the previous growing season suggest that allocations to leaves and flowers are determined before conditions in the current season become evident. If this is the case, *Pinguicula vulgaris* may have limited ability to respond to short-term changes in resource availability (section 1.2.3).

Vegetative propagules that are physically distinct from the perennating organ may enable trade-offs between vegetative propagation and growth, if resources are independently allocated to gemmae and winter buds. However, gemmae are essentially axillary buds, so that their formation and that of the winter bud are physiologically related and occur simultaneously. In addition, the winter bud and gemmae complete development at the end of growing season when net resource gains for the year become evident, and after fruit and seeds have matured. As a result, growth of the winter bud and gemmae may be positively related.

2.3 Carnivory

Carnivorous plants variously attract, capture and/or digest animal prey from which they absorb nutrients that promote growth, survival, pollen production or seed set (Givnish et al. 1984). The main benefit of carnivory is from mineral nutrients, rather than increased carbon supply (Darwin 1875, F. Darwin 1878, Hepburn et al. 1920, Harder and Zemlin 1967, Heslop-Harrison 1976, Aldenius et al. 1983). Consequently, carnivorous plants typically occupy nutrient-poor sites, where the ability to absorb nutrients from animals presumably gives them a competitive advantage (Darwin 1875, Givnish et al. 1984). The minerals gained from carnivory are probably invested in photosynthetic enzymes which then increase carbon fixation and growth (Givnish et al. 1984). Most carnivorous plants occur in sunny, moist habitats (bogs, swamps, and aquatic habitats), perhaps because increased nutrient availability enhances photosynthesis most when sunlight and water are abundant (Givnish et al. 1984). However, species with adhesive traps, such as *Pinguicula*, may also require moist conditions to maintain mucus secretion glands (Schmucker and Linneman 1959, cited in Aldenius et al. 1983).

Pinguicula species trap and digest insects on the upper surface of their leaves through the actions of stalked and sessile glands. The stalked glands secrete mucopolysaccharide droplets that adhere immediately on contact with the prey and set into strong threads when drawn out. On stimulation by insects or other proteinaceous materials, the sessile glands adjacent to the insect secrete proteolytic enzymes. The sessile glands also absorb digestive products, which enter the leaf within two hours and move into the vascular tissues. Movement of nutrients out of the leaf begins within 12 h of capture (Heslop-Harrison and Knox 1971).

Insect capture by carnivorous plants depends on prey attraction and on the ability of insects to escape from traps. Prey size and strength are probably the primary factors determining which insects *Pinguicula* species capture. For example, Spanish *P. nevadense* catch few prey longer than 4 mm, whereas artificial sticky traps catch prey up to 20 mm long (Zamora 1990a). Other than size, the species caught on artificial traps and plants did not differ (Zamora 1990a). Capture of larger insects may be possible only

when they are weakened by other factors (Zamora 1990b). For catchable prey, the trapping efficiency of *Pinguicula vulgaris* rosettes significantly exceeds that of artificial traps shaped like rosettes, which suggests that prey find the plants attractive (Karlsson et al. 1987). Although there are no ultra-violet patterns on *Pinguicula* leaves, as there are in some other carnivorous genera (Joel et al. 1985), leaf color or odor may attract insects (Karlsson et al. 1987). The mean ($\pm$ SE) number of insects caught over a seven-day period by medium sized *Pinguicula vulgaris* plants (rosettes 6 cm diameter) at the Sheep River was 8 ± 1.4 insects in one week (June 23-29) and 6 ± 1.1 insects in the following week (June 30-July 6).

Ants, which are usually too strong to be captured by *Pinguicula*, rob prey from *P. nevadense* leaves (Zamora 1990b). They prefer large prey, close to the leaf margins that are visible above the mucilage and fresh enough to still contain nutrients (Zamora 1990b). Zamora (1990b) found that ants robbed 47% of the flies placed on *P. nevadense* leaves within 24 h. I made similar observations of robbery by ants in my *P. vulgaris* populations (see Chapter 4). During one trial, most of the fruit flies fed to plants were robbed within 2 h. Losses to ants probably significantly affect the plants because ants prefer large prey and steal them before nutrients are absorbed (Zamora 1990b).

The benefits of carnivory can be assessed in terms of biomass or nutrients gained. *Pinguicula vulgaris* plants increase in biomass in response to both insects and nutrient solutions in agar blocks (Aldenius et al. 1983, Karlsson and Carlsson 1984, Karlsson et al. 1991). Production of flowers, fruit and seeds are little affected by supplemental feeding, possibly because of preformation (Aldenius et al. 1983, Karlsson and Carlsson 1984, Karlsson et al. 1991). Phosphorous seems to be the most important nutrient gained through carnivory, followed by nitrogen (Aldenius et al. 1983, Karlsson and Carlsson 1984). Plants fed whole insects or complete nutrient solution in agar blocks gain more mass and have higher nutrient concentration in their tissues than plants supplied with either nutrient alone. Thus micronutrients absorbed through carnivory may enhance nutrient uptake by the roots (Aldenius et al. 1983, Karlsson and Carlsson 1984).

Pinguicula vulgaris probably does not depend solely on carnivory for mineral nutrition because plants respond to increased soil nutrients as well as to prey (Karlsson et al. 1991).

2.4 Reproductive Biology

Pinguicula vulgaris flowers allow both insect-pollination and autonomous selfing. The corollas are approximately 2 cm wide with a 0.8-1.0 cm, nectar-producing spur. The showy, purple color and the morphology of *P. vulgaris* flowers suggest long-tongued bees as the most likely pollinators. However, the Sheep River populations are rarely visited by pollinators; I observed only two clear-winged sphinx moths (*Hemaris* sp.) visiting the flowers during the two years of the study. Floral morphology facilitates autonomous selfing because the receptive surface of the stigma curls back to meet the anthers (Willis and Burkhill 1903, Hagerup 1951). Autonomous self-pollination occurs in British, Scandinavian (Willis and Burkhill 1903) and Faroese (Hagerup 1951) populations, in cool wet areas with poor conditions for pollinators.

Autonomous selfing may occur before, during, or after opportunities for outcrossing in a flower (Lloyd 1979, Lloyd and Schoen 1992). The differences in timing determine the degree to which self pollen displaces outcrossed pollen (Ockendon and Currah 1978). Delayed selfing is always advantageous because no opportunities to receive outcrossed pollen are lost, whereas competing (i.e., selfing occurs during anthesis) and prior selfing are primarily beneficial when pollinators are especially scarce (Lloyd 1992). *Pinguicula vulgaris* flowers last approximately nine days. Observations on laboratory plants showed that no flowers had selfed autonomously by day 1 ($n=23$). However, the anthers do not dehisce until day 2 or 3, which indicates the flowers are protogynous. In contrast, 75% of flowers had selfed by day 5 ($n=20$). The proportion of selfed flowers had not changed by day 9 ($n=21$), when almost all flowers wilted. Thus, selfing by *Pinguicula vulgaris* is mostly competing, although the onset of self pollination could be slightly delayed due to protogyny. Competing selfing should be

favoured at the Sheep River because pollinator abundance is low, so that competition between outcrossed and selfed pollen probably is not severe (Lloyd 1992).

Although reproductive assurance provided by self pollination probably prevents pollen limitation of fruit and seed set by *P. vulgaris*, the showy, nectar-producing flowers indicate that outcrossed pollen may be preferable to self pollen. I therefore conducted an experiment during 1992 to determine whether receipt of outcrossed pollen is advantageous for *Pinguicula vulgaris*. This study involved 30 groups of plants at Site 1, each with three flowering plants of similar size. I bagged each plant's flowers with nylon mesh bags to exclude pollinators and randomly assigned them to one of three pollination treatments: (1) control, (2) hand-outcrossed, and (3) hand-selfed. Differences between control and hand-pollinated plants should reflect the efficiency of self-pollination. If autonomous selfing results in full fruit and seed set, seed number in control and hand-selfed plants should not differ. In contrast, if outcrossing is advantageous, hand-outcrossed plants should produce more seeds than hand-selfed plants.

I pollinated flowers by removing dehiscent anthers from donor flowers with forceps and rubbing each anther on the stigma of the recipient flower. For the selfed treatment, anthers were either taken from the recipient flower or from other flowers on the same plant. For outcrossed plants, I selected donor flowers at least 1.5 m from the recipient plant to minimize the chances of using pollen from related plants or other ramets of the same genet. Most flowers were hand-pollinated twice, once on the day after anthesis and again three days later. Pollination on the first day was not always possible for the selfed treatment because anthers did not dehisce until the second or third day.

At least 65% of flowers produced fruit in all treatment groups. Plants with final bud masses (i.e. bud masses at the end of the growing season) ranging from 8 to 113 mg (the entire size range in this study) produced mature fruit. After I had established that final bud mass did not affect fruit set by flowering plants during 1992 (LOGISTIC procedure, SAS 1990: Wald Chi Square=5.95, $P>.9$, $n=66$), I used contingency table analysis (FREQ procedure, SAS 1987) to assess the effects of pollination treatment on

fruit set. Fruit set differed among pollination treatments ($X^2=6.87$, d.f.=2, $P<.05$, $n=73$), with lower fruit set in control (fruit set = 65%) than in hand-pollinated plants ($X^2=5.81$, d.f.=1, $P<.02$, $n=73$), but no difference between hand-selfed (fruit set = 81%) and hand-outcrossed (fruit set = 85 %) plants ($X^2=1.50$, d.f.=1, $P>.2$, $n=50$).

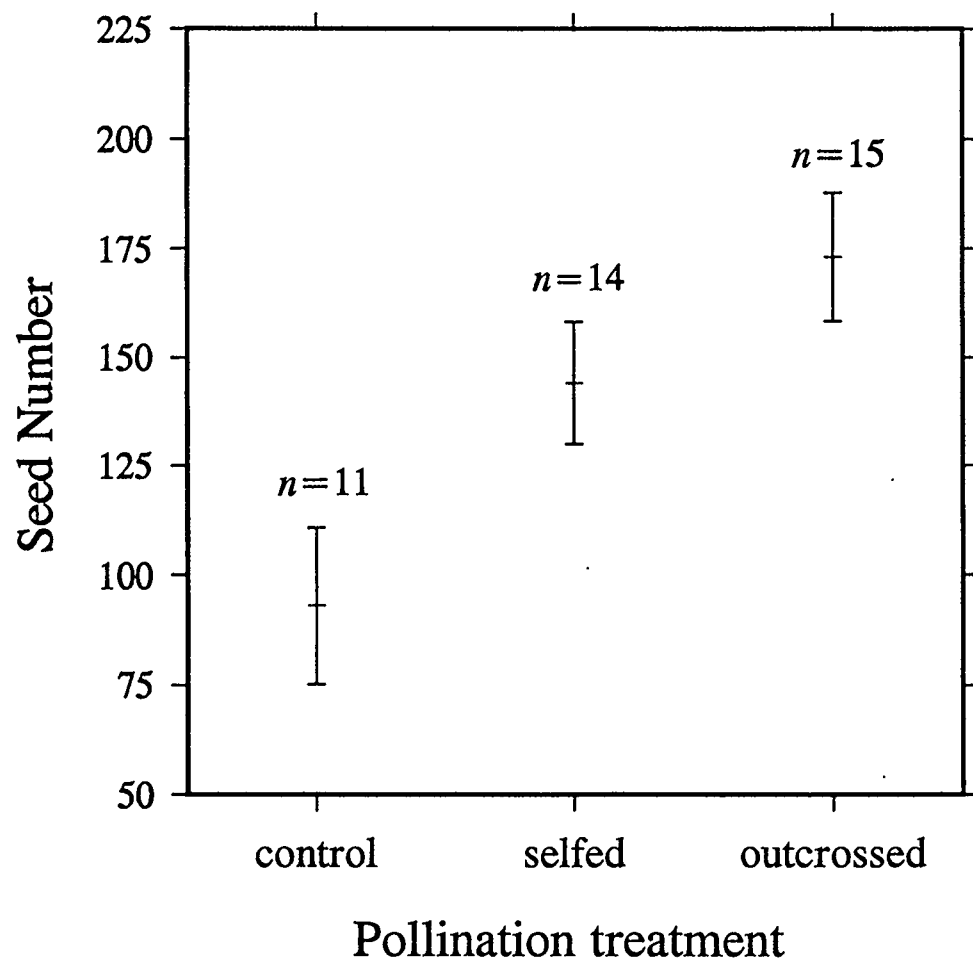
I assessed whether plants with outcrossed pollen set more seed than those with selfed pollen with one-way analysis of covariance (GLM procedure, SAS 1987). The three bagged treatments (control, hand-selfed and hand-outcrossed) and location were the main effects. Bud mass, gemmae mass, and ovule number were included as covariates in the initial model as well as two-way interactions between covariates and treatment. Nonsignificant terms were eliminated using backwards elimination. Pollination treatment significantly affected seed number ($F_{2,14}=5.39$, $P<.02$; Fig 2.2). On average, outcrossed plants produced 174 seeds per fruit, 80 more than controls ($t_{14}=3.28$, $P<.005$; Fig. 2.2). Hand-selfed plants had intermediate seed set (mean=140 seeds per fruit), which did not differ significantly from that by control ($t_{14}=2.09$, $.05<P<.06$) or outcrossed plants ($t_{14}=1.37$, $P>.1$; Fig. 2.2). Seed production did not depend on location ($F_{23,14}=1.54$, $P>.2$), bud mass, gemmae mass, gemmae number or ovule number.

Higher fruit and seed set in hand-pollinated plants indicates that *Pinguicula vulgaris* is not fully efficient in autonomously selfing. However, fruit set was still high enough in control plants for autonomous selfing to confer considerable reproductive assurance. The slightly higher seed set in outcrossed plants may simply reflect a larger number of pollen grains on the stigma (own + outcrossed) compared to selfed plants (own only). Overall, it seems that reproduction by *Pinguicula vulgaris* is more likely resource-limited than pollen-limited.

2.5 Implications for Trade-offs and Resource Allocation

Three aspects of *Pinguicula vulgaris*' biology have important implications for resource allocation. First, although they are structurally related, the perennating organ (winter bud) and vegetative propagules (gemmae) are physically distinct so that there is

Figure 2.2. Mean seed number ($\pm$ SE) in control, hand-selfed and hand-outcrossed plants. All plants were bagged to prevent pollinator visitation. See text for overall ANCOVA results.



potential for trade-offs between growth and reproduction. Second, *P. vulgaris* is fully self compatible and exhibits competing selfing. Although receipt of outcrossed pollen may be advantageous, reproduction is likely primarily resource limited. Finally, both leaf and floral primordia form during the autumn preceding flowering, indicating that *P. vulgaris* may have limited ability to respond to good conditions with immediate increases in flowering and fruiting, even though reproduction is probably resource limited.

3 THE INFLUENCES OF TRADE-OFFS AND PLANT SIZE ON RESOURCE ALLOCATION BY *PINGUICULA VULGARIS*

3.1 INTRODUCTION

3.1.1 Life History Trade-offs

Perennial plants allocate resources between sexual reproduction, vegetative propagation, and growth. Allocation to each function should depend on the fitness gained by investing in that function relative to the fitness lost through foregoing investment in other functions. Trade-offs between functions influence the changes in relative fitness that are associated with altered investment in each function (Cody 1966, Williams 1966a, b, Gadgil and Bossert 1970, Schaffer 1974, Caswell 1982).

Most empirical evidence of trade-offs involves costs of reproduction, which are well documented in plants. For example, hand pollination of species with naturally low fruit set often increases fruiting at the expense of growth and subsequent reproduction (review in Calvo 1993). Trade-offs also occur between reproduction and survival (Law et al. 1977, Paige and Whitham 1987, Gillman and Crawley 1990) and negative genetic correlations have been shown between reproduction and growth (e.g. Reekie 1991, Rameau and Gouyon 1991, Primack and Antonovics 1982). For a few species, trade-offs between sexual and vegetative propagation have been unequivocally demonstrated (e.g. Sohn and Policansky 1977, Law et al. 1983, Westley 1993). However, relative allocation to sexual and vegetative propagation are often compared in different environments (reviews in Evenson 1983, Loehle 1987, Lovett-Doust 1989), making trade-offs difficult to distinguish from the effects of plant size (section 1.2.2, also see below). Relations between vegetative propagation and growth have not been examined, probably because of developmental and physiological similarities which often make it difficult to distinguish between the two (section 1.2.3).

Because plants have several allocation options, trade-offs between sexual reproduction, vegetative propagation and growth should be clearest when allocations to all three functions are considered concurrently (Rameau and Gouyon 1991).

Comparison of the few studies that have comprehensively examined allocation to all functions (Snow and Whigham 1989, Rameau and Gouyon 1991, Mendez and Obeso 1992, Reekie 1991: see section 1.2.1) indicates that trade-offs vary between species and may depend on growth form (section 1.2.1). Furthermore, the independent effects of allocation to each of the other two functions on allocation to sexual reproduction, vegetative propagation and growth have not been considered.

3.1.2 Plant Size and Resource Allocation

The proportion of resources allocated to particular functions often changes with plant size. Such allometric investment is well established for reproduction (Samson and Werk 1986, Ohlsen 1988, Peters et al. 1988, Weiner 1988, section 1.2.2) and may also be a feature of vegetative propagation and growth, although there are few relevant data. Changes in relative allocation to vegetative propagation are sometimes associated with changes in plant size caused by varying plant density or environmental severity (Douglas 1981, Mendez and Obeso 1992, Menges 1990, but see Bostock 1980, Hartnett 1990).

Variation in relative allocation may result from variation in plant size and resource availability or from direct responses to environmental factors that affect parent and offspring fertility and survival (Gadgil and Bossert 1970, Gadgil and Solbrig 1972, Schaffer 1974). It is well established that between-site differences in relative allocation to sexual reproduction may result primarily from differences in resource availability (Samson and Werk 1986, Weiner 1988, Peters et al. 1988, Coleman et al. 1994). Between-site differences in relative allocation to vegetative propagation and growth may also reflect variation in resource availability. Many of the environmental factors postulated to affect relative allocation to sexual reproduction and vegetative propagation (e.g., plant density, light levels, others: reviewed by Abrahamson 1980, Loehle 1987, Louvett Doust 1989) also affect resource availability. Consequently differences in relative allocation to reproduction and clonal propagation may reflect differences in plant size rather than direct responses to environmental factors (cf. Samson and Werk 1986, Weiner 1988). Environmental factors may still directly affect resource allocation by

altering the slopes or intercepts of size-dependent allocation patterns (Soule and Werner 1981, Ohlson 1988, Hartnett 1990, de Ridder and Dhondt 1992, Schmid and Weiner 1993). Given allometric allocation, the effects of plant size must be considered before spatial and temporal variation in relative allocation can be attributed to the direct effects of environmental factors because resource availability, and therefore plant size, often varies between habitats (Samson and Werk 1986, Weiner 1988).

3.1.3 Objectives

In this study I investigate patterns of resource allocation by *Pinguicula vulgaris* at two sites. I address three specific questions. (1) Do trade-offs occur between sexual reproduction, vegetative propagation and growth? Because the gemmae and winter bud form simultaneously (Chapter 2) through similar physiological processes, I expect trade-offs between sexual reproduction and other functions, but not between vegetative propagation and growth. (2) Do allocation patterns vary with plant size? Absolute allocation to all three functions should increase with plant size due to increased resource availability. (3) Is there between-site variation in plant size and/or patterns of resource allocation? Plant size may vary between sites, but most variation in absolute resource allocation should reflect plant size. Therefore I predict that patterns of relative resource allocation will not vary between sites.

The compact nature of the winter bud and the annual root system (see Chapter 2) make it possible to excavate, weigh, and replant dormant winter buds without adversely affecting the plant. These features, combined with discrete and easily detached gemmae enable accurate assessment of plant size, growth, and allocation to vegetative propagation. To assess patterns of resource allocation, I measured sexual reproduction (flower, fruit and seed production), vegetative propagation and growth during one reproductive season in unmanipulated plants. Absolute allocation to each function was analyzed in terms of allocation to other functions, plant size, and site.

3.2 METHODS

3.2.1 Data Collection

This study considers growth, vegetative propagation and sexual reproduction during 1993 of plants for which the overwintering bud had been weighed during the preceding autumn. The study involved plants at two beaches with coarse, sandy soil, one facing northwest (Site 3) and the other southeast (Site 4, see section 2.1 for details). In 1992, I marked groups of four plants at each of 25 locations (100 plants) at Site 3 and six plants at each of 30 locations (180 plants) at Site 4. The plants at each location grew within 30 cm of each other (mostly 15 cm apart) and were of a similar size, with rosette diameters of at least 2 cm. By autumn of 1992, 97 plants at 25 locations at Site 3 and 123 plants at 24 locations at Site 4 remained alive. Of these plants, 81 plants at Site 3 and 105 at Site 4 survived until spring. By autumn of 1993, 79 plants at Site 3 and 95 plants at Site 4 were still living. The number of locations with live plants did not change after 1992.

During 1993, I quantified aspects of plant size, sexual reproduction and vegetative propagation. Plants were monitored every three or four days throughout the growing season to assess flower and fruit production and they were categorized as non-flowering, flowering or fruiting. Flowering plants did not set fruit. Nine plants that lost flowers to herbivory or accidents were eliminated from the study. Individual flowers were marked with jeweller's tags so that fruit from the first and subsequent flowers could be distinguished. At or close to maturity, fruit were collected and preserved in 70% ethanol. I counted mature seeds, aborted seeds and unfertilized ovules in the laboratory using a Wild-M5 dissecting microscope.

Once plants became fully dormant at the end of the growing season (Oct. 1- Oct. 17, 1993), I excavated the winter buds with their attached gemmae. I then obtained bud mass and the total gemmae mass for each bud with a Mettler PM100 digital balance and counted the gemmae. Because the same procedure had been followed in 1992 and the winter buds were replanted after removal of 1992 gemmae, I could calculate the difference between "initial" (1992) and "final" (1993) bud mass. Although I refer to this

difference as "growth," it reflects a different process from that usually referred to as growth. In *Pinguicula vulgaris*, growth represents size differences between former and current structures, rather than the size increments of a persistent structure. Thus, if the new winter bud is smaller than the previous one, growth is negative.

3.2.2 Statistical Analysis

I analyzed plant size to help determine whether site and location differences in relative allocation resulted from differences in plant size or direct effects of environmental factors. Analysis of variance (GLM procedure, SAS 1987) was used to determine whether initial bud mass differed between sites, locations, or reproductive categories (non-flowering, flowering only, fruiting). Main effects included site, location within site (random effect) and reproduction. Interactions between location within site and other main effects were not analyzed because many locations were represented by single plants. Data were log transformed prior to analysis to stabilize variances. To facilitate presentation, I back-transformed descriptive statistics, resulting in asymmetric standard errors, which I report as lower (LSE) and upper standard errors (USE).

I used analysis of covariance (GLM procedure, SAS 1987) to determine the factors affecting variation in growth and vegetative propagation. The main effects were as described above. The covariates depended on the analysis and included gemmae mass, gemmae number, growth, and either initial (1992) or final (1993) bud mass as measures of size. Except for interactions between location within site and other variables, all possible two- and three-way interactions were included in the initial model and nonsignificant terms were dropped using backwards elimination ($\alpha=.05$). Data were log transformed for both analyses to stabilize variances. Because growth was often negative, I added 200 mg to all measures of growth prior to transformation. I analyzed significant differences between reproductive categories by using *t*-tests based on Šidák's multiplicative inequality (Sokal and Rohlf 1981) to compare pairs of means adjusted for the effects of significant covariates.

Plant size was included as an explanatory variable in all analyses. Growth determines final bud mass and was therefore analyzed as a function of initial bud mass. However, it was less clear whether final or initial bud mass is the more important influence on vegetative propagation. On one hand, initial bud mass influences total resource availability. On the other, the "final" winter bud and gemmae form simultaneously, probably as a result of related physiological processes. Therefore, two analyses were conducted, one using initial (1992) bud mass, growth, and gemmae number as covariates and the other using final (1993) bud mass and gemmae number only. Nine plants that produced no gemmae were omitted from the analyses. Both models fit the data equally well (adjusted $R^2=0.85$), but the model using final bud mass provided a much simpler explanation of the data. I therefore present only the latter model below.

To determine which factors influenced successful sexual reproduction, I analyzed the relative frequency of fruiting per location in response to the effects of site, mean size, growth, or gemmae mass by logistic regression. The LOGISTIC procedure (SAS 1990) uses maximum likelihood estimates to assess the effects of explanatory variables on the proportion of fruiting plants at a location. Site was coded as a dummy variable equal to zero at Site 3 and one at Site 4. Other explanatory variables were included as covariates. Gemmae number was not included in these analyses because it was strongly correlated with gemmae mass ($r=.86$, $P<.001$, $n=47$) and total gemmae mass is probably more indicative of overall allocation to vegetative propagation. Stepwise and backwards elimination were used to determine which factors affected the probabilities that plants fruited.

Ovule and seed production by plants that produced a single fruit were analyzed using ANCOVA (GLM procedure, SAS 1987). Because fruits were harvested from only ten plants at eight locations at Site 3 and 20 plants at 13 locations at Site 4, it was not possible to include location effects in the analysis. Instead, I used mean values of dependent variables and covariates at each location. For the analysis, site was the main effect and covariates included initial bud mass, gemmae mass, growth and, for the

analysis of seeds, ovule number. Two-way interactions between site and covariates were included in the initial model and nonsignificant terms involving covariates were dropped using backwards elimination.

To test whether relative allocation to growth, vegetative propagation and ovule production varied allometrically with plant size, I examined the slopes and intercepts of partial regression coefficients for relations between these functions and bud mass. For log-transformed data, a partial regression coefficient for bud mass equal to one indicates a proportional relation between bud mass and the dependent variable. For untransformed data, an intercept of zero indicates a proportional relation. I assessed these expectations with single-sample *t*-tests.

In the analyses of growth, vegetative propagation and ovule number, two covariates affected the dependent variable. To illustrate the influence of each covariate most clearly, I adjusted the data presented in the figures for the effect of the other covariate. I first calculated a predicted value for each observation given the value of the covariate of interest based on intercepts and partial regression coefficients from the ANCOVA and the mean value of other covariate. For this adjustment, I then added the residuals from the ANCOVA to these predicted values.

3.3 RESULTS

3.3.1 Plant Size and Resource Allocation

Initial bud mass differed significantly between sites, locations within sites and reproductive categories (Table 3.1). Plants at Site 3 (mean=42 mg, LSE=39.7 mg, USE=44.0 mg, $n=72$) weighed approximately 35 mg less than those at Site 4 (mean=77 mg, LSE=72.5 mg, USE=82.6 mg, $n=91$). Initial plant size also differed significantly between all three reproductive categories (Tukey's studentized range, $P<.05$). Fruiting plants (mean=96 mg, LSE=88.9 mg, USE=103.3 mg, $n=50$) were over twice the mass of non-flowering plants (mean=44 mg, LSE=41.3 mg, USE=45.9 mg, $n=92$), whereas flowering plants (mean=70 mg, LSE=62.0 mg, USE=70.3 mg, $n=21$) were intermediate

Table 3.1. Analyses of initial bud mass, growth, and gemmae mass.

Effect	Initial Bud Mass	Growth	Gemmae Mass
Site	$F_{1,87} = 12.54^{***}$	$F_{1,122} = .34$	$F_{1,122} = 1.26$
Location(Site)	$F_{45,112} = 3.14^{***}$	$F_{45,96} = 1.29$	$F_{45,96} = 1.70$
Reproduction	$F_{2,112} = 7.33^{**}$	$F_{2,96} = 15.61^{***}$	$F_{2,96} = 7.77^{***}$
Site x Repro.	$F_{2,112} = .04$	$F_{2,96} = 1.90$	$F_{2,96} = 1.10$
Initial Bud Mass	-	$F_{1,96} = 33.38^{***}$	-
Final Bud Mass	-	-	$F_{1,96} = 35.42^{***}$
Gemmae Mass	-	$F_{1,96} = 30.36^{***}$	-
Gemmae Number	-	n.s.	$F_{1,96} = 107.31^{***}$
Initial Bud x Repro.	-	$F_{2,96} = 18.01^{***}$	n.s.

** $P < .01$, *** $P < .001$, n.s. not significant

in size. Differences in average plant size among the three reproductive categories did not depend on site (site x reproduction interaction, Table 3.1).

Although much of the variation in plant size was explained by site and location (Table 3.1), site and location did not affect growth, vegetative propagation or the probability of reproducing as long as the analyses included bud mass and, for vegetative propagation, gemmae mass. These results imply that the effects of site and location on resource allocation are largely mediated through plant size.

3.3.2 Growth

Growth during 1993 depended on initial bud mass, gemmae mass and reproduction, but not on gemmae number (Table 3.1). Growth varied positively with gemmae mass for plants in all reproductive categories (Fig. 3.1). In contrast, growth varied negatively with bud mass in all plants, but the strength of the relation depended on reproduction (Table 3.1, Initial bud x Repro interaction: Fig. 3.2). Almost all non-fruited plants gained mass during 1993 (Fig. 3.2 a, b), with small plants growing slightly more than large plants (Fig. 3.2a and b). In contrast, roughly one third of fruited plants lost mass and growth declined strongly with increasing bud mass (Fig. 3.2c). Fruited plants that lost mass weighed between 100 and 300 mg and were larger than most non-flowering and flowering plants (Fig. 3.2). Consequently, despite their reduced size, these plants remained heavier than 100 mg, large enough to fruit during the next season. The partial regression coefficients for bud mass in all reproductive categories differed significantly from -1 (non-flowering: $b \pm s_b = -.08 \pm .038$, flowering: $b \pm s_b = -.13 \pm .060$, fruited $b \pm s_b = -.41 \pm .052$) indicating that absolute allocation to growth decreases at a decelerating rate and that relative allocation decreases at an accelerating rate.

3.3.3 Vegetative Propagation

Ninety-four percent of the plants in this study produced gemmae ($n=158$). Total gemmae mass depended on final bud mass, gemmae number and reproduction (Table

Figure 3.1. Relation between growth and total gemmae mass for plants in all reproductive categories ($b \pm s_b = .11 \pm .020$). Overall ANCOVA results are in Table 3.1. Data are adjusted for the effects of bud mass (see methods).

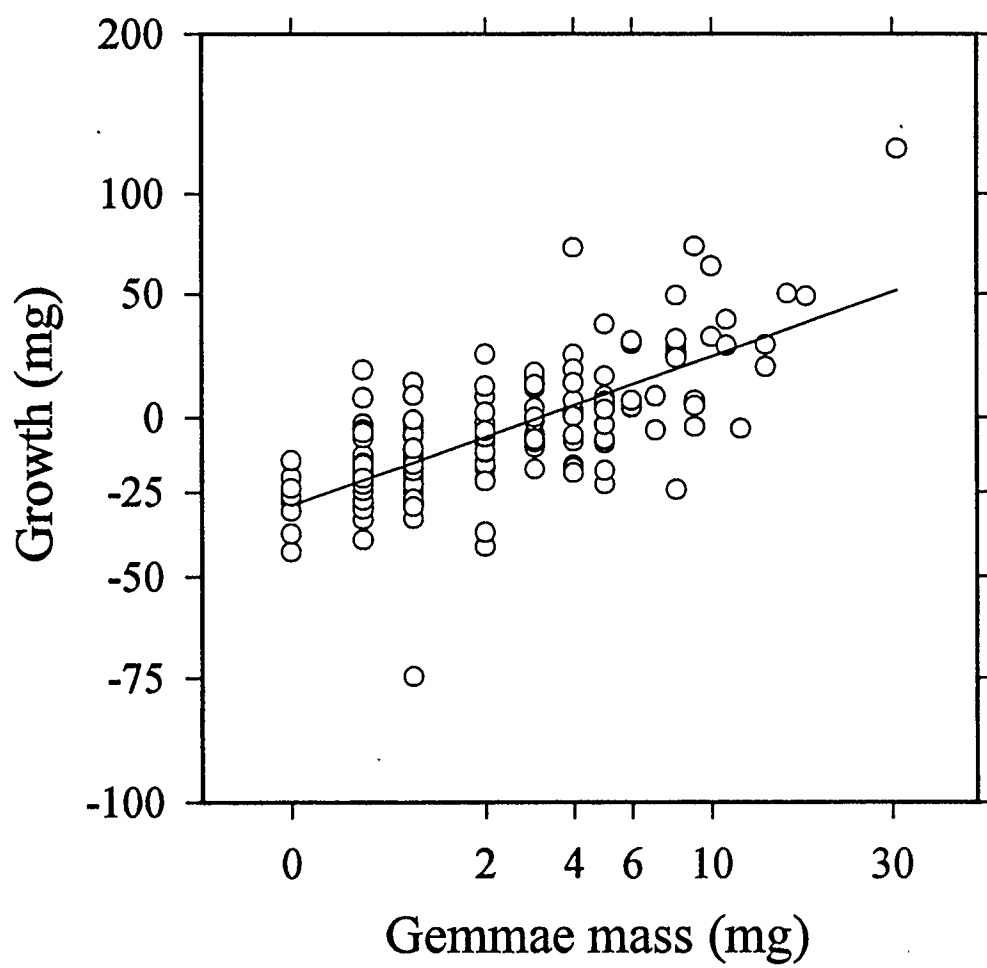
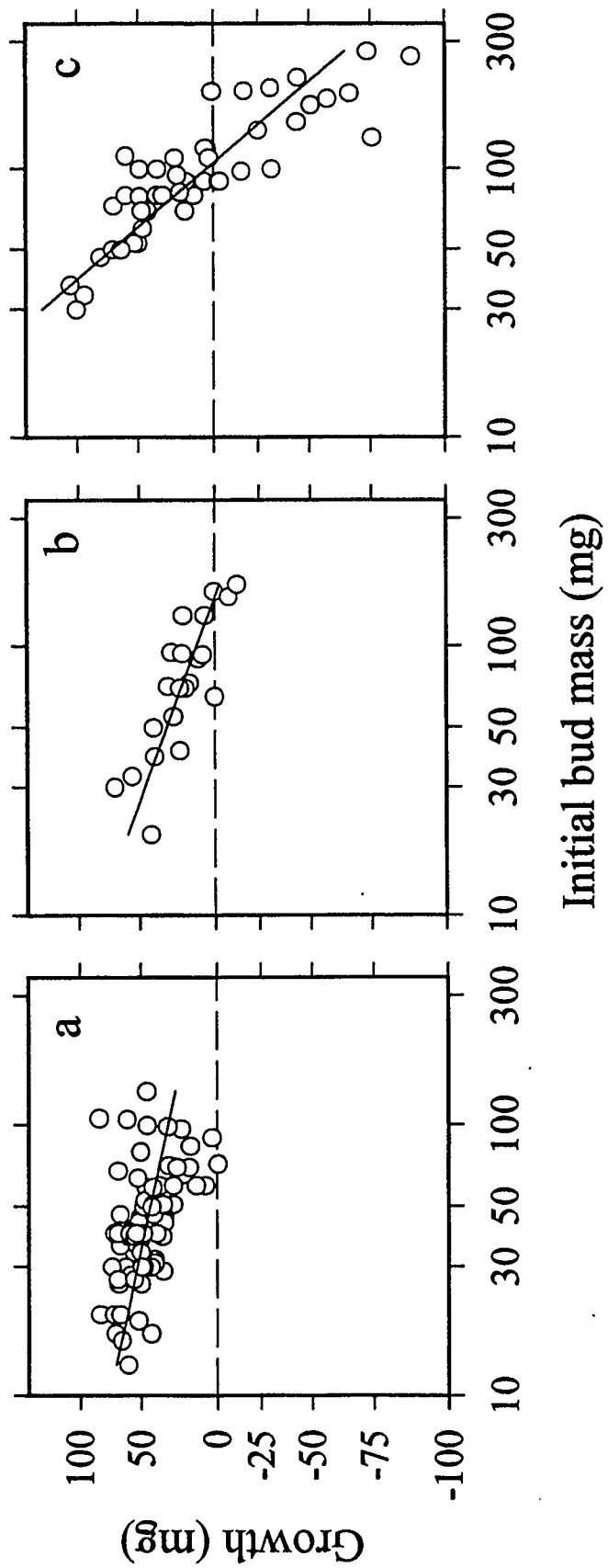


Figure 3.2. Relations between growth and initial bud mass for (a) non-flowering ($b \pm s_b = -.08 \pm .038$), (b) flowering ($b \pm s_b = -.13 \pm .060$), and (c) fruiting plants ($b \pm s_b = -.41 \pm .052$). See Table 3.1 for ANCOVA results. Data are adjusted for the effects of gemmae mass (see methods).



3.1). The partial effects of bud mass ($b \pm s_b = .61 \pm .114$, $t_{96}=5.95$, $P<.001$) and gemmae number ($b \pm s_b = .84 \pm .081$, $t_{96}=10.36$, $P<.001$) are both strong and positive (Fig. 3.3 a, b). The partial regression coefficient for $\ln(\text{gemmae number})$ did not differ from one ($t_{96}=1.97$, $P>.05$) indicating that total gemmae mass varies proportionately with gemmae number. Thus, the size of individual gemmae does not vary with the number of gemmae produced when the effects of other factors in the model are accounted for. The relation between total gemmae mass and plant size is difficult to assess from this analysis because the partial regression coefficient for $\ln(\text{bud mass})$ indicates the relation between gemmae mass and bud mass for a given gemmae number, and gemmae number may also vary with plant size. In a second analysis of gemmae mass which included only bud mass as a covariate, the partial regression coefficient for $\ln(\text{bud mass})$ did not differ from one ($b \pm s_b = 1.09 \pm .155$, $t_{97}=.54$, $P>.5$) indicating that allocation to vegetative propagation varies proportionately with plant size, so that relative allocation to gemmae is constant.

Vegetative propagation differed significantly among reproductive classes when the effects of bud mass and gemmae number were accounted for (Table 3.1). Non-flowering plants produced a greater mass of vegetative propagules than fruiting plants ($t_{96}=3.94$, $P<.001$; Fig. 3.4). Gemmae mass of flowering plants was intermediate and did not differ significantly from that of non-flowering ($t_{96}=1.40$, $P>.05$) or fruiting plants ($t_{96}=2.00$, $P>.05$; Fig 3.4).

3.3.4 Sexual Reproduction

At the two sites combined, 46% ($n=151$) of plants flowered and 70% ($n=69$) of flowering plants set fruit so that 32% of all plants set fruit. The proportion of plants fruiting at different locations varied positively with initial bud mass and negatively with growth and did not differ among sites (Table 3.2, Fig. 3.5). Few plants produced fruit at locations where the mean initial bud mass was less than 50 mg (Fig. 3.5). At these locations, most plants gained mass during the 1993 growing season and no plants lost

Figure 3.3. Effects of (a) final bud mass ($b \pm s_b = .61 \pm .114$) and (b) gemmae number ($b \pm s_b = .84 \pm .081$) on total gemmae mass in all plants. See Table 3.1 for ANCOVA results. In each plot, data are adjusted for the effects of the other covariate (see methods).

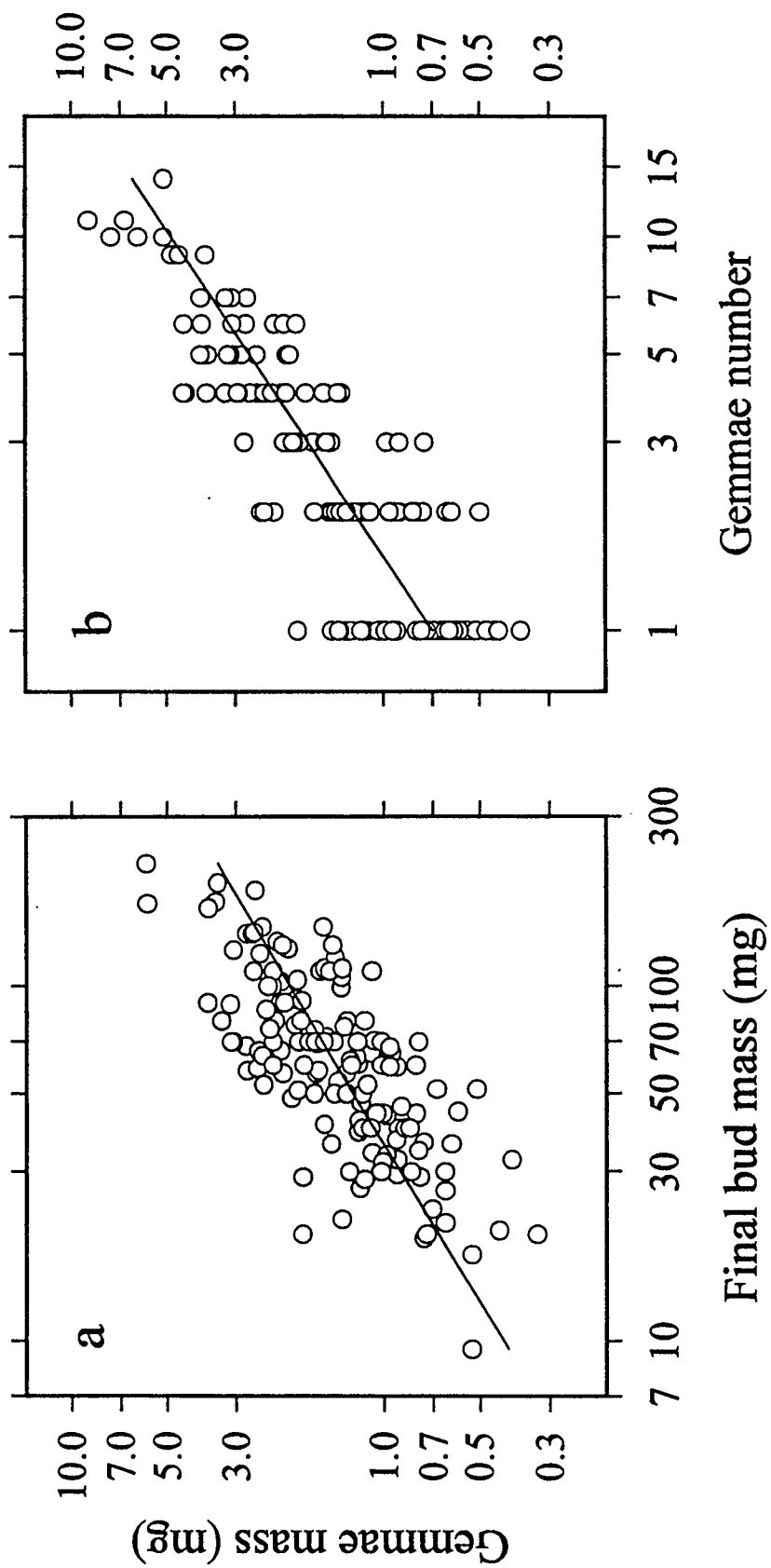


Figure 3.4. Total gemmae mass (mean $\pm$ SE) in non-flowering, flowering and fruiting plants. Overall ANCOVA results are in Table 3.1. Means are adjusted for the effects of final bud mass and gemmae number.

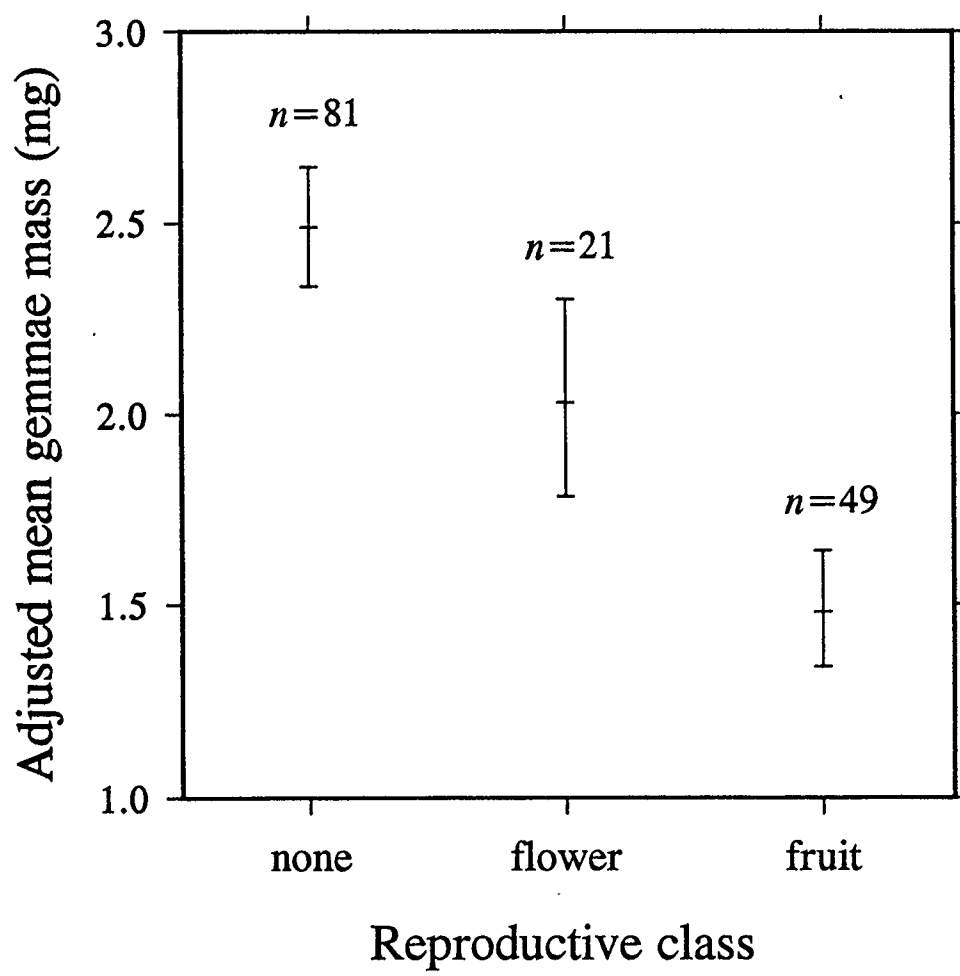
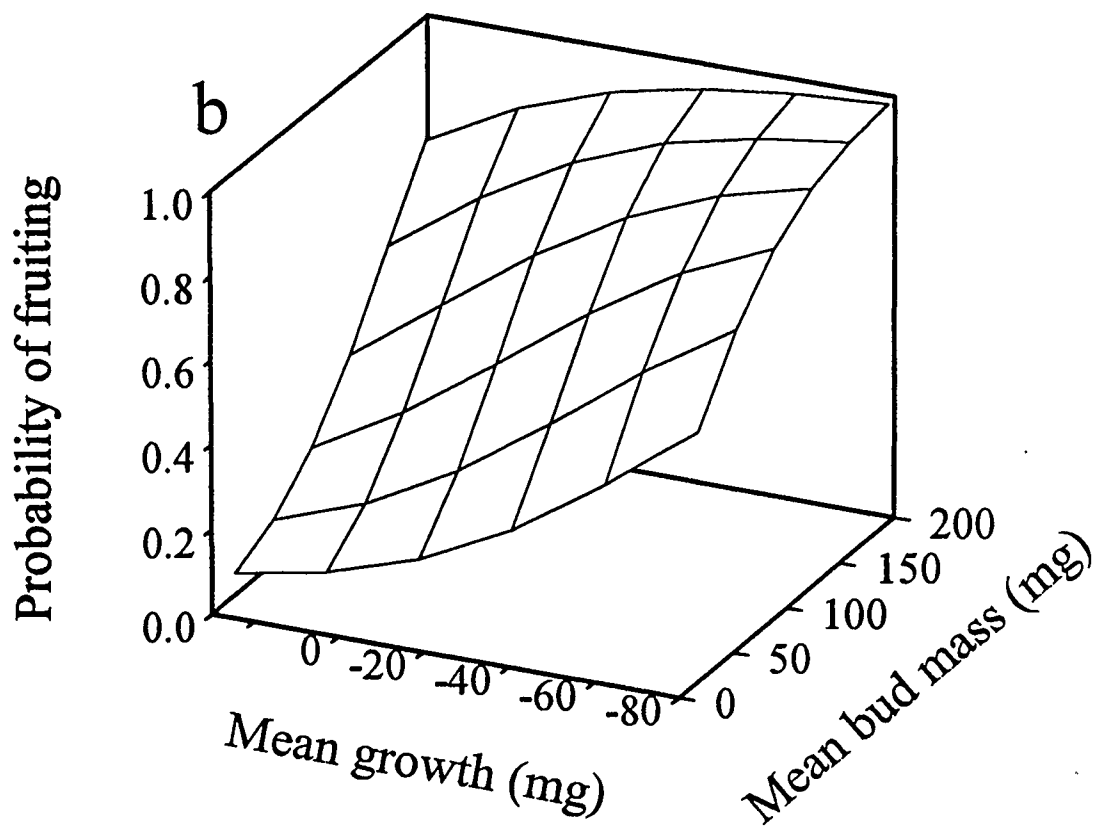
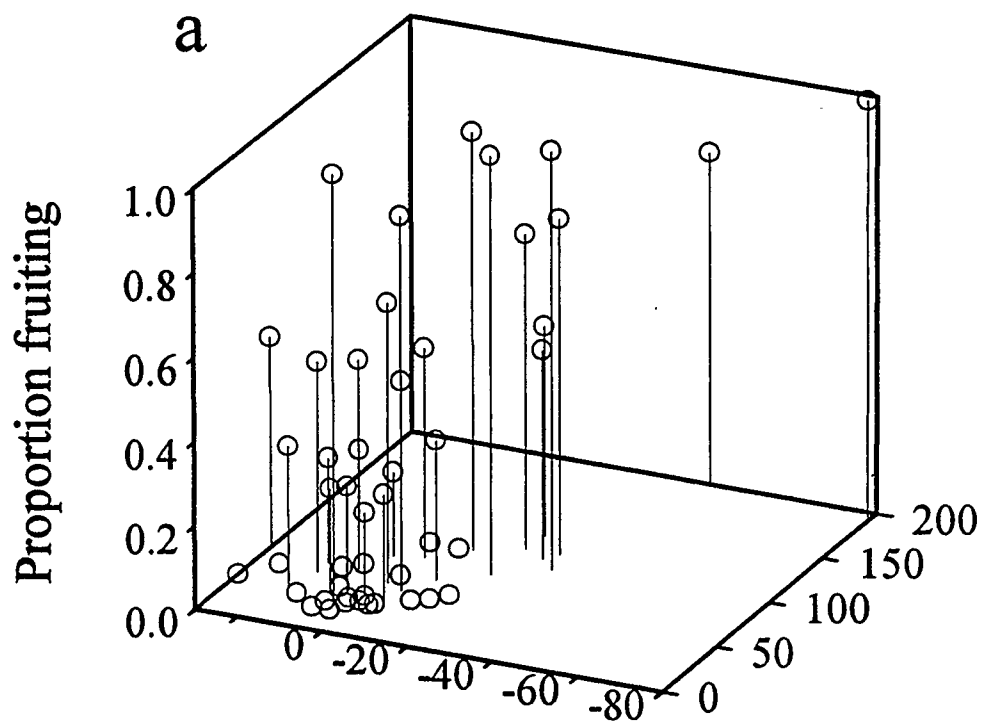


Table 3.2. Logistic regression results for factors affecting the proportion of fruiting plants per location within sites. Because site did not affect fruiting, it was eliminated from the analysis presented below.

Effect	Estimate (SE)	Wald Chi Square
Intercept	-2.52 (.533)	22.32***
Initial Bud Mass	.02 (.007)	9.95**
Growth	-.03 (.015)	4.24*

* $P < .05$, ** $P < .01$, *** $P < .001$

Figure 3.5. Proportion of plants fruiting per location within sites as a function of mean bud mass and mean growth. The predicted relation is based on logistic regression (Table 3.2).



more than 20 mg. In contrast, more than 50% of plants produced fruit at locations with mean bud masses greater than 50 mg and/or with a loss in mass exceeding 20 mg (Fig. 3.5).

Mean ovule production by fruiting plants at each location increased linearly with bud mass (Fig. 3.6a, b), but was unrelated to gemmae mass (Table 3.3). The positive intercept in the relation between bud mass and ovule number ($a \pm s_a = 153 \pm 14.4$, $t_{16}=10.61$, $P<.001$) indicates that as plant size increased, relative ovule production decreased at a decelerating rate. Growth affected ovule number positively at Site 3, but the relationship between ovule number and growth was not significant at Site 4 (Table 3.3, growth x site interaction: Fig. 3.6b).

Seed production varied positively and linearly with ovule number (Table 3.3, $b \pm s_b = .80 \pm .212$). The intercept of this relationship did not differ significantly from zero ($a \pm s_a = -28 \pm 46.4$, $t_{16} = -.61$, $P>.5$), indicating that a constant proportion (80%) of ovules developed into seeds. Although, the partial regression coefficients for gemmae mass did not differ significantly from zero at either site (Site 3: $b \pm s_b = 11.28 \pm 5.32$, $t_{16}=2.12$, $.049 < P < .05$, Site 4: $b \pm s_b = -3.84 \pm 1.87$, $t_{16} = -2.05$, $P>.05$), they did differ between sites (Site x gemmae mass interaction: Table 3.3).

3.4 DISCUSSION

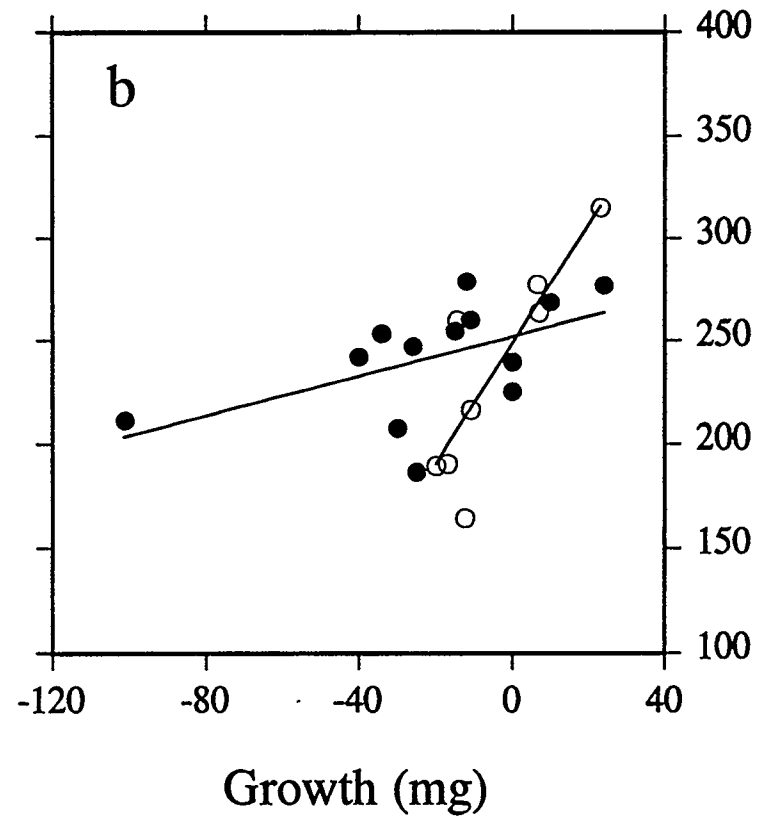
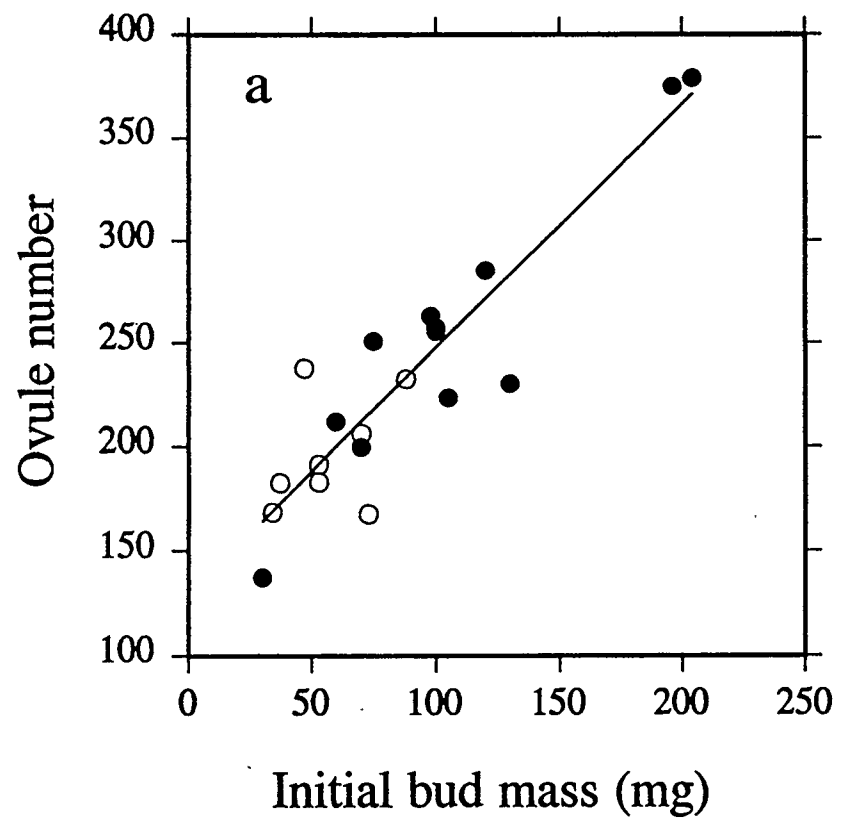
Allocation of resources to sexual reproduction, vegetative propagation, and growth in *Pinguicula vulgaris* depends on trade-offs with other functions. As predicted (objective 1), trade-offs occur between sexual reproduction and vegetative functions (growth and gemmae production), whereas vegetative propagation and growth vary positively. In particular, fruiting plants lost the most mass (Fig. 3.2), the proportion of fruiting plants varied negatively with growth (Fig. 3.4), and gemmae mass was lowest in fruiting plants (Fig. 3.4). In contrast, growth and gemmae mass were positively related (Figs 3.1, 3.3a). Positive relations between vegetative functions probably reflect physiological ties and phenology. Reduced gemmae production by fruiting *Pinguicula*

Table 3.3. Analyses of mean ovule and seed number per location.

Effect	Ovule Number	Seed Number
Site	$F_{1,16} = 13.16^{**}$	$F_{1,16} = 10.83^{**}$
Bud Mass	$F_{1,16} = 47.27^{***}$	n.s.
Growth	$F_{1,16} = 19.31^{***}$	n.s.
Ovule Number	-	$F_{1,16} = 14.34^{**}$
Gemmae Mass	n.s.	$F_{1,16} = 1.60$
Growth x Site	$F_{1,16} = 11.01^{**}$	n.s.
Gem. Mass x Site	n.s.	$F_{1,16} = 7.92^*$

* $P < .05$, ** $P < .01$, *** $P < .001$, n.s. not significant

Figure 3.6. (a) Relation between mean ovule number and mean initial bud mass per location ($b \pm s_b = 1.19 \pm .173$). Site 3 is represented by open circles and Site 4 by closed circles. (b) Relation between mean ovule number and mean growth per location at Site 3 ($b \pm s_b = 2.91 \pm .695$; open circles) and Site 4 ($b \pm s_b = .48 \pm .285$; filled circles). Overall ANCOVA results are in Table 3.3. For each plot, data have been adjusted for the effect of the other covariate (see methods).



vulgaris plants, even when the effects of final bud mass are accounted for, indicates that reproduction affects vegetative propagation and growth independently. Thus, reproduction is more costly than implied by examination of single trade-offs.

Resource allocation by *P. vulgaris* also depends on plant size. I expected absolute allocation to all three functions to vary positively with bud mass (objective 2). This was the case for vegetative propagation (Fig 3.3a) and sexual reproduction (Figs. 3.5 and 3.6a), but not for growth (Fig. 3.2). Negative relations between bud mass and growth could reflect architectural constraints on plant size and/or a size-maintaining strategy. I also predicted that site and location variation in resource allocation would be mediated through plant size (objective 3). This was true for growth, gemmae and fruit production, and ovule number (Tables 3.1, 3.2, and 3.3), indicating that environmental variation in resource allocation results largely from plant-size effects.

3.4.1 Trade-offs

Fruit and seed production reduce growth in many species (reviews in Snow and Whigham 1989, Calvo 1993). Most evidence for costs of reproduction involves plants with artificially increased fruit set, but reproductive trade-offs have also been demonstrated for plants with natural fruit set (e.g., Sohn and Policansky 1977, Snow and Whigham 1989, Zimmerman and Aide 1989, Gillman and Crawley 1990). Fruiting also reduces growth in *Pinguicula vulgaris* because the negative relation between plant size and growth was strongest in fruiting plants (Figs. 3.2 & 3.5). Elevated reproductive effort by fruiting plants probably reduced the energy available for growth.

In *Pinguicula vulgaris*, allocation to vegetative propagation depends on plant size at the end of the growing season and is therefore positively related to growth. The dependence on final size could result because gemmae are essentially axillary buds on the developing winter bud, so that gemmae and winter bud form simultaneously through similar physiological processes (section 2.2). It may also be advantageous for plants to remain large enough to reproduce in the following year. Regulation of final size may be easier if allocation to vegetative propagation is determined as the winter bud forms and

total resource accumulation becomes evident. Production of vegetative propagules is similarly related to the size of perennating organs in other bulbous (van der Valk and Timmer 1974, Barkham 1980) and corm-forming species (e.g. Snow and Whigham 1989). In contrast, the production of rhizome buds (vegetative propagation) varies negatively with growth for *Agropyron repens*, a rhizomatous grass (Reekie 1991). Contrasting relations between growth and vegetative propagation in *A. repens* and *P. vulgaris* may reflect differences in growth form and phenology. In *A. repens*, rhizome buds are initiated during the growing season, so that resources may be allocated to vegetative propagation at the expense of growth. In *P. vulgaris*, the winter bud and gemmae are structurally related and form simultaneously so that resource availability affects both similarly.

Negative relations between reproduction and vegetative propagation in bulbous, tuberous and corm-forming species could simply reflect the effects of reproduction on bulb or corm size, rather than direct trade-offs between growth and vegetative propagation, because clonal propagules form with the perennating organs. Effects of reproduction on gemmae mass that are independent of plant size (Table 3.1) indicate that direct trade-offs between reproduction and vegetative propagation occur in *P. vulgaris*. Although trade-offs between sexual reproduction and vegetative propagation have been demonstrated in other species (e.g., Sohn and Policansky 1977, Snow and Whigham 1989, Rameau and Gouyon 1991), the possibility that these trade-offs are distinct from the effects of reproduction on growth has not been considered. My results indicate that current reproduction reduces the potential for future reproduction by reducing growth of both the parent plant and vegetative propagules.

3.4.2 Plant Size and Site Effects

Between-habitat variation in relative allocation to reproduction (Samson and Werk 1986, Weiner 1988, Mendez and Obeso 1992), vegetative propagation and growth (Mendez and Obeso 1992) can result from size effects rather than from the direct effects of environmental factors. Site and location effects on resource allocation in *Pinguicula*

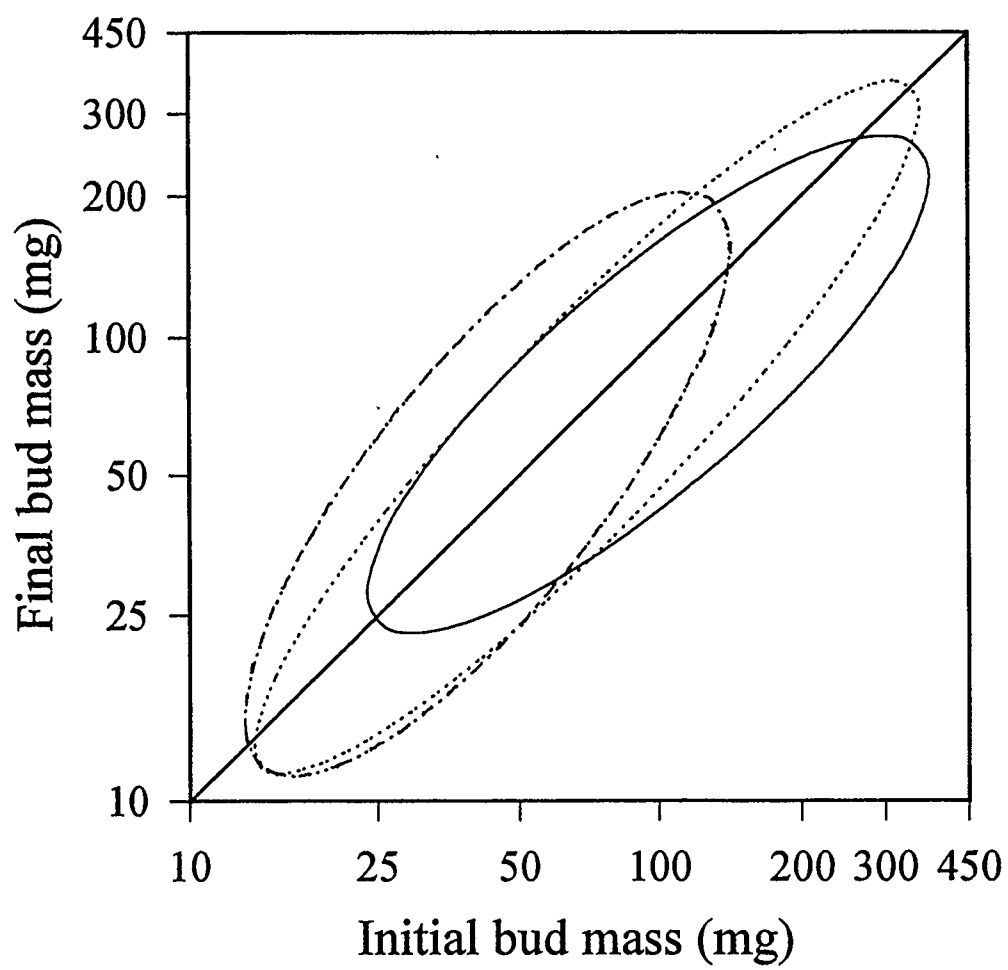
vulgaris are also largely mediated through plant size. Although the plants at Site 3 were roughly half the size of those at Site 4, site and location did not affect gemmae mass once variation due to bud mass had been accounted for. The effects of bud mass on fruit production were also the same at each site. Environmental factors may affect resource allocation directly by altering the slopes or intercepts of relations with plant size (e.g., Soule and Werner 1981, Ohlson 1988, de Ridder and Dhondt 1992, Schmid and Weiner 1993); however, except for between-site differences in the effects of growth on ovule number in fruiting plants, I did not observe such effects.

Allometric patterns of resource allocation indicate that between-habitat differences in the size distribution of *Pinguicula vulgaris* populations cause variation in relative allocation to both sexual reproduction and growth. Although the implications of allometric allocation to reproduction are well recognized (Soule and Werner 1986, Weiner 1988), the implications of allometric growth and vegetative propagation have received little consideration. My results indicate spatial and temporal variation in vegetative allocation may reflect size effects rather than direct responses to environmental factors, as is often assumed (e.g., Ogden 1974, Abrahamson 1975, 1980, Bostock 1980, Ashmun et al. 1985).

3.4.3 Plant Size and Resource Allocation

Several important aspects of the relations between plant size, growth and reproduction in *Pinguicula vulgaris* can be summarized by plotting final bud mass against initial bud mass for each reproductive category (Fig. 3.7). Differences in minimum plant size between non-fruiting and fruiting plants indicate threshold sizes for reproduction, a common phenomenon in plants (Werner 1975, Harper 1977, Gross 1981, reviews in Dafni et al. 1981, Mendez and Obeso 1992). A threshold size for reproduction in *Pinguicula vulgaris* is evident from differences in initial plant size between non-fruiting and fruiting plants (Fig 3.7). Plants below the threshold size probably have insufficient resources to sustain flower or fruit production and instead invest all resources in growth and gemmae production. However, the large overlap in

Figure 3.7. Relations between initial and final bud mass in non-flowering (dashed-dotted ellipse), flowering (dotted ellipse), and fruiting plants (solid ellipse). The solid diagonal line has a slope of one: plants falling below this line lose mass from one growing season to the next, whereas plants falling above this line gain mass. Each ellipse encompasses 95% of the data.



plant size between reproductive categories (Fig. 3.7) indicates that flowering and fruiting must depend on more than plant size alone.

Because differences in plant size reflect overall variation in resource availability, absolute allocation to all functions was expected to vary positively with plant size (cf. van Noordwijk and de Jong 1986). This was the case for sexual reproduction, as indicated by threshold sizes and an increased probability of fruiting as plant size increased beyond the threshold (Fig. 3.5). Similarly, total gemmae mass varied positively with final bud mass (section 3.4.1, above). In contrast, growth in *P. vulgaris* varied negatively with bud mass. This negative relation cannot be entirely due to reproductive costs as it was significant in non-fruiting plants (Fig 3.2). Growth and plant size may be negatively related because *Pinguicula vulgaris* does not grow beyond a maximum size. *Pinguicula* species have flat basal rosettes of leaves. As plants become larger, the extent of leaf overlap increases. Thus, rates of photosynthesis and insect capture may be maximal at intermediate plant sizes. If lifetime reproduction is maximized by allocating less to growth and more to other activities as plant size increases, growth should vary negatively with plant size.

Despite costs of reproduction and negative relations between growth and plant size, losses in bud mass by fruiting plants probably did not have serious consequences for future reproduction. Consider Figure 3.7, in which the diagonal line represents plants with equal final and initial bud masses (i.e., zero growth). Comparison of the ellipses for each reproductive category indicates that non-flowering plants generally gained mass, flowering plants maintained their original mass, and fruiting plants typically lost mass (Fig. 3.7). These differences probably reflect costs of reproduction (section 3.4.1). However, even though many fruiting plants lost mass, their average initial bud mass was more than double that of non-flowering plants (96 mg versus 44 mg: section 3.3.1) and their final bud mass still varied positively with initial bud mass. Consequently, fruiting plants maintained a mass that would allow them to fruit in the following year (Fig 3.7).

Relative allocation to sexual reproduction varies allometrically with plant size in many species (Samson and Werk 1986, Weiner 1988, Klinkhamer et al. 1990, 1992).

Relative allocation to vegetative propagation and growth may also be allometric and, due to trade-offs between sexual reproduction and vegetative functions (section 3.4.1), may be the inverse of reproductive allometries (Mendez and Obeso 1992). Relative allocation to growth by *Pinguicula vulgaris* varied negatively with plant size, whereas total gemmae mass was proportional to plant size. If large plants allocate proportionately more resources to activities other than growth or gemmae production, then relative allocation to sexual reproduction should vary positively with plant size. Although relative allocation to ovule number by fruiting plants varied negatively with plant size, it is possible that total reproductive effort increased with plant size. Assessment of relative ovule number considers only a subset of plants and does not incorporate investment in flowers, pollen, or fruit. In addition, the probability of fruiting increased with plant size.

This study demonstrates the influence of both physiological trade-offs between sexual reproduction and other functions and the role of plant size in determining resource allocation by *Pinguicula vulgaris*. Costs of reproduction decrease both growth and vegetative propagation. Consequently, plants do not reproduce until they are sufficiently large to incur costs to growth without jeopardizing their chances of future reproduction.

4 RESOURCE AVAILABILITY AND ALLOCATION OPTIONS IN *PINGUICULA VULGARIS*

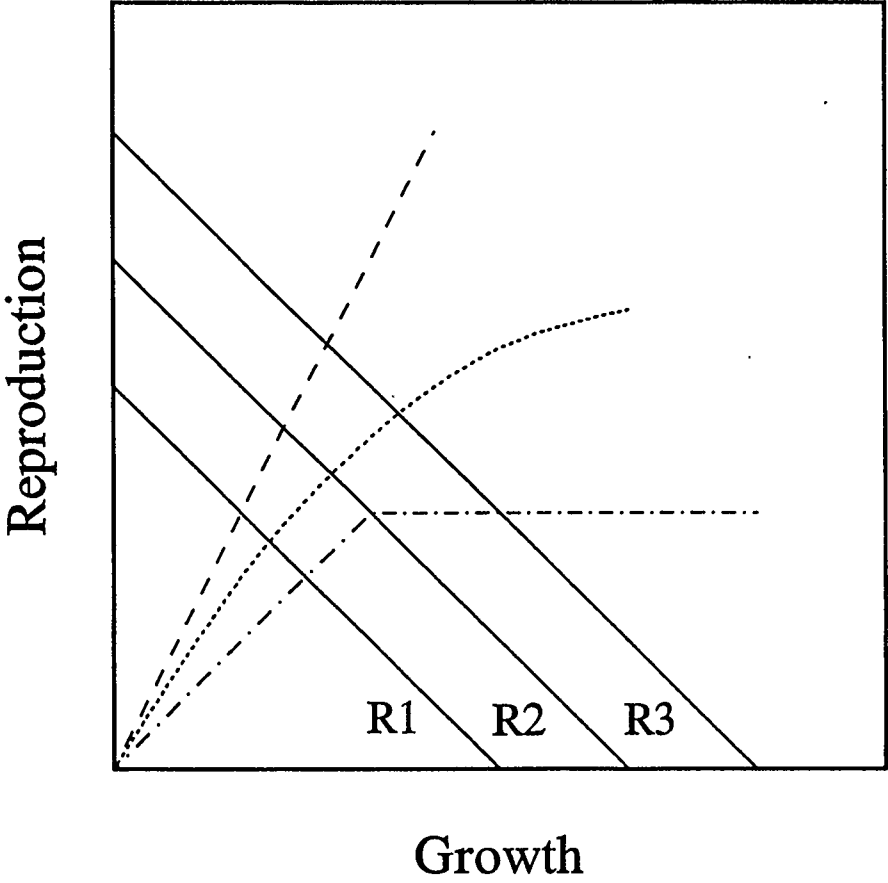
4.1 INTRODUCTION

4.1.1 Resource Limitation of Lifetime Reproduction

Resource availability limits lifetime reproduction by many organisms. In plants, positive relations between seed production and plant size (Samson and Werk 1986, Weiner 1988, Schmid and Weiner 1993, Chapter 3) reflect the dependence of reproduction on resource availability. Further evidence for resource limitation is provided by reproductive costs (i.e. trade-offs between reproduction and other functions), which have been documented in many species (reviews in Snow and Whigham 1989, Calvo 1993, Chapter 3). In addition, reduction of resource demands by the removal of flowers or fruit often increases fruit or seed set of the remaining flowers (e.g. Van Stevenick 1957, Galen et al. 1985, Queller 1985, Ehrlén 1992). Finally, fertilizer and water increase reproductive yield in wild (van Andel and Vera 1977, Willson and Price 1980, McCall and Primack 1985, Delph 1986, Boeken 1989, Vaughton 1991, Campbell and Halama 1993) as well as agricultural species.

Spatial and temporal variation in resource availability (McCall and Primack 1985, Vaughton 1991, Campbell and Halama 1993) should select for plants that are responsive to fluctuating resource levels. Figure 4.1 summarizes potential responses by perennial plants to increased resource availability. The solid lines indicate a trade-off between reproduction and growth. At each resource level, increased allocation to one function results in decreased allocation to the other, hence the negative slopes. A plant's position on the trade-off line reflects relative allocation to growth and reproduction. The dashed and dotted lines represent possible changes in absolute allocation to growth and reproduction as resource availability changes. Perennial plants allocate resources to growth and vegetative propagation as well as to current reproduction. Thus, perennial species could respond to increased resources by increasing absolute allocation to all three functions. In this case, relative allocation to all functions and trade-offs between functions would remain constant over a range of resource levels (cf. van Noordwijk and

Figure 4.1. Three hypothetical patterns of resource allocation to reproduction and growth. The solid lines represent a linear trade-off between growth and reproduction at three different resource levels (resource availability increases from R1 to R3). The straight dashed line represents constant allocation patterns, regardless of resource availability, because the proportion of available resources allocated to growth and reproduction is the same at all three resource levels. The dotted line represents a plant that increases the proportion of available resources allocated to growth relative to reproduction as resource availability changes. The dashed-dotted line represents a plant with upper limits to reproductive allocation. Once R2 is reached, this plant can increase allocation to growth but not to reproduction as resource levels increase.



de Jong 1986: Fig 4.1, dashed line). Alternatively, extra resources may be allocated preferentially to one or more functions, so that changes in resource availability alter patterns of resource allocation (Fig 4.1, dotted line). The extreme case of preferential allocation occurs when allocation to one function has an upper limit: consequently, once the limit is reached, resources can only be allocated to other functions (Fig. 4.1, dashed-dotted line).

4.1.2 Resource Allocation by Perennial Species

How plants respond to increases in resource availability should depend on the flexibility of allocation patterns and on the relative advantages of allocation to each function. Advantages of increasing current reproduction include the certainty of producing at least some offspring capable of contributing to future generations (review in Stearns 1976). These benefits must be balanced against those associated with growth and vegetative propagation. Investment in vegetative functions increases the resource-garnering ability of the genet and therefore its ability to produce seeds in the future (Reekie and Bazzaz 1987a). It is probably always advantageous to use some extra resources for current reproduction because survival until the next reproductive episode is never certain. Consequently, perennial species do increase current fruit or seed production when resource levels increase (e.g. van Andel and Vera 1977, Willson and Price 1980, McCall and Primack 1985, 87, Boeken 1990, Vaughton 1991).

When increases in current reproduction are prevented and/or survival until the next reproductive episode is fairly certain, lifetime reproduction may be increased through growth or vegetative propagation. Pollen limitation (Bierzychudek 1981, Galen et al. 1985, McCall and Primack 1985), meristem limitation (Watson 1984, Ericksson 1985, Geber 1990, Casper and Neisenbaum 1993), and preformation of floral primordia during the preceding season (Sørensen 1941, Hartsema 1961, Billings and Mooney 1968, Mark 1970, Dafni et al. 1981) can all set an upper limit on fruit and seed production (section 1.2.3). In species with preformation, resource levels in one year often influence flower and fruit production in the next (e.g., Hill-Cottingham and

Williams 1967, Mark 1970, Boeken 1989, Svensson et al., 1993). Thus, some perennial species probably respond to increased resource availability by increasing investment in future rather than in current reproduction.

Plants with preformation should evolve means of adjusting reproduction upwards to take advantage of fluctuations in resource availability (cf. Lloyd 1980). Two possibilities exist. First, plants may produce more flower primordia or flowers than they can mature into flowers or fruit (review in Mark 1970). A second, less expensive means of exploiting extra resources for reproduction would be to simply increase seed number in existing fruit. Seed number per fruit increases in response to resource supplementation in several species (Willson and Price 1980, Delph 1986, Ehrlén 1992, Campbell and Halama 1993).

Nutrient availability may affect future reproduction directly as well as indirectly through increased growth and vegetative propagation. Seeds have high concentrations of phosphorous, nitrogen and potassium (van Andel and Vera 1977, Bloom et al. 1985), so that nutrient enhancement in one year may directly increase seed output in subsequent years if such nutrients can be stored rather than used for growth. For example, fertilization of *Banksia spinulosa* in one year did not affect flowering in the following year but did increase fruit set (Vaughton 1991). If the effects of fertilization on future reproduction were mediated through increased growth, flowering should also have increased. Similarly, after a year of heavy seed production the nutrient status of the rest of the plant may be impoverished, reducing subsequent reproduction until nutrient stores can be replenished. Several studies have shown negative relationships between reproduction in one year and both growth and flowering or fruiting in the next (e.g., Montalvo and Ackerman 1987, Zimmerman and Aide 1989, Snow and Whigham 1989, Ackerman and Montalvo 1990, Primack and Hall 1990, Gillman and Crawley 1990, Eggert 1992), but the possibility that reproduction in one year may affect subsequent reproduction independently of size has not been explored.

Because growth and vegetative propagation may often be positively related (Chapter 3), Figure 4.1 does not apply to the responses in allocation to these functions

following resource supplementation. However, options do exist for the distribution of resources between growth and vegetative propagation. Resources could be distributed proportionately between each function or allocation to one or the other could be favoured. Small plants often allocate proportionately more resources to growth than large plants due to threshold sizes of reproduction (Werner 1975, Harper 1977, reviews in Dafni et al. 1981, Mendez and Obeso 1992). Growth may also be favoured when ramets compete for space or light (Abrahamson 1975, 1980). Conversely, relative allocation to growth may decrease as reproductive plants become large because architectural constraints may reduce the advantages of large size (Chapter 3). Allocation to vegetative propagation also increases the opportunity for physical spread and exploitation of resources, so that the genet may reach larger sizes than would be possible if all resources were allocated to growth of a single ramet (Williams 1975, Abrahamson 1980).

4.1.3 Objectives

This study investigates resource allocation in *Pinguicula vulgaris* in response to resource supplementation. Several aspects of the biology and habit of *P. vulgaris* suggest resource limitation and may influence its response to resource supplementation. The nutrients available for growth and reproduction by *P. vulgaris* are probably limited by insect abundance because the plants grow in wet, nutrient-poor soil and derive most of their nutrients from insects (Aldenius et al. 1983, Karlsson and Carlsson 1984, Karlsson et al. 1991). The ability to self-pollinate autonomously and to complete seed set in selfed fruits (Chapter 2) also indicates that reproduction is more likely to be limited by resource than pollen availability.

The objectives of this study are two-fold. The primary objective is to determine whether patterns of resource allocation and trade-offs change with increased resource availability. Preformation of leaf and flower primordia may prevent *Pinguicula vulgaris* from increasing reproduction in the current year, except by increasing the proportion of ovules matured into seeds, so that extra resources should be allocated to growth and

vegetative propagation. The secondary objective is to determine whether past reproduction affects future reproduction directly or indirectly through plant size. Because flower and fruit production are size related in *P. vulgaris* (Chapter 3), I expect costs of previous reproduction to be mediated through plant size. I address these objectives by comparing resource allocation to sexual reproduction, vegetative propagation and growth during 1993 by control plants and plants fed fruit flies. To correct for initial variation in resource availability, my analyses accounted for plant size at the beginning of the growing season. I also examined reproductive success in relation to a plant's fruiting status during the preceding year.

4.2 METHODS

4.2.1 Data Collection

During 1992, I selected four plants at each of 30 locations as study subjects at Site 2, a side channel on the east bank of the Sheep River (see Chapter 2 for details). Plants in each group were of a similar size, with rosette diameters of at least 3 cm, and had flower buds. The plants were monitored every three to four days during the growing season (daily during flowering) to assess flower and fruit production. At the end of the season, I categorized all plants as non-flowering, flowering or fruiting. By definition, flowering plants did not set fruit. When plants became fully dormant at the end of the growing season (Sept. 20 - Oct. 3), I excavated the winter buds and attached gemmae. I weighed winter buds, and total gemmae mass for each bud with a Mettler PM100 digital balance and counted the gemmae. I then replanted the winter buds in their original locations. By autumn of 1992, 110 of the original 120 plants marked were alive. One hundred and three of these plants at 27 locations survived until the 1993 growing season.

In May, 1993, half the plants at each location (usually two but sometimes one if not all plants at that location survived the winter) were randomly assigned to a resource supplementation treatment and the remaining plants were left as controls. "Fed" plants received two or three freshly killed fruit flies on their leaves twice a week. In the fourth week of the 18-week growing season (June 14), I observed ants removing fruit flies from

the plants. To prevent further interference by ants, I surrounded all plants with 5-cm high wire mesh enclosures whose bases were covered with Tanglefoot[®]. All enclosures were in place by June 23, by which time plants that subsequently flowered had buds but no mature flowers.

To test the effects of enclosures on natural prey, I selected 15 pairs of non-experimental plants and caged one plant in each pair. The leaves of enclosed plants captured significantly fewer prey. The mean difference ($\pm$ SE) in prey capture between pairs of enclosed and open plants over a seven-day period was 7 ± 1.5 insects in one week (June 23-29) and 4 ± 1.4 insects (June 30-July 6) in the following week. The differences were significant in both weeks (paired-sample *t*-test, Week 1: $t_{12}=4.46$, $P<.001$, Week 2: $t_{12}=2.90$, $P<.02$). Because the cages reduced natural prey, I caged both control and fed plants to maintain a difference in insect availability between treatments in the feeding experiments.

I collected data on sexual reproduction, vegetative propagation, growth, and plant size. The plants were monitored for flower and fruit production as in 1992. Three plants that lost flowers to herbivory or accidents were eliminated from the study. At or close to maturity, fruit were collected and preserved in 70% ethanol. I used a Wild-M5 dissecting microscope to count mature seeds, aborted embryos and unfertilized ovules; these were summed to obtain total ovule number. Weighing of winter buds and gemmae (Oct. 3-8) were as described for 1992. As in Chapter 3, growth was calculated as the difference between initial and final winter bud mass. By the end of the study, 89 of the original 120 plants remained alive.

To assess the effects of increased growth due to feeding on reproductive potential, I also examined the influence of bud size on the production of flower primordia. The data used in this analysis were collected in 1992 from four sites, including the site used for all other aspects of this study. The three other sites were Sites 3 and 4 (Chapter 2) and an additional site approximately 2 km upstream from the site used for this study.

4.2.2 Statistical Analysis

I used analysis of covariance (GLM procedure, SAS 1990) to analyse growth and vegetative propagation. Main effects included location (random effect); reproductive category (non-flowering, flowering, fruiting), and feeding treatments. Initially, fruiting category in 1992 (fruiting, non-fruiting) was also included as a main effect. However, fruiting in 1992 did not affect growth or vegetative propagation in 1993, so I removed it from the analyses. Covariates included bud mass (either initial or final, see below), gemmae mass, gemmae number, and growth. All possible two-way interactions were included in the initial models, except those involving location, and nonsignificant terms were dropped using backwards elimination ($\alpha=.05$). Interactions involving location were excluded because several locations were represented by single plants. Data were log transformed for both analyses to stabilize variances. Because growth was often negative, I added 100 mg to all measures of growth prior to analysis. To facilitate presentation, I back-transformed descriptive statistics, resulting in asymmetric standard errors, which I report as lower (LSE) and upper (USE) standard errors. I analyzed significant differences between reproductive categories with *t*-tests based on Šidák's multiplicative inequality (Sokal and Rohlf 1981) to compare pairs of means adjusted for the effects of significant covariates. When more than one covariate affected the dependent variable, data presented in the figures were adjusted for the effects of the other covariate (see Chapter 3 for details).

Because I measured winter bud mass in autumn of 1992 and 1993, I could have included either initial or final bud mass as a size indicator in my analyses of growth, vegetative propagation and reproduction. Growth was analyzed as a function of initial bud mass because final bud mass depends on growth. Initial size also influences sexual reproduction more than final size because allocation to flowers and fruit occurs before final size is determined. Whether initial or final bud mass primarily affect gemmae production is not intuitively obvious. On one hand, initial bud mass is an important determinant of the resources available for vegetative propagation. On the other, gemmae and the final winter bud form simultaneously and probably as part of related

physiological processes, so that total allocation to gemmae may depend more on final than initial size. To clarify the issue, I initially analyzed 1993 gemmae mass in terms of both initial and final bud mass. In the analysis originally including initial bud mass, initial bud mass was eliminated from the model. Because addition of final bud mass to this model increased R^2 from .62 to .92, I present the analysis of 1993 gemmae mass in terms of final bud mass.

I analyzed aspects of sexual reproduction with logistic regression (LOGISTIC procedure, SAS 1990) because plants produced no more than two flowers and fruit, so that I could not analyze flower and fruit production as continuous variables using ANCOVA. I analyzed the relative frequency of flowering and of fruiting by flowering plants per location during 1993 in response to the effects of mean initial bud mass, vegetative propagation, and growth by logistic regression. For each location, means were calculated separately for fed and control plants, and feeding treatment was coded as a dummy variable equal to -1 in control plants and 1 in fed plants. Continuous terms that were non-significant were eliminated using stepwise and backwards elimination.

I analyzed the proportion of plants with more than one flower primordium as a function of mean bud mass per location. Site was coded by three dummy variables. Site did not affect the probability of producing multiple flower primordia, and was therefore removed from the analysis presented below.

To determine whether previous reproduction influences current reproduction directly, I performed two analyses. First, I analyzed the proportion of plants changing fruiting status between 1992 and 1993 per location as a function of fruit production in 1992, bud mass at the end of 1992, 1993 gemmae mass, and 1993 growth. Fruiting in 1992 was coded as a dummy variable equal to -1 in non-fruiting plants and 1 in fruiting plants. Feeding was not included in this analysis because it didn't affect flowering and fruiting (see results in section 4.3.3) and its inclusion would have reduced sample size per feeding-treatment combination. Second, I used Stuart's test (Marascuilo and McSweeney 1977) to determine whether the proportion of plants in each reproductive category differed significantly between years. Stuart's test allows comparison of

marginal probabilities in square contingency tables when the chi-square assumption of independence is violated (Marascuilo and McSweeney 1977). Here, recategorization of plants at two times introduced a correlation between marginal probabilities. Stuart's test involves calculating 95% confidence intervals for between-year changes in marginal proportions. When the confidence interval does not span zero (no change) the difference between proportions is considered significant.

Because feeding may increase the number of seeds per fruit, I originally intended to analyze the effects of feeding on seed production. However, low fruit numbers in 1993 (only 25 plants set fruit) coupled with losses due to herbivory or accidents meant that I was only able to harvest fruit from 15 plants. Although seed set was slightly higher in fed plants (mean $\pm$ SE=134 $\pm$ 22.8, $n=5$) than in control plants (122 $\pm$ 15.8, $n=10$), the difference was not significant ($t_{13}=0.44$, $P>.6$) and the sample size was too small for more detailed analysis.

4.3 RESULTS

4.3.1 Growth

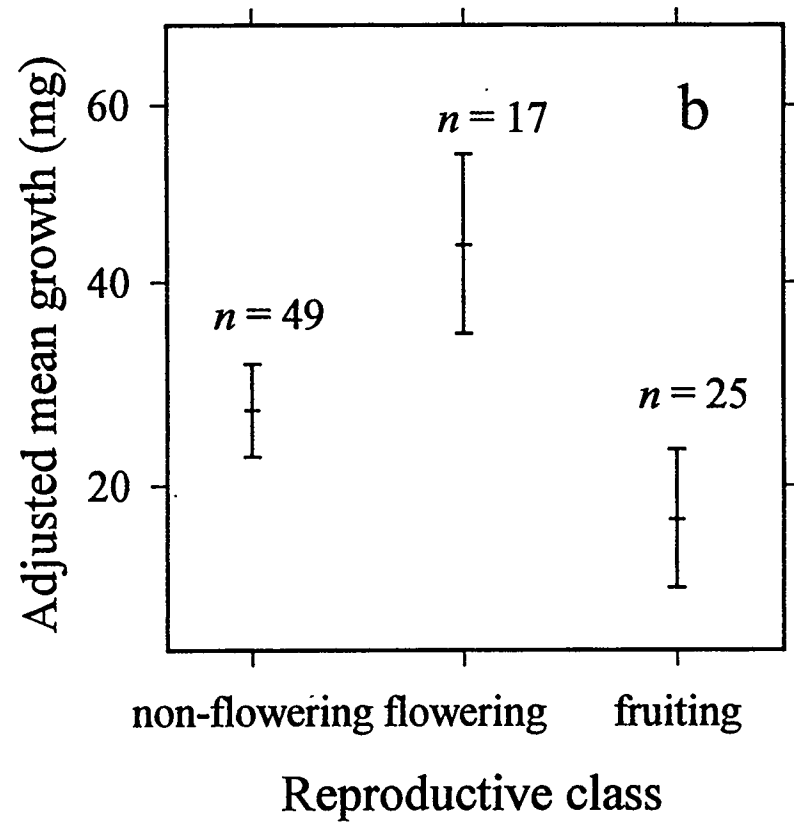
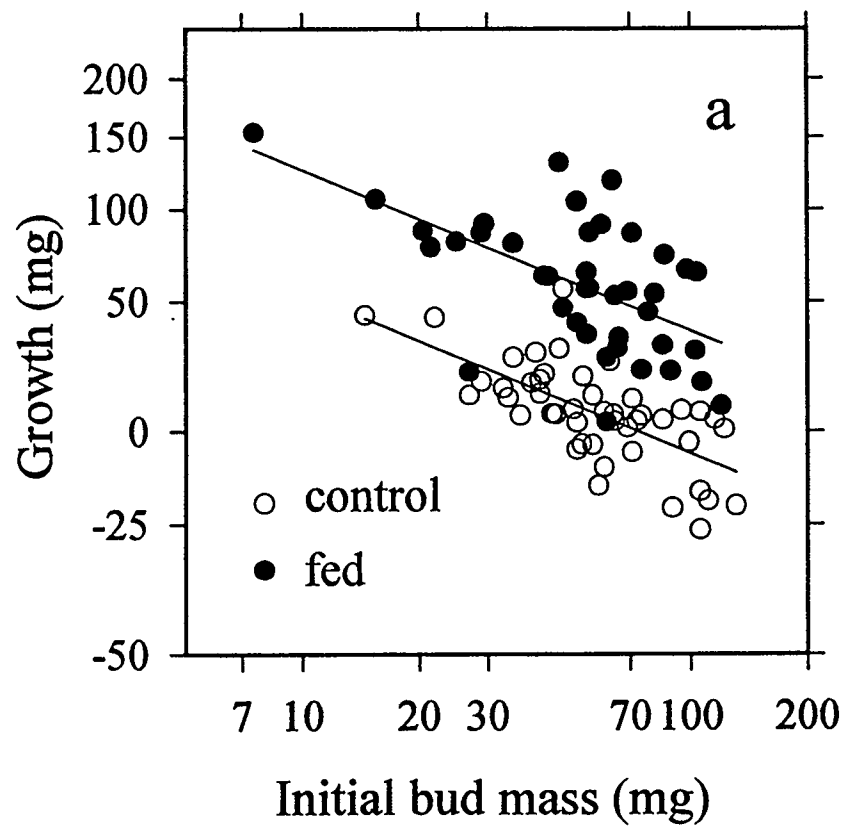
Feeding increased growth dramatically. Analysis of variance (effects were location and feeding treatment) indicated that initial bud mass (for all plants, mean bud mass=54 mg, LSE= 51.2 mg, USE= 57.3 mg) did not differ between feeding categories ($F_{1,59}=0.14$, $P>.7$), whereas final bud mass did ($F_{1,59}=67.85$, $P<.001$). Mean final bud mass was 106 mg (LSE=99.6 mg, USE=113.1 mg) in fed plants and 60 mg (LSE=55.8 mg, USE=64.3 mg) in control plants. Location, feeding treatment, reproductive category and initial bud mass significantly affected growth (Table 4.1). Growth varied negatively with initial bud mass (Fig. 4.2a), indicating that larger plants grow less than smaller ones in both relative and absolute terms. Fed plants (adjusted mean growth=56 mg, LSE=50.4 mg, USE=62.1 mg) grew much more than controls (adjusted mean growth=7 mg, LSE=2.6 mg, USE=10.7 mg) and, for a given plant size, there was very little overlap between fed and unfed plants (Fig. 4.2a). Feeding did not affect the slope

Table 4.1. Analyses of growth and vegetative propagation

Effect	Growth	Gemmae Mass
Location	$F_{25,54}=2.48^{**}$	$F_{24,32}=1.44$
Feeding	$F_{1,54}=54.37^{***}$	$F_{1,32}=6.27^*$
Reproduction	$F_{2,54}=3.28^*$	$F_{2,32}=3.15$
Feed x Reproduction	$F_{2,54}=.07$	$F_{2,32}=.26$
Initial bud mass	$F_{1,54}=13.31^*$	-
Final bud mass	-	$F_{1,32}=10.89^{**}$
Gemmae number	n.s.	$F_{1,32}=58.80^{***}$
Gemmae no x Feed	-	$F_{1,32}=5.23^*$

* $P<.05$, ** $P<.01$, *** $P<.001$, n.s. not significant

Figure 4.2. (a) The relation between growth and initial bud mass for control and fed plants ($b \pm s_b = -.22 \pm .061$). Data are adjusted for the effects of reproduction and location. (b) Growth (mean $\pm$ SE) by non-flowering, flowering and fruiting plants. Means are adjusted for the effects of initial bud mass, feeding, and location. Overall ANCOVA results for both panels are in Table 4.1.



of the relation between growth and bud mass (Table 4.1, Feed x reproduction interaction; Fig. 4.2a).

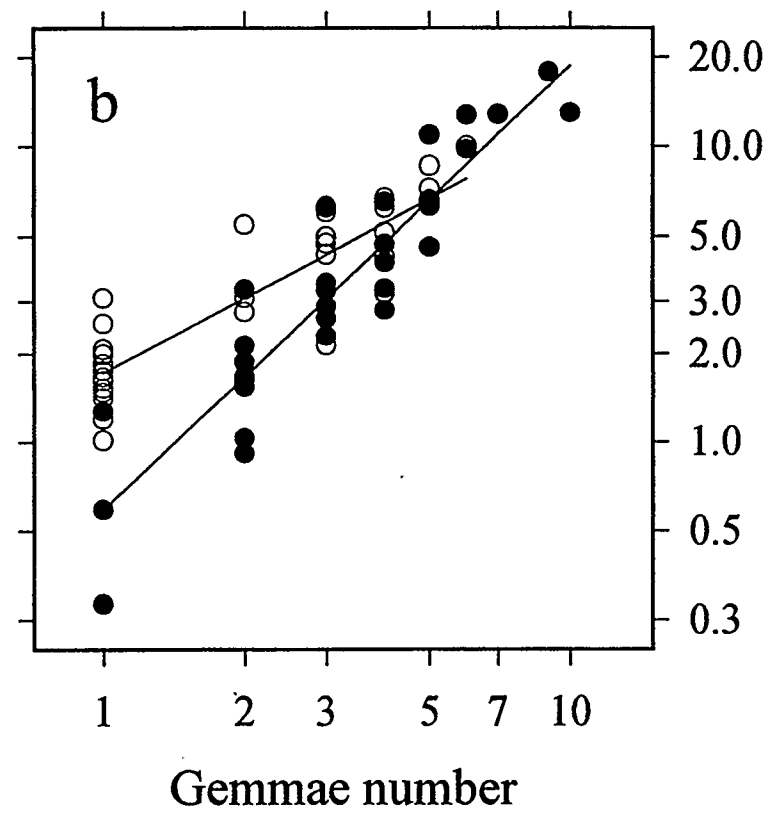
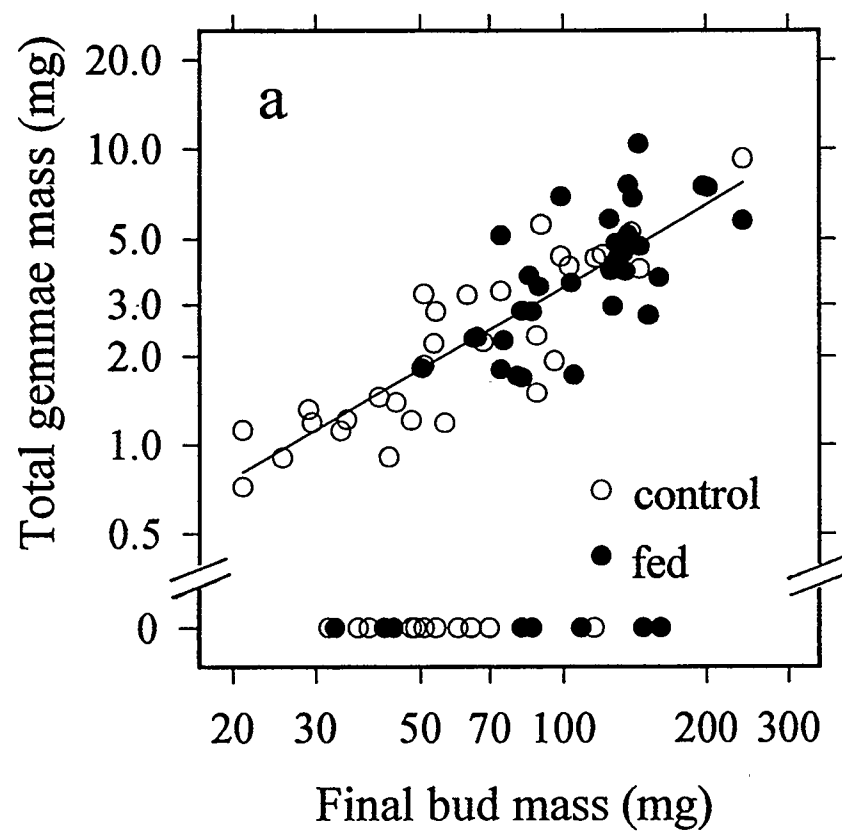
There was evidence of a trade-off between growth and fruit production. When the effects of plant size and feeding were accounted for, fruiting plants grew 17 mg on average, significantly less than flowering plants which grew an average of 44 mg ($t_{54}=2.56$, $P<.01$; Fig 4.2b). Non-flowering plants grew an intermediate amount (27 mg) which did not differ significantly from growth by either flowering ($t_{54}=1.68$, $P>.1$) or fruiting plants ($t_{54}=1.11$, $P>.2$; Fig. 4.2b). Although this result differs somewhat from my earlier finding (section 3.2.1) of significant differences in growth among all reproductive classes, the power associated with this analysis was quite low (.44). The effects of reproduction on growth did not differ between feeding treatments (repro x feed interaction, Table 4.1).

4.3.2 Vegetative Propagation

In both years most plants produced at least one gemma (87% in 1992 and 73% in 1993). No threshold size for gemmae production was apparent; plants that produced no gemmae were well within the size range of gemmae-producing plants (Fig. 4.3a). Only gemmae-producing plants were included in the analyses of gemmae mass. Analyses of 1992 and 1993 gemmae mass produced similar models, indicating that general patterns of allocation to gemmae were similar between years: only the 1993 analysis is presented below.

Gemmae mass varied positively with bud mass and gemmae number but was not significantly affected by location or reproduction (Table 4.1). Even though fed plants grew more than control plants, feeding did not change the relation between plant size and gemmae mass (Fig. 4.3a). Thus, feeding largely affected gemmae mass indirectly through its effects on growth and final bud mass. However, feeding did affect the relation between the number of gemmae produced and total gemmae mass (Fig 4.3b). The slopes and intercepts of the relation between gemmae number and gemmae mass differed between control and fed plants (Table 4.1; Fig 4.3). However, the difference in

Figure 4.3. Relations between total gemmae mass and (a) final bud mass ($b \pm s_b = .93 \pm .281$) and (b) gemmae number in control ($b \pm s_b = .84 \pm .179$) and fed ($b \pm s_b = 1.50 \pm .237$) plants. The statistical analysis involved only plants that produced gemmae. In each plot, data are adjusted for the effects of the other covariate (see Chapter 3). See Table 4.1 for ANCOVA results.



mean gemmae mass between treatments was significant only for plants that produced a single gemma. Many control plants produced a single or a few large gemma, whereas most fed plants produced several smaller gemmae (Fig. 4.3b). Thus, feeding changed the distribution of mass among gemmae.

Although the overall effect of reproduction on gemmae production in 1993 was not quite statistically significant ($F_{2,32}=3.15$, $.05 < P < .06$, Table 4.1), the more powerful analysis for a linear trend (Kirk 1982) indicated that gemmae mass decreased with increased reproductive effort (linear contrast, $F_{1,32}=5.88$, $P < .025$). These results follow a similar trend to those outlined in Chapter 2, despite limited statistical power (.39).

4.3.3 Sexual Reproduction

Flowering depended only on plant size. All plants examined had at least one flower primordium at the end of 1992 and 45% ($n=78$) produced two or more flower primordia. The probability of producing multiple flower primordia varied positively with 1992 bud mass (Table 4.2). Most locations with a mean bud mass of more than 60 mg included plants that produced more than one flower primordium (Fig 4.4a).

Only 41% ($n=85$) of the plants in the feeding experiment flowered in 1993. The probability of flowering in 1993 was positively related to initial bud mass, and unrelated to gemmae mass, growth or feeding treatment (Table 4.2). Flowering occurred at all locations where mean bud mass was greater than 62 mg and 50% or more of the plants flowered at locations where mean bud mass was greater than 78 mg (Fig. 4.4b).

Most flowering plants set fruit (71%, $n=35$) and the probability of setting fruit was independent of bud mass, growth, gemmae mass or feeding treatment (Table 4.2). Many plants changed fruiting status between 1992 and 1993 (58%, $n=89$). The probability of changing fruiting status between 1992 and 1993 depended on fruiting in 1992 and plant size at the end of 1992 (Table 4.2: 92 Bud x 92 Fruit interaction). Plants that did not fruit in 1992 were most likely to change fruiting status in 1993 if they had large overwintering buds at the end of 1992 (Table 4.2, Fig 4.5a). In contrast, for plants that fruited in 1992, a change in fruiting status was more prevalent among small plants

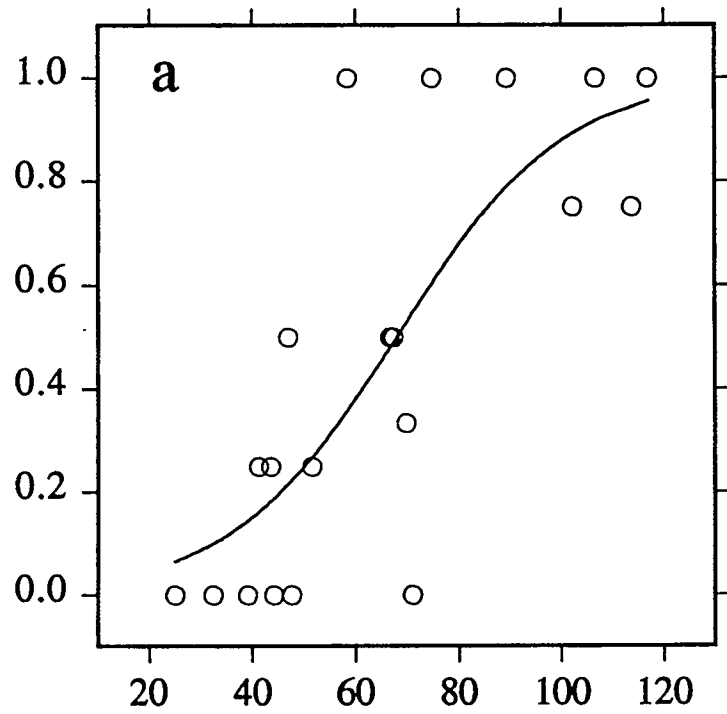
Table 4.2. Logistic regression parameter estimates and test statistics for the factors affecting proportions of: plants that produced multiple flower primordia; plants that flowered; flowering plants that fruited; and plants that changed fruiting status between 1992 and 1993.

Effect	>1 Flower primordia		Flowering		Fruiting		Δ Fruiting status	
	Estimate (SE)	Wald Chi Square	Estimate (SE)	Wald Chi Square	Estimate (SE)	Wald Chi Square	Estimate (SE)	Wald Chi Square
Intercept	-4.20 (.926)	20.57***	-6.00 (1.217)	23.97***	-2.60 (1.769)	2.16	1.06 (1.378)	.58
Feeding	-	-	.08 (.303)	.08	.07 (.307)	.06	-	-
92 Fruit	-	-	-	-	-	-	-5.30 (1.378)	14.80***
92 bud mass	.06 (.0141)	19.25***	.084 (.019)	22.41***	n.s. -	-	-.02 (.021)	.78
92 Bud x 92 Fruit	-	-	-	-	-	-	.07 (.021)	10.72**

** $P < .01$, *** $P < .001$

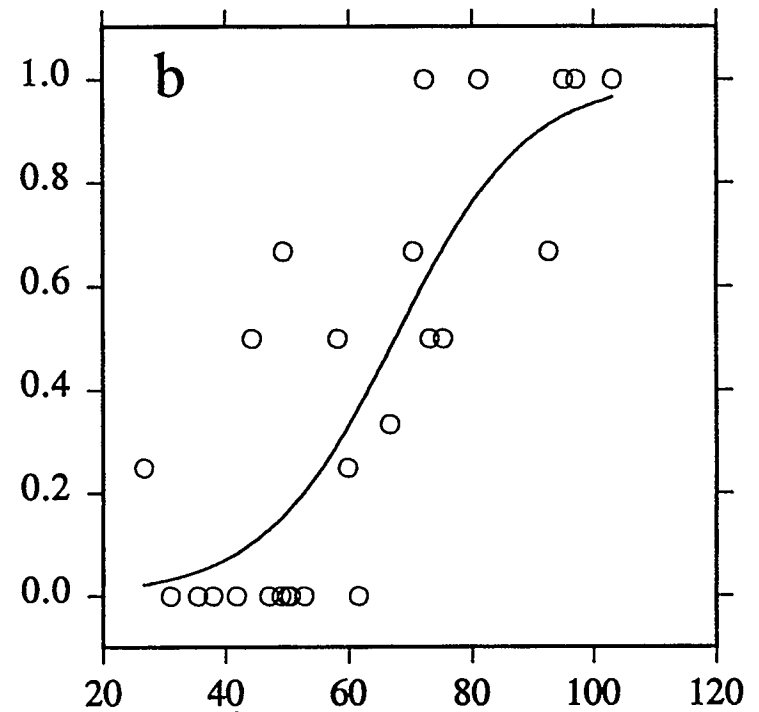
Figure 4.4. (a) The proportion of buds with more than one flower primordium as a function of mean bud mass per location at the end of 1992. These data represent plants from four sites along the Sheep River, including the site on which all other aspects of this study are based. (b) The proportion of plants flowering in 1993 as a function of mean final (1992) bud mass per location. The predicted relations in both panels are based on logistic regression (Table 4.2).

Proportion with > 1 fl. primordium



Final (1992) bud mass (mg)

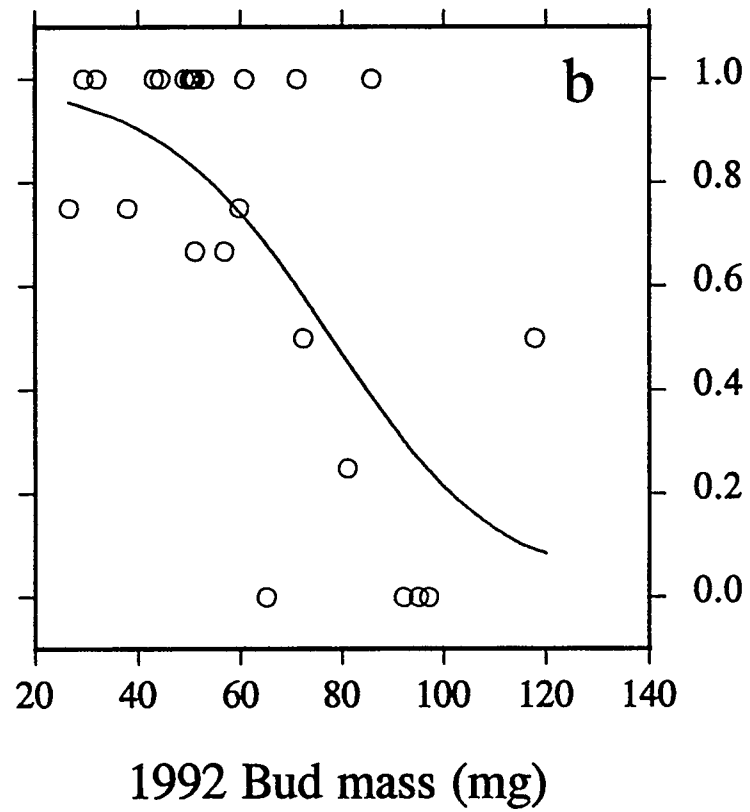
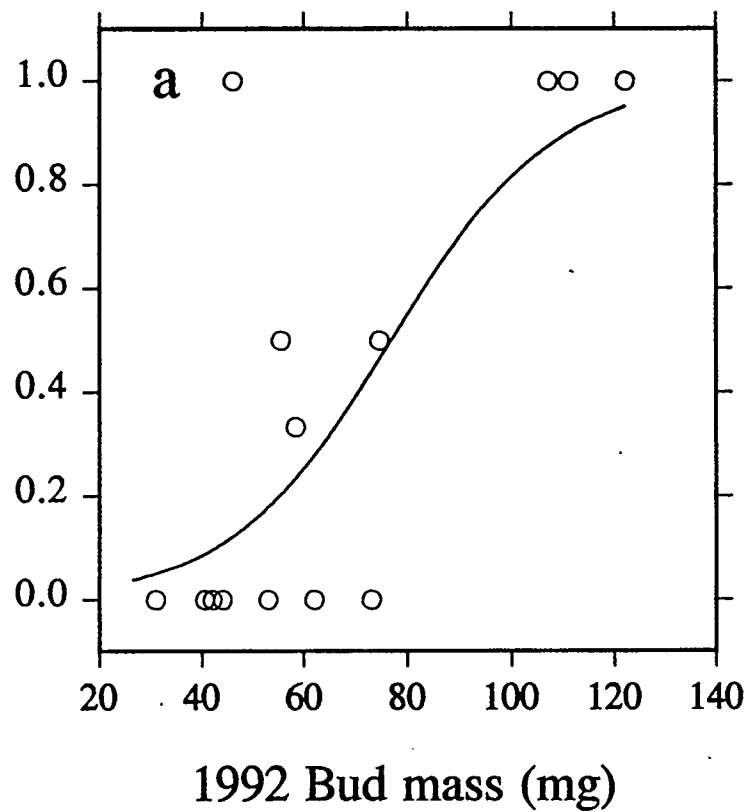
Proportion flowering in 1993



Final (1992) bud mass (mg)

Figure 4.5. The proportion of plants changing fruiting status per location between 1992 and 1993 as a function of fruiting status and mean final bud mass in 1992. The relation for plants that did not fruit in 1992 is shown in (a) and the relation for plants that fruited in 1992 in (b). The predicted relations are based on logistic regression (Table 4.2).

Proportion changing fruiting status



(Table 4.2, Fig 4.5b). This result indicates a strong influence of plant size on the dynamics of sexual reproduction in this *Pinguicula vulgaris* population.

The proportion of fruiting plants was considerably lower in 1993 (21%) than in 1992 (85%). Compared to 1992, a significantly smaller proportion of plants produced fruit during 1993 ($\Delta_{\text{fruit}} \pm 95\% \text{ C.I.} = -.44 \pm .164$) and the proportion of non-flowering plants was correspondingly higher ($\Delta_{\text{non-flower}} = .55 \pm .134$) in 1993 than in 1992. The proportion of plants that flowered but did not set fruit remained similar ($\Delta_{\text{flower}} = .09 \pm .14$).

4.4 DISCUSSION

Within-season changes in resource availability can affect seasonal allocation to sexual reproduction, growth and vegetative propagation in various ways (Fig. 4.1). Preformation of floral primordia sets an upper limit to seasonal flower and fruit production by *Pinguicula vulgaris*. Consequently, resource supplementation did not increase reproduction during the same season, even though positive relations between reproduction and plant size indicate resource limitation of sexual reproduction. Instead, extra resources increased growth and vegetative propagation, and therefore the potential for future reproduction (Fig 4.1, dashed-dotted line). Similar allocation patterns may occur in other species with preformation. Although feeding increased allocation to growth and gemmae in *P. vulgaris*, it did not affect relations with plant size. Thus, resource availability does not affect size-dependent strategies of allocation to growth and vegetative propagation.

4.4.1 Resource Availability and Allocation to Sexual Reproduction, Growth, and Vegetative Propagation

The dramatic growth response to feeding (Fig. 4.2) indicates that insect availability is an important factor limiting growth of *Pinguicula vulgaris* at this site. That growth is limited by the nutrients supplied through insect ingestion is not surprising, given that the plants generally grow in areas with ample moisture and sunlight and that

carnivory is an adaptation to nutrient-poor habitats (Givnish et al. 1984). Nutrient limitation of growth is common in carnivorous plants and nutrients supplied to the leaves often increase growth in *Pinguicula* and other genera (e.g., Darwin 1978, Harder and Zemlin 1967, Aldenius et al. 1983, Karlsson et al. 1991, Karlsson and Pate 1992).

The cages used to exclude ants may have created “starved” and fed rather than “control” and fed treatments. Consequently, my results may exaggerate the importance of resource limitation to *Pinguicula vulgaris*. However, on average, growth in control plants was slightly positive (approximately 7 mg) and patterns of resource allocation did not differ much between control plants in this study and uncaged plants at Sites 3 and 4 (Chapter 3) or between unfed plants and the same plants in 1992 (results not shown, but see section 4.3.2). In addition, elimination of ant robbery may balance the losses in prey caused by the cages. Thus, it seems that caging probably had little effect on resource allocation by control plants.

Feeding also indirectly increased overall allocation to vegetative propagation. Vegetative propagation in *P. vulgaris* depends on total resource accumulation by the end of the growing season (Chapter 3). Consequently, gemmae production is correlated with final rather than initial bud mass (Fig 4.3a). Although feeding did not change the relation between gemmae mass and final bud mass, fed plants grew larger than control plants and therefore had greater gemmae masses (Fig 4.3a). Feeding also changed the distribution of mass among individual gemmae (Fig 4.3b); control plants were more likely to produce a single large gemma. This could have been because control plants were less likely to have sufficient resources to divide between multiple gemmae and they therefore allocated all available resources to a single gemma (see Ebert 1994).

In contrast to growth and gemmae production, flowering and fruiting depended only on initial bud mass and were unaffected by increased resources in the current year (Table 4.2). These results agree with previous work on *Pinguicula vulgaris* and probably reflect preformation (Aldenius et al. 1983, Karlsson et al. 1991). Preformation of floral primordia during the autumn preceding flowering occurs in many arctic, alpine, desert and spring flowering perennials (review in Sørensen 1941, Hartsema 1961,

reviews in Billings and Mooney 1968, Mark 1970, Dafni et al. 1981). Reproductive output by such species, including *P. vulgaris* (Svensson et al. 1993), may depend on temperature, rainfall, or nutrient availability in the previous, rather than in the current, year (Mark 1965, Hill-Cottingham and Williams 1967, Billings and Mooney 1968, Mark 1968, Boeken 1990, Svensson et al. 1993). In general, the effects of previous resource levels on reproduction are probably mediated through the size of perennating structures (Barkham 1980, Boeken 1989), such as the overwintering bud of *P. vulgaris*.

Lifetime reproduction by all organisms is governed by internal factors such as growth form and physiology and external factors such as mate or resource availability (Partridge and Sibly 1991). Although preformation probably increases reproductive success by enabling plants to flower early or in short growing seasons, *P. vulgaris* and other species with preformation seem unable to increase current reproductive output significantly in response to increased resource availability. Therefore, preformation may restrict the ability of some species to take advantage of short-term fluctuations in resource availability. To a certain extent, constraints imposed by preformation can be overcome by allocation of resources to future activities. The positive effects of feeding on the mass of the incipient winter bud (see above), coupled with positive relations between initial bud mass and number of floral primordia, flowering and fruiting, indicate that, like other species (Boeken 1989), *Pinguicula vulgaris* can use extra resources to increase future reproduction.

Survival is uncertain, so that it is always beneficial to allocate some supplemental resources to reproduction. Therefore, plants with preformation should evolve means of increasing reproduction to take advantage of fluctuations in resource availability (cf. Lloyd 1980). Two possibilities exist. First, plants may produce more flower primordia or flowers than they can mature into flowers or fruit (e.g.'s in Mark 1970). *Pinguicula vulgaris* does produce "extra" flower primordia that normally are not matured (Chapter 2); however, my feeding experiment did not significantly increase flower production. Because *P. vulgaris* individuals are small and few flowered, each additional flower probably represents a relatively large increase in reproductive expenditure.

Consequently, feeding may have been insufficient to support increases in flower number. Alternatively, interference by ants may have meant that effective feeding began too late to increase flower production; the plants were already in bud when ant robbery was detected. A second, less expensive means of exploiting extra resources for reproduction would be simply to increase seed number in existing fruit. This may occur in *Pinguicula vulgaris*, although I had insufficient data to assess the possibility. Resource supplementation increases seed number per fruit in several species (Willson and Price 1980, Delph 1986, Ehrlén 1992, Campbell and Halama 1993).

Nutrient availability may affect future reproduction directly through storage of nutrients for future use, as well as indirectly through growth and vegetative propagation (Vaughton 1991). I did not test the effects of nutrient additions on future reproduction directly, but other results indicate that reproduction depends primarily on plant size. Although many plants changed fruiting status between 1992 and 1993, the change was mediated through plant size (Fig 4.5b). Furthermore, flowering and fruiting in 1993 did not depend on nutrients supplied through feeding in 1993. Thus, costs of reproduction in *Pinguicula vulgaris* seem to be mediated through effects on plant size. The coincident reductions in future growth and reproduction resulting from increased fruit set which occur in many species (e.g., Montalvo and Ackerman 1987, Zimmerman and Aide 1989, Snow and Whigham 1989, Ackerman and Montalvo 1990, Primack and Hall 1990, Eggert 1992) may also reflect the effects on reproduction on plant size, rather than direct trade-offs between reproduction in consecutive years.

The delayed effects of resource supplementation on reproduction by species with preformation have implications for the detection of resource limitation of lifetime reproduction. Failure to increase current reproduction in response to resource supplementation does not rule out the possibility that reproduction is resource limited. Allocation of resources to growth and future reproduction is a possibility for all perennials because even species that can increase current reproduction may still allocate some resources to future activities (e.g. Montalvo and Ackerman 1987, Vaughton 1991).

4.4.2 Resource Supplementation and Patterns of Resource Allocation

Feeding did not alter costs of reproduction to growth and vegetative propagation. If resource supplementation offsets costs of reproduction, effects of reproduction should differ between feeding treatments. Instead, trade-offs between reproduction and other functions persisted under elevated resource levels, because plants cannot increase reproduction in response to feeding (see above). Consequently, plants allocated all extra resources to other functions regardless of reproductive status. Because feeding increased allocation to growth and vegetative propagation, but not to sexual reproduction, fed plants allocated relatively more resources to growth and vegetative propagation than control plants.

Feeding elevated the relation between plant size and growth but did not change the slope (Fig. 4.2a), indicating that the relations between growth and plant size remain constant under different resource levels. As suggested in Chapter 3, the negative relationship between growth and initial bud mass may be explained by architectural constraints which reduce the advantages of further growth by large plants. However, if this were the case, a decreasing proportion of resources should be allocated to growth as plant size increases. It seems that plants of a given size allocate a set proportion of their resources to growth and do not change this proportion in response to increased resource availability. The effects of feeding on vegetative propagation were largely mediated through increased growth and final plant size in fed plants, indicating that allocation to vegetative propagation depends primarily on total resource accumulation by the end of the growing season. Thus, resource availability does not alter size-dependent allocation to growth and vegetative propagation by *Pinguicula vulgaris*. Much within-species variation in reproductive allocation is explained by plant size (Samson and Werk 1986, Weiner 1988, Peters et al. 1988, Hartnett 1990, Thompson et al. 1991, Schmid and Weiner 1993). The effects of resource availability or other environmental factors on allocation to growth and vegetative propagation have rarely been studied explicitly (but

see Mendez and Obeso 1992). My results and those of Mendez and Obeso (1992) indicate that growth and vegetative propagation may also primarily depend on plant size.

This study demonstrates that growth form and developmental phenology can influence resource allocation by plants. Given preformation of floral primordia, current reproduction may not increase in response to resource supplementation even though, ultimately, resources do limit reproduction. Consequently, responses to increased resource availability may be more complex than a simple increase in allocation to all functions. Although increases in current reproduction may be prevented by preformation or other factors, perennial plants can still increase lifetime reproduction by increasing allocation to growth and vegetative propagation, which both promote future reproduction.

5 CONCLUDING DISCUSSION

5.1 Factors Influencing Resource Allocation by Plants

Biological and environmental factors such as plant size, growth form and developmental phenology, the ability to propagate vegetatively, and pollen availability can influence trade-offs and patterns of resource allocation in plants (reviewed in Chapter 1). My research illustrates how these factors interact to affect resource allocation in *Pinguicula vulgaris*. Other plant species share aspects of *P. vulgaris*' biology that have important influences on resource allocation. Consequently, trade-offs and allocation patterns displayed by *P. vulgaris* may apply more generally, particularly to species with similar phenologies and habits. In this section, I use the results of Chapters 2, 3 and 4 to speculate about size-dependent strategies of resource allocation in *Pinguicula vulgaris* and consider my results in the context of general resource allocation strategies by plants.

5.1.1 Plant Size and Resource Allocation

Size-dependent resource allocation in *Pinguicula vulgaris* likely reflects evolved strategies for survival and reproduction. Allocation to growth varies negatively with plant size whereas allocation to reproduction varies positively with plant size (Chapters 3 & 4). Although large reproductive plants often lost mass, they generally remained large enough to flower in the following year (Chapter 3). This result implies that *Pinguicula vulgaris* plants allocate sufficient resources to the incipient winter bud to maintain a size compatible with flowering in the following season, and allocate remaining resources to reproduction. The success of this strategy probably varies between years. For example, if flowering or fruiting were prevented in one season by flooding (1992, Site 4), then plants would reach larger sizes. Conversely, after a season of particularly heavy fruiting (1992, Site 2), many plants may be too small to flower in the following year (see section 4.3.3). Such flexibility would allow plants to respond to environmental variation in resource availability or favorable conditions for flowering and fruiting.

Allocation to vegetative propagation also depends primarily on plant size. When gemmae mass is considered only as a function of plant size (gemmae number omitted from the analysis), allocation to vegetative propagation increases proportionately with plant size (Chapter 3). Opportunities for gemmae establishment and growth are limited unless the soil is disturbed by ungulate hooves, digging by small mammals, or floods because the leaves of the parent plant often cover gemmae (section 2.2). Proportional allocation to gemmae may be constant because the probabilities of floods or other disturbances do not change with plant size.

Even though reproductive costs to vegetative propagation (Chapter 3) and the effects of increased resource availability (Chapter 4) are largely indirect and mediated through their effects on plant size, independent trade-offs occur between vegetative propagation and reproduction. Because opportunities for gemmae establishment are limited, growth may be sufficiently important that it is better to forego some vegetative propagation and remain large enough to reproduce in the future. Thus, it seems that the relative benefits associated with growth (i.e. increased survival and reproductive potential) may exceed those of vegetative propagation.

5.1.2 Growth Form and Developmental Phenology

Both final bud mass and total gemmae mass in *Pinguicula vulgaris* depend on resource accumulation by the end of the season (Chapters 3 and 4). The close tie between vegetative propagation and growth in *Pinguicula vulgaris* probably reflects the fact that gemmae are essentially axillary buds on the winter bud. Several forms of vegetative propagation involve structures that are developmentally and physiologically linked to the perennating structures (e.g., bulbils, cormels, tubers). Therefore, allocation to vegetative propagation in other species may also reflect the size of the perennating organ.

Phenology and growth form also influence trade-offs in *Pinguicula vulgaris*. Trade-offs occur between sexual reproduction and vegetative functions (growth and vegetative propagation), probably because formation of the winter bud and gemmae

occur during the growing season and therefore coincide with fruit and seed maturation. In contrast, developmental and physiological ties may prevent trade-offs between growth and vegetative propagation (see above). Thus allocation options and opportunities for trade-offs in *P. vulgaris* reflect phenology and habit. Similar situations probably occur for other species. For example, opportunities for trade-offs between growth and reproduction are greater in *Eriophorum scheuchzeri* than its congener *E. vaginatum* because allocation to growth and reproduction coincide in the former species but not in the latter (Mark and Chapin 1989). Similarly, the arrangement of modules and meristem availability may restrict patterns of resource allocation in rhizomatous and stoloniferous species (Watson 1984, Ericksson 1985, Geber 1990, but see Bishop and Davy 1985).

Preformation of floral primordia has several implications for resource allocation by *Pinguicula vulgaris*. Preformation restricts *P. vulgaris*' ability to increase current reproduction in response to short-term increases in resource availability, so that extra resources must be invested in future reproduction (Chapter 4). However, plants with preformation may also be able to exploit increases in resource availability by maturing extra flower primordia or increasing seed set, options which I did not explore thoroughly. Preformation occurs in many perennial species, probably with implications for resource limitation similar to those described for *Pinguicula vulgaris*.

5.1.3 Strategies of Resource Allocation

My interpretation of resource allocation in *Pinguicula vulgaris* infers size-related strategies and a strong influence of growth form and developmental phenology on allocation decisions. Many features of *P. vulgaris*' biology, which I interpret as important influences on resource allocation, are common to numerous species and there is evidence that these species may allocate resources similarly to *P. vulgaris* (section 5.1.2, above). These observations imply that plants with similar growth form and developmental phenology may employ similar strategies of resource allocation.

Some evidence that reproductive and resource allocation strategies correspond to growth form exists in the literature. For example, the timing of flowering reflects

developmental phenology and affects the potential for trade-offs. Flowering times of animal-pollinated angiosperms in Japan and Carolina are strongly influenced by phylogenetic membership (family) and “life form” (tree, shrub, vine, annual, perennial, biennial: Kochmer and Handel 1986). Both families and life forms can have characteristic developmental phenologies and growth forms. Similarly, British trees, shrubs, herbs, and bulb- and corm-forming species have different flowering peaks, which may result from differences in plant development (Grainger 1939). Finally, desert annuals show suites of morphological and physiological traits which may reflect developmental “programs” and taxonomic affiliation, as well as adaptations to the desert environment (Fox 1989, 1990).

5.2 Demographic Consequences of Physiological Trade-offs

Physiological responses to environmental conditions during growing seasons govern demographic traits such as fertility and survival (section 1.1). Below I consider the demographic implications of my findings in light of a recent study of the long-term demography of *Pinguicula vulgaris* (Svensson et al. 1993) and outline the physiological responses that probably underlie the demographic trends Svensson et al. observed.

Svensson et al. (1993) studied three *Pinguicula* species; my discussion will be confined to *P. vulgaris*. From 1984 to 1991, Svensson et al. followed *P. vulgaris* plants growing in ten permanent 50 cm x 50 cm quadrats. The quadrats were randomly distributed among sparsely vegetated, solifluction terraces in a subalpine heath near the Abisko Scientific Research Station in Swedish Lapland. They mapped each quadrat once a year, shortly after flowering, and recorded the position, size and flower number of each plant. Size was estimated by multiplying the length of the longest leaf by the number of leaves. “Seedlings” were plants less than 4 mm. in diameter that had not been previously recorded. Consequently, no seedling data were collected in 1984. Svensson et al. constructed stage-based projection models (Caswell 1989) based on the observed transition probabilities between stages and size classes to determine rates of population growth, stable size distributions and elasticity values. *Pinguicula vulgaris* had five size

classes and, for each size class, plants were divided into stages (vegetative or flowering). Seeds formed a separate class.

Svensson et al. (1993) did not mention vegetative propagation, nor are gemmae mentioned in any previous studies of *Pinguicula vulgaris* by Karlsson and colleagues (section 2.2). The lack of vegetative propagation could reflect the small size of Swedish plants, which had a maximum leaf length of 21 mm, or the harsh subalpine conditions. The longest leaf length of my plants was approximately 60 mm. Variable gemmae production also occurs in Alberta populations (L.D. Harder, pers. comm., July 1994). The existence of gemmae should increase the population growth rate, either by increasing the number of individuals (treating ramets as individuals) or by increasing genet longevity (Caswell 1989). Clearly, knowledge of gemmae establishment rates would be needed to assess these effects.

Environmental factors influenced reproduction in Swedish *Pinguicula vulgaris* populations (Svensson et al. 1993). Flowering varied positively with mean summer temperature during the previous year. Svensson et al. (1993) suggested preformation as a possible explanation for the correlation. My observations on developmental phenology (section 2.3) and positive correlations between winter bud mass and production of flower primordia (section 4.3.3) confirm their speculations. Together, our results imply that conditions in one year influence fecundity in the following year through effects on plant size.

Year, plant size, and stage all influenced the fate (flowering, vegetative or dead) of Swedish *Pinguicula vulgaris* plants. Larger sizes increased probabilities of surviving to and flowering in the following season. Conversely, flowering reduced probabilities of survival and subsequent flowering (Svensson et al. 1993). The correlations between plant size, flowering and survival in Swedish populations probably reflect physiological costs of reproduction to growth (e.g., Chapters 3 & 4) and their demographic consequences. Because the physiological costs of fruiting exceed those of flowering (Chapters 3 & 4), demographic costs of reproduction may be underestimated if all flowering plants are considered reproductive. However, failure to distinguish between

fruiting and non-fruiting plants may not have particularly severe consequences because most flowering *P. vulgaris* plants set fruit as a consequence of autonomous selfing (Chapter 2, also see Willis and Burkhill 1903, Hagerup 1951).

Survival of established plants had the strongest influence on rates of population growth in Swedish *Pinguicula vulgaris* populations. A similar situation may exist in Sheep River populations where resources were allocated in a manner ensuring that plants maintain relatively constant sizes and, probably, survival probabilities (see section 5.1.1 and figure 3.7). Resource allocation to growth and propagation should reflect the relative importance of these functions in determining rates of population growth and, therefore, fitness (Caswell 1989).

The combined results of Svensson et al. (1993) and my experiments and observations (Chapters 2 through 4) reveal how physiological responses by organisms may affect demographic traits and therefore lifetime reproduction. Ultimately, patterns of resource allocation should evolve to maximize lifetime reproduction within the constraints imposed by trade-offs, growth form, and developmental phenology.

LITERATURE CITED

- Abrahamson, W. G. 1975. Reproductive strategies in dewberries. *Ecology* **56**:721-726.
- Abrahamson, W. G. 1980. Demography and vegetative reproduction. Pages 89-106 in O.T. Solbrig, editor. *Demography and evolution in plant populations*. Blackwell Scientific, London, UK.
- Ackerman, J. D. and A. M. Montalvo. 1990. Short and long term limitation to fruit production in a tropical orchid. *Ecology* **71**:263-272.
- Aldenius, J., B. Carlsson and S. Karlsson. 1983. Effects of insect trapping on growth and nutrient content of *Pinguicula vulgaris* L. in relation to the nutrient content of the substrate. *New Phytologist* **93**:53-59.
- Armstrong, R. A. 1982. A quantitative theory of reproductive effort in rhizomatous perennial plants. *Ecology* **63**:679-686.
- Armstrong, R. A. 1984. On the quantitative theory of reproductive effort in clonal plants: refinements of the theory, with evidence from goldenrods and mayapples. *Oecologia (Berlin)* **63**:410-417.
- Ashmun, J. W., R. L. Brown, and L. F. Pitelka. 1985. Biomass allocation in *Aster acuminatus*: variation within and among populations over 5 years. *Canadian Journal of Botany* **63**:2035-2043.
- Ayre, D. J. and R. J. Whelan. 1989. Factors controlling fruit set in hermaphroditic plants: studies with the Australian Proteaceae. *Trends in Ecology and Evolution* **4**:267-272.
- Barkham, J. P. 1980. Population dynamics in the wild daffodil (*Narcissus pseudonarcissus*), I. clonal growth, seed reproduction, mortality and the effects of density. *Journal of Ecology* **68**:607-633.
- Bierzzychudek, P. 1981. Pollinator limitation of plant reproductive effort. *American Naturalist* **117**:383-840.
- Billings, W. D. and H. A. Mooney. 1968. The ecology of arctic and alpine plants. *Biological Reviews* **43**:481-530.

- Bishop, G. F. and A. J. Davy. 1985. Density and the commitment of apical meristems to clonal growth and reproduction in *Hieracium pilosella*. *Oecologia* (Berlin) **66**:417-422.
- Bloom, A. J., F. S. Chapin, III and H. A. Mooney. 1985. Resource limitation in plants - an economic analogy. *Annual Review of Ecology and Systematics* **16**:363-392.
- Boeken, B. 1989. Life histories of desert geophytes - the demographic consequences of reproductive biomass partitioning patterns. *Oecologia* (Berlin) **80**:278-283.
- Boeken, B. 1990. Life histories of two desert species of the bulbous genus *Bellevallia*. The relation between biomass partitioning and water availability. *Oecologia* (Berlin) **82**:172-179.
- Boeken, B. and Y. Gutterman. 1989. The annual cycle of *Sternbergia chusiana* of the Negev Desert. *Journal of Arid Environments* **16**:271-282.
- Bostock, S. J. 1980. Variation in reproductive allocation in *Tussilago farfara*. *Oikos* **34**:359-363.
- Calvo, R. N. 1993. Evolutionary demography of orchids: intensity and frequency of pollination and the cost of fruiting. *Ecology* **74**:1033-1042.
- Campbell, D. R. and K. J. Halama. 1993. Resource and pollen limitations to lifetime seed production in a natural plant population. *Ecology* **74**:1043-1051.
- Casper, B. B. and R. A. Neisenbaum. 1993. Pollen versus resource limitation of seed production: a reconsideration. *Current Science* **65**:210-214.
- Caswell, H. 1982. Optimal life histories and the maximization of reproductive value: a general theorem for complex life cycles. *Ecology* **63**:1218-1222.
- Caswell, H. 1989. *Matrix Population Models*. Sinauer Associates, Sunderland Massachusetts, USA.
- Cody, M. L. 1966. A general theory of clutch size. *Evolution* **20**:174-184.
- Coleman, J. S., K. D. M. McConnaughay, and D. D. Ackerly. 1994. Interpreting phenotypic variation in plants. *Trends in Ecology and Evolution* **9**:187-191.
- Cook, R. E. 1979. Asexual reproduction: a further consideration. *American Naturalist* **113**:769-772.

- Dafni, A., D. Cohen and I. Noy-Meir. 1981. Life-cycle variation in geophytes. *Annals of the Missouri Botanical Garden* 68:652-660.
- Darwin, C. 1875. *Insectivorous plants*. Appleton, London, UK.
- Darwin, F. 1878. Experiments on the nutrition of *Drosera rotundifolia*. *Journal of the Linnaean Society of Botany, London* 17:17-32.
- Delph, L. C. 1986. Factors regulating fruit and seed production in the desert annual, *Lesquerella gordonii*. *Oecologia (Berlin)* 69:471-476.
- de Ridder, F. and A. A. Dhondt. 1992. The reproductive behaviour of a clonal herbaceous plant, the longleaved sundew *Drosera intermedia*, in different heathland habitats. *Ecography* 15:144-153.
- de Steven, D. 1988. Genet and ramet demography of *Oenocarpus mapora* ssp. *mapora*, a clonal palm of Panamanian tropical moist forest. *Journal of Ecology* 77:579-596.
- Douglas, D. A. 1981. The balance between vegetative and sexual reproduction of *Mimulus primuloides* (Scrophulariaceae) at different altitudes in California. *Journal of Ecology* 69:295-310.
- Ebert, D. 1994. Fractional resource allocation into few eggs: *Daphnia* as an example. *Ecology* 75:568-571.
- Eggert, A. 1992. Dry matter economy and reproduction of a temperate forest spring geophyte, *Allium ursinum*. *Ecography* 15:45-55.
- Ehrlén, J. 1992. Proximate limits to seed production in a herbaceous perennial legume, *Lathyrus vernus*. *Ecology* 73:1820-1831.
- Eriksson, O. 1985. Reproduction and clonal growth in *Potentilla anserina* L. (Rosaceae): the relation between growth form and dry weight allocation. *Oecologia (Berlin)* 66:378-380.
- Evenson, W. E. 1983. Experimental studies of reproductive energy allocation in plants. Pages 249-274 in C.E. Jones and J.R. Little, editors. *Handbook of experimental pollination biology*. Van Nostrand Reinhold, N.Y., USA.

- Fox, G. A. 1989. Consequences of flowering-time variation in a desert annual: adaptation and history. *Ecology* **70**:1294-1306.
- Fox, G. A. 1990. Components of flowering time variation in a desert annual. *Evolution* **44**:1404-1423.
- Gadgil, M. and W. H. Bossert. 1970. Life historical consequences of natural selection. *American Naturalist* **104**:1-24.
- Gadgil, M. and O.T. Solbrig. 1972. The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. *American Naturalist* **106**:14-31.
- Galen, C., T. E. Dawson and M. L. Stanton. 1993. Carpels as leaves: meeting the carbon cost of reproduction in an alpine buttercup. *Oecologia (Berlin)* **95**:187-193.
- Galen, C., R. C. Plowright and J. D. Thomson. 1985. Floral biology and regulation of seed set and seed size in the lily, *Clintonia borealis*. *American Journal of Botany* **72**:1544-1552.
- Geber, M. A. 1990. The cost of meristem limitation in *Polygonum arenastrum*: negative genetic correlations between fecundity and growth. *Evolution* **44**:799-789.
- Gillman, M.P. and M. J. Crawley. 1990. The cost of sexual reproduction in ragwort (*Senecio jacobaea*). *Functional Ecology* **4**:585-589.
- Givnish, T. A., E. L. Burkhardt, R. E. Happel and J. D. Weintraub. 1984. Carnivory in the bromeliad *Brocchinia reducta*, with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist, nutrient-poor habitats. *American Naturalist* **124**:479-497.
- Grainger, J. 1939. Studies upon the time of flowering of plants. Anatomical, floristic and phenological aspects of the problem. *Annals of Applied Biology* **26**:684-704.
- Gross, K. L. 1981. Predictions of fate from rosette size in four "biennial" plant species: *Verbascum thrapus*, *Oenothera biennis*, *Daucus carota*, and *Tragapogon dubius*. *Oecologia (Berlin)* **48**:209-213.

- Hagerup, O. 1951. Pollination in the Faroes - in spite of rain and poverty in insects. *Biologiske Meddelelser* 18:1-48.
- Haig, D. and M. Westoby. 1988. On limits to seed production. *American Naturalist* 131:757-759.
- Harder, R. and I. Zemlin 1967. Förderung der Entwicklung und des Blühens von *Pinguicula lusitanica* durch fütterung in axenischer Kultur. *Planta* (Berlin) 73:181-193.
- Harper, J. L. 1967. A Darwinian approach to plant ecology. *Journal of Ecology* 55:247-270.
- Harper, J. L. 1977. Population biology of plants. Academic Press, London.
- Harper, J. L. and J. Ogden, 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. *Journal of Ecology* 58:681-698.
- Hartnett, D. C. 1990. Size-dependent allocation to sexual and vegetative reproduction in four clonal composites. *Oecologia* (Berlin) 84:254-259.
- Hartsema, A. M. 1961. Influence of temperature on flower formation and flowering of bulbous and tuberous plants. *Encyclopedia of Plant Physiology* 16:123-167.
- Hepburn, J. S., F. M. Jones and E. Q. St. John. 1920. The absorption of nutrients and allied phenomena in the pitchers of the Sarraceniaceae. *Journal of the Franklin Institution* 189:147-184.
- Heslop-Harrison, Y. 1976. Enzyme secretion and digest uptake in carnivorous plants. *Perspectives in Experimental Botany* 2:443-476.
- Heslop-Harrison, Y. and R. B. Knox. 1971. A cytochemical study of the leaf-gland enzymes of insectivorous plants of the genus *Pinguicula*. *Planta* 96:183-211.
- Hill-Cottingham, D.G. and R.R. Williams. 1967. Effect of time of application of fertilizer nitrogen on the growth, flower development, and fruit set of maiden apple trees, var. Lord lambourne, and on the distribution of total nitrogen within the trees. *Journal of Horticultural Science* 42:319-338.

- Hirshfield, M. E. and D. W. Tinkle. 1975. Natural selection and the evolution of reproductive effort. *Proceedings of the National Academy of Science* 72:2227-2231.
- Holler, L. C. and W. G. Abrahamson. 1977. Seed and vegetative reproduction in relation to density in *Fragaria virginiana* (Rosaceae). *American Journal of Botany* 64:1003-1007.
- Jain, S. K. 1976. The evolution of inbreeding in plants. *Annual review of Ecology and Systematics* 7:479-495.
- Janzen, D. H. 1977. What are dandelions and aphids? *American Naturalist* 111:586-589.
- Jennerston, O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conservation Biology* 2:359-366.
- Joel, D. M., B. E. Juniper and A. Dafni. 1985. Ultraviolet patterns in the traps of carnivorous plants. *New Phytologist* 101:585-593.
- Karlsson, P. S. 1986. Seasonal pattern of biomass allocation in flowering and nonflowering specimens of three *Pinguicula* species. *Canadian Journal of Botany* 64:2872-2877.
- Karlsson, P. S. 1988. Seasonal patterns of nitrogen, phosphorus and potassium utilization by three *Pinguicula* species. *Functional Ecology* 2:203-209.
- Karlsson, P. S. and B. Å. Carlsson. 1984. Why does *Pinguicula vulgaris* trap insects? *New Phytologist* 97:25-30.
- Karlsson, P. S., K. O. Nordell, B. Å. Carlsson and B. M. Svensson. 1991. The effect of soil nutrient status on prey utilization in four carnivorous plants. *Oecologia (Berlin)* 86:1-7.
- Karlsson, P. S., K. O. Nordell, S. Eirefelt and A. Svensson. 1987. Trapping efficiency of three carnivorous *Pinguicula* species. *Oecologia* 73:518-521.

- Karlsson, P. S. and J. S. Pate. 1992. Contrasting effects of supplementary feeding of insects or mineral nutrients on the growth and nitrogen and phosphorous economy of pygmy species of *Drosera*. *Oecologia* (Berlin) **92**:8-13.
- Karlsson, P. S., B. M. Svensson, B. A. Carlsson and K. O. Nordell. 1990. Resource investment in reproduction and its consequences in three *Pinguicula* species. *Oikos* **59**:393-398.
- Karoly, K. 1992. Pollinator limitation in the facultatively autogamous annual, *Lupinus nanus* (Leguminosae). *American Journal of Botany* **79**:49-56.
- Kirk, R. E. 1982. *Experimental Design*. Brooks/Cole, Monterey, California, USA.
- Klinkhamer, P. G. L., T. J. de Jong and E. Meelis. 1990. How to test for proportionality in the reproductive effort of plants. *American Naturalist* **135**:291-300.
- Klinkhamer, P. G. L., E. Meelis, T. J. de Jong and J. Weiner. 1992. On the analysis of size dependent reproductive output in plants. *Functional Ecology* **6**:308-316.
- Kochmer, J. P. and S. N. Handel. 1986. Constraints and competition in the evolution of flowering phenology. *Ecological Monographs* **56**:303-325.
- Law, R. 1979. Ecological determinants in the evolution of life histories. Pages 81-103 in R. M. Anderson, B. D. Turner and L. R. Taylor, editors. *Population dynamics*. Blackwell Scientific Publications, Oxford, U.K.
- Law, R., A. D. Bradshaw and P. D. Putwain. 1977. Life history variation in *Poa annua*. *Evolution* **31**:233-246.
- Law, R., R. E. D. Cook and R. J. Manlove. 1983. The ecology of flower and bulbil production in *Polygonum viviparum*. *Nordic Journal of Botany* **3**:559-565.
- Lloyd, D. G. 1979. Some reproductive factors affecting the selection of self-fertilization in plants. *American Naturalist* **113**:67-79.
- Lloyd, D. G. 1980. Sexual strategies in plants I. An hypothesis of serial adjustment of maternal investment during one reproductive session. *New Phytologist* **86**:69-79.
- Lloyd, D. G. 1992. Self and cross-fertilization in plants. II. The selection of self-fertilization. *International Journal of Plant Science* **153**:370-380.

- Lloyd, D. G. and D. J. Schoen. 1992. Self- and cross-fertilization in plants. I. Functional dimensions. *International Journal of Plant Science* 153:358-369.
- Loehle, C. 1987. Partitioning of reproductive effort in plants: a benefit-cost model. *Oikos* 49:199-208.
- Lovett Doust, L. 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*) I. The dynamic of ramets in contrasting habitats. *Journal of Ecology* 69:743-755.
- Lovett Doust, J. 1989. Plant reproductive strategies and resource allocation. *Trends in Ecology and Evolution* 4:230-234.
- Marascuilo, L. A. and M. McSweeney. 1977. Nonparametric and distribution-free methods for the social sciences. Brooks / Cole, Monterey, California, USA.
- Mark, A. F. 1965. Flowering, seeding and seedling establishment of narrow leaved snow tussock, *Chionochloa rigida*. *New Zealand Journal of Botany* 3:180-193
- Mark, A. F. 1968. Factors controlling irregular flowering in four alpine species of *Chionochloa*. *Proceedings of the New Zealand Ecological Society* 15:55-60.
- Mark, A. F. 1970. Floral initiation and development in New Zealand alpine plants. *New Zealand Journal of Botany* 8:67-75.
- Mark, A. F. and F. S. Chapin. 1989. Seasonal control over allocation to reproduction in a tussock-forming and a rhizomatous species of *Eriophorum* in central Alaska. *Oecologia (Berlin)* 78:27-34.
- McCall, C. and R. B. Primack. 1985. Effects of pollen and nitrogen availability on reproduction in a woodland herb, *Lysmachia quadrifolia*. *Oecologia (Berlin)* 67:403-410.
- McCall, C. and R. B. Primack. 1987. Resources limit the fecundity of three woodland herbs. *Oecologia (Berlin)* 71:431-435.
- Mendez, M. and J. R. Obeso. 1992. Size-dependent reproductive and vegetative allocation in *Arum italicum* (Araceae). *Canadian Journal of Botany* 71:309-314.

- Menges, E. S. 1990. Environmental correlations with male, female, and clonal biomass allocation in the forest herb, *Laportea canadensis*. *American Midland Naturalist* 124:171-180.
- Montalvo, A. M. and J. D. Ackerman. 1987. Limitations to fruit production in *Ionopsis utricularioides* (Orchidaceae). *Biotropica* 19:24-31.
- Moss, E. H. 1983. *Flora of Alberta*. University of Toronto Press, Canada.
- Ockendon, D. J. and L. Currah. 1978. Time of cross- and self-pollination affects the amount of self-seed set by partially incompatible plants of *Brassica oleracea*. *Theoretical and Applied Genetics* 52:233-237.
- Ogden, J. 1974. The reproductive strategy of higher plants II. The reproductive strategy of *Tussilago farfara* L. *Journal of Ecology* 62:291-324.
- Ohlson, M. 1988. Size dependent reproductive effort in three populations of *Saxifraga hirculus* in Sweden. *Journal of Ecology* 76:1007-1016.
- Paige, K. N. and T. G. Whitham. 1987. Flexible life history traits: shifts by scarlet gilia in response to pollinator abundance. *Ecology* 68:1691-1695.
- Partridge, L. and R. Sibly. 1991. Constraints in the evolution of life histories. Pages 3-12 in R.H. Harvey and T. R. E. Southwood, editors. *The evolution of reproductive strategies*. The Royal Society, London, UK
- Peters, R. H., S. Cloutier, D. Dube, A. Evans, P. Hastings, H. Kaiser, D. Kohn and B. Sarwer-Foner. 1988. The allometry of the weight of fruit on trees and shrubs in Barbados. *Oecologia (Berlin)* 74:612-616.
- Pietropaolo, J. and P. Pietropaolo. 1986. *Carnivorous plants of the world*. Timber Press, Portland, Oregon, USA.
- Pitelka, L. F., S. B. Hansen and J. W. Ashmun. 1985. Population biology of *Clintonia borealis* I. Ramet and patch dynamics. *Journal of Ecology* 73:169-183.
- Pitelka, L. F., D. S. Stanton and M. O. Peckenhams. 1980. Effects of light and density on resource allocation in a forest herb, *Aster acuminatus* (Compositae). *American Journal of Botany* 67:942-948.

- Primack, R. B. and J. Antonovics. 1982. Experimental ecological genetics in *Plantago*. VII. Reproductive effort in populations of *P. lanceolata* L. *Evolution* **36**:742-752.
- Primack, R. B. and P. Hall. 1990. Costs of reproduction in the pink lady's slipper orchid: a four year experimental study. *American Naturalist* **136**:638-656.
- Queller, D. C. 1985. Proximate and ultimate causes of low fruit production in *Asclepias exaltata*. *Oikos* **44**:373-381.
- Rameau, C. and P.-H. Gouyon. 1991. Resource allocation to growth, reproduction and survival in *Gladiolus*: the cost of male function. *Journal of Evolutionary Biology* **4**:291-307.
- Rathcke, B. and E. P. Lacey. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**:179-214.
- Reekie, E. G. 1991. Cost of seed versus rhizome production in *Agropyron repens*. *Canadian Journal of Botany* **69**:2678-2683.
- Reekie, E.G. and F.A. Bazzaz. 1987a. Reproductive effort in plants 1. Carbon allocation to reproduction. *American Naturalist* **129**:876-896.
- Reekie, E. G. and F. A. Bazzaz. 1987b. Reproductive effort in plants. 3. effect of reproduction on vegetative activity. *American Naturalist* **129**:907-919.
- Reekie, E. G. and F. A. Bazzaz. 1992. Cost of reproduction as reduced growth in genotypes of two congeneric species with contrasting life histories. *Oecologia (Berlin)* **90**:21-26.
- Richards, A. J. 1986. *Plant Breeding Systems*. George Allen and Unwin, London, UK.
- Sackville-Hamilton, N. R., B. Schmid and J. L. Harper. 1986. Life-history concepts and the population biology of clonal organisms. *Proceedings of the Royal Society, London, Series B*. **232**:35-57.
- Samson, D. A. and K. S. Werk. 1986. Size dependent effects in the analysis of reproductive effort in plants. *American Naturalist* **127**:667-680.
- SAS. 1987. *SAS/STAT guide for personal computers*. Version 6 edition. SAS Institute, Cary, North Carolina, USA.

- SAS. 1990. SAS technical report P-200, SAS/STAT software: CALIS and LOGISTIC procedures, release 6.04. SAS Institute, Cary, North Carolina, USA.
- Schaffer, W. M. 1974. Selection for optimal life histories: the effects of age structure. *Ecology* **55**:291-303.
- Schmid, B. and J. Weiner. 1993. Plastic relationships between reproductive and vegetative mass in *Solidago altissima*. *Evolution* **47**:61-74.
- Schnell, D. E. 1976. Carnivorous plants of the United States and Canada. J. F. Blair Publishing, Winston-Salem, North Carolina, USA.
- Schoen, D. J. and A. H. D. Brown. 1991. Whole and part flower self-pollination in *Glycine clandestina* and *G. argyrea* and the evolution of autogamy. *Evolution* **45**:1651-1664..
- Sih, A. and M. Baltus. 1987. Patch size, pollinator behavior, and pollinator limitation in catnip. *Ecology* **68**:1697-1690.
- Snow, A. A. and D. F. Whigham. 1989. Costs of flower and fruit production in *Tipula discolor* (Orchidaceae). *Ecology* **70**:1286-1293.
- Sohn, J. J. and D. Policansky. 1977. The costs of reproduction in the mayapple, *Podophyllum peltatum* (Berberidaceae). *Ecology* **58**:1366-1374.
- Sokal, R. R. and F. J. Rohlf. 1981. Biometry, 2nd edition. W.H. Freeman, San Francisco, USA.
- Sørensen, T. 1941. Temperature relations and phenology of the northeast Greenland flowering plants. *Meddelelser om Grønland* **125**:1-305.
- Soule, J. D. and P. A. Werner. 1981. Patterns of resource allocation in plants, with special reference to *Potentilla recta* L. *Bulletin of the Torrey Botanical Club* **108**:311-319.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* **51**:3-47.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York, USA.

- Svensson, B. M., B. Å. Carlsson, P.S. Karlsson and K. O. Nordell. 1993. Comparative long-term demography of three species of *Pinguicula*. *Journal of Ecology* **81**:635-645.
- Thompson, B. K., J. Weiner and S. I. Warwick. 1991. Size-dependent reproductive output in agricultural weeds. *Canadian Journal of Botany* **69**:442-446.
- Tuomi, J., T. Hakala and E. Haukioja. 1983. Alternative concepts of reproductive effort, costs of reproduction and selection in life history evolution. *American Zoologist* **23**:25-34.
- van Andel, J. and F. Vera. 1977. Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition. *Journal of Ecology* **65**:747-758.
- van der Valk, G. C. and M. J. G. Timmer. 1974. Plant density in relation to tulip bulb growth. *Scientia Horticulturae* **2**:69-81.
- van Noordwijk, A. J. and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist* **128**:137-142.
- Van Steveninck, R. F. M. 1957. Factors affecting the abscission of reproductive organs in yellow lupins (*Lupinus luteous* L.). *Journal of Experimental Botany* **8**:373-381.
- Vaughton, G. 1988. Pollination and seed set of *Banksia spinulosa*: evidence for autogamy. *Australian Journal of Botany* **36**:663-642.
- Vaughton, G. 1991. Variation between years in pollen and nutrient limitation of fruit-set in *Banksia spinulosa*. *Journal of Ecology* **78**:389-400.
- Venable, D. 1992. Size-number trade-offs and the variation of seed size with plant resource status. *American Naturalist* **140**:287-304.
- Watson, M. F. 1984. Developmental constraints: effect on population growth and patterns of resource allocation in a clonal plant. *American Naturalist* **100**:687-690.

- Weiner, J. 1988. The influence of competition on plant reproduction. Pages 229-245 in J. Lovett Doust and L. Lovett Doust, editors. *Plant Reproductive Ecology*. Oxford University Press, New York.
- Weiner, J. and
- Werner, P. A. 1975. Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.) *Oecologia* (Berlin) 20:197-201.
- Westley, L. C. 1993. The effect of inflorescence bud removal on tuber production in *Helianthus tuberosus* L. (Asteraceae). *Ecology* 74:2136-2144.
- Williams, G. C. 1966a. *Adaptation and Natural Selection*. Princeton University Press, Princeton, New Jersey, USA.
- Williams, G.C. 1966b. Natural selection, the costs of reproduction and a refinement of Lack's principle. *American Naturalist* 100:687-690.
- Williams, G. C. 1975. *Sex and Evolution*. Princeton University Press, Princeton, New Jersey, USA.
- Willis, J. C. and I. H. Burkill. 1903. Flowers and insects in Great Britain. Part III. Observations on the most specialized flowers of the Clova Mountains. *Annals of Botany* 17:539-571.
- Willson, M. F. 1983. *Plant reproductive ecology*. Wiley and Sons, Toronto, Canada.
- Willson, M. F. and P. W. Price. 1980. Resource limitation of fruit and seed production in some *Asclepias* species. *Canadian Journal of Botany* 58:2229-2233.
- Zamora, R. 1990a. The feeding ecology of a carnivorous plant (*Pinguicula nevadense*): prey analysis and capture constraints. *Oecologia* (Berlin) 84:376-379.
- Zamora, R. 1990b. Observational and experimental study of a carnivorous plant - ant kleptobiotic interaction. *Oikos* 59:368-372.
- Zimmerman, J. K. and T. M. Aide. 1989. Patterns of fruit production in a neotropical orchid: pollinator vs. resource limitation. *American Journal of Botany* 76:67-73.
- Zimmerman, M. and G.H. Pyke. 1988. Reproduction in Polemonium: assessing the factors limiting seed set. *American Naturalist*. 131:723-738.