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EFFECTS OF EXOTIC SPECIES AND SOIL DEPTH ON A RARE SERPENTINE
JEWELFLOWER

A Thesis

Presented to

The Faculty of the Department of Environmental Studies
San José State University

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science

by

Allison R. Green

December 2004

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ABSTRACT

EFFECTS OF EXOTIC SPECIES AND SOIL TYPE ON A RARE SERPENTINE JEWELFLOWER

by Allison R. Green

Nutrient-poor serpentine soils act as refugia for native plant species due to competitive pressure by exotic species that have invaded California's grasslands. However, some exotic species have recently evolved to tolerate deep serpentine soils, thereby jeopardizing these biologically rich refugia. I hypothesized for this study that *Streptanthus albidus* var. *peramoenus* (Most Beautiful Jewelflower) is restricted to shallow serpentine soils due to competition from exotic annual plants occurring in neighboring deep serpentine soils. I performed a factorial experiment manipulating the presence of exotic plant species in shallow and deep soils within patchy serpentine grassland habitat. Results show *Streptanthus albidus* var. *peramoenus* to be successful in deep serpentine soil areas when exotics were removed. It follows, then, that populations of this plant may be expanded through restoration efforts focused on reducing neighboring exotic plant abundance.

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CHAPTER 1

INTRODUCTION

California's grasslands have been permanently altered by the invasion of exotic grasses and forbs (Heady 1988). However, grasslands occurring on unique serpentine soil, derived from ultramafic serpentinite rock, commonly harbor many native grassland species. Some of these species are endemic to serpentine substrate and are, therefore, quite rare (Kruckeberg 1984 and 1992, Harrison 1999). Introduced grasses are typically not abundant in these areas due to their intolerance of the poor nutrient availability and high toxicity of the serpentine soil environment (Huenneke 1990). Thus, serpentine grasslands offer an opportunity to study a complex mix of larger ecological issues, namely invasion ecology, edaphic endemism, rare plant ecology, and the refugia concept for native species. When combined with the goal of protecting Earth's biodiversity and native floral communities, these ecological issues present a dramatic challenge in our pursuit of sound conservation methods.

Serpentine soil areas can be particularly challenging to manage because of the substantial number of rare and endangered species found in these habitats (Kruckeberg 1992). In order to ensure the persistence of these rare plant populations, land managers must be provided with ecological information on these plants and the community in which they exist. To that end, this study was designed to collect information on the germination success, survivorship, and fecundity of a rare serpentine annual plant and its surrounding community within the context of exotic species and variable soil type. The study species,

Streptanthus albidus var. *peramoenus* (E. Greene) Kruckeb., commonly called Most Beautiful Jewelflower, is a rare annual plant found on areas of serpentine substrate in the San Francisco and Monterey Bay areas, California.

My research uses a small-scale factorial experiment manipulating the presence of exotic plant species in two soil conditions within serpentine habitat to understand how soil conditions and exotic plant competition may interact to influence the demographic performance (germination, survivorship, and fecundity) of the jewelflower. I located a total of 48 study plots in two soil types in three areas of serpentine grassland on the property. In each study plot I sowed 50 *S. albidus* var. *peramoenus* seeds in a grid so I could track each individual plant. In order to determine the role played by exotic plant competition in limiting the distribution and demographic performance of *S. albidus* var. *peramoenus*, I removed all exotic plants from half of the study plots. I measured the germination success, survivorship, and number of flowers and seeds for each sown plant at five-week intervals to assess the plant's demographic performance. I also measured the composition of the serpentine grassland community in both shallow and deep soils. Soil tests were conducted at each of the three sites.

This thesis is presented in six chapters and two appendices. Chapter 2, Related Research, sets the scene of the experiment conceptually and immediately follows this Introduction (Chapter 1). In Chapter 3, Objectives and Methods, I describe my research objectives and hypotheses, experimental design, the study area, and the data collection and statistical methods. In Chapter 4, Results, I

provide the results to the statistical analyses and qualitative comparisons for *S. albidus* var. *peramoenus* demography, community level effects, and physical effects such as soil characteristics and the amount of photosynthetically active light available to the plants. Chapter 5, Discussion, considers these results with regard to the ecological information provided in the related research section and other sources. Finally, I conclude the study in Chapter 6, Conclusion, where I provide recommendations for land managers, ideas for further research based on my findings, and discuss some limitations to my study. I have also included an Appendix A called the Regulatory Framework for Rare Plant Protection in California where I examine the regulations pertinent to the conservation of rare plants such as the study species, and an Appendix B that lists the species found in experimental plots.

Not only will this study provide information useful to land managers and owners where this plant is found (e.g., Santa Clara County Parks, Santa Clara County Open Space Authority, California State Parks, and other agencies and private landowners), but it provides ecological insights into rare plants in serpentine grasslands, as well as some information on how to manage for these unique habitats.

CHAPTER 2

RELATED RESEARCH

Biological invasions are occurring at an alarming rate throughout the world due to the disintegration of traditional biogeographic boundaries (Elton 1958, D'Antonio and Vitousek 1992, Schierenbeck 1995). Unlike geologic time, biota now regularly move around the world as a result of human activities involving travel and trade, with plant and animal species being introduced into new areas either deliberately or accidentally (D'Antonio and Vitousek 1992). Charles Elton wrote a seminal work on invasion ecology in 1958, and noted the gravity of the current age of biological invasion: "We must make no mistake: we are seeing one of the greatest historical convulsions in the world's fauna and flora" (Elton 1958, Mooney and Cleland 2001, 5446).

These worldwide biological invasions have dramatically affected California's biodiversity. In fact, the invasion of exotic species into California's grasslands is widely regarded as one of the most explicit biological invasions that has occurred in recent history (Mooney *et al* 1986).

Within this thesis chapter, I describe first the historical aspects of the dramatic alteration of California's grasslands and the major phases of the introduction of exotic grassland species. Then, the following section details the ecology behind the invasion of Mediterranean species into the State's native grasslands. Bringing the focus closer to this thesis study, the third section outlines the characteristics of serpentine soils and its grassland habitat. Finally, I

close the chapter with a discussion of those ecological concepts that are important to unique edaphic areas such as serpentine grasslands.

Changes in California's Grasslands

California is one of the most floristically diverse and biologically rich areas in the world, with 5,862 documented plant species and endemic species that consist of over 24 percent of the native flora (Stebbins and Major 1965, Mooney 1988, Kruckeberg 1992, Hickman 1993). This high level of biodiversity can be attributed to California's large range in latitude (approx. 32° - 42° N), a complex geologic history that has resulted in highly variable topography and a multitude of soil types, and a unique climatic history that, when combined with its geologic history, includes the development of a wide variety of microclimates throughout the state (Raven and Axelrod 1978). While all of these factors created California's distinctive biogeographic mosaic, this heterogeneous landscape has been heavily influenced by the invasion of exotics species.

California's Mediterranean climate with cool, wet winters and dry, hot summers has not only provided optimal conditions for native flora, but exotic species from the Mediterranean region have also readily adapted to this environment. In fact, 1,045 species, or almost 25 percent of California's flora, are considered to be exotic (Ornduff *et al* 2003). The invasion of exotic species into California is regarded as one of the most dramatic in the world (Mooney *et al* 1986) and has a history closely tied with the change of land use and exploration by humans during the past 450 years.

What exactly is an exotic species? In California it is generally regarded as a species introduced by Europeans, primarily the first explorers and missionaries, although there is also the possibility Native Americans could have introduced exotic species into the landscape through trade and travel. The term “exotic” is not applied to those species that migrated into the state as part of the trinity of geofloras (the Arcto-Tertiary, Neo-Tropical Tertiary, and the Madro-Tertiary) through geologic time; rather, these species are considered to be native to California.

Some ecologists believe the exotic annual grasses should be regarded as permanent members of California’s grasslands and, thus, should no longer be regarded as non-native species (Heady 1988). However, that topic is highly controversial amongst ecologists and native plant restorationists and is beyond the scope of this thesis.

California’s Original Grasslands

A complicated and unresolved ecological question is what the composition of California’s present grasslands was prior to European contact. There are generally two schools of thought: first, the grasslands were comprised predominantly of perennial bunchgrass species such as *Nasella pulchra* and *Danthonia californica* with interspersed annual flowering forbs, and, second, and in contrast, of only annual flowering forbs such as the California poppy, *Eschscholzia californica*, and other wildflowers and grasses (Mooney et al 1986).

The fact that relict stands of native grassland are extremely rare complicates the issue because there is little evidence of this early and original grassland.

However, despite the ongoing debate, the majority of researchers have declared their belief in the bunchgrass theory formulated by Shantz and Zon in 1924 (Mooney et al 1986). For example, Heady (1988, 495) stated, "*Stipa pulchra*, beyond all doubt, dominated valley grassland." Recently, however, research supports the forbs-only view. Solomeshch and Barbour (2004) contend that while portions of California's grasslands did indeed derive from bunchgrass prairie, some grasslands derived from forb-dominated vegetation. These views are continuously debated among grassland specialists and enthusiasts, providing ample fodder for researchers to detect signs of what may have been.

Regardless of the original composition of California's grasslands and the fact this pristine landscape is the subject of debate, there is little controversy over the fact that exotic grasses and forbs have permanently changed the California grasslands. In order to better understand this change in California's grasslands, some description of the history behind the introduction of exotic grassland plant species is necessary.

History of Exotic Introductions

Native Americans were the first people to populate the state of California, with several prehistorians placing their presence beginning 12,000 to 14,000 years ago (Moratto 2004). By manipulating their local landscapes through burning, pruning, and collecting vegetation, these people regularly gleaned resources for

food, shelter, tools, and items for trading with other tribes (Blackburn and Anderson 1993). While it is possible that plants and seeds were introduced to California from areas that are now other states and eventually became naturalized in the landscape, it is well accepted that the major period of introduction of exotic grassland species occurred upon the arrival of European explorers and settlers.

The majority of California's exotic grassland species originate from the Mediterranean region that is bordered by southern Europe, Turkey, the western countries of the Middle East, and northern Africa. As California's first visitors from this region were from Europe, so too are the exotic plant species these individuals introduced into the landscape. The first European explorers to reach the shores of California, such as Juan Rodríguez Cabrillo, Gaspar de Portolá, and Sir Francis Drake, reportedly arrived from Europe in ships loaded with livestock and fodder as well as dry ballast containing plant material with seeds that could have made their way into California's native vegetation (Heady 1988). Heady (1988) opines that any one trip to explore the coastal lands from these sailing vessels laden with exotic plant material could have brought seeds onshore, particularly those excursions that included horses with plant seeds in their intestines.

In the 1920's and 1930's George Whiting Hendry, an agronomy professor at University of California, Davis, performed some admirable detective work to more accurately gauge the original composition of California's grasslands and find out what species early explorers introduced to the landscape. According to

Hendry (1931) several exotic species common in California's grasslands today were found in the adobe bricks used to build several of the missions. His studies suggest these exotic species were already established prior to the mission-building era.

Despite being initially introduced prior to the establishment of California's missions, this event undoubtedly played a large role in the continued distribution and establishment of these alien plants. In just one year the missionaries traveled north along California's Coast Range, possibly carrying exotic plants and seeds they used as fodder for their livestock. The first mission was established in 1769 in at San Diego and the second in 1770 in Carmel. The closest mission to the study area is Santa Clara, founded in 1777. Seeds from fodder of Mediterranean grasses were probably spread into the landscape as the explorer's animals grazed on native grassland. Because there was continual overland travel between missions, the assumption is that there were ample opportunities for animals to spread exotic seeds across the Coast Range landscape.

Heady (1988) discusses the introduction of exotic plant species in terms of four major groups or phases. The first phase was during the early exploration period, prior to the 1760's. Based on Hendry's adobe brick analyses, several exotic species were already established: *Erodium cicutarium*, *Sonchus asper*, *Hordeum leporinum* (now *H. murinum* ssp. *leporinum*), *Lolium multiflorum*, and *Avena* spp. (Gordon 1977).

According to Heady (1988), the second major phase of the introduction and spread of exotic plants occurred in the early 1800's through the 1870's, a time when the missions were terminated and livestock grazing increased. Livestock predominantly grazed around the missions and on Mexican land grants early in the century. However, the livestock industry greatly expanded, with the highest number of cattle occurring around 1862 and the greatest number of sheep occurring about 1876. By many accounts, eventually much of California's native grasslands was overgrazed at this time (Heady 1988). The drought of the 1860's further stressed overgrazed grassland species, allowing the better adapted exotic annual grasses to dominate the landscape (Mooney *et al* 1986). Throughout the latter half of the 1800's, California experienced a boom of mining towns and roads, thereby exacerbating the spread of the exotic plant species into native grasslands.

The dominant plants introduced and established in the second phase (at least in reference to the general region of this study) include *Erodium* spp. and *Medicago polymorpha* for sheep forage, along with grasses such as *Bromus* spp., *Gastridium ventricosum*, and *H. murinum* ssp. *leporinum* (*Hordeum leporinum*) (Crampton 1974). The 1880's saw the third major group of introductions; the two main species include *Bromus rubens* (now *B. madritensis* ssp. *rubens*), *Centaurea melitensis*. The fourth phase is recent and is perhaps even still occurring. The major grass introduced most recently that impacts Central Coast grasslands is *Brachypodium distachyon* (Heady 1988). In summary, many exotic grassland species we see today had been introduced and spread in areas of California's

Coast, Transverse, and Peninsular Ranges prior to 1800, and many researchers conclude it was the latter part of that century that saw the greatest expansion of these exotic species.

Invasion Ecology

Just as important as delineating how exotic grassland species arrived in California is the ecology behind the invasion of these species. Many exotic grassland species have life history characteristics that allow them to easily overtake native flora in California's broad array of plant communities. Further, once an exotic species becomes established in its new habitat, it can provoke permanent changes in the landscape (Vitousek 1986), namely the exclusion and ultimate extinction of native species (Mooney 1988).

In this section, I will discuss both the immediate effects of invasive grassland species on the grassland ecosystem and native vegetation and, as well, the long-term, evolutionary implications for the grassland ecosystem as a whole. After that, I will then bring the focus to California grasslands and discuss the specific biological traits exotic species have that make them successful competitors in the Coast Range grasslands. Last, I will explicate how human land use activities exacerbated the invasion process.

The introduction of exotic species changes environments by the disruption of various elements in ecosystems, primarily microclimates and fire regimes. Annual exotic grasses accumulate more litter than native perennial grasses, which, in turn, can influence soil temperature and moisture (D'Antonio and

Vitousek 1992). As a result of this change in microclimate, seed germination, seedling growth, and nutrient availability within the soil can be altered as well (D'Antonio and Vitousek 1992).

Because grasslands are found in areas with distinct dry seasons and periodic drought (Risser 1988), fire is an important feature of this environment replete with dry fuel (Heady 1988, D'Antonio and Vitousek 1992). Invasive exotic grassland species can alter the frequency, area, and intensity of natural fire regimes via their morphological differences from native forbs and perennial grasses (Vitousek 1986, D'Antonio and Vitousek 1992). A grassland's abundant vertical dead material with large surface to volume ratios that dry out quickly and the rapid recovery rate of grasses after fires result in a positive-feedback fire cycle in the grassland ecosystem (D'Antonio and Vitousek 1992). While exotic species easily colonize cultivated and disturbed areas (Elton 1958, Orians 1986), they also readily invade native, or pristine, and generally undisturbed areas, such as the grasslands of the study area, directly affecting the positive-feedback fire cycle. Fire is also essential to grasslands to exclude trees and shrubs (Gurevitch *et al* 2002), a point well known to early settlers of California who regularly burned shrublands to maintain grassland environments for grazing (Heady 1988).

In addition to affecting ecosystem properties, competitive effects by exotic species are resource-based, forcing native species to compete for water, light, and other resources. In general this occurs as a result of the invaders' abilities to 1) access resources in the ecosystem when the native species are inactive or where

native species cannot reach, or 2) use resources more efficiently than the native species (Vitousek 1986). For example, exotic annual grassland species can utilize water more efficiently than native perennial species because exotic annual grasses are better at drawing down moisture to their root systems than native grasses ((D'Antonio and Vitousek 1992). In other words, with grasslands already an area of low soil moisture (Risser 1988), native perennial species (with longer roots) must compete with exotic annual grasses (with shallow roots) for water. These modified rates of resource uptake also eventually alter large-scale ecosystem disturbance effects (D'Antonio and Vitousek 1992). According to D'Antonio and Vitousek (1992), the combination of advanced water uptake capabilities of exotic annual grasses alters the water holding capacity of an area, which in turn can affect the local microclimate and flammability of the vegetation and its resultant fire regime.

Competition for light, or shade tolerance, is one of the principle physical factors that guide competitive pressures in grasslands. Although light itself is essentially in infinite supply, the canopy created by exotic annual grasses that germinate early in the growing season prevents later-germinating native grasses and forbs from photosynthesizing enough to survive (Gurevitch *et al* 2002, personal observation). D'Antonio & Vitousek (1992) concur, as they determined that the photosynthetic ability of native competitors in California's grasslands is reduced by rapidly growing annual grasses. Further, McGraw and Levin (1998) researched survivorship of the federally endangered *Chorizanthe pungens* var. *hartwegiana* Rev & Hardham (Polygonaceae; the Ben Lomond Spineflower), an

annual plant confined to the harsh growing conditions of the Zayante sandhill soils in the Santa Cruz Mountains, CA. Because growth of this plant was more successful on soil types other than its native soil, they found shade to be a primary cause of the edaphic endemic's limited distribution because it is a poor competitor for light among other species.

Evolutionary processes are also greatly affected by exotic species. In their study, Mooney and Cleland (2001) examined the impacts of invasions on native species and found several ways exotic species spurred different evolutionary trajectories. One of the most straightforward ways is through competitive exclusion where the native species is simply extirpated from the ecosystem. Another is through niche displacement, when the exotic species force native species into ever-narrowing ranges of ecological conditions. While hybridization with exotic species can create new species, these new species become additional competitors in the environment, which in turn places more competitive pressure on natives, possibly resulting in extinction.

There are several life history traits of California's invasive grassland species that result in dramatic disruptions in the habitat, including temporal, climatic, reproductive, and overall flexibility within the environment. Exotic annual grasses have temporal advantages over native perennial grasses. Perennial grasses not only have slower growth rates in California's winter growing season, but they also have low reproductive output their first year (Jackson 1985). Annual grasses, on the other hand, have high reproductive output, giving them the ability to readily outcompete young perennial grasses,

particularly seedlings (Jackson 1985). More specifically, *Avena* sp. and *Bromus* sp. have been shown to be self pollinating, thereby increasing their advantage over perennial grasses to colonize new areas (Harrison *et al* 2001). This temporal advantage of annual grasses is one reason why these exotic grass species are usually the first to populate disturbed areas, for they are able to colonize and regenerate before the perennial grasses become established (Orians 1986).

Exotic grassland species also have more advantageous reproductive methods than California's native species and flexible use of resources in the grassland environment. The high success rate of these invaders is a result of shorter life cycles (annual v. perennial) and high population growth rates as a result of allocating much energy toward reproduction (Orians 1986). By producing large amounts of seed often, invasive annual grasses exhibit increased levels of plasticity that may contribute to these plants' ability to rapidly evolve to efficiently utilize a variety of resources in the environment (Baker and Stebbins 1965, Jackson 1985, Orians 1986). Wind pollination and dispersal is also an important contributor to their success because there are no mutualistic requirements (e.g., pollinators, birds) to depend on for regeneration (Orians 1986). It is important to note, however, that there are cases when species with these characteristics are not invasive, as well as instances when species without these characteristics are invasive (Orians 1986).

As discussed earlier, California's exotic annual grasses came from the Mediterranean region. Jackson (1985) performed a study to compare and contrast California's grassland environments with those around the

Mediterranean region. Surprisingly, she found that despite the obvious success of these grasses in California as a climax community, there are not similar annual grasslands in the Mediterranean region. Rather than existing as a later successional stage, annual grasses in the Mediterranean regions are typically ruderal species that exist mainly along roadsides, cultivated fields, and other disturbed areas. Further, California's long summer droughts, perhaps regarded as a relative extreme in Mediterranean dry-summer climate zones, apparently favor the dominance of these exotic annual grasses (Jackson 1985). Despite these differences, these species thrive in deep soils with high cation exchange capacity and high levels of winter rains as they do in their native Mediterranean climate areas (Jackson 1985).

Particularly pertinent to California's land use history, exotic annual grasses are not only preadapted to a Mediterranean climate, but they prefer open and disturbed habitats (Jackson 1985) such as those overgrazed during the Spanish period. In contrast, perennial grasses are at a competitive disadvantage by having to expend energy to regenerate after being overgrazed (Jackson 1985, Gurevitch *et al* 2001). Prior to the introduction of livestock, grazing pressure on native perennial grasses and forbs was substantially less as early grazers like the pronghorn antelope and tule elk were much more mobile than livestock, resulting in a more periodic grazing regime (Heady 1988).

Further, the life history of the exotic annual grasses allows them to set seed very early in the winter growing season, allowing them to get an earlier start than the perennials, and therefore are the first in the season to soak up

available nutrients and water (Gurevitch *et al* 2002). Of course, this cycle is compounded in low rainfall years, such as the California drought of the 1860's (Heady 1988, Gurevitch *et al* 2002). All of these biological characteristics contributed to the incursion and eventual replacement of so much of California's perennial grasslands.

In summary, exotic species become successful invaders when competing against physically stressed plants (Orians 1986), such as plants overgrazed, experiencing drought, or living in adverse serpentine conditions where nutrients are less abundant. I will elaborate on the serpentine soils and this unique grassland habitat in the next section.

Serpentine Ecology

Within California's grassland regions there are some edaphic areas that host particularly diverse grassland landscapes - one of these is serpentine soil. There are a limited number of vegetation types that can tolerate serpentine soil; the most common communities found on serpentine include chaparral scrub and grassland (Kruckeberg 1984). Although only a few communities are adapted to serpentine, it is notable that serpentine endemics make up 10 percent of the total endemic flora of California. This seems like a large number given only 1.0 percent of California's surface area is comprised of serpentine soils (Kruckeberg 1984).

In this section, I will describe the ecology of serpentine grasslands by, first, discussing the biotic characteristics and origination of serpentine soils.

Second, the above-ground serpentine environment will be described, by characterizing serpentine grassland communities, by looking at ways this vegetation has historically been affected by exotic species, investigating the dynamic interaction between the native and exotic vegetation and the size of serpentine soil areas, and considering the notion of refugia. Finally, I will discuss the concepts of endemism and rarity in the serpentine environment.

Serpentine Soils

Serpentinitic soils are derived from the parent rock serpentinite, a type of ultramafic rock often found near areas of geologic faulting where hydrothermal alteration of parent material occurs (Proctor and Woodell 1971, Malpas 1992). The serpentinitic bedrock in the coast ranges is largely derived from ultramafic intrusives within the Franciscan sedimentary rock complex during the Mesozoic age. Exposure of this rock took place during the late Pliocene or early Pleistocene epochs, depending on the rate of erosional weathering of overlying marine and igneous deposits (Kruckeberg 1984, Arianoutsou *et al* 1993). In the study area and its vicinity, the serpentine soils derived from this bedrock are derived from California's Montara upland serpentinitic series (Kruckeberg 1984).

Serpentine areas have been described as "barrens" due to the commonness of outcrops of bedrock and the paucity of vegetation (Kruckeberg 1984). Commonly, these areas consist of coarse clay-like sediments and gravelly substrate. The porous nature and lack of water holding capacity of serpentine

soils has a microhydrologic effect on plants by creating a xerophytic environment (Brooks 1987).

What makes serpentine soil so unique is its distinct chemistry. These soils typically have low calcium to magnesium ratios (typical ranges are from 0.1 to 0.7; Kruckeberg 1984, Brooks 1987) and often have a high content of heavy metals such as chromium (Cr), nickel (Ni), and iron (Fe). The low levels of calcium (Ca^{2+}) and high levels of magnesium (Mg^{2+}) and other metals coincide with low levels of nitrogen (N) and phosphorus (P), which are the primary nutrients required by most plants. As a result, the serpentine soil environment is inimical to plant growth and overall productivity (Turitzin 1982, Kruckeberg 1984 and 1992, Malpas 1992). Some researchers contend magnesium can directly prevent calcium uptake by plants, forcing plants living on serpentine soil to be tolerant of magnesium (Brooks 1987). Further, levels of these nutrients and metals differ between serpentine locations as a result of variations in climatic regime, age of serpentinite bedrock, topographical relief, and the biological activity (Turitzin 1982, Arianoutsou *et al* 1993). Although these levels differ, the ratio of the chemical values typically remains the same (Brooks 1987).

Because nitrogen is one of the most important plant nutrients, it is necessary to discuss its role in serpentine soils. In order to overcome nitrogen deficiency in serpentine soils, most plant species depend on symbiotic relationships with their roots and surrounding bacteria and mycorrhizal fungi (Campbell and Reece 2002). In all soils, most usable nitrogen (NO_3^-) is derived mainly from organic material in the form of ammonium (NH_4^+) but also from the

atmosphere, and is converted to NO_3^- by way of nitrogen-fixing bacteria. In general, the low overall productivity of serpentine grasslands often results in levels of nitrogen that are likewise low (Brooks 1987). When serpentine grasslands are experimentally fertilized with nitrogen and phosphorus, overall diversity is decreased and the dominance of a few highly competitive species is promoted (Harrison 1999b, Huenneke et al 1990).

Serpentine Grassland Environment

Just as serpentine soil has distinct features, it is not surprising that grassland areas on serpentine soils also exhibit unique vegetation characteristics, creating a noticeable difference of vegetation cover between serpentine and non-serpentine areas. One of the most noticeable differences is the greater biodiversity in serpentine areas. The poor nutrient conditions in serpentine soil areas promote lower productivity and less competition that usually allows a higher number of species to coexist (Turitzin 1982, Huenneke 1990, Harrison 1999). Moreover, species usually found only on serpentine soil are often regarded as poor competitors yet survive because they are able to tolerate low levels of Ca^{2+} (Brooks 1987, Harrison 1999). When compared to non-serpentine grasslands, serpentine grasslands typically have sparse vegetation cover due to the shorter stature of grasses and forbs that result from the combination of toxic and nutrient-poor soil (Brooks 1987, Kruckeberg 1992). The low nutrient levels and xerophytic nature of serpentine environments often result in plants that vary ecotypically and morphologically from non-serpentine soil areas (Brooks 1987).

This environmentally driven phenotypic plasticity is clearly evident within the serpentine landscape. According to Kruckeberg (1992), some of the greatest visual differences between serpentine and non-serpentine grassland species composition can be found in California. The zones where serpentine soil meets non-serpentine soils are usually sharp boundaries with sudden changes in species composition (Mason 1946, Kruckeberg 1992). These boundaries are readily evident due to the high levels of species richness on serpentine soils and the non-serpentine exotic-dominated grassland environment.

Serpentine Soils and Invasive Exotic Grasses

As described in the earlier section on the historical change of California's grasslands, the State's rich biodiversity is now threatened by the introduction and invasion of exotic species (Heady 1988, Mooney 1988). More specifically, much of California's remaining grassland habitats are now dominated by introduced exotic grasses and forbs such as *Avena* sp., *Bromus* sp., and *Lolium* sp., *Hordeum* sp., *Erodium* sp. (Baker 1986, Mooney *et al* 1986, Heady 1988, Huenneke 1990, Kruckeberg 1992, Harrison 1999).

These introduced species commonly outcompete California's native grassland flora in non-serpentine grassland areas and become naturalized, dominant species in these landscapes. In some cases they permanently change the ecological structure of these areas (Heady 1988, Mooney 1988). Because these exotic species are generally less abundant in areas of serpentine soils, presumably due to its toxicity and lack of nutrients (Kruckeberg 1992, Harrison

1999) these environments are often considered “refugia” for native grasses and forbs. Put differently, they may be considered the only remaining areas of California’s native, pre-invasion, grassland flora (Murphy and Ehrlich 1989, Huenneke 1990, Harrison 1999).

However, exotic grasses are now threatening these refugia for two reasons: first, annual grasses are able to adapt to serpentine soil areas in relatively short periods of time, and, second, another direct threat appears in the form of nitrogen deposition. Demographic advantages of the exotic annual grasses such as higher seed output, reduced levels of seed predation, and a large seed bank all contribute to their ability to evolve adaptation to serpentine soils (Jackson 1985, D’Antonio and Vitousek 1992). Nitrogen deposition is the fallout of excess nitrogen onto areas downwind from anthropogenic activities such as transportation, agriculture, power plants, and industry; it can occur either from the air (dry) or by water (wet) (Fenn *et al* 2003).

As a specific threat to diversity on serpentine refugia for native grassland species, nitrogen deposition provides additional nitrogen that can allow exotic grasses to succeed in this otherwise adverse, yet biologically rich environment (Weiss 1999). The extra nitrogen added to the system will change, perhaps permanently, the entire serpentine grassland community (Fenn *et al* 2003). My study area, with its patchy serpentine grassland habitat, lies downwind of the entire San Francisco Bay Area, which results in a high potential for anthropogenic nitrogen deposition. Estimated deposition rates for this study area in south San Jose is one of the highest in the Bay Area, with 10-15 kilograms

of nitrogen per hectare being deposited annually (Weiss 1999). Weiss (1999) has studied the effects of dry nitrogen deposition throughout Santa Clara County and has found that the exotic grass *Lolium multiflorum* is expanding its range onto previously inhospitable parts of the serpentine landscape. As a result, the grass is outcompeting *Plantago erecta*, the main host plant species for the endangered Bay Checkerspot butterfly (Weiss 1999).

Endemism and Rarity in the Serpentine Landscape

Over twenty-four percent of California's flora is considered to be endemics and serpentine endemics make up 10 percent of them (Hickman 1993, Kruckeberg 1984). Edaphic endemics are considered plants that thrive in very local conditions and further, a plant found only on serpentine soils is an excellent example of a narrow (edaphic) endemic (Mason 1946). As noted earlier, these plant species thrive on unique serpentine soils because they can take advantage of reduced competition yet tolerate the low levels of calcium, nitrogen, and phosphorous levels and high levels of magnesium (Kruckeberg 1954 and 1984, Brooks 1987, Harrison 1999). According to Kruckeberg (1992, 59), there are four main types of serpentine plant species:

(1) endemics, narrowly restricted to serpentine [also known as *bodenstets* species (Kruckeberg 1954)]; (2) local indicator species showing high fidelity to but not restricted to serpentine; (3) wide-ranging species that occur in a variety of habitats underlain by both normal (zonal) and ultramafic soils (also known as *bodenvag* species); (4) species that are excluded from ultramafics.

Despite these well-defined classifications, ecologists remain uncertain if plant species commonly found on serpentine soil are endemics or indicator species of serpentine soil environments. As a result, several studies have investigated the dynamic interaction between serpentine endemics and bodenvag species, such as some highly competitive exotic grasses. These serpentine endemics and indicator plant species are weak competitors and have sparse populations (Brooks 1987, Harrison 1999), as evidenced by Kruckeberg's 1954 study on the competitive ability of a serpentine endemic. Kruckeberg (1954) found that *Streptanthus glandulosus*, a congener of the study species, *Streptanthus albidus* var. *peramoenus*, was unable to compete against weed seedlings in non-serpentine soil. However, the weeds were unable to grow in serpentine soil while *S. glandulosus* survived. Additionally, Proctor and Woodell (1975) performed a similar experiment in the field with *Plantago erecta*, an associate of *S. albidus* var. *peramoenus*. Like *S. glandulosus*, *P. erecta* could not survive off serpentine with other species; rather it only survived in plots cleared of other vegetation.

In order to clarify if a plant is a serpentine endemic, several studies have examined the evolutionary history of these plants for clues to their origin. In one analysis of endemism in California's flora, Stebbins and Major (1965) categorized endemics as paleoendemics, or relict species, contrasted with neoendemics, or newly evolved species as a result of a change in the environment of the plant population. Put differently, paleoendemics were once widespread across large areas, including serpentine and non-serpentine, and competitive pressures led to

range contraction resulting in their present disjunct populations (Brooks 1987). Neoendemics, on the other hand, typically exist in single populations that have experienced minimal range expansion (Mayer and Soltis 1994). Mayer and Soltis (1994) researched the evolutionary patterns of the *Streptanthus glandulosus* complex, which includes the study species *Streptanthus albidus* var. *peramoenus*, and found that *S. albidus* var. *peramoenus* is indeed a paleoendemic. This possibility is easily understood when the small, scattered populations in Santa Clara, Alameda, and Contra Costa Counties are considered.

Clearly, the complexities of competition in the serpentine environment are important to understand. Further, Kruckeberg and Rabinowitz (1985) suggest studies should be performed that investigate why serpentine endemics are excluded from more common habitats. Although it has been established that *S. albidus* var. *peramoenus* is an endemic species, there have been no studies investigating this species' competitive abilities in the serpentine environment. Moreover, manipulative experiments in competitive plant removal and seed sowing are few and such an experimental approach should be applied to endemics (Kruckeberg & Rabinowitz 1985). To that end, this study examines competitive effects of exotic species on a rare serpentine endemic plant by way of an exotic removal treatment and seed sowing.

Before describing the study species and the specifics of this thesis research, the concept of rarity must be addressed due to its importance in the serpentine grassland environment. To begin a discussion of rarity, perhaps it is easiest to begin with a description of what is not rare. Logic suggests that a

common, not rare, species is one that is very abundant across several habitats in a broad geographic range. One can infer, then, three aspects of rarity for a species: geographic range, habitat specificity, and the local population size (Rabinowitz 1981). Several different levels of rarity exist depending on the whether a plant's range is large or small, how many different types of habitats it lives in, and how large a population is within that habitat. Serpentine endemics serve as excellent examples of very rare species.

The notion of rarity cannot be clearly separated from that of endemism. While a species may be endemic to a region, that does not make it rare (Kruckeberg and Rabinowitz 1985). *Sequoia sempervirens*, for example, is endemic to the coastal area of California but within that area it is a common conifer (Stebbins and Major 1965). On the other hand, plant species that exist in only a small portion of a geographic province or floristic region are considered rare (Kruckeberg and Rabinowitz 1985), such as the study species. According to Rabinowitz (1981), plants generally become rare as a result of low competitive abilities and their populations are sustained as natural selection favors those traits that allow the population to persist.

For many endemic serpentine plants, small geographic range and limited extent of serpentine soil areas are coupled with narrow habitat specificity within the serpentine soil environment. As a result many of these endemic plants are considered very rare species (Rabinowitz 1981). *S. albidus* var. *peramoenus*, for example, has a very narrow geographic range with only a few populations in Santa Clara, Alameda, and Contra Costa Counties. And, as noted, these

populations are found only on serpentine soils. Further, personal observations indicate the size of these populations is small and very localized. All of these attributes collectively speak to its status as a rare and endemic plant.

Species of Study: *Streptanthus albidus* var. *peramoenus*

Fig. 1. *Streptanthus albidus* var. *peramoenus* (E. Greene) Kruckeb. (All photos by author unless otherwise noted.)

The study species, *Streptanthus albidus* var. *peramoenus* (E. Greene) Kruckeberg (Brassicaceae), commonly called Most Beautiful Jewelflower, is a rare annual found only on areas of serpentine substrate in the San Francisco Bay area (Alameda, Contra Costa, and Santa Clara Counties; Fig. 1). It was originally designated as part of the *Streptanthus glandulosus* complex by Greene in 1906, a group that underwent a revision in its taxonomic treatment in 1958 by Arthur Kruckeberg

(Kruckeberg 1958; Mayer, Soltis, and Soltis 1994b).

Observations of this plant's life history show germination beginning in December and occurring in additional pulses through March. Flowers are borne on racemes beginning as early as late March that develop into long cylindrical siliques with a septum separating two rows of variable numbers of brown-black seeds by June and July. These fruits passively dehisce in late August through September. The seeds are probably gravity and wind-dispersed over short distances due to a wing located on one side of each seed.

This plant is currently listed as “1B” by the California Native Plant Society and is therefore considered rare and endangered. Although the U.S. Fish and Wildlife Service (USFWS) designated the study species as a Category 1 candidate for proposed listing as threatened or endangered in 1990, however, the Category 1 status was dropped in 1996 because a proposal for listing was not provided. Even though many Category 1 species become candidate species, *S. albidus* var. *peramoenus* did not; it is now a USFWS “Species of Concern.”

According to the USFWS Draft Recovery Plan (1998), information about its reproduction (e.g., pollination biology, seed bank dynamics), response to natural disturbances such as fire, and success with various methods of propagation is required in order for land managers to adequately manage this plant and recover its populations (USFWS 1998). Information is also lacking for how this plant interacts with exotic species that coexist in the grassland habitat. Additionally, although the morphology of the study species has been described taxonomically, the plant’s ecology and phenology have not been formally studied. To provide this requisite information, this thesis research aims to document life history information about *Streptanthus albidus* var. *peramoenus*, and, as well, investigate how the plant is affected by the presence of exotic grassland species.

CHAPTER 3

OBJECTIVES AND METHODS

Research Objectives and Hypotheses

The overarching objectives of this study are concerned with the conditions for success of rare endemic plants, as well as the dynamic community interrelationships in the serpentine grassland. The alteration of California's grasslands by exotic species underscores the importance of serpentine soils as refugia for native plant species. Highly competitive effects of exotic grassland species, combined with their rapidly evolving adaptation to exist in unique serpentine soils, have forced native species to retreat even farther within the serpentine soil environment to extremely harsh shallow soil areas amidst rocky outcrops. While rare native plants found only in shallow serpentine soils are now ecologically restricted to this inimical environment due to competition pressure from exotics, they may have once had a much larger historical distribution.

Although it is perhaps impossible to know exactly the composition of California's native grassland communities in their natural state, through experimental manipulations it may be possible to test whether rare native plants now restricted to shallow serpentine soil areas may have once existed in neighboring deep serpentine soil areas currently occupied by exotics. More specifically, one can test whether *Streptanthus albidus* var. *peramoenus*, now restricted to shallow serpentine soils near serpentinite rock outcrops, may have

once had a larger distribution that included deep serpentine soils prior to the invasion by exotic species (Fig. 2).

Soil chemistry can vary greatly within the serpentine soil environment due to geomorphological and topographical characteristics, such as the proximity of the soil to serpentinitic rock outcrops, the amount of time the soil has been exposed for weathering and subsequent plant colonization, and the possibility of alluvial deposition from remote sources (Kruckeberg 1984, Brooks 1987, Harrison *et al* 2001). To this end, quantifying soil chemistry within serpentine grassland environments can explicate differences in microsites such as areas of exotic-dominated deep serpentine soil and areas of native-dominated shallow serpentine soil.

Exotic-dominated grasslands are more densely vegetated compared to the sparsely vegetated and native-dominated areas of shallow serpentine grasslands. The amount of light (Photosynthetically Active Radiation (PAR)) available to plants is directly related to the amount and type of vegetation cover. It follows, then, that light availability plays a large role in defining the interspecific, or between species, competition in these varying environments. Therefore, it is important to measure the amount of light available to experimental populations of *Streptanthus albidus* var. *peramoenus* in deep and shallow serpentine soils.

Soil moisture is also variable in the serpentine soil environment (Brooks 1987), particularly in patchy environments such as the study site that consist of both deep and shallow serpentine soils. Because plant growth can be limited by moisture availability within the soil, and there are vegetative differences in deep

and shallow serpentine soil areas, measuring this characteristic within this study is important.

As such, the objectives of this study address the following questions.

Can populations of *Streptanthus albidus* var. *peramoenus* be expanded from shallow serpentine soils near rock outcrops to deep serpentine soil areas currently dominated by exotic grasses?

Are there differences in soil characteristics in shallow and deep serpentine soil areas that may affect the success of *Streptanthus albidus* var. *peramoenus*, and the surrounding native plant community?

How does the amount of light in shallow and deep serpentine soil areas affect the success of *Streptanthus albidus* var. *peramoenus*?

Is there a difference in soil moisture in shallow and deep serpentine grassland areas?

In order to determine how exotic competitors and soil depth affect *Streptanthus albidus* var. *peramoenus* and its surrounding plant community, five hypotheses are tested in this study.

H₁: Exotic species have a significant effect on germination of *Streptanthus albidus* var. *peramoenus* in both deep and shallow soils.

H₂: Exotic species have a significant effect on survivorship of *Streptanthus albidus* var. *peramoenus* in both deep and shallow soils.

H₃: Exotic species have a significant effect on fecundity of *Streptanthus albidus* var. *peramoenus* in both deep and shallow soils.

H₄: Soil type has a significant effect on native species richness and percent native cover.

H₅: Exotic species have a significant effect on native species richness and percent cover of native species in both shallow and deep soil types.

Fig. 2. Serpentine grassland landscape. *Streptanthus albidus* var. *peramoenus* is currently found in the shallow soils associated with the rocky serpentine outcrop as shown in the foreground. It may have once had a larger distribution in the deep soil areas currently dominated by exotic species.

Study Area

This study was conducted in areas of patchy serpentine grassland in the San Francisco Bay area, California within a 273 hectare property located at 37° 09' 053" N and 121° 47' 041" W at an average elevation of 335 meters (Fig. 3). Located in the Central Coast region of California, the climate is Mediterranean, with most

of the rain occurring between the months of October through April (Fig. 4). The dry season is typically late May through September or early October. As a result, the winter (wet) growing season is from late October or early November through late May or early June.

Fig. 3. Serpentine grasslands present in the study area.

Fig. 4. Climograph of San Jose, Santa Clara County, California.

The property, located in the northeastern portion of the Santa Cruz Mountains, was purchased from a private land owner by the Santa Clara County Open Space Authority (SCCOSA) in Fall of 2000 and has remained closed to the public for resource analysis since that time. Sporadic cattle grazing occurred on the property for 70 years until the SCCOSA purchased the property (Pat Congdon, personal communication). Although flora in many serpentine grasslands in California have been negatively affected by overgrazing (USFWS 1998), native serpentine flora have persisted. The study area was used by the previous owner to host outings for individuals and groups hunting quail, doves, turkeys, and deer. A road bisecting the property was built in approximately 1985 to 1990 (Pat Congdon, personal communication). Use of the road has remained minimal over the years, and it now serves as the primary access to the property for the SCCOSA and researchers (Fig 5). This study was part of the initial resources analysis performed

Figure 5. A satellite picture of the South San Francisco Bay Area with the study area circled in red showing its relationship to the greater San Jose area and Santa Clara Valley. (Photo courtesy of NASA)

by the SCCOSA.

Although the property consists of rolling hills and steep terrain covered by oak woodland, chaparral, grassland areas, the grassland experiments were performed solely on serpentine soils. These serpentine grassland areas are patches between approximately one-half to four hectares, and are located predominately along grassy ridges within a mosaic of oak woodland, manzanita, and chaparral scrub communities. The serpentine grasslands used for this experiment consists of both shallow serpentine soils amidst serpentinite rock outcrops and deep serpentine soils that are near, but not among, the outcrops.

Research Design

To test the hypotheses, I used a small-scale factorial experiment and manipulated the presence of exotic plant species on two soil types, shallow and deep. Forty-eight randomized rectangular $.5 \text{ m}^2$ (1m x .5m) plots were established on three small patches of serpentine grassland habitats (subsequently referred to as Sites 1, 2, and 3) within the larger study area. Sixteen plots were located at each of the three sites, with eight plots located on shallow soil and eight plots located on deep soil (Fig. 6).

I established all plots based on personal observation of major vegetation differences in three separate but generally homogenous sites of patchy serpentine grassland. Shallow soil was determined by the proximity of

Layout of One Plot

Fig. 6. Research design. Layout of plots and a visual depiction of a single plot with the sowing grid enlarged.

serpentinite rock outcrops, predominance of gravel in the soil, and the presence of *Streptanthus albidus* var. *peramoenus* and other serpentine endemic species [*Dudleya setchellii* (Santa Clara Valley *Dudleya*), *Lessingia micradenia* var. *glabrata* (Smooth *Lessingia*), *Linanthus ambiguus* (Serpentine *Linanthus*)]. Soil in these areas was gravelly and shovel test pits could not penetrate more than 10 cm because of the shallow soil depth.

Deep soil plots were established in areas with high percent cover of vegetation that were dominated by exotic annual grass species, and where shovel test pits of at least 30 cm deep could be performed. Soil samples were taken at each of the six general plot locations (shallow and deep at each of the three sites) to determine soil characteristics. The soil testing process is described further in the data collection section.

Field reconnaissance is commonly used as a method of placing plots in serpentine grassland experiments because vegetative differences and unique patterns in species composition indicate the presence and absence of serpentine soil (Kruckeberg 1985, Harrison *et al* 2001). Further, the habitat of a rare species, such as the study species, at the landscape level is expected to be distinct and conspicuously contrast with neighboring habitats (Kruckeberg and Rabinowitz 1985). To this end, differences in vegetation and habitat characteristics between shallow and deep serpentine soil areas are readily recognizable at the study site. However, Proctor and Woodell (1971) did note serpentine soils are highly variable depending on the particular chemical and mineral makeup of the parent rock, serpentinite. Further, Harrison *et al* (2001) noted that serpentine alluvium, or soil “runoff” from patches of serpentine soil, could confound the effect serpentine soil has on vegetation in non-serpentine soil at the landscape level. As a result, the sharp boundaries of vegetation type that typically occur in patchy serpentine environments may be obscured.

On November 10, 2002, the 48 plots were permanently marked with wood stakes. Within each soil type, exotic plants were removed in four of the eight

plots at each of the three sites, chosen randomly, immediately following the first rain of the season (November 7, 2002). I performed subsequent exotic removal treatments approximately every six weeks. During fieldwork, I concluded that to remove the exotics prior to tabulating the cover and richness data would not provide an accurate depiction of what occurred at the community level regarding native species recruitment and exotic species invasion. This method follows that used by Miller and Duncan (2004) who removed reinvading weeds from exotic removal plots when plots were monitored for germination.

I used vegetative characteristics to identify grass seedlings early in the season before they started flowering, including ligules, auricles, collars, leaf blade ribs, leaf shape, node shape, presence of trichomes and hairs, stems or culms (hollow or solid or rolled), sheaths (open or closed), the throat (overlapped and/or had hairs), and characteristics of the seed attached to the seedlings, if available. Conservative measures dictated that I remove the seedlings only when completely identified so if I was unable to identify a seedling based on vegetative characteristics at the time, I either waited until additional vegetative characteristics appeared as the seedling grew or until the species flowered. If I was unable to identify a plant early in the season, I waited until the plant flowered so I could properly identify it. If it was an exotic species, I removed it at that time and in subsequent treatments.

Fig 7. Nodes of grass seedlings in March 2003. The auricles, or small appendages of (a) *Hordeum murinum* ssp. *leporinum* are visibly different from (b) *Lolium multiflorum*.

Within each of the 48 plots, I sowed 50 *S. albidus* var. *peramoenus* seeds on November 15, 2002 at an approximate depth of 2 mm. Seeds were sown using a wood grid to ensure accurate placement and subsequent monitoring of germination, seedlings, and plants. The wood grid had fifty 2.5 cm diameter holes (in a 10 x 5 pattern), and one seed per hole was placed for a total of 2,400 seeds (Fig. 8). This method follows field methods utilized by Pavlik (1993), McGraw (2004), and Menges (personal communication) in ecological studies that evaluate experimental treatment effects on the demographic performance of rare and endangered plants.

The source seed was collected July 22 and 23, 2002 from naturally-dehiscing fruits and, due to the rarity of the study species, no more than five percent of a single plant's seed was collected. The seeds were collected from plants located in a disturbed road cut area near two of the grassland study sites

in order to minimize any damage to the population of *S. albidus* var. *peramoenus* occurring in the nearby grassland.

In order to ensure the seeds sown in the plots experienced growing conditions that were similar to the surrounding grassland vegetation (which

Fig. 8. Seed grid.

received rainfall on November 7, 2002), water was applied when no rain was forecast for at least ten days following the sowing treatment. Using a 3 gallon capacity polyethylene sprayer (Fig. 9), approximately one half gallon of water was sprayed in each plot in the area of the sowing grid after the exotic

removal treatment and seed sowing. Rain gauges were set up December 7, 2002 (two at each study site for a total of six) to obtain a more accurate measure of precipitation throughout the study.

I used Hitchcock (1969) and Hickman (1993) to identify vegetative characteristics of grasses and the following sources to identify flowering grasses and herbaceous species: Beidleman and Kozloff (2003), Corelli and Chandik (1995), Crampton (1974), Hickman (1993), Munz (1959),

Fig. 9. Polyethylene sprayer.

Matthews (1997), Robbins (1970), Thomas (1961), the Grower's Weed Identification Handbook from the University of California's Division of Agriculture and Natural Resources (1998), and Whitson (2002).

At the conclusion of the study, all experimental plants were removed July 8, 2003.

Data Collection

Based on the life history of *S. albidus* var. *peramoenus*, I collected data in four census periods, six weeks apart, during the weeks of February 10, March 24, May 5, and June 11, 2003. I measured ten variables for each of the 2,400 experimentally sown seeds, from germination to mortality (Table 1). Naturally occurring *S. albidus* var. *peramoenus* plants in the plots were not measured.

Table 1. *S. albidus* var. *peramoenus* variables measured.

date of germination (date first observed)	number and length of inflourescences (flowering stems)
survivorship	number of flowers
plant height	number of fruits
number of leaves	longest fruit length
longest leaf length	number of seeds per fruit per plant

At each census date, I used visual estimation to collect the percent cover of each species as well as the overall percent native cover and percent exotic cover in each plot. Percent cover data were collected before exotics were removed for each experimental plot in order to obtain an accurate picture of the serpentine grassland community. Total species richness (total number of species), exotic

species richness, and native species richness were also collected for each plot during each census period.

Because chemicals vary greatly within the serpentine soil environment (Brooks 1987), quantifying soil characteristics was a key component to this study. I categorized soil cover class information by adapting the California Native Plant Society Vegetation Sampling relevé methodology, using the following variables:

finer: includes sand, mud	stone: 25> diameter
gravel: >0.3, <10 cm diameter	bedrock
cobble: 10-25 cm diameter	litter: organic matter covering ground.

Amounts of cations, elements, and cation exchange capacity were measured in soil tests throughout the study (Table 2). In summer of 2003, I collected a total of six liter-sized samples, one for each soil location (deeper and shallow) at each of the three sites. I gathered soil from three areas within each soil location and homogenized them into one sample, following a procedure recommended by Soil and Plant Laboratory, Santa Clara, California. The following season in July 2004, an additional 20 soil samples were collected from 10 randomly selected plots in both deep and shallow soils. These samples were tested for Ca^{2+} , Mg^{2+} , K^+ , and sodium (Na^+).

Table 2. Characteristics measured in 2003 soil tests.

Nitrogen (NO_3^-)	Ammonium (NH_4^+)
Phosphorus (P)	Potassium (K^+)
Calcium (Ca^{2+})	Magnesium (Mg^{2+})
Iron (Fe)	Nickel (Ni)
Overall Cation Exchange Capacity (CEC)	CEC for % Ca^{2+} and % Mg^{2+}

Sequoia Analytical (Morgan Hill, CA) performed the tests for Nickel (Ni) and Cation Exchange Capacity (CEC). Soil and Plant Laboratory, Inc. in Santa Clara performed all remaining tests. Permission to collect soil was granted by the Santa Clara County Open Space Authority (Pat Congdon, personal communication).

Soil depth was also measured in every plot. Depending on soil depth, 20 to 60 strikes were made with a two-pound sledge hammer on a 1.7 cm diameter steel rod at least two areas within each plot. Due to variability of soil depth within the serpentine grassland environment (Brooks 1987), particularly in shallow soil plots (personal observation), multiple depth measurements per plot were made in order to obtain an average depth.

On March 11, 2003, I measured the amount of Photosynthetically Active Radiation (PAR) available to plants in each plot (PAR is the energy between 400 and 700 nm of the electromagnetic spectrum) using sensors and dataloggers manufactured by LiCor (LI-190SA sensor, LI-1400 datalogger, 2003S Mounting and Leveling Fixture, and the

Fig 10. LiCor-1400 Datalogger, LI-190SA sensor with mounting and leveling fixture. (Photo courtesy of Li-Cor, Inc.)

standard 10 ft (3.0 m) cable) (Fig. 10). PAR data were collected as a way to gauge the amount of evapotranspiration the study species was experiencing in each treatment type as well as the amount of light available to the plants. Early to mid March appeared to be a crucial point for the survival of *S. albidus* var. *peramoenus* germinants (personal observation). PAR was measured in micromoles of quanta per second per square meter ($\mu\text{mol/s}^2/\text{m}^2$). The accuracy of the sensor is calibrated to within $\pm 5\%$ traceable to the National Institute of Standards and Technology.

Soil moisture measurements were attempted in all plots in both deep and shallow soils, and were scheduled to continue throughout the duration of the study. Two types of soil moisture meters were used: a Kelway Soil pH and Moisture Meter and a Time Delay Reflectometer (TDR) with 20cm rods. Neither unit was able to measure soil moisture for shallow soils due to the insufficient soil depth. Another possible reason the units were not able to measure soil moisture in these shallow soil areas was because there was a high amount of gravel that may have precluded soil from completely surrounding the unit and/or probes, which is required to obtain a reading.

Statistical Analyses

I used a two-way analysis of variance (ANOVA) to test the response of *Streptanthus albidus* var. *peramoenus* germination to the exotic removal treatment and soil type (SPSS for Mac OS X 2003). Similarly, I used a repeated measures ANOVA to test for exotic and soil effects on percent native and exotic cover as well as overall, native, and exotic species richness over the four census periods

performed during the experiment. The model used included Exotics, Soil, and the interaction between Exotic and Soil. I transformed the germination data using logarithm to the base ten and proportional percent cover data using arcsin-square root (Gotelli 2004, Zar 1999). All data tested quantitatively are given as $\pm$ 1 standard error of the mean (Gotelli 2004) and confidence limits were set at 95% ($\alpha = .05$).

For survivorship and fecundity data, I made qualitative comparisons by examining the number of seeds experimentally sown, the number of those seeds that germinated and survived, and the number of new seeds that were produced by survivors.

All soil test results were analyzed qualitatively except for the soil collected in July 2004. The results of the later samples were analyzed using a t-test to determine if the difference in cations available to plants in the 10 randomly chosen shallow plots and 10 randomly chosen deep plots was statistically significant.

CHAPTER 4

RESULTS

This chapter presents the research results both qualitatively and quantitatively. Information regarding the fitness of *Streptanthus albidus* var. *peramoenus* in the various treatments is presented first, and includes sections on germination, survivorship, and fecundity. This section on the plant's demography tests the first three hypotheses. In the second section, Community Effects, hypotheses four and five are tested. Within that section, the vegetation cover portion includes overall percent cover, percent native cover, and some information on the percent cover of certain rare species found in this serpentine grassland community. The community level results also include a portion on species richness that addresses overall species richness, native species richness, and exotic species richness. Finally, a section on physical factors includes the results of soil tests and analyses, as well as data on available photosynthetic light.

Streptanthus albidus var. *peramoenus* Demography

Germination

Overall, exotic removal stimulated *S. albidus* var. *peramoenus* germination in both deep and shallow soils (2-way ANOVA, $F_{1,35} = 6.880$, $p < 0.013$), but the effect was greater in deep soils than in shallow soils (2-way ANOVA soil depth

by exotic removal, $F_{1,35} = 5.438$, $p < .026$) (Fig. 11; Table 3). Soil depth alone was not significantly different for germination.

Germination rate was highest in deep serpentine soil exotic removal plots, with 11.8% of the 600 sown *S. albidus* var. *peramoenus* seeds germinating, and the lowest rate was in deep soils with exotics present, with 1.2% of sown seeds germinating.

Figure 11. Mean and standard error for germination of *S. albidus* var. *peramoenus* for both exotic removal and soil depth treatments effects.

Survivorship

An experimentally sown plant was considered to have survived if it lived long enough to produce a seed-bearing fruit. Out of the 2,400 *S. albidus* var. *peramoenus* seeds sown, only 32 (1.3%) plants survived to produce seed for the

following year's population (Fig. 12, Table 3). In deep soils, no plants survived to produce flowers with exotics present, while 12 plants survived to produce fruits with seeds where exotics were removed. In shallow soils, five plants sown with exotics survived to produce seed-bearing fruit, and 15 plants survived to produce fruit with seeds with exotics removed. Due to the low number of survivors, inferential statistics were not applied to these data.

Fig. 12. Survivorship of *S. albidus* var. *peramoenus*.

Fecundity

Fecundity was determined by the number of seeds produced by each experimental plant that survived. Across all soil types, with and without exotics, the experimental *S. albidus* var. *peramoenus* population produced a total of 2,225 seeds (Fig. 13). Because no plants survived in deep soil with exotics, no seeds were produced. In exotic removal plots in deep soil, 96 seeds were produced.

Plants grown in shallow soil produced 2,129 seeds, with 466 seeds produced in shallow soil with exotics and 1,663 seeds were produced in shallow soil without exotics (Table 3). Due to the low number of plants that produced seed, inferential statistics were not applied to the fecundity data.

Fig. 13. Fecundity of *Streptanthus albidus* var. *peramoenus*.

Table 3. Demography of experimental population of *S. albidus* var. *peramoenus*. The number of germinants, survivors, and fecundity of *S. albidus* var. *peramoenus* are provided for each treatment combination.

	Seeds Sown	Germination	Survivorship	Fecundity
Deep soil no Exotics	600	70 (11.8%)	12	96
Deep soil with Exotics	600	7 (1.2%)	0	0
Shallow Soil no Exotics	600	48 (8%)	15	1663
Shallow Soil with Exotics	600	34 (5.7%)	5	466
TOTALS	2,400	159	32	2225

Community Effects

Vegetation Cover

While overall percent cover was consistently low in shallow soil, the highest overall percent cover occurred in deep soil plots with exotics (Fig. 14). Two-way ANOVA results confirm that overall percent cover was significantly higher in deeper soil than in shallow soil and where exotics were present rather than removed, but the effect of the exotic removal treatment was stronger in deep soil (exotics: $F_{(1,42)} = 31.313$, $p < .0001$; soil: $F_{(1,42)} = 5.953$, $p < .02$; exotic*soil: $F_{(1,42)} = 4.109$, $p < .05$).

Fig. 14. Overall percent cover at peak season.

Shallow soil showed consistently greater percent native cover throughout the growing season, in both exotic species treatments (Fig. 15). Percent native cover was significantly higher in shallow soils than deep soils when exotics were

removed. Further, both shallow soils with exotics and deep soils with exotics removed had significantly higher percent native cover than deep soil plots with exotics (census 1: $F_{1,42} = 42.837$, $p < 0.0001$; census 2: $F_{1,41} = 36.804$, $p < 0.0001$; census 3: $F_{1,41} = 41.026$, $p < 0.0001$; census 4: $F_{1,40} = 20.892$, $p < 0.0001$). By June, almost no exotic species had survived in the shallow soil plots, and they had been removed from all exotic removal plots, resulting in percent native cover figures $>91\%$. Further, only native species had survived in shallow soil plots at this time. The effects of exotics and the exotics by soil interaction effect were not statistically significant for percent native cover in any one census period. A repeated measures ANOVA showed the effect of soil depth ($F_{1,41} = 47.118$, $p < 0.0001$) was significant and the effect of exotic removal ($F_{1,41} = 2.937$, $p < 0.094$) showed a strong trend for percent cover of native species through the duration of the field season (Fig. 15).

Fig. 15. Mean percent native cover over time for each treatment combination.

In addition to *S. albidus* var. *peramoenus*, three rare plants appeared in the plots: *Calystegia collina* ssp. *venusta* (South Coast Range Morning Glory, perennial), *Lessingia micradenia* var. *glabrata* (Smooth Lessingia, annual), and *Linanthus ambiguus* (Serpentine Linanthus, annual). The rare plant *C. collina* ssp. *venusta* was found only in shallow soil plots and most often accounted for no more than five percent of the overall vegetation in the plot. Species *L. micradenia* var. *glabrata* was more prevalent throughout the array of plots in all four census periods. As a seedling in the first census (February), *L. micradenia* var. *glabrata* made up 15% of vegetation in 23 out of the 24 shallow soil plots while it accounted for no more than 5% of vegetation in four deep soil plots without exotics. Over the course of the growing season *L. micradenia* var. *glabrata* increased in cover, up to 10% in deep soil plots without exotics and up to 20% in shallow plots (with and without exotics), with the largest percent cover occurring in shallow plots with exotics removed. Serpentine Linanthus (*Linanthus ambiguus*) was found only in shallow soil with no exotics during March through May and never accounted for more than 5% of the vegetation cover in the plot. Naturally recruiting *S. albidus* var. *peramoenus* appeared in only in shallow soil plots, both with and without exotics, throughout the growing season and accounted for 5% or less of the vegetation.

Species Richness

Shallow soil supported significantly more species overall than did deep soil throughout the growing season (2-way ANOVAs, census 1: $F_{1,42} = 19.941$, $p < 0.0001$; census 2: $F_{1,41} = 27.464$, $p < 0.0001$; census 3: $F_{1,41} = 36.662$, $p < 0.0001$; census 4: $F_{1,40} = 7.111$, $p < 0.0001$; repeated measures ANOVA, $F_{1,41} = 22.511$, $p = 0.001$; Fig. 16). Exotic removal had no detectable effect on overall species richness in either soil type.

Fig. 16. Overall species richness (both native and exotic species) throughout the growing season across treatments.

Most of this species richness was due to native species richness in shallow soil (2-way ANOVAs census 1: $F_{1,42} = 46.753$, $p < 0.0001$; census 2: $F_{1,41} = 47.496$, $p < 0.0001$; census 3: $F_{1,41} = 58.723$, $p < 0.0001$; census 4: $F_{1,40} = 13.194$, $p = 0.001$; repeated measures ANOVA, $F_{1,38} = 37.673$, $p < 0.0001$; Fig. 17). Exotic species

Fig. 17. Native species richness over time.

richness was significantly lower in shallow soils throughout the growing season (2-way ANOVAs, soil depth, census 1: $F_{1,42} = 20.961$, $p < 0.0001$, strong trend in census 3: $F_{1,41} = 3.794$, $p < 0.058$, census 4: $F_{1,41} = 14.681$, $p < 0.0001$; repeated measures ANOVA, soil depth, $F_{1,41} = 13.597$, $p = 0.001$; Fig 18). Further, in the second census period at peak season for exotic annual grasses, deep soil control plots where exotics were not removed showed a higher exotic species richness than deep soil treatment plots. Exotic removal had no detectable effect on native or exotic species richness in either soil type.

Fig. 18. Exotic species richness over time.

Physical Factors

Soil Characteristics

The cation exchange capacity (CEC) of all soil samples was in the normal range for silt/ clay soils (Table 4) and showed a moderate concentration of exchange sites. The base exchange capacities for Ca^{2+} were consistently lower than those for Mg^{2+} and, as a result, had low Ca^{2+} to Mg^{2+} ratios.

Saturation extract analyses were performed to measure pH and the amount of other elements, including Ca^{2+} and Mg^{2+} (Table 5). The pH level is only slightly acidic. The Ca^{2+} to Mg^{2+} ratio for these tests is included in the table as well. Ca^{2+} levels were consistently lower than Mg^{2+} levels in each plot location, however, the results were not consistent between sites. For example, Site 1 shallow soil showed the same amount of Ca^{2+} as Site 2 deep soil, while the deep

soil sites in general shows higher levels of Ca^{2+} overall. A t-test indeed showed a significant difference in Ca^{2+} levels between deep and shallow soils ($F_{1,18} = 10.269$, $p = 0.005$; Fig. 19). Deep soils had higher levels of Mg^{2+} than the shallow soils; the mean level of Mg^{2+} for deep soils was 45.4 and 20.8 for shallow soils. A t-test of Mg^{2+} levels in deep and shallow soils did not show a significant difference. For nickel, Site 3 showed the largest difference between shallow and deep soil areas (2900 mg/kg and 820 mg/kg, respectively). There were not enough soil samples to run a t-test for nickel.

Table 4. Soil characteristics. The cation exchange capacity (CEC) of each soil sample, the percent of Ca^{2+} and Mg^{2+} of the total soil CEC, and their $\text{Ca}^{2+}:\text{Mg}^{2+}$ ratio.

	Overall CEC (meq/100 gm)	% Ca^{2+} of CEC	% Mg^{2+} of CEC	$\text{Ca}^{2+}/\text{Mg}^{2+}$ ratio
Shallow	21.5	27.9%	69.3%	.40
Shallow	31.5	19.4	79.3	.24
Shallow	29.1	25.8	71.2	.36
Deep	38.0	41.6	56.9	.73
Deep	33.9	23.0	75.1	.31
Deep	28.5	39.2	58.9	.67

Potassium was higher in shallow soils (mean = .150 meq/1) than in deeper soils (mean = .110 meq/1). Further, a t-test showed there was a marginal statistical difference between shallow and deep soils ($F_{1,18} = 4.235$, $p = 0.054$). Mean levels of sodium were higher in deeper soils (mean = 1.090) and lower in shallow soils (mean = 0.850). This difference was statistically significant according to a t-test ($F_{1,18} = 5.434$, $p = 0.032$; Fig. 20).

Table 5. Saturation extract analyses for 2003 soil tests. All results are reported as parts per million (ppm) except Nickel, which is reported as mg/kg, and pH.

	Shallow			Deep		
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
pH	6.5	6.8	6.5	6.9	6.7	6.4
Calcium, Ca^{2+}	16.3	11.2	14.8	34.3	16.4	25.2
Magnesium, Mg^{2+}	19.5	21.0	21.8	52.2	52.4	31.6
$\text{Ca}^{2+}/\text{Mg}^{2+}$ ratio	.84	.53	.68	.66	.31	.80
Phosphorus, P	.23	.13	.22	.35	.30	.27
Potassium, K	5.10	4.15	5.35	4.28	4.10	4.78
Iron, Fe	.37	.19	.57	.22	.16	.32
Nickel	650	1900	2900	870	1000	820

Fig. 19. Mean calcium levels in deep and shallow soil.

Fig. 20. Mean sodium levels in deep and shallow soil.

Mean soil depth in shallow soil plots was 14.4 cm and 30.3 cm in deep soil plots. A t-test confirmed this difference as statistically significant ($F_{1,44} = 204.44$, $p < 0.0001$; Fig. 21).

Fig. 21. Mean soil depth in deep and shallow plot areas.

Light Levels

Germination of *S. albidus* var. *peramoenus* was less in low amounts of photosynthetically active radiation (PAR) and higher when amounts of PAR were above about $1500 \mu\text{mol/s}^2/\text{m}^2$. Deep soil plots with exotics had a mean PAR level of $573.28 \mu\text{mol/s}^2/\text{m}^2$ while the total mean PAR in deep soil plots with exotics removed was $1571.86 \mu\text{mol/s}^2/\text{m}^2$, a significant difference resulting in $998.58 \mu\text{mol/s}^2/\text{m}^2$ (2-way ANOVAs, exotic removal: $F_{(1,41)} = 26.535$, $p < .0001$; soil depth: $F_{(1,41)} = 25.948$, $p < .0001$; exotic removal by soil depth interaction: $F_{(1,41)} = 18.026$, $p < .0001$; ANCOVA with PAR as a covariate for germination, exotic removal: $F_{1,41} = 9.880$, $p = 0.003$; exotic removal by soil depth interaction effect: $F_{1,41} = 5.105$, $p = 0.029$; Fig. 22). Mean PAR levels in shallow soil plots were high in both exotic removal treatments, with $1565.77 \mu\text{mol/s}^2/\text{m}^2$ in plots with exotics and $1662.00 \mu\text{mol/s}^2/\text{m}^2$ in plots without exotics.

Fig. 22. Amount of Photosynthetically Active Radiation (PAR) in deep and shallow soils for treatment and control plots. PAR units are $\mu\text{mol/s}^2/\text{m}^2$.

CHAPTER 5 DISCUSSION

This section discusses whether the results presented in the previous chapter confirmed the hypotheses for this study. Briefly, the results from this factorial experiment did indeed validate the first and fourth hypotheses. However, there was not enough data to run statistical analyses for the second and third hypotheses so these were qualitatively analyzed. The fifth hypothesis was not validated. These results are explained in detail.

First I explain the demography of *Streptanthus albidus* var. *peramoenus* with regard to the first three hypotheses that test the effect of exotic species on this plant's germination, survivorship, and fecundity, respectively. Next I discuss the effects of the experimental treatments at the community level. Hypotheses four and five state that both soil type and exotic species, respectively, had a significant effect on both native species richness and percent native cover. Lastly, I look at the physical effects present in the experiment, including soil characteristics, light levels, as well as patch dynamics. While hypotheses were not advanced for any of the physical effects, this discussion is relevant to the plant's context in the serpentine grassland community.

Streptanthus albidus var. *peramoenus* Demography

Germination

As hypothesized, germination of *S. albidus* var. *peramoenus* was clearly successful in deep soil areas with no exotic species and in shallow soil areas with

and without exotics. Lowest success occurred in the deep soil control plots where exotics were present. Not surprisingly, germination success was low in deep soil plots with exotics, an environment that had a mean percent cover of 94.5%, with over 80% of that cover comprised of exotic species at peak growing season. The similarity of germination success in shallow soil control and exotic removal treatment plots is probably a result of the low overall vegetation cover of the shallow soil areas and less interspecific competition. It should be noted that no *S. albidus* var. *peramoenus* plants are naturally found in deep serpentine soil areas dominated by exotic species, rather, these plants are restricted to shallow soils near rocky outcrops.

A similar study with an exotic removal treatment and sown seeds of a rare species [*Pachycladon cheesemanii* (Brassicaceae)] by Miller and Duncan (2004) showed similar results. In exotic removal treatment plots in open rocky outcrops, germination rates ranged between 2.1% to 8.4% of total seeds sown. Further, the rate of germination in exotic-dominated grassland plots was very low at 0.2% of total seeds sown.

The fact that *S. albidus* var. *peramoenus* germinated most successfully in areas without exotics provides substantial evidence that it is restricted to the most inimical areas of the serpentine grassland environment due to competition from exotics. This finding confirms previous research that several native species found abundantly on serpentine today are commonly found in sparse amounts, if at all, on non-serpentine because of high levels of competition from exotic grasses and forbs (Huenneke 1990). Further, Baskin and Baskin (1988) also found

that edaphic endemics can grow equally well in deep and shallow (“outcrop”) soil types, and it is competition that restricts these species to shallow soils rather than needed biological requirements.

Survivorship

Qualitatively, exotic species did have an effect on those plants sown in deep soils because the highest survivorship occurred in deep soil plots without exotics and no plants survived in deep soil plots with exotics present. The six plants that did manage to germinate in deep soils with exotics present were all etiolated and died early in the season. In shallow soil areas, survivorship was higher in experimental plots where exotics were removed. It follows, then, that, as hypothesized, exotic species did have a large effect on survivorship in deep soils while the effect of exotic species in shallow soils was less noticeable.

Several of the sown plants in the deep soil plots without exotics produced flowers that also resulted in sterile, unfertilized, fruits. Moreover, these plants were sown in experimental plots established in deep serpentine soil grassland dominated by exotic grasses, as opposed to where these plants are naturally found: in shallow serpentine soil areas rich in native, non-grassy species. Because the exotic grasses in the deep soil areas essentially create a monoculture with few flowering species to attract pollinators, it is possible, therefore, that the sterile fruits on the sown *S. albidus* var. *peramoenus* plants in deep soil areas could be caused by the absence of requisite pollinators.

In a related study, Wolf (2001) found the serpentine endemic *Calystegia collina*, a rare plant and an associate of my study species, had significantly lower fruit production in small patches than in large swaths of serpentine grassland even though there were no differences in the number of pollinators or the number of pollinator visits between these two areas. However, Wolf did speculate that pollinators in large outcrops were more likely to be carrying compatible pollen. The issue of pollination of *S. albidus* var. *peramoenus* may be confounded by the fact only a few populations of the plant exist, do not consist of large numbers of plants, and often occur on small patches of serpentine soil.

Fecundity

The low number of seeds produced in deep soil areas when exotics were experimentally removed could be due to the absence of *S. albidus* var. *peramoenus* pollinators, or, lack of compatible pollen, as several of the fruits recovered from plants in these areas were sterile and did not produce seed. Wolf (2001) demonstrated that lower reproductive success of *Calystegia collina*, an associate edaphic endemic of the study species, received significant amounts of incompatible pollen from other populations on neighboring small patches of serpentine. Further, patchiness of the serpentine grassland environment is inherently fragmented, and fragmented habitats have been known to reduce fecundity levels in plants (Hobbs and Yates 2003).

Low fecundity could also have resulted from the presence of micro-organisms in the deep soil areas. Previous research has found that root rot as a

result of soil-borne fungi negatively effected plant fecundity (Erneberg 2002). Further, in the benchmark 1957 study, Tadros contended that the presence of such microorganisms is dependent on calcium levels; they were only present in areas with soil higher in calcium. In this study, although deep serpentine soils had a low calcium to magnesium ratio, these areas had significantly higher calcium levels than the shallow serpentine soil areas. One can infer, then, that microorganisms would be more likely to exist in deep serpentine soil areas of the study site, and not in shallow serpentine soil areas. The presence of microorganisms, then, could have caused the low seed production in sown *S. albidus* var. *peramoenus* plants in deep serpentine soil areas.

Lastly, the low fecundity in deep serpentine soil exotic removal plots could have been a result of competition from exotic grass seedlings appearing in the six-week intervals between exotic removal treatments and data censuses. Exotic grass competition has been shown to reduce not only plant size and survivorship, but also reproductive output (Pavlik *et al* 1993, Miller and Duncan 2004). As hypothesized, raw numbers show that exotic grassland species did indeed reduce fecundity in both deep and shallow serpentine soils.

Community Effects

Soil depth did not have a significant effect on percent cover of exotic species but did have a significant effect on percent cover of native species and native species richness. It is interesting to note that percent native cover was

approximately 60% greater in deep soil without exotics than deep soil with exotics at peak season.

Did the exotic species removal treatment have a significant effect on both native species richness and percent cover of native species in both soil depths? While percent native cover was greater in shallow soil plots than deep soil plots, there was no significant result for the exotic removal treatment in either soil type. The increase in percent native cover from deep to shallow soils was possibly not great enough to detect an effect of exotic removal. This could be due to collecting percent cover data at the end of each six-week period, which was before I removed exotics. To illustrate, several deep soil exotic removal plots were inundated with exotic grass seedlings at the time of data collection, and these plots included in the percent cover data for that plot (Fig. 23). The larger number of exotic species in exotic removal plots in deep soil in the beginning of the growing season likely occurred because the resulting reduction in competitive pressure allowed more types of exotic species to coexist in the same area.

While all treatment effects were significant for overall percent cover, only the effect of soil was significant for overall species richness. Further, overall species richness at peak season hovered between 10-16 species per half-meter square plot, regardless of soil and exotic removal treatments. This figure is similar to Harrison's (1999b) finding that in areas of serpentine and nonserpentine grassland, the number of species was consistently between 10-15 per m². Although plots in my study all occurred in various types of serpentine

soil, the deep and shallow soil environments were significantly different in terms of species richness. For example, in May, when the majority of *Streptanthus albidus* var. *peramoenus* are in bloom, deep soil supported an average of 8.5 species while shallow soil supported an average of 14 species. Overall richness dropped at the end of the season as the number of annual plants perished, as the exotic annual grasses and forbs would have run their course by the end of the growing season. In this study, there were no exotic species alive in shallow soils and only one exotic species present in deep soil plots by the fourth census period at the end of the growing season in June.

Fig. 23. Photographs of an experimental deep soil plot in March. *a*, This is the vegetation that was censused after the first six-week period (the plot is marked by four wood stakes; the flag is in the bottom right corner); *b*, the same plot after I performed the exotic removal treatment.

One possible explanation for higher native species richness in shallow soil plots is that deep soil plots have been invaded by exotics for a long time and therefore would not support a seed bank for naturally recruiting native species. Moreover, the shallow soil plots support plant associations high in native species

and accordingly would have a seed bank high in native seeds, thereby allowing for natural recruitment to occur.

Physical Effects

Soil Characteristics

An atmosphere of debate exists among researchers as to whether it is Ca^{2+} or Mg^{2+} that limits plant growth in the serpentine environment. One of the first researchers to address this question was Walker in 1954. He found that low Ca^{2+} levels was the most limiting factor in the serpentine soil environment. However, because experiments performed by adding Ca^{2+} resulted in no significant effect on plant growth, several researchers have concluded it is the high level of Mg that is the limiting factor in limiting overall productivity (Brooks 1987, Turitzin 1982). Further, some studies have shown magnesium to actually inhibit the uptake of Ca^{2+} by plants (Brooks 1987). However, according to Turitzin (1982), low calcium levels may still serve as a limiting factor by excluding exotic species from invading serpentine areas. Harrison (1999) confirmed that speculation by providing evidence that under high levels of Ca^{2+} exotic species increased while serpentine-endemic species decreased, thereby suggesting Ca^{2+} as a limiting factor for plant productivity. Another study found that exotic grasses in particular were more abundant on serpentine sites with higher $\text{Ca}^{2+}/\text{Mg}^{2+}$ ratios (Armstrong and Huenneke 1992).

This study confirmed these later findings in that both percent cover of exotic species and exotic species richness were higher in the deep serpentine soil

plots that had significantly higher levels of Ca^{2+} than neighboring shallow soil plots. Further, I found that *S. albidus* var. *peramoenus* is able to tolerate low levels of Ca^{2+} and high levels of Mg^{2+} . As such, the study species was successful in high Ca^{2+} areas only if exotic species were removed. The fact that deep serpentine soil areas that are higher in Mg^{2+} than shallow soils supported a higher percentage of exotic species than shallow serpentine soils provides additional evidence that exotic species that are tolerant of high levels of Mg^{2+} are more abundant where Ca^{2+} levels are high, and that, in this case anyway, Mg^{2+} does not appear to inhibit Ca^{2+} uptake by the exotic species, as proposed by Brooks (1987). It stands to reason, therefore, that *S. albidus* var. *peramoenus* should find refuge from exotics in the lower Ca^{2+} shallow soils.

The cation exchange capacity (CEC) is a measure of how well a soil can adsorb and exchange cations (positively charged ions.) The CEC for each soil sample was normal, meaning there were a moderate number of exchange sites in the soil where cations important to plants (e.g., Ca^{2+}) can be taken up by roots. Although there are a normal number of cation exchange sites, the percent Ca^{2+} exchange capacity was consistently lower than the percent Mg^{2+} exchange capacity, as is common in serpentine soils. As a result, all samples showed that plants in these areas must tolerate generally high levels of Mg^{2+} and low levels of Ca^{2+} , although these values did fluctuate depending on the depth of the soil. These results are consistent with the results of the saturation extract analyses.

Light Levels

The amount of available photosynthetically active radiation (PAR) also appeared to be important in the germination success of *S. albidus* var. *peramoenus*. The fact that deep soil plots with exotics had much lower mean PAR than other deep soil plots with no exotics demonstrates the competition for light amongst plants in deep soil plots with exotics. The small difference in amounts of PAR in shallow soil plots, regardless of exotic removal treatment, is indicative of the sparse vegetation cover in this environment. Given that several studies (D'Antonio & Vitousek 1992, McGraw and Levin 1998, Gurevitch *et al* 2002) have found light to be a limiting factor in the competitive abilities of endemics and other plant species, one could conclude that low levels of PAR are the reason for the low germination rate and lack of survivorship of *S. albidus* var. *peramoenus* in deep serpentine soil areas dominated by exotic species.

Patch Dynamics

Serpentine soils are found throughout the state in small patches as well as in large continuous areas (Mason 1946, Harrison 1999 and 2001). This study area is a prime example, with serpentine patches ranging in size between .40 and 4.04 hectares interspersed by non-serpentine oak woodland and grasslands. Harrison (1999 and 2001), who defines a small patch of serpentine soil as from less than half a hectare to 3 hectares, has shown the number of exotic species is higher on patchy serpentine soils than on continuous areas. Further, small patches of

serpentine soil that have low Ca^{2+} levels may be more resistant to invasion by exotics (Harrison 1999a).

While continuous and patchy serpentine areas typically share the same soil nutrient characteristics, they differ in terms of the level of invasibility by exotic species (Harrison 1999a). This difference can be explained by the greater edge effect on the small patches that enable a large number of propagules to enter the serpentine area from non-serpentine areas (Harrison 2001). Research has shown that exotic species thrive on serpentine soils where Ca^{2+} levels are high. However, in this study there was one of three plot locations (Site 2) that had a moderately low Ca^{2+} level, yet supported a substantial presence of exotic species in the deep soil control plots (mean percent cover for three exotic species was 40% *Brachypodium distachyon*, 40% *Lolium multiflorum*, and 25.0% *Avena barbata*). This could confirm Harrison's speculation that small patches have an increased edge effect and propagule availability due to the patchiness of the landscape, and invasion could occur even in low Ca^{2+} conditions. (Harrison 1999a and 2001).

Indicative of the edge effects in patchy serpentine grassland environments, propagules of several exotic species are placing competitive pressure on populations of the study species, *S. albidus* var. *peramoenus*. Mayer and Soltis (1994a, 1994b) found that the study species exists only on small patches of serpentine soil with populations often consisting of fewer than 30 plants. In the study area they are directly affected by the rapidly invading exotic grass *Avena barbata* (slender wild oat). In the deep serpentine soil plots, the

percent cover of exotic *Avena barbata* averaged 14.1% of the total vegetation in the plots. Further, and perhaps more telling, is the same exotic grass made up 11.3% of the total vegetation in the shallow soil plots where *S. albidus* var. *peramoenus* is naturally found. *Avena* species, which have been found to be strongly associated with small patches of serpentine soils, can therefore be enabling the evolution of serpentine-tolerance in patchy, heterogeneous landscapes such as the study area (Harrison 2001). Further, *Avena* species readily grows on serpentine soil (Proctor and Woodell 1975), a fact that provides evidence of the short evolutionary time needed for these exotic species to adapt serpentine tolerance based on their

Fig. 24. *Lolium multiflorum* Lam. (Italian ryegrass)
USDA-NRCS PLANTS
Database / Hitchcock,
A.S. (rev. A. Chase). 1950

relatively recent introduction into California (Brooks 1987). The direct effects of exotic species like *Avena barbata* on *S. albidus* var. *peramoenus* have not been previously studied.

Two additional exotic annual grasses clearly dominated the percent cover of vegetation, one occurred early in the growing season and the other dominated the latter part. The first invasive species to appear was *Lolium multiflorum* Lam., or Italian ryegrass, a species found in almost every county in California except of few along the eastern spine of the state (CalFlora 2004; Fig. 24). Native to Eurasia (Hickman 1993), the plant is on

California Invasive Plant Council's (Cal IPC) 1999 Exotic Plant Pest List (Cal IPC 1999). *L. multiflorum* does well in freshwater wetland areas such as vernal pools and seeps (Cal IPC 1999, CalFlora 2004), and was most common in the study site on deep soil areas that held moisture longer than shallow soil areas (personal observation). Further, *L. multiflorum* readily invaded the areas weeded for the exotic removal treatment, as evidenced by mean percent cover of 7.3% in experimental shallow soil plots and 29.7% in deep soil plots where I removed exotics. Although this grass is an exotic species, recall that I measured the percent cover in each plot prior to removing the exotics in order to gauge community level growth and recruitment in the experimental plots, hence their initial presence in experimental plots.

Later in the season there was a notable invasion of an annual Mediterranean grass, *Brachypodium distachyon* (L.) Beauv., or purple false brome (Hickman 1993; Fig. 25). Also on the Cal IPC's 1999 Exotic Plant Pest List and an invasive weed throughout the state from the southern border to the Mendocino and Butte Counties in the north (Cal IPC 1999, Calflora 2004), this grass was the third most dominant exotic grass in the study. This plant peaked in

Fig. 25. *Brachypodium distachyon* (L.) Beauv. (Purple False Brome)
USDA-NRCS PLANTS Database / Hitchcock, A.S. (rev. A. Chase). 1950

May with a mean percent cover of almost 39.4% in deep soil plots with exotics and 17.6% in shallow soil plots with exotics.

In summary, the relative fitness, or demographic success, of *S. albidus* var. *peramoenus* is characteristic of an edaphic endemic. A poor competitor, germination was successful in deep serpentine soils when exotic species were removed. Further, survivorship and fecundity were also highest when exotics were removed. In addition to competitive pressures from exotic species, *S. albidus* var. *peramoenus* exhibits a low shade tolerance. However, the fact the plant is able to survive in shallow serpentine soils poor in nutrients gives the plant a competitive edge in these inimical conditions.

At the community level, the serpentine grassland community surrounding the study species mirrored the difference in soil type, as native species richness and percent native cover were higher on shallow soils. The amount of light available to plants varied between the shallow and deep soil environments, with intense competition for light occurring in deep serpentine soils dominated by exotic grasses. Soil characteristics were an important determinant for vegetation cover supported, as the amount of calcium appeared crucial to exotic plants' ability to invade the deep serpentine soil areas. All of these elements, demographic success of edaphic endemics, competitive pressures for resources such as light, and high variability in soil nutrients, engender a dynamic environment in the serpentine grassland ecosystem.

CHAPTER 6

CONCLUSION

California's distinctive ecological history is closely tied with what one finds in the current landscape, particularly so in the grasslands. For the past 300 years, the state's grasslands have been inundated with non-native plant species that have effectively replaced earlier landscapes known for their native bunchgrasses and flowering plants. Today, nutrient-poor serpentine soils serve as spotty remnants of these once extensive native communities.

However, exotic grasses and forbs are rapidly adapting to harsh serpentine soils. Their ability to invade farther into these serpentine refugia will continue to alter native species composition, thereby reducing the biodiversity of these biologically rich areas. Moreover, rare plants endemic to these areas are increasingly threatened by extirpation.

By examining the effects of exotic species and serpentine soil depth on *Streptanthus albidus* var. *peramoenus* and its surrounding plant community, this study provides a contribution to the effort to understand, and even restore, rare plant populations in California's native grasslands. By experimentally manipulating exotic species in deep and shallow serpentine soils, I conclude that *S. albidus* var. *peramoenus* is indeed able to expand its population into deeper serpentine soil environments when exotic species are reduced or eliminated. Further, based on the increase in native species richness and the percent cover of native species in the grassland community when exotics were removed in deep

serpentine soils, I also conclude that the native plant community within the serpentine refugia can be restored and expanded in these areas. These results suggest that it may be possible to expand other serpentine endemic plants to these deep serpentine soil areas as well. Through the active cooperation of scientists and resource managers, ecosystem-based adaptive management methods can help ensure that rare plant populations and their surrounding plant communities can be maintained and even expanded.

Recommendations

Resource managers of serpentine grassland areas are in a unique position to preserve California's biological history. Further, California's government has instituted a number of laws to encourage such acts of preservation, particularly for rare plant species (see Appendix A). Based upon my study, recommendations can be made to land managers on how best to manage these unique areas. While my overarching recommendation is to expand the serpentine refugia, there are several components that must be considered.

The first component addresses removing or reducing exotic grassland species. Because of the persistence and high adaptability of exotic species, land managers should prioritize areas where exotic species removal should take place. More specifically, my results show land managers should prioritize removing exotic species in deep soils around serpentinite rock outcrops to help expand refugia of native plant communities and rare plant populations. Reducing the presence of exotic grassland species in these areas would lower the competitive

environment and give the native species in the neighboring serpentine refugia a chance to obtain the resources they need for establishment.

Because there are so many different ways to remove or reduce exotic species, the second component to expanding the refugia is for land managers to employ adaptive management methods when effecting change in dynamic ecosystems such as patchy serpentine grasslands. This type of management is an ongoing process that requires treating management methods and actions as experiments, monitoring the success of these endeavors, and adjusting them accordingly based on their findings. Further, new scientific findings should be incorporated into management methods whenever possible. Educating and involving the public should also be a key component of an adaptive management policy. Fortunately, the stewards of the study site, the Santa Clara County Open Space Authority, already employ several of these adaptive management methods.

The third component to expanding the refugia is to establish a seed bank. After removing or reducing exotic grassland species in neighboring deep serpentine soil areas, it would be helpful to sow seed in these deeper soils from extant native species in nearby serpentine refugia. Establishing a seed bank may help restore native plant populations within the serpentine refugia. This may also be necessary to dilute the long-standing monocultures of exotics grasses in deep serpentine soil areas. Further, in the absence of competition from exotic species, sowing native plant seed might help establish populations of native flowering plants to attract pollinators needed to maintain new populations of *Streptanthus*

albidus var. *peramoenus* and other native plants. Demographic monitoring of newly established plant populations, especially populations of rare plants, should be initiated when seeds are sown and continued as part of a permanent monitoring regime performed by land managers.

Further Research

There are three major areas of further research that would help to clarify the dynamic nature of patchy serpentine grassland: pollination studies, studies on the effects certain exotic species have on rare edaphic endemics, and research on different methods for exotic species removal. Pollination studies of *Streptanthus albidus* var. *peramoenus* would provide additional guidance in the expansion of these plant populations. More specifically, in this study some *S. albidus* var. *peramoenus* plants in deep soil exotic removal plots had sterile fruits. This could be the result of low pollination rates, a lack of vital mutualistic relationship(s) needed for pollination to occur, habitat isolation due to the scattered nature of the plant's populations, or a combination thereof. I suggest that once exotic species are removed or reduced in deep serpentine soil areas near rocky outcrops, seeds from plant species that are associates of *S. albidus* var. *peramoenus* could be sown to help attract pollinators that would then increase fecundity so populations of the study species could persist.

Another area of research that would be valuable to the persistence of serpentine refugia is examining the effects of specific exotic plants (*Avena* spp., *Lolium multiflorum*, or *Brachypodium distachyon*) on rare edaphic endemic species.

Patchy serpentine grasslands are particularly susceptible to invasion of exotics as the increased edge effect promotes accessibility of propagules of these plant species. Further, as noted earlier, the direct effects of exotics like *Avena barbata* on *S. albidus* var. *peramoenus* have not been researched. In this study *Lolium multiflorum* and *Brachypodium distachyon* were also very invasive and deserve further research on how their advancement into the refugia would affect edaphic endemics.

Further research should also investigate the effects of different exotic species removal methods on rare serpentine endemics and the surrounding community. Varied regimes of grazing, burning, and mowing are all worth examining closely. The Santa Clara County Open Space Authority opined that grazing is the most cost-effective option for them (Pat Congdon, personal communication). To that end, beneficial research projects include studying how grazing by cattle, goat, and sheep at varied frequencies, seasons, and intensities affect deep and shallow serpentine plant communities. Further, sowing seeds of rare plant species under these various grazing regimes would provide additional information as to whether or not these populations could be expanded or restored.

REFERENCES

- Allen, W. H. 1994. Reintroduction of endangered plants: biologists worry that mitigation may be considered an easy option in the political and legal frameworks of conservation. *Bioscience* 44(2): 65-8.
- Arianoutsou, M., P.W. Rundel, and W.L. Berry. 1993. Serpentine endemics as biological indicators of soil elemental concentrations. Pages 179-189 in Bernd Markert, ed., *Plants as Biomonitors: indicators for heavy metals in the terrestrial environment*. Weinheim, Germany: Verlagsgesellschaft mbH.
- Armstrong, J.K. and L.F. Huenneke. 1992. Spatial and temporal variation in species composition in California grasslands: the interaction of drought and substratum. Pages 213-233 in Baker, A.J.M., J. Proctor, and R.D. Reeves, eds., *The vegetation of ultramafic (serpentine) soils*. Andover: Intercept.
- Baker, H.G. and G.L. Stebbins. 1965. *The Genetics of Colonizing Species*. New York: Academic Press.
- Baskin, Jerry M. and Carol C. Baskin. 1988. Endemism in rock outcrop plant communities of unglaciated eastern United States: an evaluation of the roles of the edaphic, genetic and light factors. *Journal of Biogeography* (15): 829-840.
- Bass, Ronald E., Albert I. Herson, and Kenneth M. Bogdan. 1999. *CEQA Deskbook: a step-by-step guide on how to comply with the California Environmental Quality Act*. Point Arena, CA: Solano Press Books.
- Beidleman, Linda H. and Eugene N. Kozloff. 2003. *Plants of the San Francisco Bay Region: Mendocino to Monterey*. Berkeley, CA: University of California Press. 507 pp.
- Bittman, Roxanne. 2001. The California Natural Diversity Database: a natural heritage program for rare species and vegetation. *Fremontia*, vol. 29 (3-4): 57-62.
- Blackburn, Thomas C. and Kat Anderson, eds. 1993. *Before the Wilderness: Environmental Management by Native Californians*. Menlo Park, CA: Ballena Press.
- Brooks, R.R. 1987. *Serpentine and its vegetation: a multidisciplinary approach*. Portland, OR: Dioscorides Press.

- CalFlora: Information on California plants for education, research and conservation. 2004. [web application]. The CalFlora Database [a non-profit organization]: Albany, California. Accessed frequently throughout 2002 - 2004. URL: <http://www.calflora.org>
- California Department of Fish and Game. 1977. Native Plant Protection Act. Internet, accessed August 5, 2003. URL: http://www.dfg.ca.gov/hcpb/species/t_e_spp/tespp.shtml,
- _____. 1984. California Endangered Species Act, Fish and Game Code 2050-2085. Internet, accessed August 5, 2003. URL: http://www.dfg.ca.gov/hcpb/ceqacesa/cesa/incidental/cesa_policy_la_w.shtml,
- California Department of Fish and Game, Conservation Planning. Last updated July 18, 2002. Internet, accessed August 5, 2003. URL: <http://www.dfg.ca.gov/hcpb/conplan/conplan.shtml>.
- California Department of Fish and Game, Threatened and Endangered Species. Last updated August 19, 2003. Native Plant Conservation statement. Internet, accessed August 19, 2003. URL: http://www.dfg.ca.gov/hcpb/species/t_e_spp/nat_plnt_consv.shtml.
- California Department of Fish and Game, Natural Diversity Database. July, 2003. *Special Vascular Plants, Bryophytes, and Lichens List*. Biannual publication, Mimeo. 88 pp.
- California Exotic Pest Plant Council. 1999. Exotic Plant Pest List. (<http://ucce.ucdavis.edu/files/filelibrary/5319/4898.pdf>, October 19, 1999). California Exotic Pest Plant Council, California.
- California Native Plant Society. 1999. Open Letter calling for Equal Protection for Plants under the Federal Endangered Species Act, June 24, 1999. Internet, accessed August 5, 2003. URL: <http://www.cnps.org/archives/archives.htm>.
- Campbell, N.A. and J.B. Reece. 2002. Biology. Sixth edition. Benjamin Cummings: San Francisco.
- City of San Jose. Last updated July 30, 2002. Internet, accessed August 23, 2003. URL: http://www.ci.san-jose.ca.us/planning/sjplan/Habitat_consarea/hca-Index.html.
- CNPS. 2001. *Inventory of Rare and Endangered Plants of California* (sixth edition). Rare Plant Scientific Advisory Committee, David P. Tibor, Convening Editor. California Native Plant Society: Sacramento, CA.

- Corelli, Toni and Chandik, Zoe. 1995. *The Rare and Endangered Plants of San Mateo and Santa Clara County with Photographs and Illustrations*. Half Moon Bay, CA: Monocot Press.
- Crampton, Beecher. 1974. *Grasses in California*. University of California Press: Berkeley.
- D'Antonio, Carla M. and Peter M. Vitousek. 1992. Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change. *Ann. Rev. Ecol. Syst.* 23: 63-87.
- Elton, C.S. 1958. *The ecology of invasions by animals and plants*. London: Methuen.
- Erneberg, Marianne. 2002. The process of plant invasion with focus on the effects of plant disease. PhD diss., The Royal Veterinary and Agricultural University, Copenhagen, Denmark.
- Fenn, M.E., R. Haeuber, G.S. Tonnesen, J.S. Baron, S. Grossman-Clarke, D. Hope, D. A. Jaffe, S. Copeland, L. Geiser, H.M. Rueth, and J.O. Sickman. 2003. Nitrogen emissions, deposition, and monitoring in the western United States. *BioScience* 53(4): 391-403.
- Fiedler, P. 1991. Mitigation related transplantation, translocation and reintroduction projects involving endangered and threatened and rare plant species in California. Sacramento, CA: California Department of Fish and Game. 82 pp.
- Gordon, Burton L. 1977. *Monterey Bay Area Natural History and Cultural Footprints*. Pacific Grove, CA: The Boxwood Press.
- Gotelli, Nicholas J. and Aaron M. Ellison. 2004. *A Primer of Ecological Statistics*. Sunderland, Massachusetts: Sinauer Associates, Inc.
- Gurevitch, J., S. M. Scheiner, and G. A. Fox. 2002. *The Ecology of Plants*. Sunderland, Massachusetts: Sinauer Associates, Inc.
- Harrison, S. 1999a. Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. *Ecology* 80(1): 70-80.
- _____. 1999b. Native and alien species at the local and regional scales in a grazed California grassland. *Oecologia* 121: 99-106.
- Harrison, S., K. Rice, and J. Maron. 2001. Habitat patchiness promotes invasion by alien grasses on serpentine soil. *Biological Conservation* 100: 45-53.

- Heady, Harold F. 1988. Valley Grassland. Pages 491-514 in Barbour, M. and J. Major, eds. *Terrestrial Vegetation of California*. California Native Plant Society Special Publication Number 9.
- Hendry, George W. 1931. The adobe brick as a historical source. Reporting further studies in adobe brick analysis. *Agricultural History* V(3): 110-127.
- Hickman, J. C. ed. 1993. *The Jepson Manual: Higher Plants of California*. Berkeley: UC Press.
- Hitchcock, C. Leo, Arthur Cronquist, Marion Ownbey, and J.W. Thompson. 2001. *Vascular Plants of the Pacific Northwest. Part 1: Vascular Cryptograms, Gymnosperms, and Monocotyledons*. Seattle: University of Washington Press. 1969.
- Hobbs, Richard J. and Colin J. Yates. 2003. Impacts of ecosystem fragmentation on plant populations: generalizing the idiosyncratic. *Australian Journal of Botany* 51(5): 471-488.
- Howald, A.M. 1996. Translocation as a mitigation strategy: lessons from California. In: D.A. Falk, C.I. Millar, and M. Olwell eds. *Restoring Diversity: Strategies for Reintroduction of Endangered Plants*. Washington, DC: Island Press.
- Huenneke, L. F., S.P. Hamburg, R. Koide, H.A. Mooney, P.M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71(2): 478-491.
- Jackson, L. 1985. Ecological origins of California's Mediterranean grasses. *Journal of Biogeography* 12: 349-361.
- Kruckeberg, A. 1954. The ecology of serpentine soils. III Plant species in relation to serpentine soils. *Ecology* 35: 267-274.
- . 1984. *California Serpentine: Flora, Vegetation, Geology, Soils and Management Problems*. Berkeley: University of California Press.
- Kruckeberg, A. and D. Rabinowitz. 1985. Biological aspects of endemism in higher plants. *Ann. Rev. Ecol. Syst.* 16: 447-479.
- Kruckeberg, A. 1992. Plant life of western North American ultramafics. Pages 31-73 in B.A. Roberts and J. Proctor, eds., *The Ecology of Areas With Serpentinized Rocks: A World View*. Netherlands: Kluwer Academic Publishers.

- Major, Jack. 1988. California climate in relation to vegetation. Pages 11-74 in Barbour, M. and J. Major, eds. *Terrestrial Vegetation of California*. California Native Plant Society Special Publication Number 9.
- Malpas, J. 1992. Serpentine and the geology of serpentinized rocks. Pages 7-30 in B.A. Roberts and J. Proctor, eds., *The Ecology of Areas With Serpentinized Rocks: A World View*. Dordrecht, Netherlands: Kluwer Academic Publishers.
- Mason, H.L. 1946. The edaphic factor in narrow endemism. I. The nature of environmental influences. *Madroño* 8: 209-226.
- Matthews, Mary Ann. 1997. *An Illustrated Field Key to the Flowering Plants of Monterey County and Ferns, Fern Allies, and Conifers*. California Native Plant Society, Sacramento, CA. 401 pp.
- Mayer, Michael S. and Pamela S. Soltis. 1994a. The evolution of serpentine endemics: a chloroplast DNA Phylogeny of the *Streptanthus glandulosus* complex (Cruciferae). *Systematic Botany* 19(4): 557-574.
- Mayer, Michael S. and Pamela S. Soltis. 1994b. The evolution of the *Streptanthus Glandulosus* complex (Cruciferae): genetic divergence and gene flow in serpentine endemics. *American Journal of Botany* 81(10): 1288-1299.
- McGraw, Jodi M. and Anna L. Levin. 1998. The roles of soil type and shade intolerance in limiting the distribution of the edaphic endemic *Chorizanthe pungens* var. *hartwegiana* (Polygonaceae). *Madroño* 45(2): 119-127.
- McGraw, Jodi M. 2004. The interacting effects of natural disturbances and competition with exotic plant species on native plants in sandhills habitat of central coastal California. Ph.D. diss., University of California, Berkeley, California.
- Miller, Alice L. and Richard P. Duncan. 2004. The impact of exotic weed competition on a rare New Zealand outcrop herb, *Pachycladon cheesmanii* (Brassicaceae). *New Zealand Journal of Ecology* 28(1): 113-124.
- Mooney, H.A., S.P. Hamburg, and J.A. Drake. 1986. The Invasions of Plants and Animals Into California. Pages 250-272 in Harold A. Mooney and James A. Drake, eds, *Ecology of Biological Invasions of North America and Hawaii*. New York: Springer-Verlag New York, Inc.
- Mooney, H. A. 1988. Lessons from Mediterranean-climate Regions. Pages 157-165 in E.O. Wilson, ed., and Frances M. Peter, assoc. ed., *Biodiversity*. Washington, D.C.: National Academy Press.

- Mooney, H.A. and E.E. Cleland. 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences of the United States of America* 98(10): 5446-5451.
- Moratto, Michael J. 2004. *California Archeology*. 2d ed. Salinas: Coyote Press.
- Munz, Philip A. and David D. Keck. 1973. *A California Flora (and Supplement)*. Berkeley, CA: University of California Press.
- Murphy, D.D., P.R. Ehrlich. 1989. Conservation biology of California's remnant native grasslands. Pages 201-211 in Huenneke, L.F. and H.A. Mooney, eds, *Grassland Structure and Function: California Annual Grassland*. Dordrecht, Netherlands: Kluwer Academic Publishers.
- Orians, G.H. 1986. Site Characteristics Favoring Invasions. Pages 133-148 in Harold A. Mooney and James A. Drake, eds, *Ecology of Biological Invasions of North America and Hawaii*. New York: Springer-Verlag New York, Inc.
- Ornduff, Robert, Phyllis M. Faber, Todd Keeler-Wolf. 2003. *Introduction to California Plant Life*, Revised Edition. Berkeley, California: University of California Press.
- Pavlik, Bruce M., Daniel L. Nickrent, and Ann M. Howald. 1993. The Recovery of an Endangered Plant. I. Creating a New Population of *Amsinckia grandiflora*. *Conservation Biology* 7(3): 510-526.
- Proctor, John and Woodell, Stanley R.J. 1971. The Plant Ecology of Serpentine. I. Serpentine vegetation of England and Scotland. *Journal of Ecology* 59(2): 375-395.
- Proctor, J. and S.R.J. Woodell. 1975. The ecology of serpentine soils. *Adv. Ecol. Res.* 9: 255-366.
- Rabinowitz, D. 1981. Seven forms of rarity. Pages 205-217 in Hugh Synge, ed., *The Biological Aspects of Rare Plant Conservation*. New York, New York: John Wiley & Sons, Ltd.
- Raven, Peter J. and Daniel I. Axelrod. 1978. *Origin and Relationships of the California Flora*. Sacramento, CA: University of California Press.
- Risser, Paul G. 1988. Diversity in and among grasslands. Pages 176-180 in E.O. Wilson, ed., and Frances M. Peter, assoc. ed., *Biodiversity*. Washington, D.C.: National Academy Press.
- Robbins, W.W., Margaret K. Bellue, and Walter S. Ball. *Weeds of California*. Sacramento, CA: California Department of Food & Agriculture.

- Roberson, Emily. 2001. Management of Rare Plants under State and Federal Endangered Species Law: A CNPS Perspective. *Fremontia* vol. 29: 3-4.
- San Diego Multiple Species Conservation Program. Last updated August 12, 2003 Natural Community Conservation Planning website, accessed August 23, 2003. URL: <http://www.dfg.ca.gov/nccp/index.html>.
- Schierenbeck, Kristina A. 1995. The threat to the California flora from invasive species: problems and possible solutions. *Madroño* vol 42(2): 168-174.
- Solomeshch, Ayzik I. and Michael G. Barbour. 2004. *Could California grasslands all have been derived from bunchgrass prairie?* Ecology and Management of California Grasslands conference held in Berkeley, California 2-3 April 2004; Internet, accessed October 3, 2004. URL: <http://cbc.berkeley.edu/grass/Abstracts.htm>.
- SPSS for Mac OS X 2003. SPSS 11.0.2, standard version, released April 15, 2003. Chicago: SPSS Inc..
- Stebbins, G. Ledyard and Jack Major. 1965. Endemism and speciation in the California flora. *Ecological Monographs* vol 35(1): 1-35.
- Tadros, T.M. 1957. Evidence of the presence of an edapho-biotic factor. *Ecology* 38(1): 14-23.
- Thomas, John Hunter. 1961. *Flora of the Santa Cruz Mountains of California: a manual of the vascular plants*. Stanford, CA: Stanford University Press. 434+ pp.
- Turitzin, S.N. 1982. Nutrient limitations to plant growth in a California serpentine grassland. *American Midland Naturalist* 107(1): 95-99.
- UC Oakland Division of Agriculture and Natural Resources. Revised 1998. *The Grower's Weed Identification Handbook*. Berkeley, CA: University of California.
- USDA-NRCS PLANTS Database, Hitchcock, A.S. (rev. A. Chase). 1950. *Manual of the grasses of the United States*. USDA Misc. Publ. No. 200. Washington, DC. Internet, accessed July 11, 2004. URL: http://plants.usda.gov/cgi_bin/plant_profile.cgi?symbol=BRDI2.
- US Department of the Interior. Fish and Wildlife Service. 2003. *Endangered Species Act "Broken" – Flood of Litigation Over Critical Habitat Designation Hinders Species Conservation*, by Hugh Vickery and Megan Durham. May 28, 2003. Washington, D.C.

- U.S. Fish and Wildlife Service. 1998. *Recovery Plan for Serpentine Soil Species of the San Francisco Bay Area*. Portland, Oregon. 330+ pp.
- Vitousek, P.M. 1986. Biological Invasions and Ecosystem Properties: Can Species Make a Difference? Pages 163-176 in H.A. Mooney and J.A. Drake eds. *Ecology of Biological Invasions of North America and Hawaii*. Volume 7. New York: Springer-Verlag.
- Weiss, S. B. 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conservation Biology* 13(6): 1476-1486.
- Whitson, Tom D, ed. 2002. *Weeds of the West*. Jackson, Wyoming: Grand Teton Lithography. 628+ pp.
- Zar, Jerrold H. 1999. *Biostatistical Analysis, Fourth Edition*. Upper Saddle River, New Jersey: Prentice Hall.

Personal Communication

- Congdon, Patrick, Resource Manager, Santa Clara County Open Space Authority, personal communication, ongoing between April 2002 through January 2004.
- McGraw, Jodi, Ph.D., Plant Ecologist, Consultant, personal communication, May 2002 to May 2004.
- Menges, Eric S., Ph.D., Archbold Biological Station, Lake Placid, FL, personal communication, August 2002.

APPENDIX A

REGULATORY FRAMEWORK FOR RARE PLANT PROTECTION IN CALIFORNIA

Several state and federal policies govern the protection of rare plants and their habitats in California, creating a complex network of laws and regulations. While these independent pieces of legislation are run by different government entities, there are many areas where their jurisdictions and processes overlap. There are two primary reasons why this overlap occurs: the chronological order these policies were enacted into law, and, second, the knowledge and resources about rare plants have changed over time.

In the discussion that follows, I briefly discuss the federal and California policies that protect rare plants. The two major federal laws discussed here that protect rare plants are the National Environmental Policy Act (NEPA, 1970) and the federal Endangered Species Act (FESA, 1973). At the state level, there are five major policies and entities discussed that exist to further the protection of rare plants: the California Environmental Quality Act (CEQA, 1970), the Native Plant Protection Act (NPPA, 1977), the California Endangered Species Act (CESA, 1984), a subset of CESA called the Natural Community Conservation Planning Act (NCCP Act, 1991), and the California Natural Diversity Database (CNDDDB). Within the description of each policy, I will note the law's date of inception, the intent of the law, the governing entity, the areas of overlap with other legislation, and the rare plant definitions or special lists specific to that

policy. Finally, I will examine the ways these policies protect rare plants and/or their habitats.

National Environmental Policy Act (NEPA), 1970

Between January 1, 1970, the day the National Environmental Policy Act (NEPA) became law, and 1974, legislative initiatives and policies were enacted as a result of a growing consciousness of ongoing environmental degradation. NEPA was developed to give the federal government the opportunity to help ensure that every person acts as responsible stewards of our nation's natural resources, balancing the use of those resources with the risk of further environmental degradation. NEPA called for the creation of the Council of Environmental Quality (CEQA) that oversees the implementation of the Environmental Impact Statement (EIS) process, a process developed to apply the latest science and public input to environmental decisions. NEPA proved to be a premiere example of environmental policy in the United States.

Although NEPA was regarded as revolutionary for environmental protection, the Act provides limited protection for rare plants, particularly since NEPA pertains only to projects in which a federal entity is the lead agency. NEPA does, however, protect rare plants populations during the creation of a draft EIS. During the first three years of the NEPA process before the inception of the Federal Endangered Species Act (FESA) in 1973 (described in the next section), mention of endangered and rare plants occurred only when individuals with knowledge of local flora engaged in the public comment period during the

EIS process. However, since the inception of FESA, all federally endangered, threatened, and candidate plant species and their associated habitats on federal land are required to receive protection or suitable mitigation under NEPA.

In contrast to plants receiving protection under the FESA, the protection of unlisted but “rare” plants is based entirely on input from various federal and state agencies, non-profit groups, and individuals. For example, the US Fish and Wildlife Service maintains a nationwide list of rare plants called “Species of Concern” that do not receive official protection under FESA but can be recommended for protection under NEPA. This list contains unlisted rare plants as well as those already formally listed as candidate, threatened, and endangered.

California’s rare plants that are included in the USFWS “Species of Concern” list are from a list maintained by the California Department of Fish and Game’s Natural Diversity Database (CNDDDB, described below). The non-profit California Native Plant Society also maintains a list of rare and endangered plants called the *Inventory of Rare and Endangered Plants of California* (2001). While this list will be described in greater detail below, the plants in this list are included in the federal EIS process. Further, plants listed as highest protection priority in the CNPS *Inventory* (2001) are called “special status species” by the Bureau of Land Management and “sensitive species” by the US Forest Service (CNPS 2001). Both of these federal government agencies focus efforts directed toward protecting rare plants when possible.

Once all rare plant populations affected by the federal level project are acknowledged in the draft EIS, the final EIS document typically includes approved mitigations or other arrangements to minimize harm to plants listed under FESA as well as Species of Concern. In those cases when an EIS is not required, the potential destruction of rare plants is not discussed under NEPA.

Federal Endangered Species Act (FESA), 1973

Perhaps one of the most well known conservation policies in the United States, the federal Endangered Species Act of 1973 has been continually debated since its inception. At the brunt of the controversy is the very entity charged with maintaining the FESA - the United States Fish and Wildlife Service (USFWS). The entire Act is fraught with ongoing controversy, by environmentalists and groups suing the USFWS to protect additional species, to private landowners demanding the recognition of their right use their property the way they want, regardless of what species happen to live on their land. Just last May, the US Department of Interior (USDI) issued a press release on behalf of the USFWS stating that more than two-thirds of the FESA \$9.077 million budget is being spent on complying with court orders and settlement agreements for designation of critical habitat for already listed species (US Department of Interior 2003).

In addition to the overlap that occurs with NEPA, as described above, there are three main areas where FESA overlaps with policies developed in California: the California Environmental Quality Act (CEQA), the California

Endangered Species Act (CESA), and the maintenance of the California Natural Diversity Database (CNDDDB). These areas of overlap will be discussed under each of those policies in the following sections.

There are many pros and cons to the Federal Endangered Species Act. One of the major benefits of FESA is that when species are listed, not only are the existing individuals protected, but their existing and potential habitat is protected as well. Even though this is a benefit, it is also the part of FESA that is forcing the USFWS to spend money in the courts resolving designated habitat complaints, when it could be used to list additional species. FESA also requires the issuance of “take” permits for federally listed species; the regulations regarding these permits are generally strict and help to ensure entire populations of listed species will not be harmed.

Another benefit to the species listed under FESA is the development of recovery plans as required by Section 4 of the act. Recovery plans often include the latest scientific information regarding both listed species and federal Species of Concern, designated by the USFWS (Roberson 2001). For example, in 1998, the USFWS released the *Recovery Plan for Serpentine Soil Species of the San Francisco Bay Area* that includes information on *Streptanthus albidus* var. *peramoenus*, an unlisted yet rare plant. These recovery plans, while valuable, have no legal backbone for implementation. As well, there is no funding available to do so.

While the FESA protects listed animal species wherever they occur in the United States, FESA only protects listed plant species if they live on federal land. To that end, the protection for many listed plant species is minimal, because

many plant populations are so small they are located only on privately owned land. If landowners elect to decimate a threatened or endangered plant, there is no provision in FESA that can stop them. Put differently, FESA only protects plants officially listed as a candidate, threatened, or endangered species that exist on federal land; there is no specific provision in FESA that protects unlisted rare plants in other locations.

California Environmental Quality Act (CEQA), 1970

California's population boom in the middle of the 20th century created an unprecedented demand for housing and other development throughout the state. As a result, much of the natural beauty that prompted people to flock to California in the first place was lost. In an effort to help conserve its natural resources, in 1970 the California Legislature signed into law the California Environmental Quality Act (CEQA).

Modeled after NEPA, CEQA was originally written to cover only projects done by state agencies. However, the 1972 case of *Friends of Mammoth v. Board of Supervisor of Mono County* 8 Cal. 3d 247 forced California's legislation to expand CEQA's regulatory capacity to include private projects as well (Bass 1999). Like NEPA, CEQA implements a process of environmental impact analysis by requiring Environmental Impact Reports (EIRs, rather than an EIS for NEPA) from project proponents, or lead agencies, to avoid significant impacts to California's environmental and historical resources through approved mitigations and project alternatives.

Although CEQA requires many formal environmental analysis documents and a public comment period, the power of CEQA has been debated. While indeed providing additional opportunities for protection of rare, threatened, and endangered species, the lead agency has the power to decide if the benefits of a project (e.g., economic growth, production of jobs) outweigh the impacts on rare and endangered flora (CEQA Guidelines § 15093 and 15091(a)(3), Bass 1999). As a result, even though under CEQA projects are supposed to “avoid or minimize environmental damage where feasible” (CEQA Guidelines §15021(a)), there are many instances when rare and endangered plant populations have been lost in the name of progress (Bass 1999).

Nonetheless, rare plants are protected to some degree under CEQA. During the writing of the EIRs, the project proponent or hired consultants must by law recognize rare plants in a required botanical surveys. From 1970 to about 1974, prior to the inception of the California Endangered Species Act (CESA, 1984), rare plants were protected only if individuals with knowledge of the local flora were consulted. But it wasn't until the first CNPS *Inventory of Rare and Endangered Plants of California* was published in December 1974 that agencies and botanists had a resource for rare plant protection.

In addition to federal and state endangered species listed under the FESA and CESA respectively, California's Department of Fish and Game (DFG) recommends that plants listed as 1A, 1B, and 2 in the CNPS *Inventory* (2001) specifically be addressed in CEQA projects (California Department of Fish and Game, *Threatened and Endangered Species* 2003). Plants listed as 1B are the

highest priority because they are deemed as rare, threatened, or endangered in California have limited habitat (such as serpentine grasslands), and are in low numbers or in limited numbers of populations. Not only is it mandatory that 1B plants be recognized in botanical surveys for proposed projects, but all of them are eligible for listing under the CESA. Further, 1B plants meet the requirements for protected plants under the Native Plant Protection Act (NPPA, 1977,) and the CESA. Both the NPPA and CESA will be discussed in detail in the following sections.

The study species, *Streptanthus albidus* var. *peramoenus*, is one of 45 species or subspecies in Santa Clara County listed in the CNPS *Inventory* as “1B” (CNPS 2001). A good example of CEQA in action concerns the protection of the study species at the study site. In order to fulfill their mission, the Santa Clara County Open Space Authority (SCCOSA) is in the middle of establishing a trail for recreational use on the study property. However, at least two CNPS 1B plants are located near or along the trail, the study species and *Lessingia micradenia* var. *glabrata* (Smooth Lessingia). In order to establish the trail, a CEQA review must be done and the existence of these rare plants must be addressed and harm to them avoided (or mitigated). Because the SCCOSA is a government entity, it can serve as its own lead agency. To this end, the SCCOSA finds itself in the odd situation where it would require itself to obtain necessary permits, devise a trail that prevents any impact to these rare plant populations, and/or create a mitigation strategy that their own agency will be able to both agree on and comply with.

Public Participation in the CEQA Process

One of the main ways individuals and groups can affect the CEQA process in protecting rare and endangered plants is to utilize the public comment period during the creation of environmental impact documents through Notices of Preparation (NOP), Negative Declarations, Initial Studies, Draft and Final Environmental Impact Reports (EIRs), Environmental Assessments (EAs), and Wetland Fill Applications. It is important for these groups to notify the lead agency, as well as other stakeholders in a project, of the presence of rare and endangered species and sensitive habitat areas like serpentine rock outcrops and grasslands that commonly harbor rare and endemic taxa. The public comment opportunities in the CEQA process is the way individuals and groups, such as the California Native Plant Society and National Audubon Society, can influence a project.

It is very important that comments are submitted to ensure the least impact will occur on any native plant populations or that sound mitigation strategies are developed for a project. While avoidance of impacts to the flora is the best practice, it is also sometimes unrealistic. Comments are typically made to ensure all rare species are accounted for in species lists of project areas, especially unusual, rare, listed, or candidate taxa such as those on List 1B in the CNPS *Inventory*. Further, comments can help to minimize destruction of native plant resources by providing scientifically-based information and ensure policies are consistent with CNPS's Statement Opposing Transplantation as Mitigation

and their Mitigation Guidelines for Rare, Threatened, or Endangered Plants. Also, comments can encourage the use of native plants in all landscaping that would not disrupt the genetic integrity of nearby native wild populations through hybridization. Comments should also discourage the use of exotic species in projects, particularly those species that are known to be aggressive and invasive and could threaten the stability of native plant populations (such as Mediterranean grasses). Finally, cumulative impacts on rare plants and their populations should be brought forth through the commenting process for all EIRs.

California's Native Plant Protection Act (NPPA), 1977

The Native Plant Protection Act (NPPA, 1977) was the first piece of legislation that allowed California's Department of Fish and Game (DFG) to designate plant species as rare, threatened, and endangered. To this end, the NPPA was essentially a prequel to CESA, an act that has since formalized the process of species protection and instilled stricter regulations regarding the protection of listed species. The NPPA also gave the California DFG the ability to require permits or written record of when these newly listed rare and endangered plants were going to be destroyed, collected for propagation, exportation, importation, or sold.

Even though NPPA was intended to "preserve, protect and enhance endangered or rare native plants of California (Fish and Game Code §1900) through listing species and requiring "take" permits, it actually allowed for

widespread destruction of rare plants. This is primarily due to the large number of exemptions made in the law for commercial activities. In addition to public utilities that impact native vegetation in order to provide service to the public, landowners who want to harvest timber in accordance with a legal timber harvest plan, mine, clear a canal, lateral ditch, or roadside of vegetation, and clear land for agricultural use, may proceed with these activities that destroy rare plants.

Commercial activities can only proceed, however, if the public utilities and landowners give California's DFG ten days notice of their planned activity so the Department could salvage these plants (transplant them to another location, Fish and Game Code §1913). Further, the burden was on the DFG to notify all private landowners and public utilities these unique plants resided on their property. If landowners were not notified by the DFG, these landowners were not required to give the ten-day notice. As a result, countless rare and endangered plant species were simply lost due to landowners' lack of concern or ignorance.

If the DFG did not act immediately to locate suitable habitat for the plants and transplant them during the ten day period, the rare and endangered plants and their habitat were destroyed. Granted, even when populations of these plants were transplanted, there was little likelihood they would survive the ordeal. According to Fiedler in a 1991 study for the DFG, only 15% of cases involving transplantation were effective, even under the most favorable conditions. Two other researchers also found the majority of transplantation (or

translocation) efforts to be unsuccessful (Allen 1994, Howald 1996). While originally created to protect rare and endangered plants, NPPA has weak provisions that instead allowed dramatic destruction of California's rare and endangered flora.

In taking a step back from the discussion of the NPPA, it is important to note the timing when California's network of botanists joined forces and knowledge to create the multitude of resources we have today on rare and endangered plants. Originating in a 1968 card file maintained by G. Ledyard Stebbins of California plants with a distribution less than 100 miles, the CNPS *Inventory of Rare and Endangered Plants of California* grew into the major resource that currently serves botanists, consultants, naturalists, and government agencies throughout California and the rest of the United States (CNPS 2001). In the early years of CEQA, from 1970 to late 1974, there was no formal list of rare plants in the state that agencies, consultants, and botanists could easily access. As a result, the protection of rare plants in acts such as NEPA, CEQA, and NPPA depended largely on the inclusion of botanists' local knowledge of rare flora in environmental impact documents and projects. In December 1974, however, the first edition of CNPS's *Inventory* was published. This initial edition of the *Inventory* in 1974 named 1,393 rare and endangered plants in contrast with the sixth edition used today that describes a total of 2,073 plants. As the *Inventory* was growing, so was the number of new environmental protection laws being proposed (CNPS 2001).

California Endangered Species Act (CESA), 1984

With FESA serving as an example of species protection for over ten years, the California state legislators drafted their own Endangered Species Act and signed it into law in 1984. Expanding on California's NPPA, CESA further delineated the categories for listed species to include the current 218 candidate (species under review by DFG for listing), threatened (will be endangered in foreseeable future if action is not taken), and endangered (remaining populations are in immediate jeopardy) (DFG 2003). Like the NPPA, CESA continues to give the DFG the ability to require permits for scientific collecting and research or for incidental take of threatened, endangered, and/or candidate species during an approved project. Unlike the NPPA however, the provisions in CESA are stricter, resulting in more protection for listed species.

CESA does not provide protection for unlisted rare plant species. According to the DFG, when CESA was signed into law, all rare animals were listed as threatened under CESA but only those plants already designated as threatened and endangered under the NPPA were incorporated into the Act; although eligible, plants listed as rare under the NPPA were never included (California Department of Fish and Game, Threatened and Endangered Species 2003). However, the Act did establish a process so individuals and non-profit organizations such as CNPS could petition for a species to be listed as threatened or endangered. One reason why individuals would want to submit a petition for listing a species under CESA is when projects are proposed, the DFG or other lead agencies would not be able to choose the benefits of a project over the

protection of listed species. In all cases, significant, unmitigated, and/or unavoidable impacts on these plants must be avoided under CESA (Roberson 2001).

Recent legal developments have both strengthened and weakened CESA. In 1997, Governor Pete Wilson signed Senate bill 879 into California law. Among other items, this law enacted stricter regulations for take permits and required that listed species incur no net loss of individuals or habitat. Although great strides were made, the following year, then-Attorney General Dan Lungren, in concert with commercial interests, submitted an opinion stating that the 1977 NPPA rules for take and destruction of listed and unlisted rare and endangered plants take priority over CESA. The Lungren opinion has not swayed the current California State Legislature that continues to opine that priority lies with CESA laws that protect plants. As the debate continues today, the fate of rare and endangered plants in California hangs in the balance.

Natural Community Conservation Planning Act (NCCP Act), 1991

One of the most recent developments in conservation policies for rare plants is the Natural Community Conservation Planning Act of 1991. Essentially an addition to CESA (Fish & Game Code §2800-2840), the NCCP Act was created to promote voluntary cooperation between private landowners, federal, state, and local government agencies such as the USFWS, DFG, and local cities and municipalities, as well as other interested groups (DFG website). Under the NCCP Act, formal agreements are drawn up that allow the protection of rare and

endangered species while ensuring the needs of private landowners are met. These agreements serve as a Habitat Conservation Plan (HCP) under the Federal Endangered Species Act (§ 10(a)(1)(B)) and Natural Community Conservation Plans under the NCCP Act. Each HCP/NCCP are required to go through both the NEPA and CEQA processes for public comment. Further, each agreement must be submitted to both the USFWS and the DFG to ensure that all permits, authorizations, and other regulations regarding listed and unlisted species are met.

While the San Diego area has taken the lead with its Multiple Species Conservation Program agreement among twelve cities, a local water district, and the military to protect the coastal sage scrub community from urban sprawl, the City of San Jose recently entered into an agreement with Santa Clara County and the Santa Clara Valley Water District to create a HCP/NCCP by 2006 (California's NCCP website and City of San Jose website, 2003). Natural Community Conservation Plans are steadily gaining in popularity as a conservation tool through the state. However, it remains to be seen if the San Jose/Santa Clara County/Santa Clara County Water District agreement will specifically address rare plants in this area, namely *Streptanthus albidus* var. *peramoenus*.

California Natural Diversity Database (CNDDB), 1979

Originally the brainchild of The Nature Conservancy in 1979, the California Natural Diversity Database (CNDDB) is a trove of information on rare

and endangered plants, animals, and vegetation communities. The DFG's Habitat Conservation Division Wildlife and Habitat Analysis Branch maintains the CNDDDB so that information can be disseminated to government agencies, professionals in the private sector, and parties interested in conserving California's biodiversity. The conservation goals of the CNDDDB extend far beyond California, however, since it is part of a larger database maintained by The Nature Conservancy called "NatureServe" (Bittman 2001). The NatureServe database is made up of those similar to CNDDDB from all over the United States, Canada, and Latin America and is thus able to report prioritized conservation information on a regional basis. It is in this way that the CNDDDB contributes to the preservation of worldwide biodiversity.

With regard to rare plant conservation, the almost 20,000 records of rare plants listed on the CNDDDB gain legal protection through several policies noted above, including NEPA, CEQA, NPPA, and the Natural Community Conservation Plans through the NCCP Act (Bittman 2001). To that end, government agencies like the USFWS regard rare plants listed in the database as unofficial "Species of Concern" and these species are then afforded protection by the USFWS under NEPA. At the state level, because all plants listed in the CNPS *Inventory* are also listed in the CNDDDB, those rare plants not listed under CESA are protected under CEQA, NPPA and NCCPs. Species that are added to the database are either listed under FESA and/or CESA as endangered, threatened, rare, or as a candidate /proposed species for reasons such as rarity, threats such

as development, the species is associated with a rapidly declining habitat type, or more information is needed (DFG Native Plant Conservation Statement 2003).

***Streptanthus albidus* var. *peramoenus* as a Species of Concern in the CNDDDB**

The study species, *S. albidus* var. *peramoenus*, is listed in the CNDDDB. Additionally, because that database is part of the larger, worldwide NatureServe, it has both a state ranking and a global ranking; these rankings inform government agencies and conservation groups of a plant's priority when considering land management or other land use activities in designated habitat.

For subspecies, such as the study species, the rank is two-fold with the "G" portion being the rank of the species and the "T" portion the rank of the subspecies. To illustrate, its global rank of G2T2 means there are from 6 to 20 occurrences, 1,000 to 3,000 individuals, or its populations exist on 2,000 to 10,000 acres (809 to 4046 hectares). The state ranking of *S. albidus* var. *peramoenus* is S2.2; the first "2" has the same meaning as the global rank and the second "2" designates it as "threatened" (as opposed to "very threatened" or "no current threats known") (California Department of Fish and Game, Natural Diversity Database 2003). The CNDDDB also lists this plant as a Species of Concern and is therefore included on a list of "potentials" for listing as maintained by the USFWS and as mentioned earlier, part of the CNPS *Inventory* lists as category 1B (California Department of Fish and Game, Natural Diversity Database 2003). The author has completed the Field Survey Form to include the populations studied in this thesis research in the CNDDDB.

The state and federal policies describe here is the first step toward conserving California's unique biological history and diversity. The second step is enforcing these regulations and the third step is expanding them. The outlook for *S. albidus* var. *peramoenus* and other rare plants in serpentine environments can be positive if the plant is afforded continued protection through CEQA, the records in the CNDDDB are maintained, and additional protection is eventually provided under the CESA.

APPENDIX B

SPECIES LIST

This list is comprised of native and exotic plants found in experimental plots; plants located outside of experimental plots are not included. Scientific names throughout the study are listed according to The Jepson Manual (Hickman 1993). Common names were determined by The Jepson Manual (Hickman 1993), Plants of the San Francisco Bay Region (Beidleman and Kozloff 2003), and CalFlora: Information on California Plants for Education, Research and Conservation (2004). The status of rarity was determined by The Jepson Manual (Hickman 1993) and the CNPS Inventory of Rare and Endangered Plants of California (2001).

Scientific Name*	Family	Common Name	Status**	Rare?
<i>Sanicula bipinnatifida</i>	Apiaceae	Purple Sanicle	N	
<i>Achillea millefolium</i>	Asteraceae	Common Yarrow	N	
<i>Ancistrocarphus filagineus</i>	Asteraceae	Wooly Fishhooks	N	
<i>Calycadenia multiglandulosa</i>	Asteraceae	Sticky Rosinweed	N	
<i>Centaurea melitensis</i>	Asteraceae	Tocalote, Maltese Star Thistle	E	
<i>Crepis capillaris</i>	Asteraceae	Smooth Hawk's-beard	E	
<i>Eriophyllum confertiflorum</i> var. <i>confertiflorum</i>	Asteraceae	Wooly Sunflower, Yellow Yarrow	N	
<i>Hemizonia congesta</i> ssp. <i>luzulifolia</i>	Asteraceae	Hayfield Tarweed	N	
<i>Hypochaeris glabra</i>	Asteraceae	Smooth Cat's Ear	E	
<i>Lessingia micradenia</i> var. <i>glabrata</i>	Asteraceae	Smooth Lessingia	N	Yes
<i>Microseris douglasii</i>	Asteraceae	Douglas Microseris	N	
<i>Microseris elegans</i>	Asteraceae	Elegant Microseris	N	
<i>Sonchus asper</i> ssp. <i>asper</i>	Asteraceae	Prickly Sow Thistle	E	
<i>Taraxacum officinale</i>	Asteraceae	Common Dandelion	E	
<i>Cryptantha flaccida</i>	Boraginaceae	Flaccid Cryptantha	N	
<i>Lepidium nitidum</i> var. <i>nitidum</i>	Brassicaceae	Common peppergrass	N	
<i>Streptanthus albidus</i> ssp. <i>peramoenus</i>	Brassicaceae	Most Beautiful Jewelflower	N	Yes
<i>Minuartia douglasii</i>	Caryophyllaceae	Sandwort	N	
<i>Silene gallica</i>	Caryophyllaceae	Windmill Pink	E	
<i>Calystegia collina</i> ssp. <i>venusta</i>	Convolvulaceae	So. Coast Range Morning Glory	N	Yes
<i>Crassula connata</i>	Crassulaceae	Pygmy-weed	N	
<i>Astragalus gambelianus</i>	Fabaceae	Dwarf Milkvetch	N	
<i>Lotus humistratus</i>	Fabaceae	Short-podded Trefoil	N	
<i>Lotus purshianus</i>	Fabaceae	Spanish Clover	N	
<i>Lotus strigosus</i>	Fabaceae	Bishop Lotus	N	
<i>Lotus wranglianus</i>	Fabaceae	Chile Trefoil	N	
<i>Lupinus bicolor</i>	Fabaceae	Miniature Lupine	N	
<i>Lupinus succulentus</i>	Fabaceae	Arroyo Lupine	N	
<i>Medicago polymorpha</i>	Fabaceae	California Burclover	E	
<i>Monardella douglasii</i>	Fabaceae	Douglas Monardella	N	
<i>Salvia columbariae</i>	Fabaceae	Chia	N	
<i>Trifolium wildenovii</i>	Fabaceae	Tomcat Clover	N	
<i>Erodium botrys</i>	Geraniaceae	Broadleaf Filaree	E	

Scientific Name*	Family	Common Name	Status**	Rare?
<i>Erodium cicutarium</i>	Geraniaceae	Redstem Filaree	E	
<i>Geranium molle</i>	Geraniaceae	Dove's Foot Geranium	E	
<i>Sisyrinchium bellum</i>	Iridaceae	Blue-eyed Grass	N	
<i>Calochortus venustus</i>	Liliaceae	Butterfly Mariposa Lily	N	
<i>Chlorogalum pomeridianum</i> var. <i>pomeridianum</i>	Liliaceae	Common Soap Plant	N	
<i>Dichelostemma capitatum</i>	Liliaceae	Bluedicks	N	
<i>Camissonia graciliflora</i>	Onagraceae	Hill Sun Cup	N	
<i>Clarkia purpurea</i> ssp. <i>purpurea</i>	Onagraceae	Winecup Clarkia	N	
<i>Eschscholtzia californica</i>	Papaveraceae	California Poppy	N	
<i>Plantago erecta</i>	Plantaginaceae	California Plantain	N	
<i>Avena barbata</i>	Poaceae	Slender Wild Oat	E	
<i>Brachypodium distachyon</i>	Poaceae	Purple Falsebrome	E	
<i>Bromus hordeaceus</i>	Poaceae	Soft Chess	E	
<i>Bromus madritensis</i> ssp. <i>rubens</i> (B. <i>rubens</i>)	Poaceae	Foxtail Chess	E	
<i>Gastridium ventricosum</i>	Poaceae	Nit Grass	E	
<i>Hordeum murinum</i> (var. <i>leporinum</i>)	Poaceae	Barnyard Foxtail	E	
<i>Lamarckia aurea</i>	Poaceae	Goldentop Grass	E	
<i>Lolium multiflorum</i>	Poaceae	Italian Ryegrass	E	
<i>Nasella pulchra</i>	Poaceae	Purple Needle Grass	N	
<i>Vulpia microstachys</i> var. <i>pauciflora</i>	Poaceae	Common Hairy Leaf Fescue	N	
<i>Gilia tricolor</i>	Polemoniaceae	Bird's Eyes Gilia	N	
<i>Linanthus ambiguus</i>	Polemoniaceae	Serpentine Linanthus	N	Yes
<i>Phlox gracilis</i>	Polemoniaceae	Slender Phlox	N	
<i>Eriogonum nudum</i>	Polygonaceae	Naked Buckwheat	N	
<i>Anagallis arvensis</i>	Primulaceae	Scarlet Pimpernel	E	

* historic names in parentheses

** N=native, E=exotic