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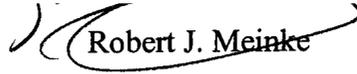
)(Robert J. Meinke

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Plagiobothrys hirtus (Boraginaceae) is a state and federally listed endangered plant found only in Douglas County, Oregon. This vernal pool endemic has historically been threatened by agricultural conversion of seasonal wetlands in the Sutherlin area, and is currently being eradicated as habitat is lost due to the rapid urban development occurring in southern Oregon. To promote the conservation of *Plagiobothrys hirtus*, plants were produced in the greenhouse and transplanted into field sites to augment the size of two diminishing natural populations. This work also resulted in propagation, cultivation, and transplantation protocols which are expected to be used in future reintroductions. Greenhouse-grown plants were installed in six plots within three soil moisture zones at each of the two sites, and were randomly assigned one of four treatments: weeded, fertilized, both weeded and fertilized, or left untreated as controls. Success of the transplants was evaluated by monitoring survival and fecundity. Transplants were most successful in the wettest zones; fertilization before transplanting, and above-ground removal of competing vegetation increased transplant success, although the effect of these treatments varied with soil moisture. Transplant success was correlated with plant

community composition; as the proportion of vegetation comprised of wetland species increased in plots, the proportion of transplants surviving also increased. Knowledge regarding successful cultivation and transplantation of *P. hirtus* will be useful for future reintroduction projects, as will the ability to identify sites likely to support created populations of this rare species. We also investigated the life history and ecology of *P. hirtus*, by comparing this rare species with *P. figuratus*, a common, closely related congener. Although the two species are similar in morphology, breeding system, pollination ecology, and seed germination, they differed in life history strategy, as *P. hirtus* was determined to be facultatively perennial, while *P. figuratus* is strictly annual. When grown together in the greenhouse, plants of *P. hirtus* continued to grow and flower as long as resources were abundant, and could propagate vegetatively, while those of *P. figuratus* died after flowering ceased. When compared with its common relative, flowers of *P. hirtus* occurring in natural populations received similar numbers of pollinator visits and set comparable amounts of seed. The breeding system and seed germination biology of the two species were also similar. Based on these investigations, *P. hirtus* would appear to have more options from a reproductive strategy standpoint, yet the species is naturally much rare and more narrowly distributed.

CONSERVATION BIOLOGY OF
PLAGIOBOTHRYS HIRTUS (BORAGINACEAE):
EVALUATION OF LIFE HISTORY
AND POPULATION ENHANCEMENT

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Major Professor, representing Botany and Plant Pathology

Redacted for privacy

Chair of Botany and Plant Pathology

Redacted for privacy

Dean of Graduate School

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Dedicated to

Erin Emily Amsberry Abood

CONSERVATION BIOLOGY OF *PLAGIOBOTHRYS HIRTUS* (BORAGINACEAE): EVALUATION OF LIFE HISTORY STRATEGY AND POPULATION ENHANCEMENT

Chapter 1

Introduction

"If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering."

Aldo Leopold, 1948

Why spend scarce economic resources to preserve a nondescript roadside weed indistinguishable from a dozen others? What is the value of a woodland snail that ten years ago no one knew existed? Why protect a weedy-looking white forget-me-not when we can readily grow prettier blue ones? And what possible purpose could there be in perpetuating a moss? In other words, why should we, as a society, be willing to spend limited resources to conserve rare species? Questions about the value of biodiversity can be answered in various ways - the conservation of native plants can be discussed within practical, aesthetic, ethical, and ecological community contexts.

Native plants have the potential to make practical contributions to agriculture, medicine, and ornamental horticulture. Wild plants may contain presently unutilized genes for disease resistance, cold hardiness, and other beneficial traits; these genes can potentially contribute to our currently genetically homogenous agricultural crops (Affolter 1997). Several cancer cures initially synthesized from wild plants have been in the news in the last few years - taxol from *Taxus brevifolia*, and vinblastine from *Cantharanthus roseus* -

and 25% of prescriptions are currently filled with drugs which contain active ingredients that are extracted or derived from plants (World Resources Institute 1995). Herbal remedies have also been hypothesized to be more effective than chemically synthesized medicines due to multiple interactive components present in plant compounds (Johnson 1997). As well as making contributions to agriculture and medicine, native plants provide an influx of new material for the horticultural industry. Ornamental plant nurseries are constantly searching for new native plants with ornamental value, and for new genetic material to contribute to future garden hybrids. For example, the latest catalog from Park's Seed advertises 134 "new" varieties of flower and vegetable seed, many resulting from the hybridization of previously unutilized genetic stock, combined with genes from existing species and cultivars (Park 2000). The extinction of native plants permanently prevents their future use. Today's weed may be tomorrow's agricultural savior, miracle drug, or latest garden fashion; the removal of these plants from the pool of those potentially available for practical purposes may eliminate an unforseen opportunity to improve our existence.

As well as providing practical benefits, protecting natural areas and conserving biodiversity increases the enjoyment of our daily lives. John Muir, perhaps, says it best - " Everybody needs beauty as well as bread, places to play in and pray in, where nature may heal and give strength to body and soul alike." (1912), and "There is no repose like that of the green deep woods. Here grow the wallflower and the violet. The squirrel will come and sit upon your knee, the logcock will wake you in the morning..." (1938). This

delight in nature can be intensified by the thrill of discovering a rare plant or animal species (Stebbins 1980). People often ascribe higher value to a scarce item (Drury 1980), as demonstrated by the excitement shown by birders when sighting seldom seen birds or the exhilaration of a child who receives a gift of a "rare" Beanie Baby. Rare plants contribute to our enjoyment of nature, as well as providing the thrill of exclusive discovery.

Although possibly less concrete than practical or aesthetic arguments, the ethical justification for conserving biodiversity is no less compelling. Aldo Leopold, in 1948, advocated the creation of a land ethic to "enlarge the boundaries of the community to include soils, waters, plants, and animals..." Almost 40 years later, a majority of people expressed the same sentiments, supporting "the value of non-human life independent of the usefulness of the non-human world for human purposes" (Naess 1986). In his surveys, Naess (1986) found that most respondents in the general population, as well as the prominent leaders he interviewed, agreed that plants and animals should be conserved regardless of their practical benefits to humans. Currently, Leopold's idea of a land ethic remains popular (The Aldo Leopold Foundation 2000, Lubchenco and Vergun 2000), and continues to influence conservation policy in the U.S., and throughout the world.

As well as promoting the concept of nature as a community, Leopold believed that our lack of sufficient information about the importance of individual components in any but the simplest systems requires the protection of all members of that community. At the

present time, we do not know if this lack of information will eventually be resolved through future study, or if biological systems are intrinsically indefinable. However, some methods for evaluating the importance of individual components have been proposed. The "keystone species" concept identifies specific taxa within a system as being critically important (as pollinators, predators, forage producers, etc.); without them, the community they inhabit would not survive (Begon et al. 1990). The ecological guild model allows us to speculate about the function and value of a specific organism within a system (Begon et al. 1990), but at the current time, we rarely have sufficient information to make decisions regarding the dispensability of any given component. Until, (and if) we learn the function and value of every component, as well as understand the interactions among components, we should heed Leopold's advice and make every attempt to keep them all.

Once the benefits of protecting biodiversity have been determined, how do we go about initiating the process of conservation? Searching for the answer to this question provides the force behind the development of conservation biology. This field is a multi-disciplinary science that has evolved in response to the crisis confronting biological diversity today (Soulé 1985). Made up of population biology, taxonomy, ecology, and genetics, with contributions from economics, ornamental horticulture and agriculture, conservation biology has two goals: first, to understand the effects of human activities on species, communities, and ecosystems, and second, to develop practical approaches to preventing the extinctions of species and, if possible, to reintegrate endangered species

into properly functioning ecosystems (Primak 1995). As our society becomes more complex and resource-hungry, and the population of the world continues to grow exponentially, our impacts on the global ecosystem invariably increase. Conservation biologists attempt to alleviate some of the negative anthropogenic effects, and protect the current levels of biodiversity. Hopefully, by using the tools available to us, we will be able to tinker without losing any of the parts.

Chapter 2

Population Augmentation of *Plagiobothrys hirtus*
in Douglas County, Oregon

Abstract

To promote conservation, naturally occurring populations of the federally-listed

endangered plant *Plagiobothrys hirtus* (USFWS 2000) were augmented at two sites in the

Umpqua Valley. Greenhouse-grown plants were planted in six plots within three soil

moisture zones at each of the two sites, and were randomly assigned one of four

treatments: weeded, fertilized, given both treatments, or left untreated as controls.

Success of the transplants was evaluated by monitoring survival and fecundity.

Transplants were most successful in the wettest zones; fertilization and removal of

competing vegetation increased transplant success. Transplant success was correlated

with plant community composition; as the proportion of vegetation comprised of wetland

species increased in plots, the proportion of transplants surviving also increased.

Knowledge regarding successful cultivation and transplantation of *P. hirtus* will be useful

for future reintroduction projects, as will the ability to identify sites likely to support

created populations of this rare species.

Introduction

Species are becoming extinct at an alarming rate. At no time in the history of the earth

have mass extinctions, of both plants and animals, occurred so rapidly (Lande 1988;

Guerrant 1992; Wilson 1992). It is estimated that up to 25% of the plant and animal

species that are currently recognized could become extinct within the next 50 years; many others will disappear even before they can be officially described (Wilson 1992; Myers 1993; Schemske et al. 1994). This unusually high extinction rate is presumably due to anthropogenic factors, the most important of which is habitat destruction, although overharvesting and pollution have also contributed to the demise of some species (Falk and Olwell 1992; Guerrant 1992; Wilson 1992; Reinartz 1995; King 1998).

Habitat destruction has been of particular importance to the loss of vernal pool and seasonal wetland species. One of the rarest and most endangered ecosystems, vernal pools appear during winter, when rainwater unable to seep through impervious hardpan temporarily fills shallow soil depressions. These pools vary in size from a few to hundreds of meters across, and may last for weeks or months before drying and disappearing completely (Baskin 1994). Conversion of these ephemeral wetlands to agricultural fields was identified as a major contributor to the extinction of vernal pool species as early as 1941 (Hoover 1941), and researchers currently estimate that 60-90% of pools extant at the time of European settlement have now been destroyed, along with the endemic plant and animal species associated with them (Keeley and Zedler 1998; King 1998).

This perturbing plethora of extinctions is ominous for a variety of reasons. The many thousands of species on earth interact to generate the air, water, and food that allow us to exist, as well as producing potential practical benefits for humans, and providing aesthetic

enjoyment. Although the importance of the services, such as clean air and water, that are produced by intact ecosystems may be less immediately apparent than the benefits of conserving wild plants for future medical or agricultural uses, the significance of these contributions to the continuation of human existence has recently been emphasized (Lande 1988; Noss 1997; Morell 1999). As species are lost from these interactive systems, the systems themselves begin to degrade, and at some point no longer function. Due to the extreme complexity of these interactive networks, the point at which degradation becomes irreparable is difficult to identify, and the effect of the loss of any single species or group of species on system integrity is unknown. Despite this lack of knowledge, the gravity of the increasing rate of extinctions is of great concern to modern scientists - as ecologists, botanists, and land managers, we are all responsible for determining how best to stop the accelerating extirpation of species from the lands under our jurisdiction (Noss 1997; Morrell 1999).

Multi-national conservation agreements that provide blanket protection to multiple species - at the landscape scale - will be essential to the long term prevention of ecosystem failure and subsequent wholesale environmental destruction. A global commitment to conserve biodiversity and protect intact habitat should be recognized as a critical component of conservation planning in the coming decades. However, large scale projects form only one component of an integrated approach to protecting biodiversity, and do not constitute a comprehensive remedy for the deluge of extinctions we are currently experiencing. Due to administrative reasons, as well as the limitations inherent

in large-scale ecological research, most efforts to prevent the loss of biodiversity in the United States are directed at individual species (Primack 1995). The lack of emphasis on the interactions that promote self-sustaining ecosystems which typifies this approach have encouraged some researchers to criticize species-level conservation as nothing more than "crisis-control" (Guerrant 1992). However, as the U.S. Endangered Species Act of 1973 (USFWS 1988) - the strongest legal protection for biodiversity conservation provided by our federal government - is designed to protect individual plant species (and subspecies), it would seem wise to use this valuable tool to its greatest advantage. The ESA officially recognizes the importance of biodiversity and provides a strong legislative mechanism for recovering species in danger of becoming extinct. As well as recommendations for reducing threats to currently extant populations of listed species, recovery plans under the ESA often include requirements for reintroduction of these species into suitable sites - with the idea that they will persist in their new abodes and reduce the need for further intervention on their behalf (Bowles et al. 1993; Pavlik et al. 1993a). Recovery plans for listed species include not only the biological information needed to evaluate the causes of endangerment and consequently recommend management objectives to prevent extinction, but often also require reintroduction of previously extirpated populations, with the goal of attaining a specified number of viable populations. The number of extant occurrences required, and the size of these populations, is based on the number predicted to be necessary to insure that the species is self-sustaining, and no longer in imminent danger of extinction (Schemske et al. 1994).

In fact, many potential benefits may result from reintroduction, defined as "the deliberate establishment of individuals of a species into an area and/or habitat where it has become extirpated, with the specific aim of establishing a viable, self-sustaining population for conservation purposes" (Maunder 1992). Replacing a rare species in sites from which it has been extirpated (and restoring suitable conditions to allow it to perpetuate) re-establishes a potentially important component of the original community for those sites, and promotes restoration of functioning ecosystems (Lande 1998). Restoring plant diversity in a specific locale by reintroducing rare plants may also improve the diversity of animals, insects, and other organisms in the area. For example, Fender's Blue butterfly (*Icaricia icariodes* ssp. *fenderi*), federally-listed as endangered, requires as a host Kincaid's Lupine (*Lupinus sulphureus* ssp. *kincaidii*), another endangered species, for larval development; recovery of the butterfly depends on recovery of the lupine (Wilson et al. 1997). Preventing extinction also insures that these conserved species will be available for future development and potential utilization in medicine, agriculture, and ornamental horticulture (Lande 1988; Wilson 1992; Affolter 1997).

Augmenting the size of naturally occurring, but currently declining populations can also improve the prospects for the persistence of rare species. Population size has long been known to affect breeding system, genetics, and evolutionary dynamics (Wright 1931, 1941). Maintaining population size and genetic diversity is currently one of the fundamental goals of conservation biology (Barrett and Kohn 1991). Larger, more genetically diverse populations are more resistant to the potentially negative impacts of

genetic drift, and less likely to suffer the effects of inbreeding depression (Barrett and Kohn 1991; Widen 1993). Genetic diversity also increases the ability of a population to resist pests and disease (Barrett and Kohn 1991; Huenneke 1991). Larger populations are also more likely than small ones to persist for non-genetic reasons. As well as reducing the likelihood of destruction by demographic stochasticity (Huenneke 1991; Menges 1991), or by random catastrophic events (Lesica and Allendorf 1995), increasing population size can alleviate potentially deleterious edge effects, and promote density-dependent benefits, such as the attraction of pollinators (Lande 1988; Widen 1993; Agren 1996). Due in part to these increases in visitation, larger patches typically exhibit higher levels of seed production than do small ones, improving their ability to persist, and promoting population enlargement (Jennersten 1988; Lamont et al. 1993 - but see Bigger 1999).

As well as reintroducing extirpated populations and augmenting the size of extant populations, greenhouse-grown plants can be used to create new populations. Introduction of populations into new or historic sites within the general locality of established native populations, and augmentation of existing populations, also improves the demographic dynamics of the species as a whole. In the event of extirpation of some populations due to a catastrophic event, surviving populations can serve as seed sources to re-establish new populations into vacated sites, naturally, or by human-mediated seed dispersal (Menges 1991). A larger number of populations also allows for the development of increased genetic differentiation among sites, increasing overall heritable

diversity, and providing more chances for the species to evolve in response to varying selective pressures (Huenneke 1991). As fragmentation of populations has been shown to interrupt pollinator movement, and consequently reduce seed set (Jennersten 1988; Agren 1996), reintroducing populations within a network that has been disrupted can improve pollinator services and increase fecundity of existing populations (Huxel and Hastings 1999).

As there is little protection available to plants on private land (under current state and federal laws, placing plants into currently unoccupied sites in suitable habitat in publically owned areas within the historic range of a species - even when the species is not known to have occurred in that exact location - allows for greater protection of threatened plant species. Unregulated development, excess grazing, and other activities that often occur on private land can be curtailed in these administratively protected sites, preventing extirpation due to such causes. The agencies that manage publically owned sites often have more expertise and resources to commit to plant conservation than many private landowners, and may be more inclined to promote management activities that benefit rare species.

However, routinely using the creation of new rare plant populations as a mitigating mechanism to compensate for the planned extirpation of existing populations by development is rightly disapproved of by most conservation biologists (Hall 1987; Havlik 1987; Falk and Olwell 1992; Maunder 1992; Gordon 1994; Howald 1996; Morse 1996;

Guerrant and Pavlik 1997). We simply do not have enough ecological information to confidently recreate natural systems (Falk et al. 1996). This caveat applies particularly to wetland ecosystems - their complex energy and nutrient webs, species composition, and hydrology make re-creation of a functioning wetland extraordinarily challenging (Falk and Olwell 1992; Zedler 1996).

And, in fact, the process of rare plant reintroduction has been fraught with failure (Falk and Olwell 1992; Allen 1994; Pantone et al. 1995; Howald 1996), often due to a lack of information about the characterization of appropriate sites (Hall 1987; Fiedler and Laven 1996). Soil type, including soil texture and moisture retention, is an especially important criterion for hospitable site selection, with many rare plant reintroduction failures attributable to transplantation of plants into sites containing soils inappropriate for the target species. The biological aspects of a proposed site are also important. Specific pollinators (Karron 1987) or mycorrhizal associates (Barroetavena et al. 1998) may be required, and exotics that outcompete or hybridize with the reintroduced plants should be absent. Removal of weedy exotics may be necessary for reintroduction into an otherwise suitable site (Pavlik et al. 1993b; Fiedler and Laven 1996).

The inability to propagate and grow rare plants in a cultivated setting has also contributed to the lack of successful, large scale introductions (Reinartz 1995). Difficulties in greenhouse production of transplants due to lack of information on seed germination (Pavlik et al. 1993a; Walck et al. 1999), mycorrhizal associates (Barroetavena et al.

1998), nutrient requirements, and other factors can restrict the amount of stock available for transplanting, and limit the establishment of adequately large populations. The development of protocols for propagation and cultivation of plants to be used as transplants is critical to the success of rare species recovery plans; fortunately, relevant information on plant cultivation is becoming more available as researchers realize the importance of this type of data (Affolter 1997).

Despite the many documented failures of rare plant reintroductions (Hall 1987; Allen 1994; Hurkmans 1995; Pantone et al. 1995; Brumbak and Flyer 1996; Howald 1996), there have also been encouraging successes. A created population of *Amsinckia grandiflora* at an unoccupied site within the historic range of the species appears to be successful, at least initially (Pavlik et al. 1993*b*; Pavlik 1995). Despite some initial setbacks, *Hymenoxys acaulis* var. *glabra* appears to have been successfully reintroduced in two protected sites on nature preserves in Illinois (DeMauro 1994; Guerrant and Pavlik 1997). Greenhouse grown plants of *Abronia umbellata* var. *breviflora* have been successfully transplanted into several sites on the southern Oregon coast (Kaye et al. 1998), and other reintroduction projects have shown at least preliminary success (Ferreira and Smith 1987; Bowles et al. 1993; Cully 1996; Edson 1996; McDonald 1996).

Because reintroduction has the potential to save endangered species, and the threats facing these species are often great, this process, despite its drawbacks, is one of the most valuable tools available to conservationists (Morse 1996). However, although the

usefulness of reintroduction is well-documented, the process of developing methods for successfully producing and transplanting endangered plants is still in its infancy (Reinartz 1995; Affolter 1997). In order to contribute to the available knowledge of rare plant reintroduction, we decided to focus on designing a model for easily identifying appropriate sites, and on developing propagation, cultivation, and transplantation protocols to be used by land managers interested in reintroduction. The objectives of this project are twofold: to augment the population size of *Plagiobothrys hirtus*, a federally-listed endangered plant (USFWS 2000) in two protected sites, and to develop practical methods to assist in future reintroduction projects.

Plant Description

Plagiobothrys hirtus (Greene) Johnst. (Boraginaceae) is an herbaceous plant ranging to be 50-60 cm tall and perennial, or considerably smaller and annual, depending on environmental conditions. The upper stems are distinctly hairy, and the bright green, strap-shaped linear leaves have hairy margins. Flowering stems are spreading, with paired coiled inflorescences containing many 5-10 mm, five-petaled flowers with yellow centers (Fig. 1). Flowers can produce up to four tan-colored to black nutlets each; due to fruit abortion or lack of pollination, calyces with fewer than four nutlets are often observed.

A technical description (from Abrams 1951; Peck 1961) consists of: stem stout, simple below, erect or reclining, 3-7 dm high, setose-hirsute above, with hairs spreading,
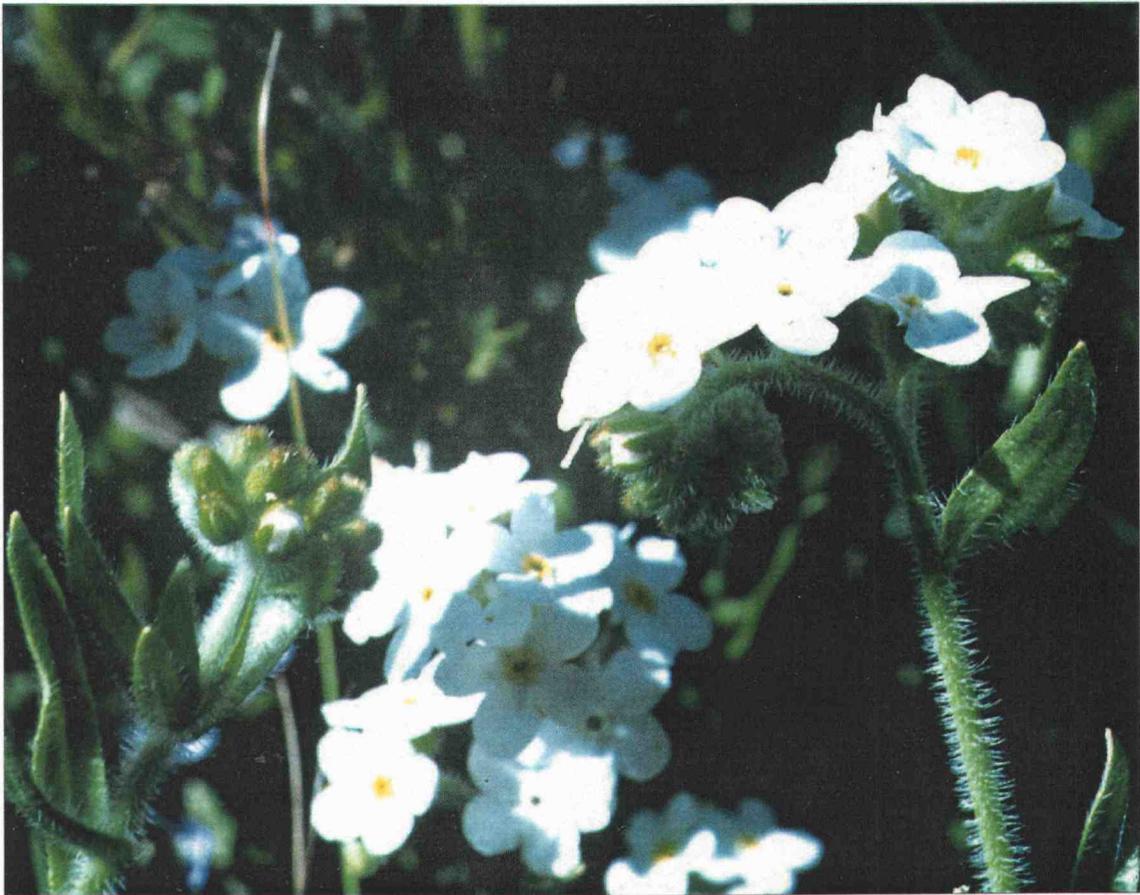
Figure 1. *Plagiobothrys hirtus* in flower. The hairy stems distinguish this species from related ones in our area.

especially on the branches, branches ascending. Leaves of the main stem opposite, connate at the base, linear 2.5-4 cm long, nearly or quite glabrous, except setose on the margins, those of the branches mostly alternate or shorter, pustulose-setose throughout with no appressed pubescence; racemes in pairs terminating the branches, bractless; pedicels slender 1-2 mm long; calyx 4 mm long in fruit, the lobes erect, densely setose-hirsute; corolla 5 mm broad; nutlets ovoid, barely 2 mm long, brownish black when fully mature, the dorsal side rounded, ridges inconspicuously reticulate, rather obscurely rugulose and tuberculate.

As do many vernal pool plants, *Plagiobothrys hirtus* produces foliage during its submerged phase that is distinctly different from that produced by emergent plants (Keeley and Zedler 1998). Immersed plants produce rosettes of glabrous, terete leaves with extensive lacunal airspace - these submerged rosettes are so distinct from the hirsute, flattened foliage produced by emergent plants as to be almost unrecognizable as the same species. This type of submerged vegetation (appropriately titled an 'isoetoid' growth form, as it is typified by the wetland plant *Isoetes*) enhances carbon assimilation in wetland habitats, and is common in seasonally aquatic plants (Keeley and Zelder 1998). In several genera, including *Plagiobothrys,* this growth form is well represented by vernal pool inhabitants, but is not present in congeneric species found outside of the seasonal wetland habitat (Keeley and Zelder 1998; Spencer and Reiseberg 1998).

Site Descriptions

In June 1996, a total of 480 greenhouse-grown transplants were installed adjacent to

small, existing native populations of *Plagiobothrys hirtus* at two wetland sites, roughly

12 miles apart (Fig. 2). The Yoncalla site, owned by the Oregon Department of

Transportation (ODOT), is located two miles north of Rice Valley immediately adjacent

to (on the east side of) Interstate 5 (T23S/R5W/S15). *Plagiobothrys hirtus* occurs in the

area, which is maintained by ODOT as a special management unit. To prevent damage to

native and experimental populations of *P. hirtus,* ODOT personnel perform routine

annual roadside mowing at this site in the fall, after seed dispersal, and use mowers that

are smaller, and set higher, than standard highway maintenance mowers. Other proposed

maintenance activities for this site are reviewed by ODOT biologists for potential impacts

on *P. hirtus* before initiation.

The Yoncalla site is open and unshaded, with *P. hirtus* flourishing throughout the low-

lying area parallel to the highway. The plants grow most densely in the deepest part of

what is, essentially, a roadside ditch, and are submerged under standing water from late

fall through spring. Like most sites that support populations of *P. hirtus*, this site is

comprised of Conser silty clay loam, a very deep, poorly drained soil found in

depressions on alluvial stream terraces at elevations of 100 to 1300 feet in the Willamette

and Umpqua Valleys. This soil is usually moist, and is saturated during the winter. An

apparent water table within this soil series is at its uppermost limit from November to

May, and the depth to aquic conditions is zero to ten inches. Although *P. hirtus* is
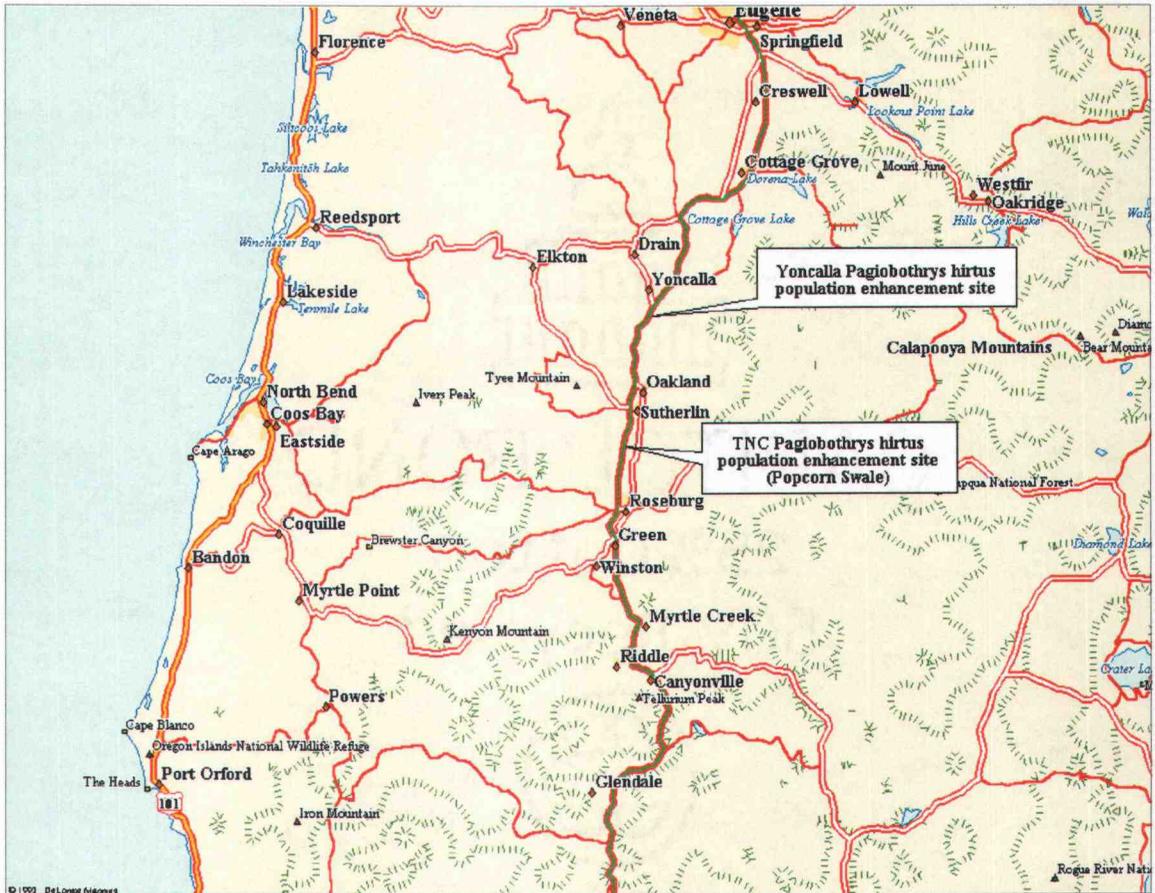
Figure 2. Location of population enhancement study sites in Douglas County, Oregon. Both sites are immediately adjacent to Interstate 5 (shown in green).

associated with Conser silty clay loam in ten of its 13 extant sites, three sites are on two

other poorly drained soils. The soil in one of those sites is comprised of Bashaw clay, and

the remaining two consist of Brand silty clay loam (Natural Resources Conservation

Service 1997; Soil Survey Division 2000).

Associated species in this site are typical of the sedge/grass-dominated open marsh in

which *Plagiobothrys hirtus* occurs; native associates include *Carex feta, Juncus effusus,*

Juncus oxymeris, Veronica scutellata, Glyceria occidentalis, and *Deschampsia*

caespitosa. Due to its close proximity to the highway, this site is highly disturbed and

subsequently suffers from an infestation of exotic weeds, including *Dipsacus sylvestris,*

Rubus discolor, and *Centaurea diffusa*. (See Appendix A for a complete species list.)

The William Oerding Popcorn Swale Preserve, owned and managed by The Nature

Conservancy (TNC) as a refuge for *Plagiobothrys hirtus*, is between Sutherlin and

Wilbur (T26/R5W/S6). Like the Yoncalla site it is adjacent to Interstate 5 (Fig. 2).

Although this site likewise supports a considerable infestation of exotic weeds, notably

Dipsacus sylvestris and *Centaurea* spp., it contains more native vegetation than the

Yoncalla site, including *Beckmannia syzigachne, Downingia yina, Camassia leichtlinii,*

and *Limnanthes douglasii*, and is partly shaded in some areas by *Fraxinus latifolia* and

naturalized *Pyrus*. (See Appendix B for complete species list.) Like the Yoncalla site, the

Popcorn Swale Preserve consists of seasonally wet meadow habitat. However, this site is

on Bashaw clay soil, another very deep, poorly drained soil formed in the alluvium of

flood plains and fans at elevations of 90 to 1,000 ft. This soil has very slow permeability; an apparent water table occurs at a depth of one ft. or above to 0.5 ft. below the surface from November to May, with flooding for long periods common from December to April (Natural Resources Conservation Service 1997, Soil Survey Division 2000).

Methods

Production of transplants. Because reintroduction attempts utilizing site-sown seed can yield poor results (Taylor 1991; Bowles and McBride 1996; Cully 1996; Kaye et al. 1998), our project exclusively used greenhouse grown transplants. These transplants were produced in the greenhouse using asexual propagation techniques (cuttings) from 20 stock plants from each site that were initially grown from seed. Asexual propagation techniques have been successfully used to create transplants for reintroduction projects with other members of the Boraginaceae (Edson 1996). Seed for stock plants was originally obtained in1994 from a cryogenic seed bank at the Berry Botanic Garden, and represents genetic material collected from the two transplant sites. Because a population may be specifically adapted to the site in which it grows (Reinartz 1995), and the choice of appropriate stock is critical to reintroduction success (Bowles et al. 1993; Guerrant 1996), transplants destined for each of the two sites were produced from stock plants grown from seed collected at that site. Cuttings were potted and then grown for two months in standard potting soil, and were fertilized with liquid fertilizer (Peter's 20-20-20©) as needed. Plants were watered daily, or immersed in water-filled trays to ensure saturation of soils. As aphid infestations are a common problem in greenhouse

cultivation of boraginaceous plants (Edson 1996; personal obervation), cuttings were treated with Safer's Insecticidal Soap© as needed. Because they were grown from simultaneously produced cuttings of the same size, plants ready for transplanting were of also of uniform size - most consisted of a single large rosette of foliage, and no flowers (Fig. 3).

Installation. After transportation to the study sites, transplants were installed along a moisture gradient in order to evaluate the importance of moisture to plant success, and to develop criteria for appropriate site selection for future reintroduction work. Moisture zones (each 40 m²), were initially delineated by observation, and were subsequently corroborated by water table measurements from soil wells. (There was a strong correlation between the average depth to water per zone with the observationally determined moisture zone; $R^2 = 0.95$.) Two sets of three moisture zones were utilized at each site, and were labeled as xeric, mesic, and hydric, although all were within the boundaries of the wetland sites. To prevent interference from naturally occurring *P. hirtus* plants, all transplant zones were located as far as possible from existing native populations present within the site (a minimum of one meter, and usually much further away). Forty plants were placed within each moisture zone, with randomization achieved by random selection of X and Y co-ordinates initiating at the southwest corner of each zone. The location of each plant was marked with a color-coded wooden stake identifying location co-ordinates and treatment applied (Fig. 4). Plants were installed by placing them in holes approximately the size of their root masses that were dug with a

Figure 3. Plants in the greenhouse ready for transplanting. At the time of planting, most plants consisted of a single rosette, with few or no elongating shoots or flowering stems.

Figure 4. Transplants blooming in August. Each transplant was marked with a color-coded wooden stake identifying location co-ordinates and treatment applied.

soil sampling shovel, then smoothing the wet field soil back in around the roots, and

immediately watering them thoroughly.

Development of site selection criteria - Evaluation of plant community composition can

be used to delineate wetlands (Wentworth et al. 1988; Committee on characterization of

wetlands 1995; Stromberg et al. 1996), and has been successfully used to identify

appropriate sites for rare plant reintroduction (Bowles et al. 1993). In our study, moisture

zones were qualitatively described by using wetland indicator species lists to evaluate the

composition of the vegetation present. A community composition score was calculated

for each moisture zone by determining the percent cover of all species at eight

randomly selected subplots within each zone, computing the average for each zone, then

utilizing numerical indicator scores for each species from the *National List of Plant*

Species that Occur in Wetlands (USFWS 1996) in a weighted average equation (Atkinson

et al. 1993):

$$\text{Weighted average} = (y_1 u_1 + y_2 u_2 \ldots + y_n u_n)/100$$

where y_1, y_2,...., y_n are the relative cover estimates for the species in the zone, and u_1,

u_2...., u_n are the indicator values for each species. Since indicator categories range from 1

to 5, zone indicator status exhibits the same range. A zone composed of all obligate

wetland species has a score of 1.00; a zone of all obligate upland species has a score of

5.00. Nativeness (relative percent cover of native vs. exotic vegetation) was also calculated for each moisture zone.

As well as determining site quality by evaluating vegetation, we measured soil moisture quantitatively in three soil wells (45 cm deep) installed in each zone (Austin 1994). Depth to ground water was measured in these wells at intervals throughout the year, and the readings from the three wells in each zone were averaged to produce the measurements used in our analyses.

Treatments. To evaluate the effect of competition from native and exotic weeds, randomly selected transplants were installed into weeded plots. As much above-ground vegetation as possible was removed from these 0.5 m² plots by weeding to ground level with a power "weed-eater" prior to placing plants. To determine if increased nutrients would enhance transplant success, randomly selected plants were given supplementary nutrients with 250 ml liquid fertilizer (Peter's 20-20-20©) in the greenhouse, one week before transport to the transplant sites. (Fertilizer was applied prior to, rather than at the time of, transplanting to prevent fertilizing existing vegetation present in the plots.) Twenty-five percent of plants received both treatments, 25% were weeded only, 25% fertilized only, and 25% were left untreated as controls. Treatments were equally distributed among 240 plants at each of the two study sites.

Evaluation. Transplants were monitored at two week intervals throughout the summer, and monthly in winter, with transplant success evaluated through measurements of survivorship, growth (stem length, ramet production), and fecundity (flower production, seed set). Data were analyzed for treatment and moisture zone effects using the General Linear Model and Mixed procedures in SAS 6.12 to perform ANOVA tests (SAS Institute 1996). Linear regression was used to analyze community composition data using Statgraphics 3.0 for Windows (Statistical Graphics Corp.1997).

Results

Mortality. The Yoncalla site is clearly a more hospitable site than Popcorn Swale for reintroduction, with 50% of transplants still alive at the end of the first summer, and 41% of the transplants surviving for one year (Figs. 5 and 6). Many *Plagiobothrys hirtus* plants were alive and thriving within the transplant zones at this site, four years after installation However, due to the clonal habit of this plant, the destruction of plot locators due to unexpected ODOT management activities, and large amounts of seedling recruitment in some zones, it is no longer possible to accurately monitor individual transplants. At Popcorn Swale, mortality was high, with only 20% survival through the first summer, and 93% of transplants dying within the first year.

In both sites, soil moisture appears to be a critical parameter influencing transplant success ($p < 0.001$), with survival rates increasing as mean soil moisture increases (Figs. 5, 6, and 7). At Popcorn Swale, all of the plants that survived the first year did so in the
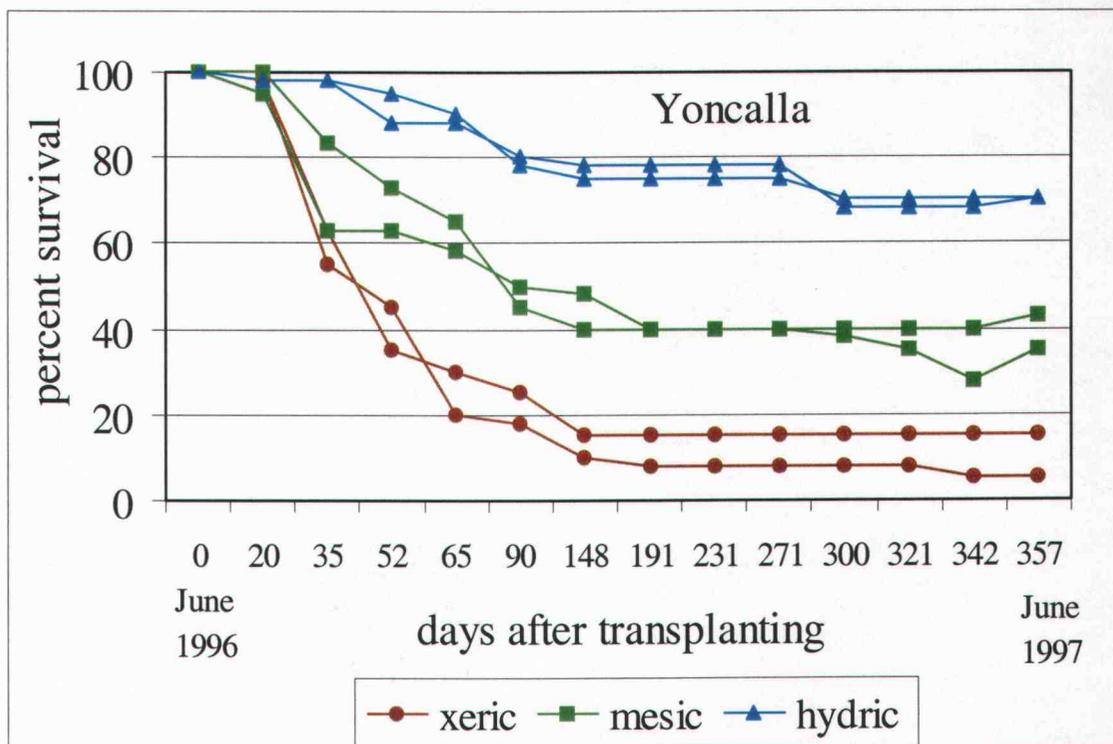
Figure 5. Survival of *Plagiobothrys hirtus* transplants at the Yoncalla site in the first year. Two hundred and forty transplants were installed at this site - two subplots containing forty plants each within each moisture zone.
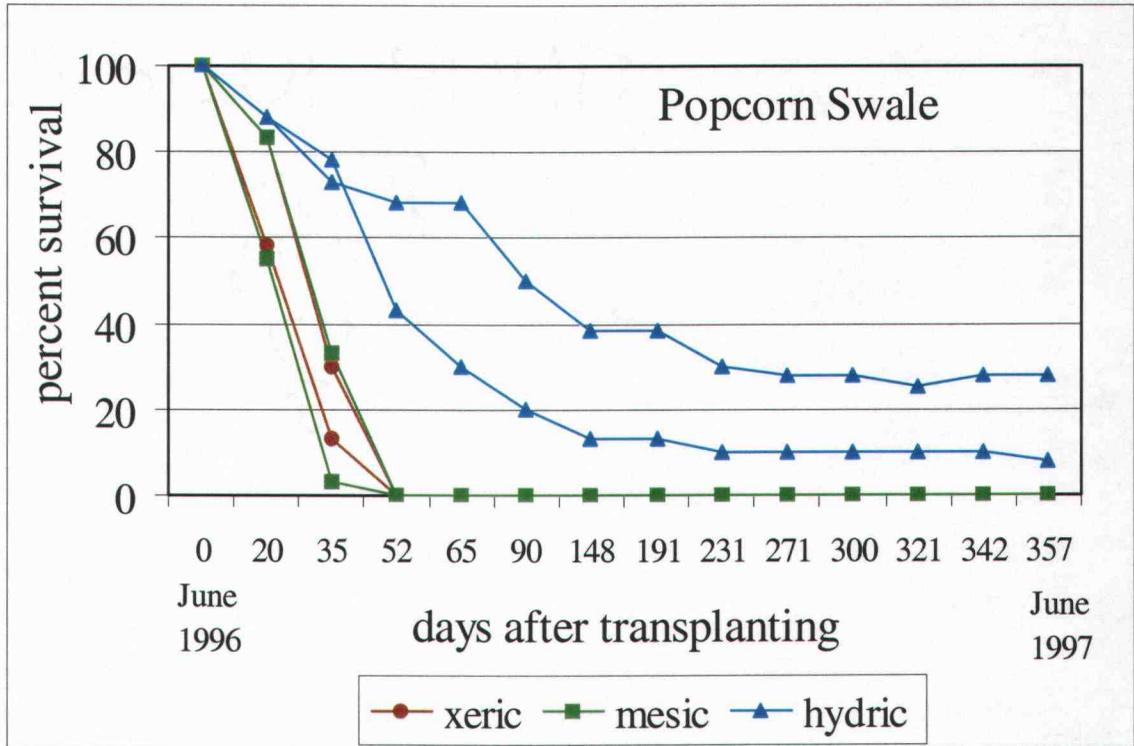
Figure 6. Survival of *Plagiobothrys hirtus* transplants at the Popcorn Swale site in the first year. Two hundred and forty transplants were installed at this site - two subplots containing forty plants each within each moisture zone.
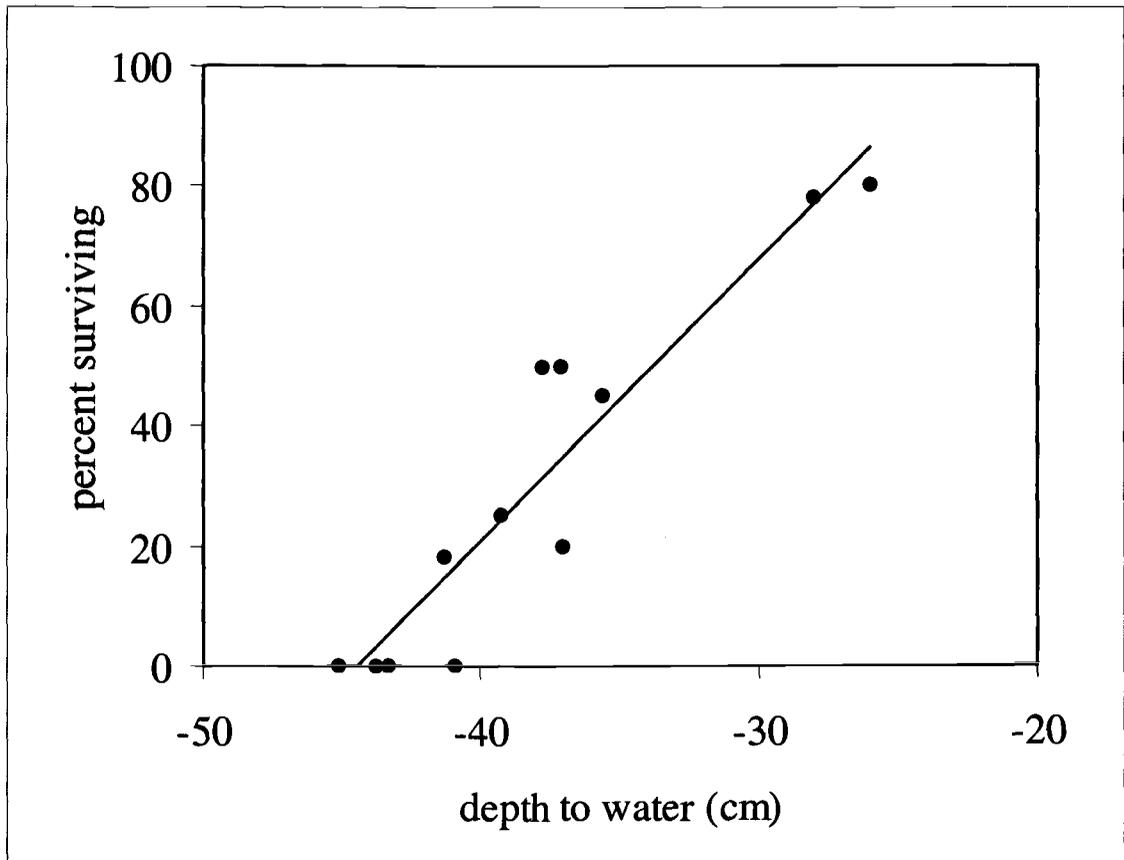
Figure 7. Survival in relation to water depth at both reintroduction sites. Points represent the depth to water, averaged throughout the year, for each of the twelve plots. Plants installed in plots with higher water tables survived better than those in drier plots. ($R^2 = 0.86$; $y = -34.62x + 18.64$; $p < 0.001$).

hydric zones. At the Yoncalla site, 61% of the one-year survivors were present in the hydric zones, 31% in the mesic zones, and only 8% in the driest zones.

Removal of competing vegetation improved establishment. Sixty-five percent of transplants in weeded plots survived through the end of the first growing season at the Yoncalla site, while 52% of those that were unweeded survived (p = 0.015). The effect of weeding at the time of transplanting continued to affect transplant survival after one year (p = 0.001), with 54% of weeded transplants, and 29% of those that were unweeded surviving. Fertilization did not significantly improve transplant survival at the end of the first growing season, or after one year (p = 0.759, and p = 0.139), but did affect survivors, at least initially (see below). At Popcorn Swale, weeding also improved survival in the first growing season (p = 0.015), with 65% of weeded transplants, and 35% of unweeded ones surviving. Low survival rates at this site prevented analysis of data past the end of the first growing season. Fertilization did not affect transplants at this site (p = 0.497).

Growth. As well as being the most important parameter influencing transplant survival, the moisture zone in which plants were installed within the wetland also significantly affected plant growth (p = 0.008). By the end of the first growing season, the mean stem length of surviving plants in the hydric zones at the Yoncalla site was 26.4 cm, 17.0 cm in the mesic zones, and 8.5 cm in the dry zones. Weeding increased stem length by an average of 4.2 cm (p = 0.006); the interaction between moisture zone and the weeding treatment was not significant (p = 0.290). However, the effect of fertilizer did depend on
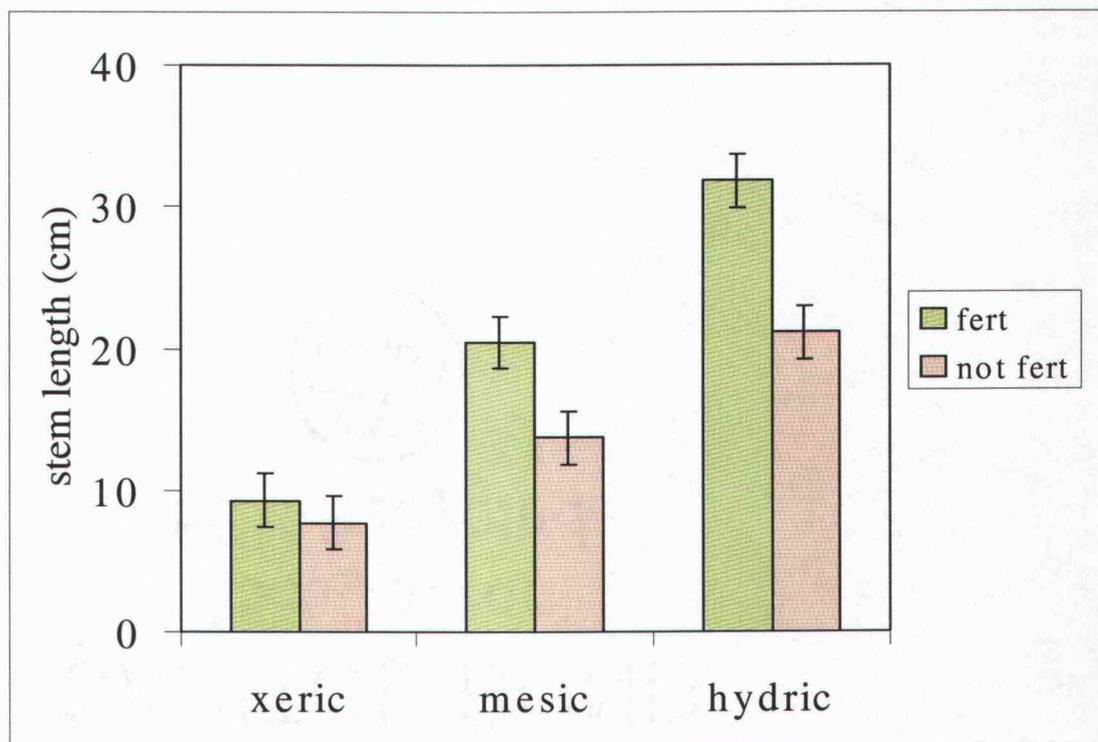
Figure 8. The effect of fertilizer on stem length. This effect was greatest in the hydric zones, less evident in the mesic zones, and not significant in the xeric zones. Error bars represent one standard error above and below the mean.

moisture zone; fertilization was most beneficial in the hydric zones (Fig. 8). The effect of treatments on growth at the Popcorn Swale site at the end of the first season was not significant (p = 0.203 for the weeding treatment, and p = 0.912 for fertilization), probably due to the low number of survivors in that site.

One year after transplanting, surviving plants continued to increase in size, producing an average longest stem 45.9 cm in length, 24.8 cm longer than the average stem produced in the first growing season. The moisture zone in which plants resided still significantly affected stem length (p = 0.002), with the smallest plants (averaging 29 cm for the longest stem) present in the xeric zones. Plants in both the mesic and hydric zones were larger (averaging 48 and 46 cm, respectively) than those in the xeric zones, although the difference between these two groups was not significant. By this time, differences in growth, as measured by stem length, were no longer affected by the fertilization and weeding treatments initiated at planting time (p = 0.466, and p = 0.939, respectively).

P. hirtus increases in size both by stem elongation and by producing ramets (rooted shoots that develop at the stem nodes, and eventually develop into independent plants as connections disintegrate). Vigorously growing plants developed large numbers of ramets; these vegetative propagules constitute the overwintering portion of the plant. Therefore, as plants mature, monitoring increases in these developing shoots is a better method of evaluating the growth and viability of this species than measuring stem length. One year after transplanting, the moisture zone in which plants were installed
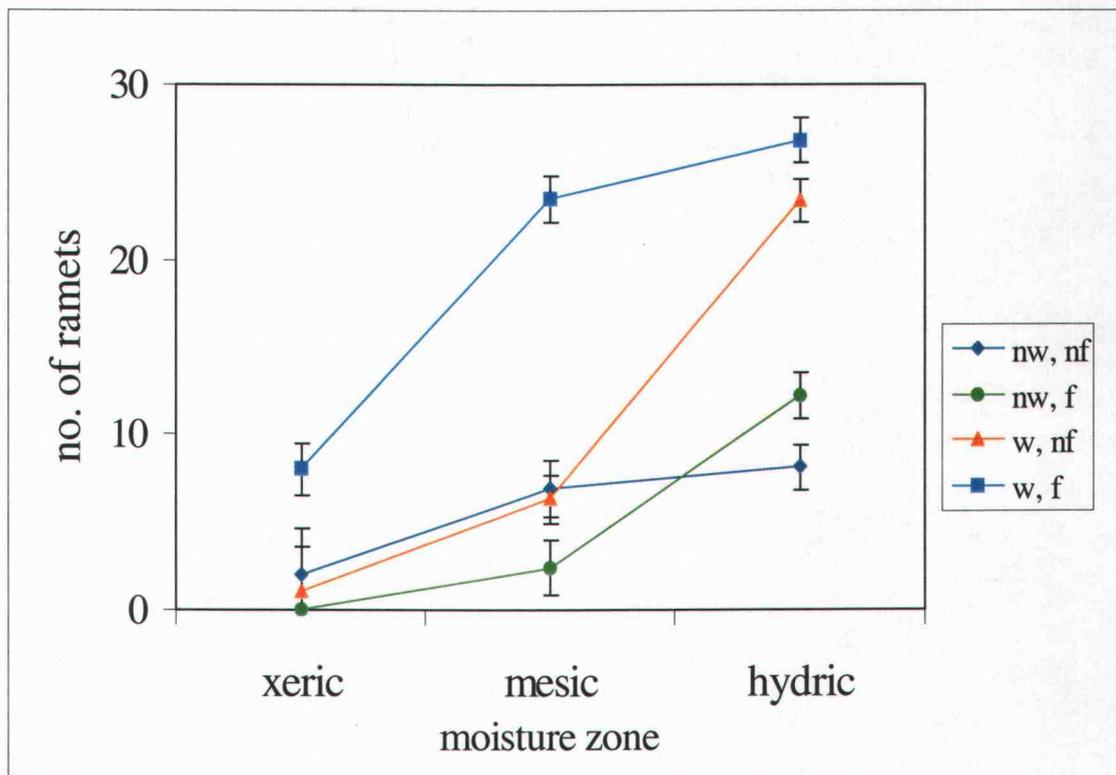
Figure 9. Effect of zone and treatments on the number of ramets produced per plant at the Yoncalla site. Plants in the mesic zones benefitted greatly from the combination of weeding and fertilization, while those in the hydric zones did well when weeded, regardless of the presence or absence of fertilizer. nw = not weeded, w = weeded, nf = not fertilized, f = fertilized. Analysis was performed on log transformed data; graphed values are back transformed. Error bars represent one standard error above and below the mean.

significantly affected this measure of success (p < 0.001) at the Yoncalla site (Fig 9). A significant interaction between the two planting treatments was also apparent (p = 0.024), and between moisture zone and the two treatments (p = 0.005). Increased soil moisture enhanced ramet production. Fertilization and weeding improved growth in the mesic zones, while weeding alone increased the number of ramets produced by plants in the hydric zones to a level similar to the weeded and fertilized plants in the mesic zones (Fig. 9).

Fecundity. By August 29, 1996, 55% of the surviving transplants at the Yoncalla site were blooming and producing filled seed. (Seeds with intact seed coats and solid interiors were considered filled.) Plants reproduced best in the hydric zones, with 79% of survivors flowering. Only 9% of survivors in the dry zone were flowering by late August, and 43% of plants in the mesic zones.

The moisture zone in which plants were installed was also a significant factor influencing the number of inflorescences produced per plant (p < 0.001), with the greatest mean number of inflorescences (4.3) produced by plants in the wettest zones. Weeding also affected the number of inflorescences produced (p = 0.016), with weeded plants averaging 2.0 inflorescences per plant, and non-weeded ones 1.1 inflorescences. Fertilization did not significantly increase the number of inflorescences (p = 0.070). At Popcorn Swale 71% of the small number of survivors (all of which were in the hydric zones) were flowering by late August, producing an average of 1.9 inflorescences.

Neither planting treatment had a significant effect on the number of inflorescences per plant at this site, probably due to the limited sample size.

One year after transplanting, all surviving plants in both sites were flowering. Plants at the Yoncalla site produced an average of 24.2 inflorescences (averaged across all zones) in this second year, 22 more per plant than were produced in the first growing season. As plants were much larger in their second year, this increased floral display is not surprising, but serves to emphasize the continuing success, both in growth and fecundity, of the transplanted stock. The number of inflorescences produced by surviving plants continued to vary in relation to moisture zone and planting treatment at the Yoncalla site; the interaction between treatments, and between moisture zone and treatments are both significant ($p = 0.042$ for the interaction of weeding and fertilization, and $p = 0.042$ for the three way interaction of both treatments and moisture zone) (Fig.10). Although the effect of fertilization on inflorescence production was not apparent in the first flowering season after transplanting (see above), the larger number of plants in flower available to analyze in the second flowering season (99 as opposed to the 80 plants flowering in the first year), as well as the larger number of inflorescences per plant, may have increased the ability of our analysis to detect the influence of fertilizer at this time.

Seeds per flower averaged 2.8 (±0.85) in the Yoncalla site in the second flowering season, representing a seed/ovule ratio of 0.70. By combining this value with the large number of flowers per inflorescence produced by *P. hirtus* at this site (mean = 19.8 ±8.8),
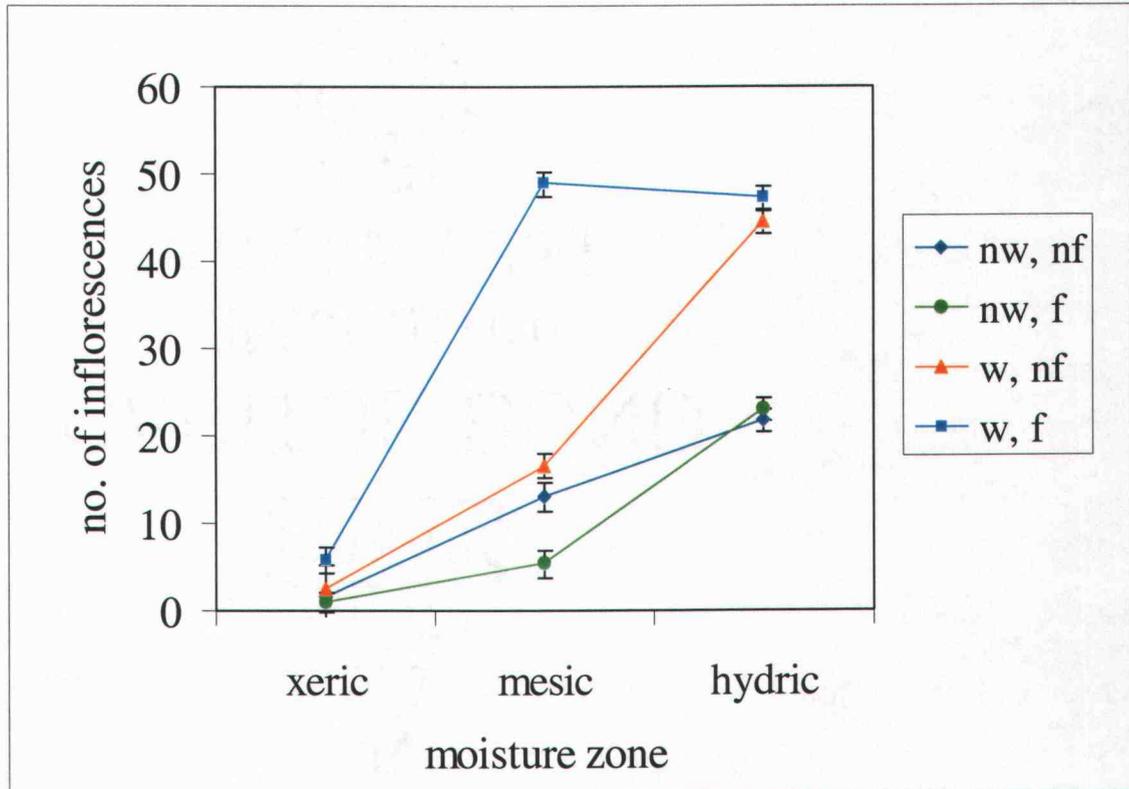
Figure 10. Effect of zone and treatment on the number of inflorescences produced per plant at the Yoncalla site. The number of inflorescences produced per plant in the mesic zones was much greater for plants which received both treatments. Weeded plants in the hydric zones produced similar numbers of inflorescences, regardless of presence or absence of fertilizer. nw = not weeded, w = weeded, nf = not fertilized, f = fertilized. Analysis was performed on log transformed data; graphed values are back transformed. Error bars represent one standard error above and below the mean.

and the large number of inflorescences produced by vigorous plants (see above), we estimated that 1342 seeds were produced by the "average" individual plant. While rough, this estimate clearly indicates that transplants were experiencing successful sexual reproduction one year after transplanting, and releasing abundant amounts of seed into the transplant area. The number of seeds produced per flower was not significantly affected by any of the factors evaluated in our study ($p > 0.05$ for moisture zone and both planting treatments). Seed/ovule ratios vary greatly among native *P. hirtus* populations (see Chapter 3), and are probably determined by multiple interacting genetic and environmental parameters not within the scope of the current study.

Recruitment. Although recruitment of new seedlings is one important criterion by which to measure the success of a created population (Pavlik 1996), this was not evaluated in our study. Offshoots from submerged overwintering stems are difficult, if not impossible, to differentiate from seedlings, making this parameter impractical to evaluate accurately. Plants that appeared to be seedlings were often observed within the plots, as many transplants set copious amounts of seed, and seeds of *P. hirtus* germinate readily under appropriate conditions (see Chapter 3).

Soil wells. As expected, soil moisture, as measured quantitatively with soil wells, has a significant effect ($p < 0.001$) on transplant survival (Fig. 7). Chronological data from soil wells (Figs. 11 and 12) also illustrate the differences in water table depth among the moisture zones, with the hydric zones in both the Yoncalla and Popcorn Swale sites
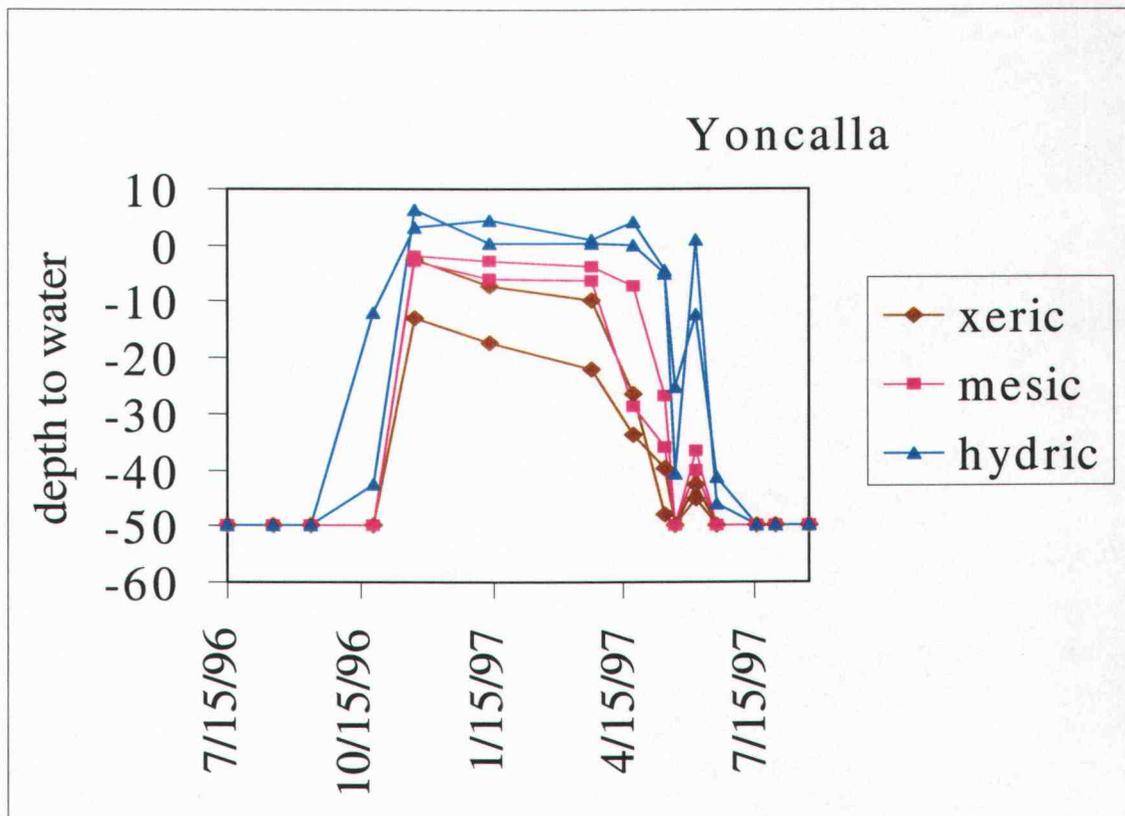
Figure 11. Soil moisture at the Yoncalla site. Negative values represent the depth below ground that water was reached, and positive values represent above-ground standing water at each sampling date.
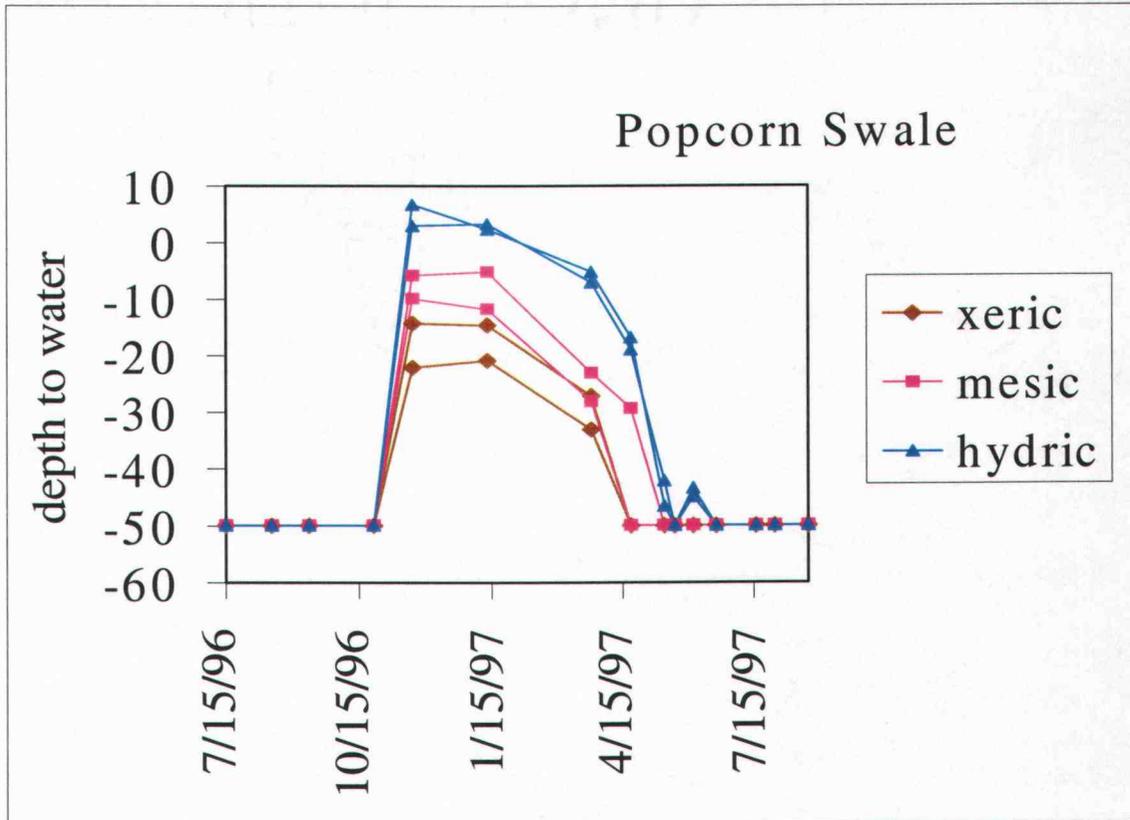
Figure 12. Soil moisture at the Popcorn Swale site. Negative values represent the depth below ground that water was reached, and positive values represent above-ground standing water at each sampling date.

retaining more water, for a longer period of time, than the other two zones. Zones designated as "hydric" were also the only areas to have above-ground standing water at any time during our monitoring period. Soil well data also demonstrate the difference in temporal changes in soil moisture between the Yoncalla and Popcorn Swale sites. Soils at the Yoncalla site responded to a greater degree to precipitation events than those at Popcorn Swale, and retained more water over a longer time period.

Site Characterization. Vegetation characterization provides a good method for identifying sites likely to support *Plagiobothrys hirtus*. The wetland community composition score for each zone, as calculated using relative percent cover estimates and wetland indicator values, correlates well with transplant success ($p < 0.001$, $R^2 = 0.85$). Sites supporting progressively more wetland species are increasingly successful as transplant sites (Fig 13).

However, because individuals of a mint found within these sites keyed alternately to *Mentha arvense*, a native species (wetland index = 1), and *Mentha pulegium*, an introduced exotic (wetland index = 2) (Hitchcock and Cronquist 1973; Hickman 1992), each data set was analyzed twice, once including the unknown mint as the native *M. arvense*, and once as the exotic *M. pulegium*. Variation in leaf and other characters of *Mentha arvense* has been documented in the North American populations, and hybridization of native *Mentha arvense* with native and introduced congeners is common in Europe (Gill et al. 1973). This portion of the analyses of the data set including *Mentha*
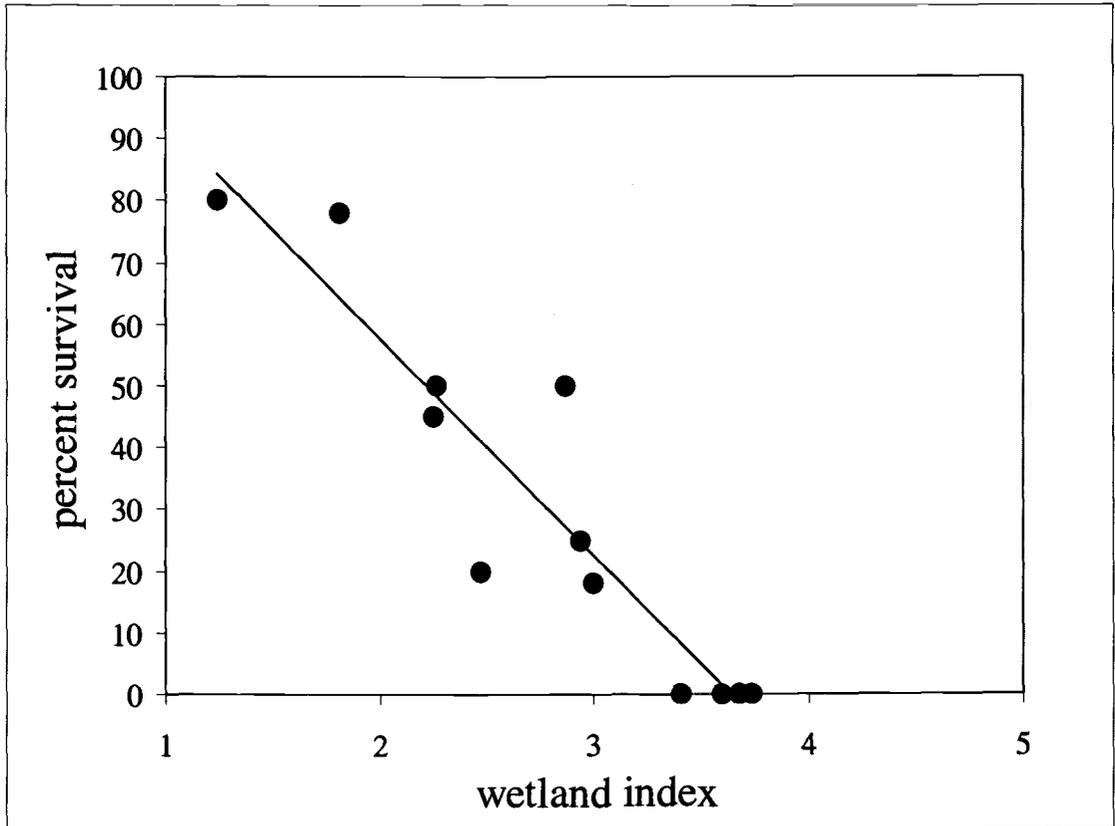
Figure 13. Percent survival of transplants increased in plots that contained more wetland species. A plot with 100% obligate wetland vegetation would have a value of 1.0; one with only obligate upland plants would have a value of 5.0 - see text for further discussion of method used to calculate wetland indexes. Plots with indexes above 3.0 did not support *P. hirtus*. (R^2 = 0.85; y = -34.98x + 127.68; p = 0.001)

pulegium provides similar statistics to the one containing *M. arvense* ($p < 0.001$, $R^2 = 0.82$); community composition is a valid indicator of transplant success, regardless of the ambiguous nature of the identity of these two mints. Transplants of *Plagiobothrys hirtus* did not survive through the first summer in zones with community composition scores greater than 3.00.

The inability to consistently identify the two species of mints in our sites made evaluation of the correlation between the transplant success and the degree of "nativeness" of each site problematic. As described above, analyses on both data sets were completed. Analysis of the data set containing *M. arvense* indicates that transplant success is greater in sites with more native vegetation ($p = 0.03$, $R^2 = 0.36$). However, this correlation is suggestive, but no longer significant, when *M. pulegium* is substituted for *M. arvense* ($p = 0.070$, $R^2 = 0.24$).

Discussion

Destruction of wetland habitat encompassing the habitat of *P. hirtus* is accelerating. Historically drained and filled for agricultural use, the few remaining wetlands in the Sutherlin area are currently imperiled by the more onerous threat of urban development. Five of the twelve known historic locations for *Plagiobothrys hirtus* no longer support the plant; three sites have been filled and converted to housing developments since the inception of our work in the area (1996). The most significant extant population of *P. hirtus* is in a large vacant lot in Sutherlin. This site has recently been drained and

surveyed in preparation for imminent development (August 2000). The destruction of these privately owned sites further increases the importance of conserving the few remaining publically owned and administratively protected populations. To prevent the extinction of *P. hirtus*, the handful of protected sites must be managed with great care, as destruction of these populations would have a dire impact on the viability of the species.

However, recovery of *Plagiobothrys hirtus* will require not only careful management of the remaining extant populations, but the augmentation of existing sites, and perhaps most importantly, the creation of a series of new, large populations in protected sites. Our experiences with identifying appropriate sites, and propagating, cultivating, and installing transplants provide important data to be used in the creation of these future populations. Protocols for these reintroduction tasks were developed with ease of use as a priority; land managers faced with mandates to manage for rare species require practical, applicable recommendations for conserving existing populations and creating new ones (Gordon 1994).

The continuing survival of transplants at the Yoncalla site, and especially their subsequent growth and reproduction, indicate that our population augmentation project was, at least initially, a success. Increasing the size of the population of *Plagiobothrys hirtus* at this site will decrease its susceptibility to the potentially negative effects of genetic drift and inbreeding depression (Barrett and Kohn 1991), as well reducing the likelihood of destruction by demographic stochasticity (Huenneke 1991; Menges 1991),

or by random catastrophic events (Lesica and Allendorf 1995). Although relatively few plants persisted at the Popcorn Swale site, several transplants installed within the hydric zones did survive (and were still evident as of July 1999), providing a slight increase in the size of this population, and possibly improving its viability.

In addition to increasing the size of existing populations, our research successfully developed protocols for identifying suitable transplant sites, and producing and planting transplants. In our study, proper site selection was an important factor affecting augmentation success. The Yoncalla site appears to be more favorable, overall, than Popcorn Swale Preserve, and within both sites, selection of areas with sufficient soil moisture is critical to transplant success, corroborating other studies that document the importance of both microsite and macrosite selection when planning rare plants reintroduction projects (Fiedler and Laven 1996).

Although selection of administratively protected sites on public land or designated preserves is critical to long-term project success, assurance that these protected sites are ecologically suited for the target species is also essential (Falk and Olwell 1992; Fiedler and Laven 1996). After evaluating vegetation community composition with a one-time measurement of percent cover, our model for identifying appropriate sites can be easily used to select potentially successful sites. As *P. hirtus* is a wetland plant, our discovery that this species does not survive in sites with wetland index scores > 3.00, and that success is greatest in areas with scores < 2.00 is not surprising; sites with scores below

2.00 can be legally delineated as wetlands based on vegetation alone, and sites with scores between 2.00 and 3.00 can be designated with additional hydrologic data (Wentworth et al. 1988; Committee on characterization of wetlands 1995). Sites with scores above 3.00 are not considered wetlands. Soil moisture data from soil wells also provides an accurate way to identify sites likely to support *P. hirtus*, but the requirement for long-term monitoring, rather than a single evaluation, probably makes this method less attractive to land managers than use of the vegetation model.

Our development of successful propagation, cultivation, and transplanting techniques also makes an important contribution to future reintroduction projects. The ability to produce vigorous stock for transplanting is a critical first step in a successful project of this type. The production of plants in the greenhouse from shoot cuttings worked well for us, and allowed for the creation of large numbers of similarly sized transplants in a timely manner. Greenhouse cultivation of plants to transplant size was also successful. *P. hirtus'* requirements for high soil moisture and scrupulous pest inspections while in the greenhouse, can be easily incorporated into most cultivation systems.

Removal of competing vegetation at the time of transplanting was helpful in promoting transplant survival, growth, and fecundity. Removal of competing vegetation before transplanting increased the fecundity of another rare forb, *Amsinckia grandifora*, with the production of inflorescences inversely correlated with the cover of competitive grasses, and the greatest reduction in fecundity evident in plots inhabited by exotic annual grasses

(Carlsen et al. 2000). Establishment of forbs, including the endangered *Rutidosis leptorrhynchoides* in Australia, has been shown to be more successful with the removal of existing vegetation at the time of planting (Morgan 1997), probably due to decreased interspecific competition and the increased availability of light, water, and nutrients (Silvertown and Lovett Doust 1993; Morgan 1997). Minimum effective gap size varies - removing vegetation in areas smaller than 100 cm^2 in some habitats (Morgan 1997), and 30 cm^2 in others (Davies et al.1999), may be ineffective in promoting transplant growth. The 50 cm^2 gaps used in our study were large enough to increase establishment and fecundity in our system, indicating that one-time vegetation removal at the time of transplanting is worthy of inclusion in reintroduction protocols for *Plagiobothrys hirtus*.

The increased growth and fecundity of weeded transplants, as long as one year after transplanting, also indicate that routine vegetation removal from existing sites may encourage persistence and recruitment of *P. hirtus*. Other studies have shown that the removal of competing vegetation from native populations of the California prairie annual *Amsinckia grandifora* (using herbicides) resulted in greater fecundity and an increase in the size of these populations (Pavlik et al. 1993). Intentional seasonal burning of the Willamette Valley by Native American tribes, and the role of these fires in maintaining existing open grasslands has been well documented (Johannessen et al. 1971), and burning has been shown to increase the growth and fecundity of rare native prairie plants in the Willamette Valley (Pendergrass et al. 1999). As the nearby Umpqua Valley probably also burned routinely, either naturally or from intentionally initiated fires, it is

likely that *Plagiobothrys hirtus* flourished in areas where frequent fires routinely removed much of the above ground herbaceous biomass. Management plans for existing native populations, as well as those that have been reintroduced, should include some form of vegetation control. As *P. hirtus* is perennial, and blooms throughout the summer with adequate moisture, care must be taken to avoid damaging plants and preventing seed set while concurrently promoting the removal of competing vegetation.

Fertilization of transplants also increased growth and fecundity, and was a particularly important addition to transplant success in mesic zones. In these zones, weeding alone did not improve ramet production, but did increase growth when combined with fertilization. The increase in nutrients provided by liquid fertilizer may have allowed transplants to grow quickly and take advantage of the openings created by the removal of competing vegetation in these marginal sites. As fertilization also increased stem length of transplants in mesic and hydric zones in the first year, as well as increasing the number of inflorescences produced, and the inclusion of fertilization in cultivation procedures is not difficult or costly, this treatment should be included whenever possible, especially when less-than-optimal sites must be utilized for transplanting.

Data collected during our augmentation projects at the Yoncalla and Popcorn Swale sites have already been used to facilitate the creation of two new populations of *Plagiobothrys hirtus* on the Bureau of Land Management North Bank Habitat Management Area (1998-1999), and have contributed to a reintroduction of the species in historical habitat as part

Figure 14. Monitoring of created population of *Plagiobothrys hirtus* at the North Bank Habitat Management Area. This population is quite successful, two years after installation, and now consists of thousands of plants.

of a large scale wetland restoration project currently in progress as a mitigation project by

Land and Water Environmental Services, Inc. (Janet Barnes, pers com). We hope that the

information gained through our experiences can contribute to the successful creation of

new populations, and that, through the continued interactive efforts of concerned parties,

P. hirtus can be reintroduced in protected sites throughout its range, eventually

recovering to the point that it will no longer be threatened with extinction (Fig. 14).

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Chapter 3

Life History Comparison of the Rare Plant, *Plagiobothrys hirtus*, and its Common Congener, *P. figuratus*

Abstract

Comparisons of reproductive and life history attributes can help explain differences in distribution and abundance of rare and common plant species. Our research on the life history of a federally endangered, narrowly endemic taxon (*Plagiobothrys hirtus*), as compared with that of a more geographically widespread congener (*P. figuratus*), revealed that *P. hirtus* is facultatively perennial, rather than annual, as was previously reported. However, few other differences were found in seed set, seed germination, or pollination ecology between the two species.

Introduction

What makes a particular species rare? Do distinctive attributes characterize uncommon taxa? Can the causes of rarity be identified? Studies that attempt to answer these questions have utilized a variety of methodologies, and have produced a wide range of explanatory hypotheses. Willis' historic theory proposing time and area as the controlling factors producing new species (Willis 1922), although quickly discounted, was an early attempt to explain the phenomenon of rarity. In a refinement of this philosophy, species can be categorized as neo-endemics i.e., rare because they have recently evolved and have not yet moved into the entire area they will ultimately occupy, or paleo-endemic, a condition which, due to geologic removal of hospitable habitat, currently occupy the final

vestiges of a once larger distribution (Stebbins 1942; Stebbins and Major 1965). Wright (1931, 1941) examined the importance of population size to genetic structure and diversity, and initiated the idea of rare species as genetically depauperate.

Later integration of many of these theories produced multi-factored models of increasing complexity, such as the "synthetic viewpoint" of Stebbins (1980), which attempted to incorporate the effects of genetics, history, and "niche breadth" to predict the incidence of rare taxa. Harper (1979), after a review of five regional floras, generalized that rare plants are likely to be zoophilous, zygomorphic, non-woody perennials, although the inability to predict the distribution of rare taxa outside of a few regions reduces the value of this model. Rabinowitz (1981) and Kruckeberg and Rabinowitz (1985), in a now widely adopted system, recognized seven forms of rarity based on local abundance, geographic distribution, and habitat specificity. In this classification, the rarest species are those that exhibit low abundance, restricted geographic distribution, and narrow habitat specificity, while other combinations of attributes constitute varying types and degrees of rarity.

Rather than searching for generalities to explain the existence of rare taxa (Griggs 1940; Mason 1946; Drury 1980), some researchers have approached the study of biotic scarcity by focusing on the biology and ecology of individual rare species. Specific rare taxa are sometimes associated with an uncommon type of habitat (Griggs and Jain 1983; Bartgis1985; Campbell et al. 1988; Lesica 1992), or affiliated with specific edaphic conditions (Kruckeberg and Rabinowitz 1985; Fiedler 1987). Some rare plants have low

seed set (Menges et al. 1986), are pollinator limited (Karron, 1987; Menges 1995), exhibit

poor competitive abilities (Clampitt 1987), or are subject to greater predation than their

common relatives (Menges et al.1986; Fiedler 1987; Gisler and Meinke 1997). Other

taxa appear to be rare due to a host of factors (Watson et al. 1994; Baskin et al. 1997),

with no single trait appearing to limit species distribution.

The distinction between naturally occurring endemism and anthropogenic rarity is of

particular interest to researchers concerned with the conservation of rare species.

Although restricted in range, presumably stable taxa with entire distributions confined to

designated Wilderness or other legally protected areas (such as *Kalmiopsis leachiana*, in

the Kalmiopsis Wilderness or *Lomatium greenmanii* restricted to a single mountaintop in

the Wallowa Mountains), are not in dire need of active management to prevent extinction.

Although their genetic diversity may be less than that of more widely distributed plants,

these species often have developed adaptations (such as the purging of deleterious

recessive alleles, and the development of self-compatibility) which prevent them from

suffering from some of the disadvantages of small population size (Schemske and Lande

1985). Assuming that their habitat remains uncompromised by human activity, these

species should be able to persist without intervention. Unfortunately, many species

thatare currently considered rare, such as Willamette Valley prairie denizens *Sidalcea*

nelsoniana and *Delphinium pavonaceum*, were once relatively abundant (Gisler and

Meinke 1997). The current decline of plants such as these is due to habitat degradation,

destruction, and fragmentation, as well as interruption of successionary progressions, lack

of pollinators, competition and hybridization with introduced weeds, and a host of other recognized, as well as yet unidentified, factors (Kaye et al. 1997).

Preservation of remaining intact habitat, as well as attempting to maintain as much as possible of naturally occurring systems within current usage patterns, will be necessary to prevent the downhill slide to extinction currently being experienced by these once common species. Natural endemics occurring outside of protected areas (such as *Plagiobothrys hirtus* or *Astragalus applegatei* of Klamath County) are at the greatest risk of all. The few small populations of such species, often within close proximity to each other, are unable to withstand the many systematic and stochastic forces assailing them. Due to the decreased genetic diversity associated with bottlenecks and depleted population sizes (Barrett and Kohn 1991; Holsinger and Gottlieb 1991), species which were once comparatively plentiful, but have suffered severe reduction in population size or number due to recent habitat loss, are at greater risk of extinction than naturally occurring endemics (Karron 1991)- especially if the endemics occupy protected habitat. Small isolated populations in legislatively unprotected areas are also likely to be extinguished by single chance events such as accidental spraying, improper or unauthorized collection, and other poorly timed or inappropriate land use activities (Huenneke 1991). Without informed intervention by land managers, the remaining populations of these imperiled species will soon disappear. An understanding of the factors that control rarity, and the integration of this knowledge into land management policy, is essential to the continued viability and recovery of rare species. In fact, the

failure of recovery efforts can be attributed largely to "the inability to isolate and assess the most important factors that contribute to the rarity in any one taxon" (Pantone et al. 1995).

One method that has been successfully utilized in identifying the biological and ecological aspects of rarity is the comparison of one or more rare taxa to a closely related common species (Primack 1980; Lack 1982; Mehrhoff 1983; Ritland and Jain 1984; Fiedler 1986, 1987; Karron 1987, 1989; Rapson and Maze 1994; Pantone et al. 1995; Baskin et al. 1997). By examining life history (Ritland and Jain 1984; Fiedler 1987), differences in breeding system and pollination ecology (Lack 1982; Mehrhoff 1983; Karron 1987, 1989), and a suite of reproductive attributes (Pantone et al. 1995), these workers were able to identify meaningful ways in which rare species differed from their more common relatives. Fiedler's (1987) comparison of rare and common *Calachortus* species emphasized the contribution of variation in life history traits to differing interspecifc levels of rarity. Seed set, bulbil production, and seedling survival rates differed between rare and common species of this genus; rare species may be inclined to more sporadic successful reproduction than their common relatives. In *Limnanthes*, life history traits such as length of time required for seed germination, time to flowering, and seedling survival rates were shown to differ between rare and common species, although not always in the expected ways (Ritland and Jain 1984). Pollinator specificity may also influence successful reproduction of common as compared to rare species, with rare plants receiving fewer pollinator visits, from fewer species of pollinators, than their

common congeners (Karron 1987). Breeding systems have also been evaluated in relation to rarity (Mehrhoff 1983); although differences between a rare and common species were documented, they did not appear to be the source of the limited distribution of the uncommon species. Although rare plants have been considered intrinsically "less fit" (as compared using an interactive suite of fitness components), than their common weedy relatives (Pantone et al. 1995), a comparison of three pairs of widespread and common species found no shared causes for the rarity of the rare species (Baskin et al. 1997). Rarity was presumably the result of a complex, interacting set of biological, edaphic, and evolutionary components. In these studies, the ultimate cause of rarity was not always identified, but comparisons of this type help to identify potentially critical factors to be addressed by land managers as they attempt to promote the recovery of these rare taxa.

Plagiobothrys hirtus (Greene) Johnst. (Boraginaceae), a federally and state listed endangered plant (ONHP 1998; USFWS 2000), with only a few small populations confined to the Umpqua Valley of southern Oregon, and its relatively widespread congener *Plagiobothrys figuratus* (Piper) Johnst. (Boraginaceae), found throughout western Oregon (Hitchcock and Cronquist 1973), are an appropriate pair for this type of rare versus common comparison. Morphologically comparable, with similar habitat preferences (and sometimes sympatric), these two species are superficially analogous. The two species are believed to be closely related, and were at one time considered to be conspecific (Chambers 1989). An investigation of the life history, breeding system, and

pollination ecology of these taxa provides an opportunity to identify specific factors which may be causing the rarity of *P. hirtus*.

Plagiobothrys hirtus and *P. figuratus,* both members of the subgenus *Allocarya* (Abrams 1951; Peck 1961; Hitchcock and Cronquist 1973; Hickman 1993), are quite similar in appearance. Both are spreading or ascending branched herbs, with bright green linear leaves and forget-me-not flowers in helicoid racemes. *P. hirtus* is the larger of the two, growing to 70 cm. tall (*P. figuratus* generally reaches only 15-45 cm), with stouter stems (4-5 mm wide as compared to approximately 2 mm in *P. figuratus*), and often larger flowers. However, although the corolla of *P. hirtus* may often exceed 1 cm in width, while that of *P. figuratus* is usually smaller at 5-10mm(Peck 1961; Hitchcock and Cronquist 1973), flower size is quite variable for both species. Flower size classes in these two species may overlap; flower size is not a reliable taxonomic character. Although the flowers may differ in size they are similar in form; both species have aromatic five petaled white flowers with yellow fornices. Each flower can produce four tan-colored to black nutlets; due to fruit abortion or lack of pollinators, calyces often contain fewer than four nutlets. These nutlets, the basis for taxonomic differentiation within *Plagiobothrys*, are remarkably similar in the two species, although the attachment scar is generally basal in *P. hirtus* (Fig. 15), and lateral in *P. figuratus*. In the field, the two taxa are readily discernable by the distinctly spreading (rather than appressed) pubescence, larger size, and facultatively perennial nature of *P. hirtus*, which easily distinguish it from *P. figuratus*, as well as other members of the genus (*P. scouleri, P.*

nothofulvus) that may be present in our area. As well as being similar in appearance, both species inhabit similar seasonally wet pools in open, generally unshaded grasslands of the Willamette and Umpqua valleys. Both occur in largely monospecific patches; associated species, when present, are members of equivalent wetland communities.

Method

Site descriptions. The *Plagiobothrys hirtus* populations used in this study occupy three sites in the Umpqua Valley in Douglas County, Oregon (Fig. 16). The lower Umpqua valley, where all three sites occur (data from Roseburg), receives a mean of 83 cm of annual precipitation (Franklin and Dyrness 1973). Most precipitation occurs from August through May, with an average of only 47 mm falling during the summer months. The January mean annual temperature for this area is 5.2°C, and the July mean temperature is 19.9°C. This area is classified as "Oregon" climate, according to the Koeppen climate classification system (Visher 1954). Two of the three sites occur on Conser silty clay loam soils, a poorly drained soil found in depressions on low alluvial stream terraces, and one on Bashaw clay, another poorly drained soil (Natural Resources Conservation Service 1997).

Plagiobothrys hirtus generally occurs in unshaded seasonally wet pools; associated species include *Beckmannia syzigachne, Brodiaea hyacinthina, Camassia leichtlinii, Carex densa, Carex feta, Centaurium umbellatum, Danthonia californica, Deschampsia caespitosa, Dipsacus sylvestris, Downingia elegans, Epilobium watsonii, Glyceria*

Figure 15. Nutlets of *Plagiobothrys hirtus*. Each flower can produce four nutlets, although due to fruit abortion, less than four are often produced. Mature nutlets are brown or black.
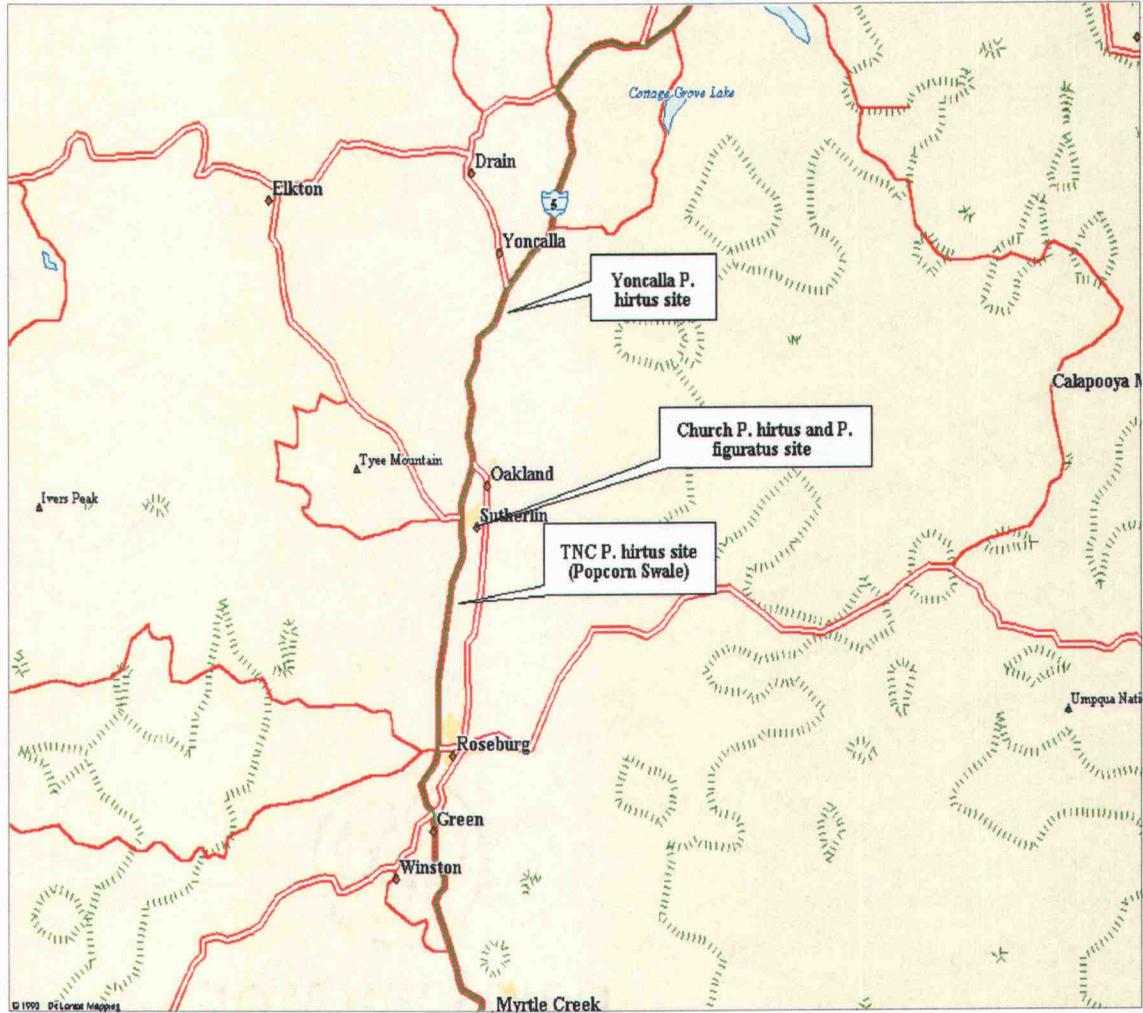
Figure 16. Location of study sites in Douglas County, Oregon. Populations of *P. hirtus* and *P. figuratus* are sympatric at the Church site. See page 70 for description of study populations.

occidentalis, Juncus effusus, Juncus oxymeris, Juncus patens, Limnanthes douglasii, Lythrum hyssopifolia, Mentha arvense/puligeum, Parentucellia viscosa, Sidalcea cusickii, Typha latifolia and *Veronica scutellata* (see appendix A for a complete list).

The Yoncalla study site (under the Yoncalla exit sign), is in the highway right-of-way owned by Oregon Department of Transportation (ODOT) two miles north of Rice Valley (T23S/R5W/S15). This site, immediately adjacent to Interstate 5, is maintained by ODOT as a Special Management Unit and is protected from potentially damaging management activities. *Plagiobothrys hirtus* flourishes in the unshaded, low-lying area parallel to the highway, and has been observed at this location since 1961 (Siddall et al. 1978).

The Church site is a privately owned lot, between a church and a trailer park on Dawn St. within the city limits of Sutherlin (T25S/R5W/S19). It is mown occasionally, and is heavily infested with exotic weeds such as *Chrysanthemum leucanthemum, Dipsacus sylvestris, Festuca arundinacea* and *Centaurea* sp. (knapweed). As *P. hirtus* occurs in small swales that have, to some extent, withstood the invasion of exotics within the site, it is more closely associated with scatterings of *Beckmannia syzigachne, Downingia elegans*, and other native wetland species. *Plagiobothrys figuratus* also occurs at this site, generally in patches a few meters away from *P. hirtus*. However, the two species also co-occur in mixed patches along a ditch that bisects the site. This site has recently

been drained and surveyed; development, with subsequent loss of this once-thriving

population of *P. hirtus,* appears imminent.

The TNC site (the William Oerding Popcorn Swale Preserve), is owned by The Nature

Conservancy (TNC), and managed as a preserve for *P. hirtus.* This site is two miles north

of Wilbur between the Interstate 5 and County Road 338 (T26S/R5W/S6). Plants

here occur in slightly shaded situations, and in full sun, and are often associated with

Limnanthes douglasii, Beckmannia syzigachne, and *Mentha puligeum.* This site is not as

disturbed as the previously described two, although, like the Yoncalla site, it is adjacent

to Interstate 5.

Populations of *P. figuratus* at E.E. Wilson National Wildlife Refuge and Finley National

Wildlife Refuge, in Benton County, were also used for seed collection and pollinator

observations (Fig.17). At E.E. Wilson, *P. figuratus* is found scattered throughout

undisturbed seasonal wetlands, while at Finley this species is found in very large, dense

monospecific patches within occasionally cultivated fields. As mentioned above, the

Church site, in Douglas County, supports populations of both species.

Life history comparison. Although considered to be an annual by taxonomic authorities

(Abrams 1951; Peck 1961), our initial observations in the field and greenhouse indicated

that *P. hirtus* could exhibit a perennial life history under optimal conditions, while *P.*

figuratus always behaved as an annual. Collected plants of *P. hirtus* kept in large pots in
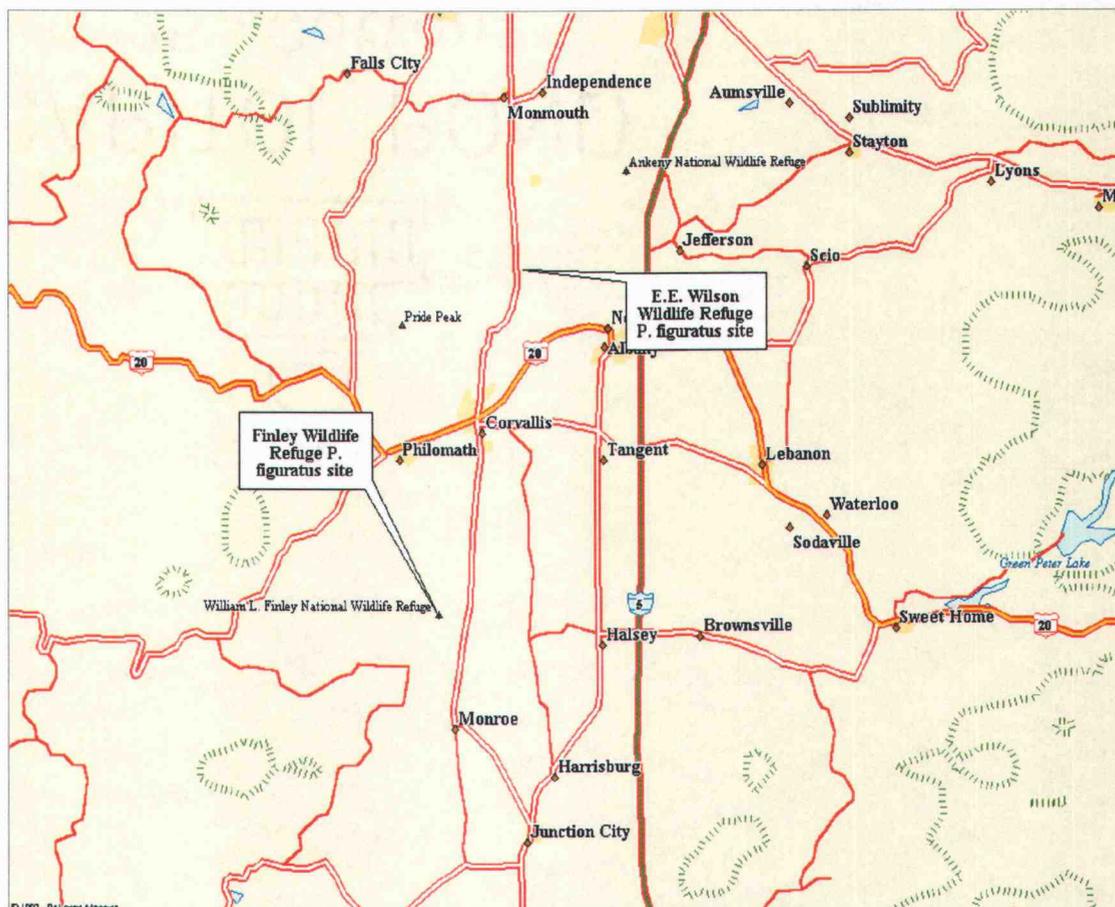
Figure 17. Sites of populations of *Plagiobothrys figuratus* used in current study. Both sites are in Benton County, Oregon, approximately 150 km north of *P. hirtus* study sites .

the greenhouse lived for three years or more, and tagged plants in the field were observed to overwinter. In order to quantitatively confirm the life history differences we initially observed, seeds from native populations of both taxa were grown in the greenhouse under ambient conditions (daily watering, no additional lighting and, standard heating and cooling).

Forty viable seeds of both taxa from collections made in 1996 at the sites described above (E.E. Wilson for *P. figuratus* and Church for *P. hirtus*), were planted in the greenhouse in seedling flats. Seeds were sown on the surface of a peat/pumice based standard potting mix available from the Oregon State University greenhouses, then covered with a thin layer of sieved soil from the same source. As *Plagiobothrys hirtus* seeds require considerable moisture to germinate well, seeds were thoroughly watered as they were planted, and kept moist until germination occurred. Seedlings were transplanted into four-inch plastic nursery pots when the first true leaves appeared; pots were kept in water-filled trays throughout the experiment in order to simulate optimal field conditions. Soluble granular fertilizer in liquid form (Peters © 20-20-20) was added uniformly to all plants twice per month. Plants were observed periodically from the time of germination until senescence (death) of all *P. figuratus* plants (February through August of 1997). Plants were considered to be flowering when at least one open corolla was evident, and were considered senescent (dead) when no green foliage could be observed.

Seed germination. Seed germination percentages differ between related species of plants, and could vary between rare and common species (Baskin et. al 1997). To evaluate potential differences in seed germination between the two species, possibly influencing relative recruitment rates and therefore distribution of *P. hirtus* and *P. figuratus*, the proportions of seeds germinating under controlled conditions were compared. As inbreeding depression can be exhibited at the seed germination stage (Schoen 1982; Widen 1993), and could influence relative distributional patterns of the two species, both manually selfed and open-pollinated seeds of each species were included in the germination tests to determine if inbreeding depression was present. Seeds were bleached briefly with a 5% bleach solution, then rinsed under running water, to prevent contamination by fungus (a common problem with seeds of some genera), and placed on bleached filter paper in petri dishes. Seeds were watered with distilled water at the initiation of the study, and kept wet throughout its duration. Twenty dishes of ten seeds of each type (*P. hirtus* open-pollinated, *P. hirtus* selfed, *P. figuratus* open-pollinated, *P. figuratus* selfed) were monitored for three weeks, with seeds counted as "germinated" when radicals could be observed (approximately 1 mm long). Seeds were germinated under ambient conditions in the lab (without additional light, at approximately 21° C).

Two germination tests were performed, the first with open-pollinated seed collected in the field from the Yoncalla site for *P. hirtus*, and from Finley Wildlife Refuge for *P. figuratus*. Selfed seed was collected from manually selfed plants growing in the

greenhouse. Flowers were selfed by squeezing the corolla tube, allowing the anthers (fused to the corolla in this genus) to contact the stigma. This procedure was developed to facilitate the selfing process, as the flower morphology of this genus makes traditional selfing methods extremely tedious. Seed set for this contact technique was not significantly different ($p = 0.95$ from a t-test) than that produced by the labor intensive manual transfer of pollen from anther to stigma under a dissecting microscope.

Due to the potential confounding effect of the environment in which the seeds matured (in the greenhouse for the selfed seed, and the potentially lower resources of the field for the open-pollinated seed), a second germination test was done using only seed matured in the field. In the field, flowers of both species were selfed by the contact technique, as they opened, and then bagged in pollination bags to prevent further naturally occurring transfer of pollen. Open pollinated seed was collected from the same sites used for the selfing procedure - the Yoncalla site for *P. hirtus* and E.E. Wilson for *P. figuratus*. Although the two species are occasionally sympatric, in the year of this study (1997), low seed production at the sites with sympatric populations prevented collection of a sufficient amount of usable seed. The procedure for this second experiment was similar to that used in the initial germination test, with six dishes of twenty seeds for each treatment. As development of mold was not a problem in the initial test (probably due to the short period required for germination in these species), seed and equipment bleaching was not deemed necessary, although watering with distilled water was continued. In both studies,

an ANOVA and Duncan's multiple range test were used to look for differences in germination among the four groups.

Field seed set. Plants that set more seed increase their chances of perpetuating their own genotypes, and are therefore more fit than their less fecund competitors Silvertown and Lovett-Doust 1993). And, because annuals and short-lived perennials rarely show a negative correlation between reproductive fitness components (i.e. higher seed set doesn't correlate positively with smaller seeds, lower seed viability, etc.), measurement of relative seed set (seed/ovule ratio) is probably a suitable method for evaluating relative fitness, at least among closely related taxa (Pantone et al. 1995). Borages, including *Plagiobothrys,* can potentially produce four nutlets per flower from a four-lobed gynoecium made up of two united carpels (Smith 1977). Seed set (seed/ovule ratio) was evaluated at four field sites (Popcorn Swale, Yoncalla, Church and a common garden site in Salem, Oregon) for *P. hirtus*, and at the Church site and E.E. Wilson for *P. figuratus,* by recording the number of realized/potential nutlets produced for all measurable calyces on each inflorescence. Due to the indeterminate nature of *Plagiobothrys* inflorescences, flowers at the top of the flowering stem continue to develop and bloom, even as seeds mature and drop from the lower calyces, making a single, one-time measurement of seed/ovule ratios for all flowers in any one inflorescence impossible. However, whenever possible, 10-20 calyces in at least three inflorescences were measured on each plant. Seed set was measured at all five sites in June1997, and at the Yoncalla site in three consecutive years.

Breeding system. An evaluation of the breeding systems of rare plants provides important insights into the potential causes of their limited distribution. Outcrossing species may exhibit greater genetic variability, and therefore be more adaptable than selfers, allowing them to persist under changing conditions, and to spread more easily into new areas. However, self-compatible species have also been proposed as successful colonizers due to their ability to produce a new population from a single propagule (Baker 1955). The ability to self fertilize may also allow maintenance of adaptive gene combinations, and promote maximum seed production without the need for cross pollination (Silvertown and Lovett-Doust 1993; Pantone et al. 1995).

The breeding systems of the two *Plagiobothrys* species were evaluated by comparing the seed set (seed/ovule ratio) and germination rates of selfed and outcrossed plants of each species. Plants were selfed by manual transfer of pollen from the anthers to the stigma of the same plant, or by the contact technique described above. Outcrossing was accomplished by manual transfer, under the dissecting scope, of pollen from one plant to the stigma of another plant. Care was taken to cross plants that were believed not to be closely related (such as those grown from seed collected from distant parts of a large population). To determine if pollen transfer by insects is required for fertilization, unmanipulated plants (n = 2148 flowers for *P. hirtus* and n = 884 flowers for *P. figuratus*) presumable grown without access to pollinators (in the greenhouse) were also included in the seed set comparison.

Pollinators. Insect visitors to *Plagiobothrys hirtus* were collected at the Yoncalla and Church sites in June 1997, and from *P. figuratus* at the Church and E.E. Wilson sites at the same time (June 1997). Pollinator specimens were pinned and identified. At the time insects were collected, pollinator visitation rates for each species were also recorded. Groups of ten plants of each species were selected, and observed for twenty minute intervals, and the number of insect visitors per unit of time to each plant was recorded. Because only one site with sympatric populations is known, and the phenology of the two species often differs, it was not possible to observe pollinators on both species at the same time. However, although observations of *P. figuratus* were not completed at the same time as those of *P. hirtus,* an attempt was made to observe on chronologically adjacent days.

Results

Life history. *Plagiobothrys hirtus* will perennate under optimal conditions, while *P. figuratus* behaves as an annual (Figs.18 and 19). Of the 40 seeds sown of each species, 28 seeds of *P. hirtus* and 25 of *P. figuratus* germinated. Germination proceeded at the same rate in both species; however, once plants began to mature, *P. figuratus* began to bloom much earlier, with most plants in flower within two months (Fig 19). Initiation of flowering was slower in *P. hirtus,* with all plants beginning to bloom by four months after sowing(Fig 20). About this same time, the most profound phenological difference between the two species became evident. Although plants of both species were well watered and fertilized, those of *P. figuratus* began to senesce as they finished flowering,

while those of *P. hirtus* remained green and continued to bloom. Senescence was

eventually complete in the annual species, while the perennial *P. hirtus* showed no

mortality throughout the six month duration of the study.

Plants of the two species grown in the greenhouse showed other life history differences as

well, although these were not quantitatively measured in this study. Plants of *P. hirtus*

can root at the nodes when in contact with water or wet soil (Fig. 20), a characteristic not

observed in *P. figuratus*. The perennial species routinely produced large rosettes with

robust stems before initiating flower stalks, while the annual *P. figuratus* bolted from a

weakly developed cluster of leaves.

In addition to exhibiting perennial behavior in the greenhouse, *P. hirtus* also overwintered

in sites where it occurs naturally. Similarly to many vernal pool plants, seeds of this

species germinate in the fall with the first rains. The plants persist as submerged rosettes

until spring, and begin to flower as soils dry in summer (Griggs and Jain 1983) (Fig. 21).

If soils remain wet for a sufficiently long period, plants begin to develop adventitious

roots at the nodes and secure themselves in the wet soil in their first growing season,

producing large mats of interconnected shoots, each with the ability to produce flowers

and seed. Although many sites where *P. hirtus* grows become quite dry by August, plants

of this species, unlike those *of P. figuratus*, typically retain small green rosettes at the

stem nodes throughout the dry period (Fig. 22), and quickly re-sprout when the rains

return. Ten tagged plants, although often somewhat lost in a dense mass of
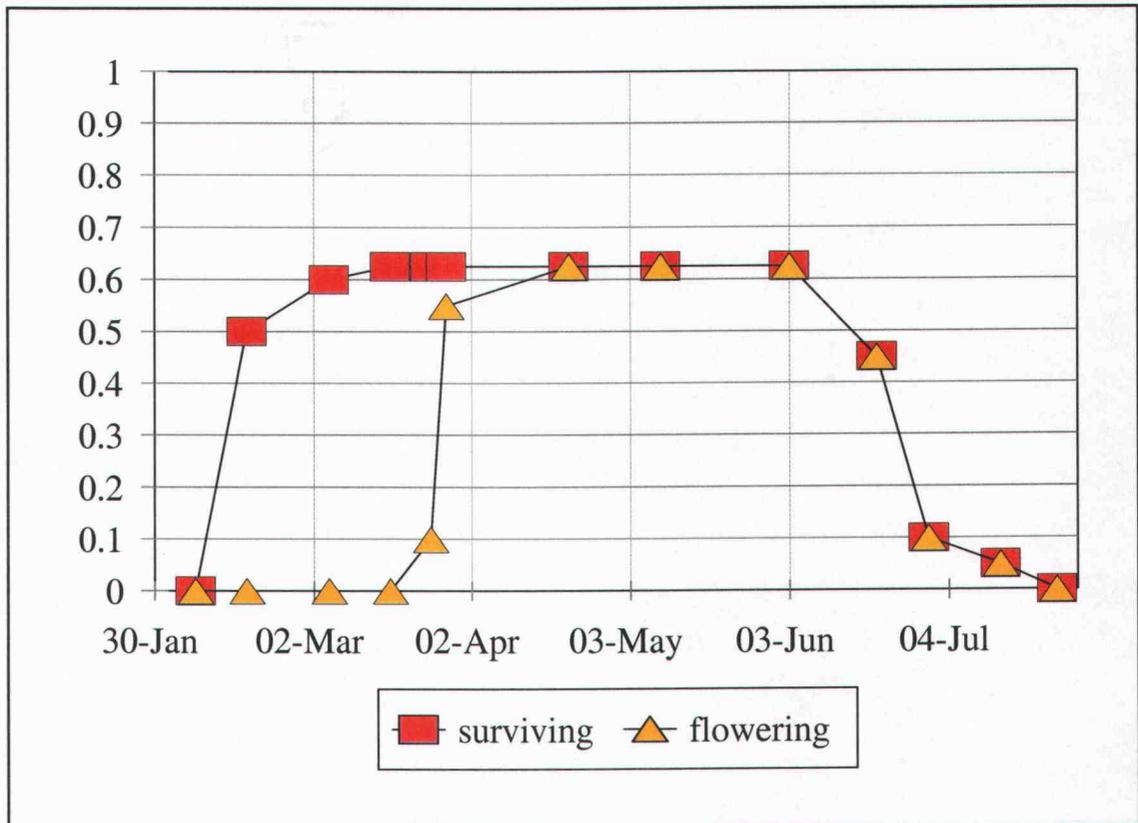
Figure 18. Proportion of *Plagiobothrys figuratus* plants germinating, surviving and flowering in the greenhouse. Plants began flowering at an earlier age than those of *P. hirtus*, (Figure 19) and began to senesce after blooming was completed.
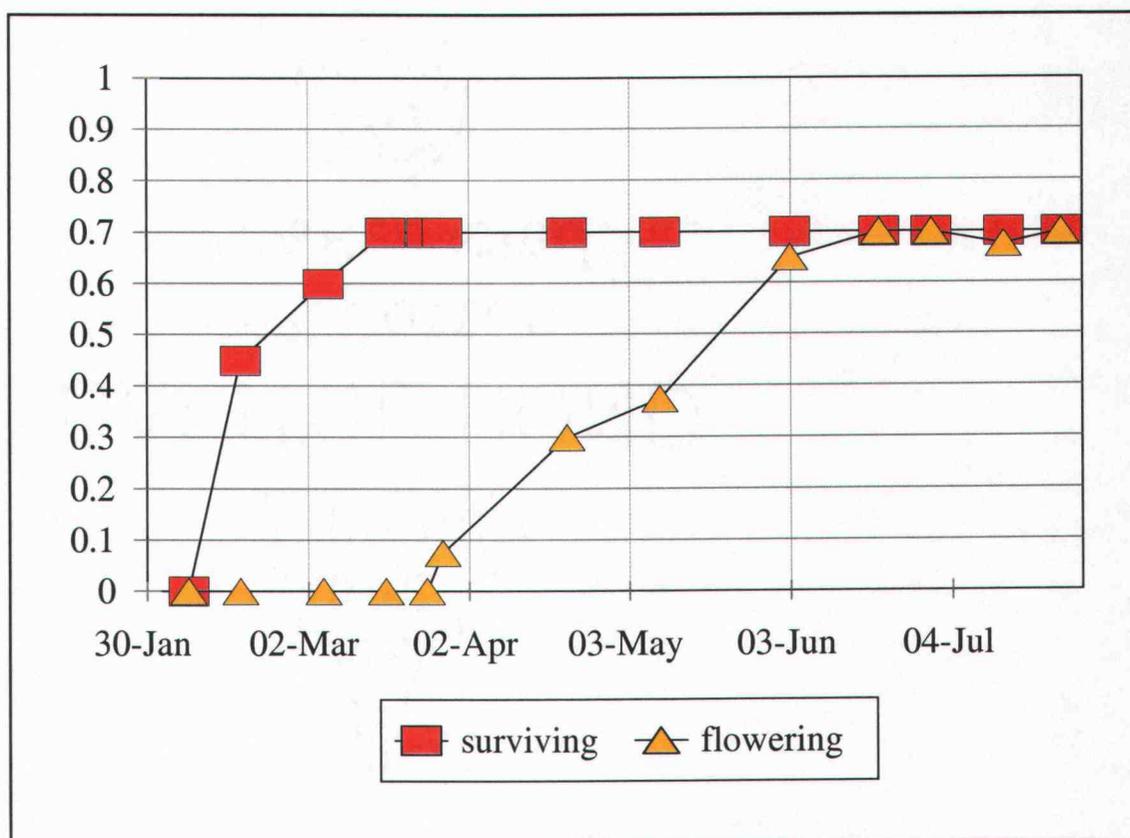
Figure 19. Proportion of *Plagiobothrys hirtus* plants germinating, surviving, and flowering in the greenhouse. Plants continued to grow and bloom throughout the length of the study, with no evidence of senescence.

Figure 20. *Plagiobothrys hirtus* plant in the field. Roots can be seen developing along the stem (which was submerged until removal for this photo). Eventually the internodes will rot away, leaving a group of independent, genetically identical ramets.

interconnected stems, were re-located for three consecutive years. Plants of *P. figuratus* did not exhibit perennating traits in any field site. This species is truly annual; tagged plants turn completely brown at the cessation of flowering and were never re-sprouted.

Seed germination. In the first germination test, seed from self-pollinated *Plagiobothrys hirtus* plants grown in the greenhouse germinated better than seed of the same species collected from open pollinated plants in the field ($p < 0.05$ from an ANOVA and multiple range test) (Fig. 23). However, in *P. figuratus*, germination was higher for field-collected open-pollinated than for selfed seeds produced in the greenhouse, ($p < 0.05$). Overall, seeds of *P. figuratus*, (both selfed and open-pollinated) showed a higher germination percentage than did *P. hirtus* (62% for *P. figuratus*, 45% for *P. hirtus*; $p < 0.05$ from a multi-factor ANOVA). However, the results of the second experiment, using field collected selfed and open-pollinated seed, differed from those of the initial study. In this second study, open-pollinated *P. hirtus* seeds germinated much better than selfed seeds from the same site ($p < 0.05$) (Fig. 24). Seeds of open-pollinated *P. figuratus* also germinated better than seed from self pollinations ($p < 0.05$). In this study, *P. hirtus* exhibited a higher overall germination percentage than *P. figuratus*, and both selfed and outcrossed seeds of *P. hirtus* germinated better than their *P. figuratus* counterparts. To evaluate possible causes for these variable results, seeds of greenhouse- and field-grown plants were weighed; seeds of greenhouse-grown *P. hirtus* seeds were heavier than seeds of the same species matured in the greenhouse (Table 1).

Figure 21. Plants emerging from a seasonal pool in late winter. Seedlings of *Plagiobothrys hirtus* are essentially aquatic, germinating when submerged and emerging as water recedes in spring.

Figure 22. Plants in summer. Both transplanted and naturally occurring *P. hirtus*
continue to bloom throughout the summer, when most other plants in the habitat have
begun to senesce.
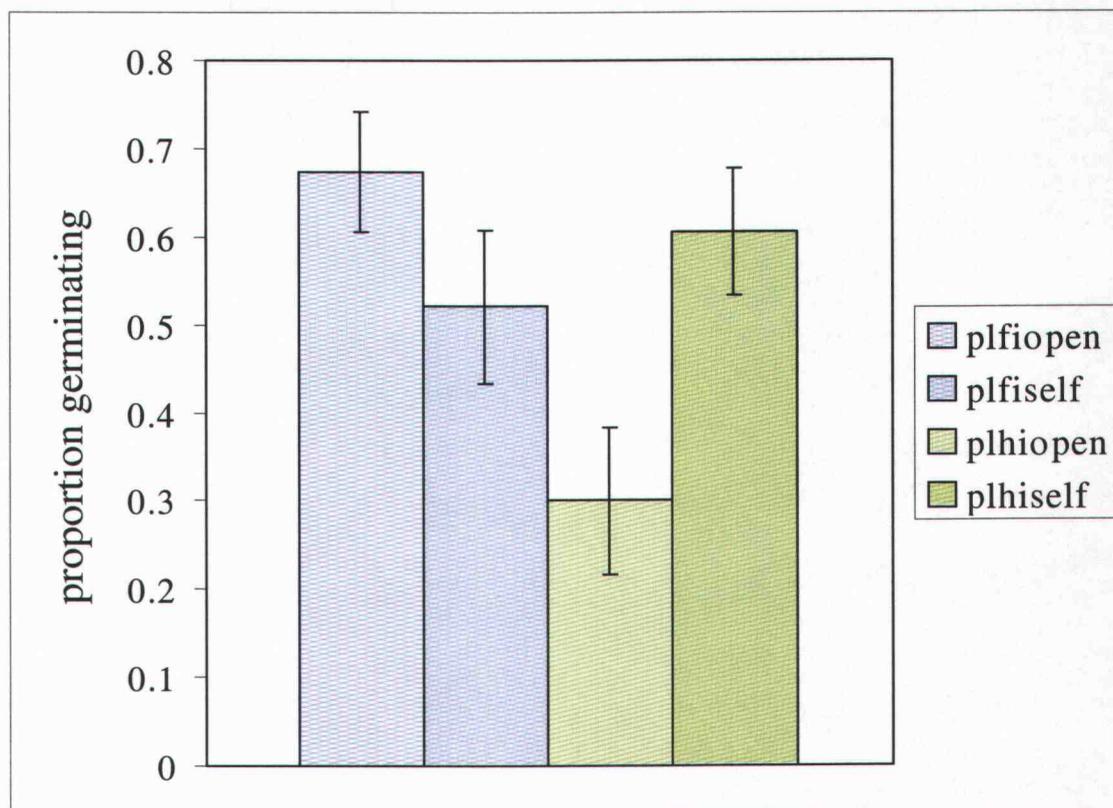
Figure 23. Germination rates of selfed and outcrossed seeds of *Plagiobothrys hirtus* (plhi) and *P. figuratus* (plfi). Open pollinated seeds were collected from field grown plants and selfed seeds were collected from plants grown in the greenhouse.

Table 1. Seed weights for *Plagiobothrys hirtus* and *P. figuratus*. Due to low seed availability, the reported values for *P. hirtus* selfed in greenhouse, selfed at Yoncalla site, and manually outcrossed in greenhouse were converted from weights for 84, 64, and 27 seeds, respectively; other weights are for 100 seeds. PLHI = *Plagiobothrys hirtus*; PLFI = *P. figuratus*.

species	treatment	seed weight/100 seeds
PLHI	manually outcrossed in greenhouse	0.12g
PLHI	selfed in greenhouse	0.13g
PLHI	selfed at Yoncalla site	0.06g
PLHI	open-pollinated at Yoncalla site	0.06g
PLHI	open-pollinated at Church site	0.08g
PLFI	selfed in greenhouse	0.06g
PLFI	open-pollinated at Finley Wildlife Refuge	0.04g
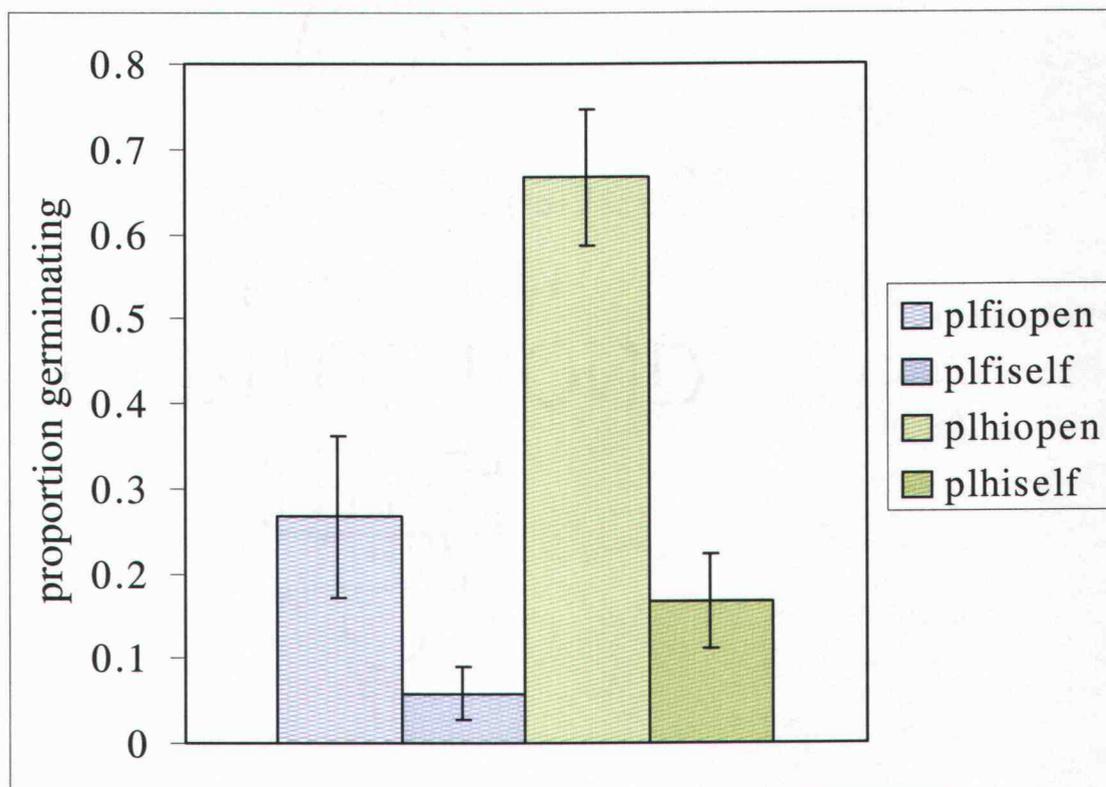
Figure 24. Germination rates of field-collected selfed and outcrossed seeds of *Plagiobothrys hirtus* (plhi) and *P. figuratus* (plfi).
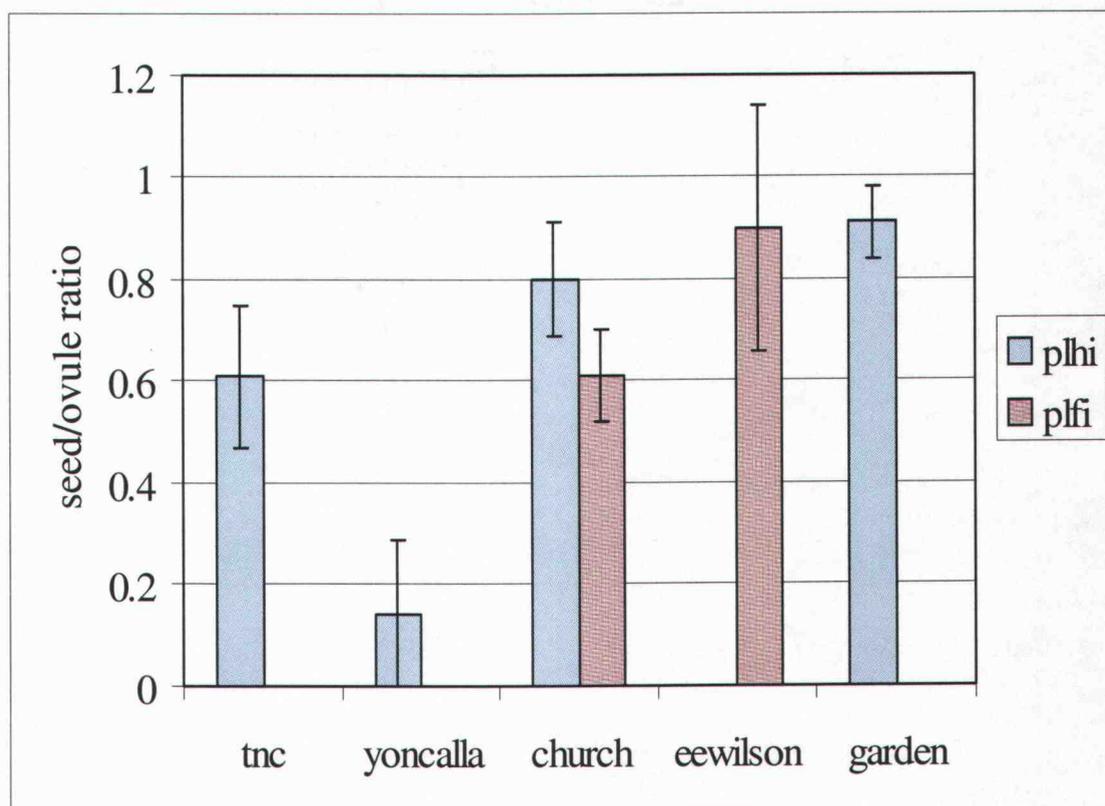
Figure 25. Seed/ovule ratios for *Plagiobothrys hirtus* (plhi) and *P. figuratus* (plfi) at five field sites. Seed set data was collected at all sites within a three week period in June 1997. Error bars represent one standard deviation above and below the mean. (plhi = *P. hirtus*, plfi = *P. figuratus;* n = 22 for tnc and yoncalla, n = 15 for church plhi, n = 11 for church plfi, n = 10 for eewilson, n = 3 for the garden)
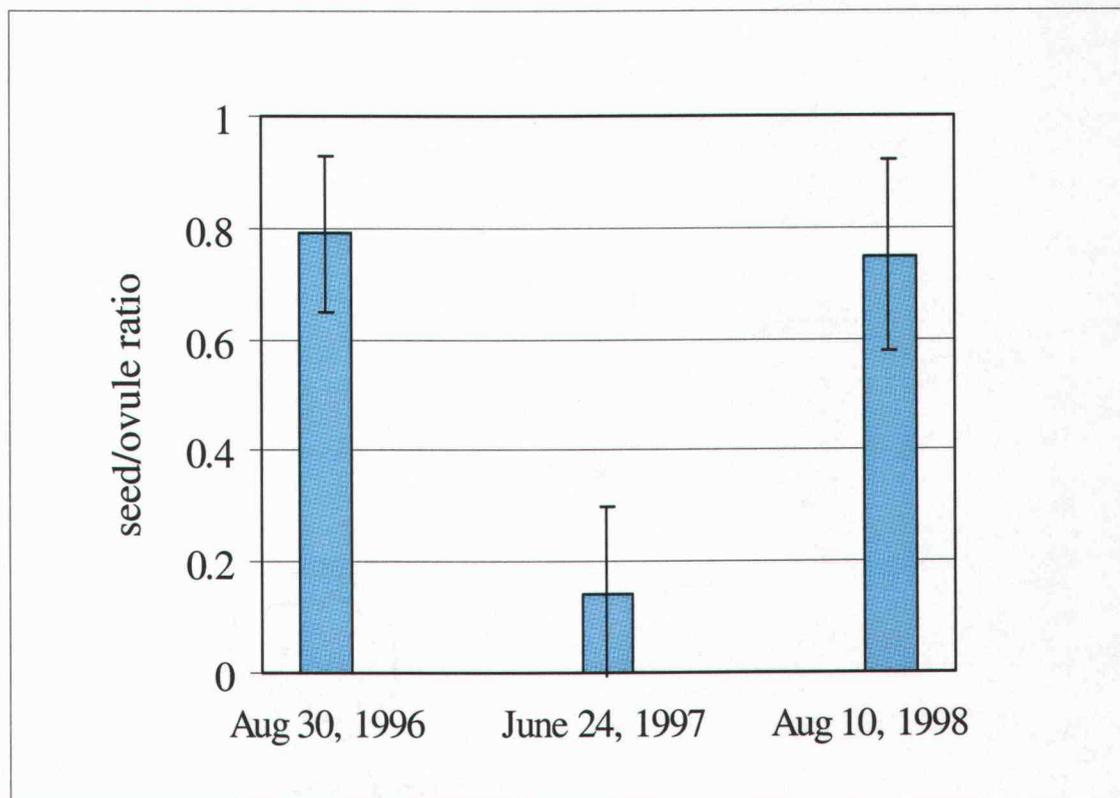
Figure 26. Seed/ovule ratios for *Plagiobothrys hirtus* at the Yoncalla site in three consecutive years. Error bars represent one standard deviation above and below the means. (n = 22 for 1996 and 1997; n = 15 for 1998).

Field seed set. Seed/ovule ratios varied between the Yoncalla, Popcorn Swale, Church, E.E. Wilson, and Garden sites (Fig. 25). Although the Yoncalla site showed significantly lower seed/ovule ratios than the other sites at the time the between-site comparison was made (June 1997), seed set at Yoncalla in 1996 and 1998 (but later in the summer, in August) was comparable to, or higher than, that from other sites (Fig. 26). Although the seed set for *P. figuratus* was lower than that for *P. hirtus* in the one site in which they occur sympatrically (the Church site), seed set for *P. figuratus* at the E.E. Wilson site was higher than or equal to that for *P. hirtus* at any site.

Breeding system. Plants of both species set little or no seed (seed/ovule ratio = 0.015 for *P. figuratus*, 0.015 for *P. hirtus*) when grown without pollinator access in the greenhouse (Fig. 27). Manual selfing of flowers resulted in a large increase in the number of seeds produced, with *P. figuratus* showing a greater increase in response to manipulation than *P. hirtus*. For *P. hirtus* the source of the pollen was not important; selfed flowers did not set a significantly different number of seeds than did flowers fertilized with pollen from another plant (p = 0.14 from a one-way ANOVA). As data from cross-pollination of *P. figuratus* were not included in this comparison, and the sample size for manually crossed *P. hirtus* was relatively small, further studies must be completed before the breeding systems of these two species can be fully understood.

Pollinators. Twelve representative floral visitors were collected from both *Plagiobothrys* species (Table 2). Many of these insects were carrying pollen in varying amounts, and
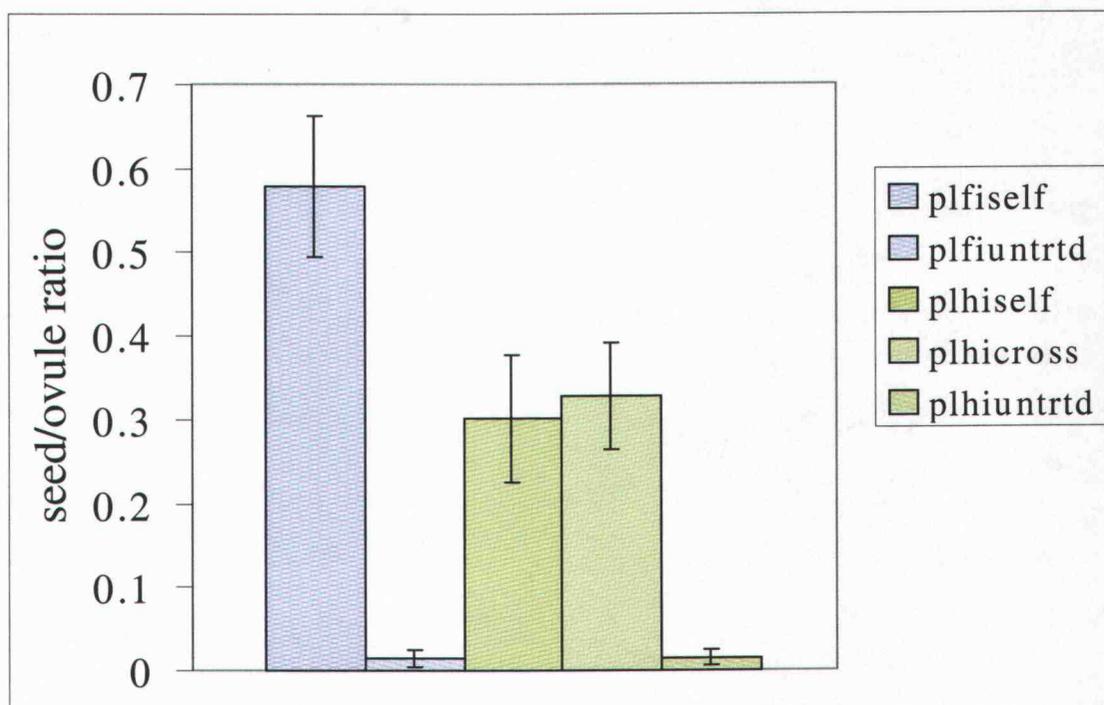
Figure 27. Seed/ovule ratios of selfed, outcrossed and untreated flowers of *Plagiobothrys hirtus* (plhi) and *P. figuratus* (plfi) grown in the greenhouse; n=69 for selfed plfi, n=85 for outcrossed plhi, n=121 for selfed plhi, n=884 for untreated plfi, and n=2148 for untreated plhi.

can be assumed to be transferring pollen between flowers in the vicinity of their collection sites. Although the source of the pollen was not evaluated, it is likely that at least some of it is from *Plagiobothrys*. Small syrphid flies and native bees were the most common visitors observed on both species at most sites, and a diurnal moth (*Ctenucha rubroscapus*) was observed frequently, throughout the flowering period, on both species at all sites. Larger-bodied pollinators, such bumble bees, honey bees and large syrphid flies (Richards 1986) were also observed on the flowers, and moved among flowers along individual inflorescences as well as moving between plants. Pollinator visitation rates were similar for the two species (Table 3), although cloudy weather during data collection for *P. figuratus* may have reduced the number of floral visitors.

Discussion

Life history. Contrary to previous reports (Abrams 1951; Peck 1961), *Plagiobothrys hirtus* is a biennial or short-lived perennial, rather than an annual plant. The ability to perennate may be an advantage in stable habitats, as an extended life span allows for more chances for successful reproduction. When compared to the annual *P. figuratus*, *P. hirtus* has the potential to flower longer, and therefore to set more seed, than its common relative, giving the rare species a longer reproductive period, as well as more reproductive "chances". However, other aspects of the life histories of the two taxa may offset this apparent advantage for the rare species. Although plants of *P. hirtus* live longer than do those of *P. figuratus*, they also require a longer period of appropriate growing conditions before initiation of flowering. In the unstable vernal pool habitats in which these plants

Table 2. Insect visitors observed on *Plagiobothrys hirtus* and *P. figuratus*, with estimates of the amount of pollen carried. (Each listed insect represents one collection - multiple individuals of each listed group were observed visiting flowers of both species at sometime during the study period). No determination was made as to pollen source. PLHI = *Plagiobothrys hirtus*; PLFI = *Plagiobothrys figuratus*.

insect visitors	present on	amount of pollen being carried
Bombus (Apidae)	PLHI, PLFI	more than 1000 grains
Bombyliidae	PLHI, PLFI	10-100 grains
Ctenucha (Arctiidae)	PLHI, PLFI	none
Halictidae	PLFI, PLFI	more than 1000 grains
Halictidae	PLHI, PLFI	10-100 grains
Hemiptera	PLHI, PLFI	none
Hemiptera	PLHI, PLFI	none
Megachilidae	PLHI, PLFI	10-100 grains
Syrphidae	PLHI, PLFI	100-1000 grains
Syrphidae	PLHI, PLFI	10-100 grains
Syrphidae	PLHI, PLFI	none
Tachinidae	PLHI, PLFI	100-100 grains

Table 3. Pollinator visitation rates for the two *Plagiobothrys* species. Plots contained 10 plants each and were monitored for an average of 140 minutes/plot. Visits/insect = the number of times an individual insect visited flowers within the plot; visits/minute = the average number of visits made by all insects within the plot in one minute; PLHI = *Plagiobothrys hirtus*; PLFI = *Plagiobothrys figuratus*.

site	date	species	visits/min.	weather	visits/insect
TNC	6/19/97	PLHI	0.28	sunny	2.4
Church	6/19/97	PLHI	0.30	sunny	1.5
Yoncalla	6/25/97	PLHI	0.52	sunny	1.8
Yoncalla	6/25/97	PLHI	0.46	sunny	2.2
Church	6/26/97	PLHI	0.57	sunny	2.6
E.E.Wilson	6/30/97	PLFI	0.15	cloudy	1.3
E.E Wilson	7/1/97	PLFI	0.28	cloudy	2.6

grow, the need for longer periods of suitably saturated conditions in order to initiate flowers (and ultimately to set seed) may severely limit the number of appropriate sites that can support viable populations of *P. hirtus*.

Although *P. hirtus* can perennate when conditions are favorable (as in the greenhouse), it can also behave like an annual in less optimal conditions. However, the need for a longer wet period to induce flowering may allow this species to flourish and reproduce in only a small subset of the seasonally wet meadow habitats available, while the potentially greater ecological amplitude of *P. figuratus* may allow it to proliferate in a wider range of environments. Narrower niche specificity as a characteristic of rare taxa has also been proposed as an explanation for limited distribution in other rare taxa (Lesica 1992, Baskin et al. 1997).

As well as helping to explain the distributional differences between the two species, the discovery of the perennial life history of *P. hirtus* has important management implications. Although attempts to conserve wetlands have increased in recent years, seasonally wet meadows are often not recognized as unique habitats, and have routinely been destroyed by agricultural conversion or development, further reducing the number of sites in which *P. hirtus* can persist. Conservation of the remaining sites for this species, as well as reintroduction into suitable unoccupied sites, will be mandatory to prevent the extinction of this unique taxon.

Management recommendations for currently protected sites based on the discovery of the perennial life cycle can also be made. Sites must remain in good condition throughout winter, as damage to habitat during the rainy season would reduce spring emergence and summer flowering. Management activities that could change the winter and spring hydrological regime should be avoided, as alteration of soil moisture at any time of year could deter the completion of the growth and reproductive cycles.

Seed germination. The results of the first germination test (using field-collected open-pollinated seed, and selfed seed from the greenhouse) are somewhat surprising - especially the higher rate for selfed vs. outcrossed seed of *P. hirtus* (Fig. 23). As lower germination rates are one manifestation of inbreeding depression (Schoen 1983; Schemske and Lande 1985), the germination rate of selfed seed could be expected to be lower, rather than higher, than that of outcrossed seed. Alternatively, if inbreeding depression is not present (due to the purging of deleterious alleles that typically occurs in small populations), or doesn't manifest itself at this stage, the germination rates of the two groups should be equal. The unexpectedly low germination rate for open-pollinated *P. hirtus* seed in our trials has several potential explanations. Selfed seeds could actually be more fit due to outbreeding depression (lack of adaption produced by the crossing of two mutually exclusively adapted genotypes) of the open-pollinated seed (Waller 1984). However, as seeds were germinated in standard conditions in the lab, it seems unlikely that the advantages of microhabitat specialization produced by selfing in a specific

environment would translate into a germination advantage in conditions other than those in which the seeds were produced.

A more likely explanation is based on the effect of the environment in which seeds ripened. In studies of seeds of the same species ripened under varying environmental conditions, those that developed under conditions of higher resources exhibited better germination rates than those grown in low resource environments (Schoen 1983; Winn 1985; Winn and Werner 1987). Plants grown in high resources also produced larger seeds than those grown in less optimal conditions, with greenhouse grown plants producing the largest seeds (Winn 1985). Furthermore, larger seeds germinated better than their smaller conspecific compatriots (Schoen 1983; Winn 1985; Winn and Werner 1987; although also see Nakamura 1988). As the selfed seeds in our initial study came exclusively from the greenhouse, and were much larger than field grown open-pollinated or selfed seeds (Table 1), the increased germination of the selfed seed is probably due to its better quality from an environmental standpoint (more endosperm, etc.), than to a genetic advantage. This effect has also been documented in other studies of inbreeding depression (Schoen 1983).

Germination test results for seeds of *P. figuratus* showed a pattern more consistent with expectations; the germination rate for selfed seeds, although they were greenhouse grown, was lower than that for open-pollinated, field collected seeds. However, the explanation behind this pattern is probably not as straight forward as it first appears. Because

inbreeding depression potentially had a greater reductive effect on seed germination in *P. figuratus* (as could be expected in a species with large population sizes, and potentially high genetic diversity [Schemske and Lande 1985]) than that seen in *P. hirtus*, this effect may have overwhelmed the positive effect of optimal seed ripening conditions. Although the conditions of seed maturation may have increased seed germination rates above what they would have been in field collected seed, their effect did not entirely compensate for the inbreeding depression exhibited by selfed seeds.

To reduce the confounding effect of seed ripening conditions, our second germination study compared open-pollinated and selfed seed collected from the same field sites (Fig. 24). The lower germination rates of selfed, as compared to open-pollinated seed, of both species, when ripened in similar conditions, imply that inbreeding depression is present at this stage. As *P. hirtus* currently occurs only in small isolated patches, the lower germination rate characteristic of seeds produced by selfed matings (or those from closely related individuals) has the potential to severely reduce seedling recruitment and compromise population viability. Maintaining adequate patch size and promoting maximum within-patch genetic diversity will be important to preserving the viability of existing populations, and is essential to the development of successful reintroduction plans.

Interestingly, the overall germination rate for *P. figuratus* was much lower, for both selfed and open-pollinated seed, in this second (as compared to the first) test. Seed of this

species was collected in a different year, at a different site, for this test; as discussed

earlier, ripening conditions vary by site and may affect germination rates. The overall

germination rate for *P. figuratus* is also lower than that for *P. hirtus* in this second test

(although higher in the first); as the seeds were collected at different sites, it is again

difficult to eliminate the effects of ripening conditions on germination rates. Due to the

many factors that affect seed viability, further germination studies are needed to make an

objective comparison of the germination rates of the two species, and to more fully

understand the genetic and environmental effects on this critical life history process.

Additional studies are also needed to look for inbreeding depression beyond the

germination stage. As well as reducing germination, inbreeding depression can manifest

itself as lowered seed set, reduced seedling viability (especially under environmental

stress), and reduced fertility of progeny (Schoen 1983; Waller 1984; Schemske and

Lande 1985; Karron 1989); all of these factors are potentially important to population

viability.

Field seed set. In addition to influencing germination rates, the site in which seeds were

collected significantly affected seed set, as measured by seed/ovule ratios (Fig. 25). The

variation in seed set may be due to between-site differences in available resources (Winn

and Werner 1987; Nakamura 1988; Menges 1995), with the highest seed set (95%)

exhibited by plants grown in a cultivated garden. Although low seed set may contribute

to reduced recruitment and population decline in rare plants (Meagher et al. 1978; Fiedler

1987; Watson et al. 1994), seed/ovule ratio, even when relatively low, is probably not a

major factor influencing the viability of either *Plagiobothrys* species. Plants of both species produce many inflorescences (5-20 for *P. figuratus*, and 10-40 for *P. hirtus*), with from 15-60 flowers per raceme and up to 4 nutlets per flower, and disperse many thousands of seeds, even in sites with relatively low seed/ovule ratios. These seeds germinate easily in a suitable (very moist) environment. As the heavy seeds of *P. hirtus* do not disperse long distances, the absence of open, suitably wet microsites, rather than lack of seed, is most likely the limiting factor controlling seedling establishment in these sites. Microsite availability has been shown to be at least as important as seed availability in determining recruitment rates in several native plant species (Eriksson and Ehrlen 1992).

Although, in general, annuals have higher seed/ovule ratios than perennials (Wiens 1984), seed/ovule ratios did not differ significantly between *P. hirtus* and *P. figuratus* in the sites that we measured. The apparent close phylogenetic relationship between the two species, despite their life history differences, may explain their deviation from expectations based on generalized annual-perennial comparisons. Although some rare plants set little seed in comparison to their more common congeners (Meagher et al. 1978; Karron 1989; Watson et al. 1994), and lack of viable seed production may affect population viability and persistence, seed set in both *Plagiobothrys* species appears to be adequately prolific to produce seedlings to fill all available habitat. Although the lighter seed of *P. figuratus* may give this species a dispersal advantage over *P. hirtus*, dispersal ability was not tested in our study.

As well as varying between sites, seed set varied within a single site over time. The low seed set measured at theYoncalla site relative to other sites in June 1997 may not be an adequate representation of overall seed production at this site, but rather an indication of a phenological difference in plants at this exceptionally wet location. Several assessments of seed set in a single year at this site demonstrate that seed/ovule ratios reached a fairly high rate (79%), but that this rate occurs approximately two months later than correspondingly high rates at other sites (Fig. 26). Due to their later emergence from the deeper pools that characterize the Yoncalla site, plants may be flowering in both sites by June, but maximum seed yield may not occur at Yoncalla until August. Seed/ovule ratios in plants with sequentially opening flowers (as in *Plagiobothrys* racemes) have been shown to change over time, irrespective of environmental conditions (Ritland and Jain 1984), and as mentioned above, seed set rates increase in response to increases in available resources. The later phenology observed in some sites may be genetically regulated; research to evaluate phenological differences in the greenhouse is currently in progress at OSU. Any one of these factors may be affecting observed differences in seed set over time. Highly variable among-year seed set rates have been documented in other rare plant species, although the cause for this phenomenon has not been determined (Fiedler 1987; Pavlik et al. 1993). However, as the seeds of *P. hirtus* lie dormant on the ground after dehiscence, and do not germinate until the soil becomes sufficiently moist in the fall, this difference in flowering season phenology probably doesn't produce differences in seedling recruitment among sites.

Breeding system. Breeding systems vary within genera; taxa with predominately

outbreeding, predominately inbreeding, and mixed mating systems can all be present

within a single genus (Jain 1976; Schemske and Lande 1985). Environmental variables

(such as pollinator abundance and flower density), as well as genetic factors, influence the

evolution of selfing from outcrossing breeding systems (Kesseli and Jain 1985). The

establishment of selfing can occur quickly, allowing variation in breeding systems to

develop among populations of the same species. The development of selfing systems can

be encouraged by small population sizes which reduce inbreeding depression through the

purging of deleterious alleles (Schemske and Lande 1985). As *P. hirtus* occurs only in

small isolated populations, this species might be expected to exhibit a predominately

selfing system. However, the populations of both *P. hirtus* and *P. figuratus* included in

our study have mixed mating systems, with selfed and open-pollination (probably

including some crosses and some geitonogamous selfs) producing seeds. More

importantly, *P. hirtus* set approximately equal amounts of seed from our artificial self and

cross-pollinations, indicating that both types of pollinations probably produce seeds in

nature. The similar seed set rates for artificial selfed and outcrossed pollinations also

indicate that inbreeding depression is not present at this stage in this species. Inbreeding

depression can occur at one or multiple stages within the life history of a species

(Schemske and Lande 1985). Although it is generally more common at the seed set stage

than during germination (Widen 1993), the point at which inbreeding depression becomes

evident depends on several factors, including breeding system and life history (Husband

and Schemske 1996). (Another potential explanation for the similar amounts of seed

produced by selfed and outcrossed plants is the possibility that outcrossed matings were actually from related plants, and so were not genetically different from the selfed matings. Although care was taken to use plants collected from distal locations, it was not possible to insure that they were truly unrelated.) Due to the lack of material available, manual outcrosses were not conducted on *P. figuratus*.

The seed set for these artificial pollinations of *Plagiobothrys hirtus* is considerably lower than field seed set (compare Figs. 26 and 27). This is probably due to inadvertently choosing non-receptive stigmas (Macior 1978), transferring a smaller pollen load than that carried by an insect, or transferring pollen only once, rather than multiple times as would occur in nature. As mentioned above, the possibility that outcrossed matings were actually consanguineous is an alternative explanation for the low seed set rates of putatively outcrossed seed as compared to those recorded for field sites.

Although *P. hirtus* and *P. figuratus* are self-compatible, they both require insect vectors (or possibly other forces, such as wind or animal movements) for regular pollination to occur (Fig. 27). The extremely low seed set produced in the absence of manual pollen transfer is important to conservation efforts for these species, as a lack of available pollinators (or ineffective pollinators) may dramatically limit seed set. As many pollinators are exceptionally susceptible to insecticides, and their populations recover slowly from decimating events (Tepedino 1979), management of sites and surrounding

areas to insure an adequate supply of insect visitors is critical to the viability of *P. hirtus* populations.

Although our initial studies indicate that the breeding systems of the two species are similar, further work is needed to quantify the potential effects of inbreeding depression on all life history stages, as well as to determine differences in seed set and seedling mortality between the two species. A molecular analysis would be a useful addition to a breeding system analysis, as it would allow an assessment to be made as to the relative percentages of open-pollinated seed produced by selfed and outcrossed pollen.

Pollinators. Lack of appropriate pollinators can affect plant fecundity and therefore species viability. Agricultural pesticide spraying, destruction of breeding habitat by development, and lack of sufficient food sources can all negatively affect pollinator densities, and reduce the reproductive success of both rare and common plants (Tepedino 1979). Furthermore, as they often depend on rare specialist pollinators for adequate pollen transfer, rare plants may suffer more than common ones from pollinator eradication, as a reduction in pollinator number may destroy the entire population of these specialized insects. Rare plants may also suffer disproportionately from a reduction in the number of available generalist pollinators, as generalists may preferentially visit common, rather than rare plants (Karron 1987). For these reasons, identifying common pollinators and estimating pollinator visitation rates is important to understanding plant rarity. Rare plants receive fewer floral visitors than their common congeners (Mehrhoff 1983;

Karron 1987; Menges 1995), but this phenomenon does not seem to be present in our *Plagiobothrys* species pair. Although further studies are needed to quantify pollinator visitation to these species, our preliminary data indicate that similar types of pollinators visited both species of *Plagiobothrys*, and that visitation rates (after consideration of weather differences) were also similar; both received adequate visits and produced large amounts of seed. Consistent visits by small flies and bees, and moths, although not highly efficient, were continuous throughout the study period, and were also observed in all sites over the course of the flowering period. These visits, combined with the more occasional visits of larger-bodied pollinators, such as large bees and flies, which were seen to visit many flowers on multiple plants within a few minutes, probably provide adequate pollen transfer to produce at least some outcrossed seed.

The number of flowers in a group (patch size) can be an important determinant of pollinator visitation rates (Richards 1986), and patch size is larger for *P. figuratus* in most sites. Both species are quite showy, fragrant, and bloom in dense patches; these attributes allow them to attract numerous floral visitors. However, our limited study of pollination ecology in *Plagiobothrys* species did not evaluate the effects of patch size or density on pollinator visitation and seed set. Future research goals include further study in this area.

Summary

The most significant difference between the two species is the life history divergence between the facultative perennial *Plagiobothrys hirtus* and the annual *P. hirtus*. The less

precocious reproduction of *P. hirtus*, as compared to *P. figuratus*, and the requirement for less ephemeral pools in order to perennate, may limit the number of habitats in which the rare species persists. As for many rare species, the factor most likely to be restricting the distribution of *P. hirtus* is the lack of available suitable habitat. The naturally limited distribution of this endemic has been exacerbated by anthropogenic loss of wetland habitat due to agricultural conversion and development; conservation of existing populations and the reintroduction of new populations into administratively protected sites are essential to maintaining the viability of *Plagiobothrys hirtus*.

Other than the notable life history divergence, few substantial differences between the two species are apparent. Both are self compatible but require pollinators to produce seed, both set seed prolifically in the field, and seeds of both germinate readily (Table 4).

Table 4. Summary of the similarities and differences between *Plagiobothrys hirtus* and *P. figuratus*.

	P. hirtus	*P. figuratus*
field seed set	variable; 0.14 - 0.91	variable; 0.61 - 0.91
inbreeding depression	present at germination	present at germination
germination	variable; 0.05 - 0.67	variable; 0.17 - 0.67
breeding system	self-compatible; pollinators required	self-compatible; pollinators required
pollinators	many	many
life history	facultative perennial	annual
flowering phenology	52 days to flower	36 days to flower

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Chapter 4

Conclusion

"Let no man expect that one lone government bureau is able--even tho it be willing--to thrash out this question alone."

Aldo Leopold,1925

The results of our research, both the comparative biology of the rare and common *Plagiobothrys* (Chapter 3), and our protocols for the cultivation and reintroduction of *P. hirtus* (Chapter 2), constitute a valuable contribution to the conservation and recovery of this rare species. Our discovery of the perennial nature of *P. hirtus* allows for improved management of sites with existing populations, provides information important to successful cultivation and transplantation efforts, and contributes to the available volume of biological knowledge of this species. Our documentation of apparently adequate levels of pollinator visitation, resulting in abundant seed set in the field, provides evidence that lack of reproduction is probably not limiting population viability. Our greenhouse investigations of breeding system and seed germination suggest that this species is not reproductively limited relative to its common congener. As is the case for many rare species, persistence of this species is most likely limited by lack of available habitat (Macior 1978; Meagher et al. 1978, Griggs and Jain 1983; Lesica 1992; Fiedler and Laven 1996). Creation of new sites in ecologically suitable and administratively protected habitat, as well as protection of the integrity of existing sites, will be essential to the recovery of this species.

Although we have now identified one of the main probable causes of the decline of *Plagiobothrys hirtus* (lack of habitat), many questions concerning its rarity remain - is it a relictual species surviving in only a few pools, while its annual, possibly derived relative moves into a much wider distribution? Or is it a newly evolved species that was just beginning to proliferate when anthropogenic habitat destruction halted its expansion? And, if *P. hirtus* has recently evolved, which species is likely to be its progenitor? These questions could potentially be addressed through a molecular phylogenetic study of *Plagiobothrys,* which could help to elucidate the relationships between the *P. hirtus* and *P. figuratus*, as well as determine the position of *P. hirtus* within the genus. Molecular analyses involving multiple populations, combined with further greenhouse studies, could also identify sites with low genetic diversity, as well as quantifying among-population differences. Information from studies such as these is useful in selecting appropriate seed sources for future reintroduction projects and identifying populations where the negative effects of low genetic diversity could be contributing to population decline.

Although the evolutionary origins and causes of rarity of *P. hirtus* remain somewhat enigmatic, we do now feel confident that we can cultivate and install transplants of this rare species, and identify habitat where reintroductions are likely to be successful. As well as addressing these biological questions, one of the goals of our work is to promote the interactive cooperation of the many agencies involved with the recovery of *P. hirtus*, and to develop a model for this type of collaboration.

Our population enhancement project involved work on sites owned by a public agency

not directly involved in conservation work (Oregon Department of Transportation -

ODOT), as well as a private conservation group (The Nature Conservancy - TNC). Not

surprisingly, these two groups were concerned with very different aspects of the

methodology of our project. Local ODOT maintenance crews were anxious to insure that

highway maintenance activities would not be unnecessarily restricted, and that our study

plots would meet their standards for roadside orderliness. TNC personnel were

concerned about disposal of clippings from our weeding procedures, and about the

feasibility of our proposed hydrologic measurement method. Biologists from both groups

were understandably concerned with possible mechanical impacts to existing native

populations, and with preventing genetic contamination through mixing of transplant

stock. By working with Nick Testa of ODOT, and Darren Borgias of TNC, we were able

to develop a plan that was acceptable to both agencies, and still met the academic

requirements of our study. Information from our research will be provided to these

managers, with the hope that our data will be useful to them in making future

management decisions.

As well as cooperating with the managers of the sites where transplanting occurred, we

worked with Oregon Department of Agriculture (ODA) and OSU to most efficiently use

the available greenhouses and other support resources. Contributions of high quality seed

from Portlands's Berry Botanic Garden also contributed to the success of our project, as

did funding from the Oregon Native Plant Society (NPSO) and The Portland Garden

Club. The interactive cooperation shown by the many private groups and public agencies involved maximized the contributions of each, and advanced the success of our project.

The lessons learned in the development and implementation of our initial enhancement projects were given a practical test in the next (post-thesis) phase of our work - introduction of *Plagiobothrys hirtus* into ecologically appropriate sites (where it has not been historically reported) on land owned by the Bureau of Land Management (BLM). The North Bank Habitat Management Area (NBHMA), between Wilbur and Glide on North Bank Road in Douglas County provided us with an administratively protected site within the Umpqua Valley, where we had the opportunity to cooperate with the BLM to create a new population of *P. hirtus*. The cultivation and transplantation experience we gained during my thesis work allowed us to efficiently produce and install more than a thousand transplants at the NBHMA. The production of healthy transplants, growth-promoting transplantation techniques, and knowledgeable site selection have allowed this project to be successful, with tens of thousands of *P. hirtus* plants now flourishing after two years. As in our earlier efforts, interagency cooperation was an important component of our success in this project, with staff from the BLM and US Fish and Wildlife Service, OSU students, and NPSO-funded interns generously contributing recommendations and advice, as well as copious amounts of labor, towards this endeavor.

As efforts to recover *P. hirtus* intensify (due to its recent Federal listing as endangered), we hope to continue to work with USFWS, ODOT, TNC, BLM, and other agencies that

manage sites that support naturally occurring or created populations of *P. hirtus*. These agencies have made important contributions toward reversing the decline of this rare species and beginning the recovery process, and we hope to include them in future recovery work. We also plan to work with the City of Sutherlin and other community groups affected by the recent listing, and to provide assistance to these groups in promoting the recovery of *P. hirtus*. Further refinement of site characterization methodology, documentation of population level genetic variation, and continued monitoring of existing sites to determine long term population viability, are planned for the future.

In 2000, in a speech about saving our Oregon salmon runs, Governor John Kitzhaber stressed the importance of working together, as citizens and as agencies, to promote the success of these conservation efforts. The introduction on the cover of a recent issue of the Endangered Species Bulletin reiterates this same point - only with co-operation among all interested parties, public and private, will our efforts towards the conservation of endangered species be successful (Bender 1999). In many ways, our efforts to conserve *Plagiobothrys hirtus* embody these recommendations. With a continuation of the co-operative venture we have begun, we truly can make a difference. Fortunately, to paraphrase Aldo Leopold (1925), one lone government bureau does not need to thrash out the question of how to recover the hairy popcorn flower alone.

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APPENDICES

Appendix A
Species list for Yoncalla site
June 27, 1996

Agrostis tenuis
Aira caryophyllea
Allium vineale
Anagallis arvensis
Asclepias speciosa
Briza minor
Brodiaea hyacinthina
Bromus tectorum
Carex densa
Carex feta
Carex unilatorales
Centaurea diffusa
Centaurium umbellatum
Convolvulus arvensis
Cirsium arvense
Cynosurus echinatus
Danthonia californica
Daucus carota
Deschampsia caespitosa
Dipsacus sylvestris
Downingia yina
Eleocharis palustris
Epilobium watsonii
Equisetum arvense
Festuca arundinaceae
Fraxinus latifolia
Galium aparine
Glyceria occidentalis
Holcus lanatas
Hordeum brachyantherum
Hypochaeris radicata
Juncus effusus
Juncus ensifolius
Juncus oxymeris
Juncus patens
Juncus bufonius
Lathyrus sylvestris
Linum perenne

Lotus corniculatus
Lythrum hyssopifolia
Mentha arvensis/Mentha puligeum
Myosotis discolor
Navarretia intertexta
Parentucellia viscosa
Plantago lanceolata
Prunella vulgaris
Rubus discolor
Rumex crispus
Ranunculus orthorhynchus
Rhus diversiloba
Rubus discolor
Scirpus microcarpus
Sidalcea cusickii
Sonchus asper
Thalictrum occidentale
Verbascum blattaria
Veronica scutellata
Vicia hirsuta
Vicia tetrasperma
Zigadenus venenosus

Appendix B
Species list for William Oerding Popcorn Swale Preserve
June 25, 1996

Agrostis tenuis

Aira caryophyllea

Allium vineale

Alopecurus pratensis

Amelanchier alnifolia

Anagallis arvensis

Beckmannia syzigachne

Bidens sp.

Briza minor

Brodiaea hyacinthina

Bromus tectorum

Camassia leichtlinii

Carex densa

Carex feta

Carex unilatorales

Centaurea diffusa

Centaurium umbellatum

Cirsium arvense

Cynosurus cristatus

Cynosurus echinatus

Danthonia californica

Daucus carota

Deschampsia caespitosa

Dipsacus sylvestris

Downingia yina

Epilobium watsonii

Festuca arundinaceae

Fraxinus latifolius

Galium aparine

Grindelia integrifolia var. integrifolia

Holcus lanatas

Hordeum brachyantherum

Hypochaeris radicata

Juncus bufonius

Juncus effusus

Juncus oxymeris

Juncus patens

Lathyrus aphaca

Lathyrus sylvestris

Limnanthes douglasii

Linum perenne

Lolium perenne

Lotus corniculatus

Lythrum hyssopifolia

Mentha arvensis/Mentha pulegium

Myosotis discolor

Myosotis laxa

Navarretia intertexta

Parentucellia viscosa

Plagiobothrys figuratus

Plantago lanceolata

Prunella vulgaris

Pyrus communis

Ranunculus orthorhynchus

Rhus diversiloba

Rosa pisocarpa

Rubus discolor

Rumex crispus

Sidalcea cusickii

Spirea douglasii

Thalictrum occidentale

Taeniatherum caput-medusae

Typha latifolia

Verbascum blattaria

Vicia tetrasperma

Zigadenus venenosus