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Abstract

Many endangered plants exist in small, declining populations and exhibit signs of poor reproductive fitness due to negative environmental pressures and/or a loss in genetic viability. The Santa Cruz tarplant (*Holocarpha macradenia*) is an extremely rare annual wildflower that has suffered many recent local extirpations. The tarplant currently exists at eleven isolated sites, only three of which have large, stable populations. This study hypothesized that individuals in the small tarplant populations are experiencing reduced reproductive fitness, primarily as a result of negative environmental forces. We looked for correlations between population size and both indicators of plant performance (seed number, seed weights, seed heads per plant, and plant size) and indicators of habitat quality (plant density, indicators of disturbance, and invasive plant presence). Primary experimental components included: comparing fitness traits of field plants to plants grown in a common garden environment, measuring indicators of habitat quality, testing the effects of self and cross fertilization in both types of the tarplant's dimorphic seeds, and performing a small-scale invasive grass removal experiment. Field plants growing in small populations produced fewer seeds, fewer seed heads, and a greater proportion of dormant seeds than plants in large populations. These trends were not observed in the greenhouse populations, leading us to believe that the effect is mostly environmental. We observed a strong correlation between population size and indicators of habitat quality and a dramatically increased rate of survival in plots where invasive plants were removed. Fewer non-dormant seeds likely represent a lack in pollination, while other negative reproductive traits may be a resource limitation stemming from invasive plant competition. Overall, we find strong evidence that the small tarplant populations are suffering from adverse environmental effects including pollen and resource limitations, invasive plants, and a lack in disturbing forces; whether these are the only or original sources of population decline has yet to be determined. We cannot rule out the possibilities of genetic problems, allee effects, or intrinsic biological attributes of the tarplant as factors reducing tarplant fitness and population size. However, this study demonstrates that negative environmental pressures are likely powerful enough to cause extirpation, therefore, intensive and proactive management, and possibly even ex-situ cultivation is needed to rehabilitate the small tarplant populations.

Chapter 1: Conservation of the Santa Cruz Tarplant

The coastal prairie, one of California's most rare habitats, exists from Monterey Bay to South-West Oregon [Appendix 1]. This study investigates the status of the Santa Cruz Tarplant (*Holocarpha macradenia*, Greene) a highly endangered coastal prairie wildflower endemic to Northern California. The US Department of Fish and Wildlife has listed the coastal prairie as the 8th most rare ecosystem in the United States, yet it continues to be destroyed through direct development and poor management. Coastal prairies are mixed communities of grasses and wildflowers that flourish on flat and gently sloping marine terrace platforms not far above the Pacific Ocean (from 100 to 400 feet in elevation). Coastal prairies are considered climax communities, as opposed to successional grasslands that will eventually converge to forests or scrublands. Some estimates have put the age of the Californian coastal prairies at 600,000 years old, thus one of the oldest, most stable ecosystems in the temperate region (Holland, 1986). At the time of European arrival in California, there were an estimated 865,000 acres of coastal prairie in California (Huenneke, 1989). Currently, less than 1%, or approximately 1,977 acres of original prairie remain (CNDDDB, 2000). The Santa Cruz tarplant is only one of many coastal prairie species facing extinction because of a severe reduction in habitat.

The county of Santa Cruz, a small county south of San Francisco, is the home to many remaining coastal prairie patches. Santa Cruz has been listed in a nation-wide study as one of the United States' major 'hot spots' for endangered plants and animals (Dobson, 1997). In some areas of Santa Cruz County, the coastal prairie supports up to 250 species of native wildflowers, including the endangered plant species *Trifolium buckwestiorum* (Santa Cruz Clover), *T. grayi* (Gray's Clover), *Plagiobothrys chorisianus* (Artist's popcornflower), *Plagiobothrys diffusus* (San Francisco Popcornflower), and *Holocarpha macradenia* (Santa Cruz Tarplant). The coastal prairies also provide habitat for a diverse array of native insects, many of which are highly

endangered (e.g., *Cicindela Ohlone*, Ohlone Tiger Beetle and *Adela oplerella*, Opler's long horned moth), and others that have already gone extinct (e.g., *Lytta molesta*, molestan blister beetle). [also see Appendix 1]

Study Species

The Santa Cruz Tarplant is an aromatic annual in the prolific tarweed tribe, Madiinae (Asteraceae), which is known for the spectacular insular radiation of Hawaiian silverswords and the widely diversified paraphyletic Californian tarweeds (Baldwin and Wessa 2000). The three other species of the *Holocarpha* genus are restricted to California meadows, but are not endangered or threatened (Hickman, 1993). A large individual of *H. macradenia* can grow up to 40 cm tall, with 10-15 rigid lateral branches and anywhere from 30-150 flowering seed heads. A smaller, stressed plant might grow 5-10 cm tall, with no branches and 1-2 flowering heads. *Holocarpha macradenia* typically occurs on soils that include a sub-surface clay component, which holds moisture longer into the growing season than the surrounding sandy soils.

The seed production of the tarplant is highly variable. Like many members of the Asteraceae family, the tarplant is characterized by dimorphic achenes. The seeds of the outermost, ray flowers produce 'dormant', ray achenes, while the innermost disk florets produce 'non-dormant', disk achenes¹. The dormant ray seeds can live an estimated 15 years in natural soil conditions, and possibly longer in cold storage, while the non-dormant seeds appear to have reduced viability after 18 months. The ray achenes collect in natural soils, waiting for environmental cues to germinate and forming an extensive seed bank, that can range from 240-40,000 seeds per square meter (Bainbridge, 1999). Casual observations (e.g., large population increases after a fire) and preliminary laboratory experiments indicate that fire is a key environmental factor contributing to the germination of dormant seeds (Bainbridge, Hayes, Barber, unpublished).

Seed dispersal from the tarplant has not been studied. Researchers who have worked on the tarplant largely agree that non-dormant seeds fall no further than several centimeters off

¹ Achenes will be referred to as seeds for the majority of this paper.

the seed head when shaken or crushed. The dormant ray seeds grow tightly bound in a sticky, glandular phyllary, which can facilitate the dispersal of the dormant seeds externally by animals or birds (CDFG, 2001). Knowledge of pollen dispersal is also limited in the tarplant, native bees, bee flies, wasps, and winged beetles have all been observed pollinating the tarplant. *H. macradenia* has been considered an obligate out-crosser (Baldwin & Bainbridge, 2000), although results of this study may contradict these previous observations.

Threats to the Tarplant and the Coastal Prairies

The California Native Plant Society defines the most significant threats to the coastal prairie ecosystem as development, habitat fragmentation, exotic weed invasion, fire suppression, and a lack of disturbance (CNDDDB, 2000). These effects are, of course, highly interrelated (e.g, fire suppression aids growth of exotics), yet are a good summary of the most significant forces effecting both the remaining coastal prairie habitat and the tarplant populations.

Development has taken perhaps the largest toll on this ecosystem. The coastal prairie habitat is divided into four marine terraces (sand deposits of different ages and locations in the coastal hills). Suburban sprawl and agricultural growth has left very few remaining intact patches of the 'first' marine terrace (located close to the sea, with prairie of approximately 100,000 years old). The second terrace around Santa Cruz has also been entirely developed with the exception of two city parks; further north it has primarily disappeared under agriculture. The third and fourth terraces have fared better, and can be found in many fragments along the north coast of California. The best tarplant habitat was probably located on the prairies of the first and second terraces; only two populations remain in these zones (Holland, 1989).

Prairie remnants are literally islands amidst a sea of concrete, as nearly 99% of the coastal terraces have been eliminated. This intensive fragmentation has significant negative effects for native wildflower populations. Widely separated populations are less likely to have opportunities for dispersal and pollination, and create channels and habitat edges for exotic invasion. Gene flow between the current tarplant sites is probably non-existent; pollinators do not

usually travel more than .5 km at one time, and most of the tarplant populations are separated by at least 2 km (CDFG, 2001).

Exotic plants have completely transformed many of California's Mediterranean-climate grasslands over the last two hundred years (Huenneke et al 1989, 1991). After settlement by the Spanish, many annual grasses and forbs native to Eurasia spread rapidly through California (Baker 1989). By the 1850's annual grass species (such as members of *Avena*, *Bromus*, and *Hordeum* genera) had largely displaced perennial bunchgrasses (Carlsen, et al 2000). The exotic annuals create a uniformly dense soil cover, as opposed to the perennial bunchgrasses, which maintain more habitat heterogeneity. The coastal prairies in the Santa Cruz area are influenced by a variety of exotic species such as annual forbs and perennial flowering plants as well as the omnipresent annual grasses [for a list of significant species see Appendix 1]. The Santa Cruz Tarplant seems to be extremely vulnerable to competitive grasses, and like other native wildflower species has been known to disappear upon proliferation of exotics or when disturbing forces were removed².

As development and fragmentation has continued in Northern California, many natural disturbance processes have been interrupted. The role of fire in prairie ecosystems has been well documented as important force in maintaining a many native communities (Kozlowski and Ahlgren 1974). Although fire may not have been such a common occurrence prior to the human occupation of California over the last 10,000 years, it was definitely an active force in this landscape and possibly occurred in catastrophic episodes. Such fires, along with herds of large herbivores that became extinct in the late Pleistocene may have been important factors in determining the persistence of the coastal prairies (Holland, 1989). The suppression of fire and cattle grazing not only threatens communities by allowing shrub and tree invasions, but can also exacerbate the problem of exotic grasses. While they may be useful as management tools, neither fire nor cattle can remove the exotics from the landscape.

² Arana Gulch, Twin Lakes, and ___ are some of the populations that have experienced nearly ten-fold increases following a fire.

Status of the tarplant

The above-described threats have taken their toll on the Santa Cruz tarplant. This species is truly teetering on the brink of extinction, only a handful of populations exist today, very few of which are likely to outlast the next decade. As their habitat has changed, the numbers of tarplant populations have declined dramatically. [see Appendix 3, Status of all Observed Populations, and Appendix 4, Population Size History]. Thirty-four native tarplant populations have been documented since 1894; fifteen were extant in 1980 and four are extant today. Only two of the remaining populations have greater than 1000 individuals, and all of them exist in the southern counties of Santa Cruz and Monterey (all native populations in the northern bay area are extirpated). The City of Santa Cruz is surprisingly progressive in regards to endangered plants, and has passed several resolutions protecting tarplant habitat. Also contributing to the protection of tarplant habitat, 1360 hectares of coastal prairie habitat have been designated as "Critical Habitat" by the Federal Department of Fish and Game (CDFG, 2001).

In the late 1970's local botanist Neil Havlik gathered seed from two natural populations facing imminent development in the north-bay county of Contra-Costa. Whole plants and seed heads were scattered in twenty-two locations that appeared to be potential tarplant habitat. The five populations that have survived until today are growing in heavily grazed regions of Wildcat Regional Park near Berkeley, and only one of these populations has greater than 1000 individuals. These re-introduced populations may face their own set of complications and threats, such as an improper seed-bank, less than ideal micro-climatic conditions, and/or a genetic bottlenecks.

Chapter 2: Population Decline and Plant Fitness

Introduction

Worldwide, plants dominate lists of rare and endangered species, with 25% of the world's vascular plants facing extinction in the next 50 years (Raven, 1987). California has the most diverse and extensive variety of plants in the United States, but many of the native wildflowers are becoming endangered at an accelerating pace. Each year, the Golden State's grasslands awe thousands of visitors and inspire local residents with their amazing show of color, yet thirty-four taxa endemic to California have gone extinct in recent years; the California Native Plant Society lists 13% of the native flora as rare or endangered (Skinner and Pavlik, 1994).

The destruction and fragmentation of native ecosystems has led to the increasing isolation of formerly common plants into small populations (Vitousek 1994, Harrison and Bruna 1999). For a number of reasons, species existing in small populations face a disproportionately high risk of extinction. Small populations are first and foremost threatened by environmental stochasticity and changes in external factors (Menges, 1991a). Another risk to small populations, as predicted in many conceptual models, is the presence of negative allee effects³. Allee effects re-enforce the concept of a minimum viable population size; as a population declines towards extinction, there is expected to be a threshold of number of individuals below which a population cannot recover, due to the loss of holistic properties in a large population (Allee, 1951). One example is the disruption of important biotic interactions, such plant-pollinator mutualisms, as plants in small populations may be less attractive to pollinators than plants in large patches, (Sih and Baltus 1987) or plants that are more sparsely arranged (Mustajarvi et al, 2001).

³ Broadly defined as the benefits conferred on an individual because of the presence of conspecifics (Steven and Sutherland, 1999)

With such threats facing small populations, it is extremely important to isolate the factors that may be causing population decline. In this study, we try to make suggestions about the cause of population decline in certain populations of the Santa Cruz tarplant. We first look at what is causing poor reproductive viability in the smaller populations, and then attempt to draw a connection between population size and reduced habitat quality. A positive relationship between population size and the reproductive viability (fitness) of individual plants has been widely theorized and demonstrated in a handful of studies; but the cause of low fitness has been rarely explained. The Santa Cruz tarplant is an example of an endangered plant suffering from extremely low population sizes and low reproductive viability, and is thus at increased risk of extirpation due to stochastic events or compounding allee effects. In the following paragraphs, we look at the evidence linking low individual fitness and population size, then explore some of the mechanisms behind this relationship.

The literature supporting generally positive relationships between population size and individual plant fitness (but not attempting to prove a cause) is reviewed here, as an increasing number of researchers are testing for fitness effects associated with small population sizes. It is not easy for researchers to prove a correlation between population size and plant performance. There is limited access to studying rare plant populations and often an absence of large populations; thus there are rarely enough data points to provide statistical power. Menges (1991) demonstrated a clear relationship between germination success and population size in *Silene regia*, while *Gentiana pneumonanthe* exhibits positive relationships between population size and a variety of life history traits (such as seedling weight and total flower production) in greenhouse-cultivated plants (Oostermeijer et al 1994). Similarly, germination success and seed size were significantly correlated with population size in *Ipomopsis aggregata* (Heschel & Paige 1995). In a study of an endangered *Sedum* species, Olfelt et al (1998) showed a positive correlation between flowering, seed set, and germination rates and estimated effective population size. Finally, Luijten et al (2000) found that the fitness of small populations (measured by seed set, germination rates, and other morphological measurements) was significantly reduced in *Arnica montana*.

Other studies have found no correlations between population size and fitness variables (Van Treuren et al. 1993; Widen 1993; Hauser & Loeschcke 1994; Ouborg & van Treuren 1995; Lammi et al. 1999).

The risk of extirpation increases in magnitude as reproductive fitness declines in small populations. Poor reproductive viability can be a result of either negative genetic or negative environmental effects. Researchers making stipulations about population size and fitness often juxtapose these two categories in an either/or scenario. Yet genetics and environmental factors can effect a population collectively and to varying degrees, while determining the relative proportion of such mechanisms can only be tested experimentally. Environmental forces that may affect the tarplant negatively include poor pollination, a lack in necessary resources, competition from invasive plants, and an absence of disturbances. In addition to negative environmental pressures, the tarplant may have suffered a loss in genetic viability as a result of declining genetic variation, accumulation of detrimental mutations, or inbreeding depression (Lynch, 1995; Lande, 1996).

Environmental differences in habitat parameters between small and large populations are considered a major factor driving variation in population size in classical ecological theory, yet there are few published studies to confirm this. Significant relationships between habitat quality and plant reproductive potential predict that populations occupying poor habitat will fall in size. For example, habitat quality largely influenced both biomass and reproductive effort in experimentally planted populations of a rare California endemic *Chorizanthe pungens* (Kluse and Doak 1999). Morgan (1999) did not perform a common garden experiment but suggests non-genetic sources of fewer seed heads produced in small populations of the grassland plant *Rutidosis leptorrhynchoides*. Carlson (2000) experimentally demonstrated that exotic annual grasses prevented normal inflorescence production in the rare forb *Amsinckia grandiflora*. Another common measure of poor habitat quality is poor pollinator presence.⁴ Pollen limitation

⁴ It is important to note the distinction between pollen limitation because of a lack of pollinators in the area (e.g., poor habitat quality as a possible cause of low population size), and a lack in pollination as a result of low population size (an allee effect, caused by the inability of small populations to draw pollinators). This paper first deals with the possibility that low pollination rates might indicate poor habitat quality, later we address the possibility of allee effects.

in small populations has been demonstrated in experimental hand-pollination of *Eupatorium* (Byer 1995) and *Lythrum salicaria* (Agren 1996). Other studies have found positive correlations between population size and plant fecundity, attributing the relationship to pollen limitation (Jennersten 1988; Lamont et al, 1993, Widen et al 1993).

In general, the evidence in published literature directly implicating environmental stress as the cause of poor fitness in small populations is meager compared to the evidence for genetically derived causes. Smaller populations had higher risks of extinction in experimentally manipulated genetic effective population sizes of *Clarkia pulchra* (Newman and Pilson 1997). There is ample evidence of genetic correlations with population size (examples: Bijlsma et al, 1991, Raijmann et al 1994), although the extent to which a loss in genetic viability (through a loss in variation, inbreeding depression, or accumulation of mutations) is to blame for reductions in fitness is difficult to determine.

In studies that are similar to this one (e.g., fitness traits are recorded both in the field and in a common garden) the results are uniformly interpreted to suggest genetic causes of poor fitness in small populations, although we might suggest that a closer analysis of many studies leaves much doubt as to the actual cause of poor fitness. Heschel & Paige (1995) attributed reduced germination of *Ipomopsis aggregata* to genetic effects because supplemental pollen increased fitness in the greenhouse plants. Fischer and Matthies (2001) tested a comprehensive array of fitness variables (in field and greenhouse plants) in *Gentianella germanica*, and assert that genetic limitations contributed more to reduced plant performance than did habitat quality, although they did not exclude the possibility of pollinator limitation. Smaller populations of *Primula veris* and *Gentiana lutea* produced fewer seeds per fruit and per plant, both traits were *not* observed in plants from the small populations in the greenhouse. Yet Kery et al (2000) states, "The inclusion of plant size (an integrated measure of habitat quality) in the statistical models did not change the relationships between fecundity and population size. Pollen limitation or inbreeding depression in small populations are therefore more likely explanations for these

patterns than is habitat quality.” In this study, we did not assume that plant size was an encompassing measure of habitat quality, and suggested a different conclusion from similar data.

Only a few studies of population size and fitness have suggested that plant performance might be an effect of both genetic and environmental stress. A lack in fire management strongly influenced finite rates of increase in *Silene regia* (Menges and Dolan 1998) while genetic variation was a close second in predicting fitness traits. In the rare *Arnica montana*, Luitjen (2000) demonstrated that small population size was correlated with reduced fitness and showed some evidence of inbreeding depression, yet they admit that this is not enough proof to disregard possible environmental effects.

The importance of examining genetic resources for rare plants is still under debate in the conservation biology field (Ellstrand and Elam, 1993 and Schemske et al, 1994), as are the traditional methods of measuring genetic variation (Podolsky 2001). Species which were formerly common and have suffered recent reductions in population extent are at a greater risk of loss of genetic variations (Huenneke 1991). As detrimental effects are manifested in the following generations, annual plants are more likely to show these symptoms sooner than perennials. The tarplant is both an annual plant and has been reduced to a tiny fraction of its former range in the last one hundred years; therefore the tarplant is a likely candidate for genetic problems. It should also be noted that the majority of studies investigating the fitness / population size connection use perennial study species. An annual plant is both more difficult to track, and will have a uniquely different set of risk factors.

There are many possible scenarios under which environmental pressures could negatively affect tarplant growth. For example, changes in the availability of necessary resources can dramatically influence native plants; falling water tables due to human use has been known to alter plant composition (Owens, 1994). Climate changes can also alter patterns of precipitation, temperature, and the frequency of extreme events, any of which could have drastic repercussions for small endemic plant populations. Available resources may limit growth for many of California's native plants because exotic annual grasses provide intense competition for water,

sunlight, and recruitment sites; thus facilitating lower seed output and smaller populations (Carlsen et al 2000). Invasive plants have also been known to alter patterns of soil-water availability in California grasslands (Holmes and Rice, 1996) and can benefit from excessive nitrogen pollution in and around urban areas (Huenneke et al, 1989). Disturbing forces such as annual fires or cattle can help reduce competition from invasive plants (Germano, 2001), and can also be necessary in creating recruitment sites while maintaining habitat heterogeneity and diversity for certain endangered species (Kotanen, 1995; Lesica, 1999). A lack of fire management was a strong predictor of low rates of finite increase in the prairie species *Silene regia* (Menges and Dolan 1998), and effected population density for the rare *Schwalbea americana* which grows in the pine forests of the southeastern United States (Kirkman et al, 1998). In addition to annual fires, large mammals have historically been significant disturbing forces for the California grasslands (Holland, 1989) yet more recently, cattle have replaced the original mammals in many California grasslands. The presence of cattle can have either a positive or a negative effect on native plants, depending on other aspects of the ecosystem, such as soil type (Safford 2001). In southern California, Germano et al (2001) found that grazing was essential in reducing the thick cover of exotic grasses, and thus necessary for the survival of threatened plants and animals (also Gilfedder 1994). It is obvious that a web of complicated environmental factors could be implicated in the population decline and poor reproductive fitness of the Santa Cruz tarplant; yet delineating such forces from genetic effects can be difficult.

Compounding the effects of adverse fitness consequences in small populations may be traits that are fundamental biological attributes of the rare species, such as normally low fecundity, poor dispersal strategies, or inherent lack of genetic variation. These intrinsic factors may constrain distribution and abundance of rare plants when influenced by factors that are extrinsic to the life history of the taxon in its native habitat (e.g. exotic competitors, lack of pollinators, habitat destruction). For example, a rare plant may not be able to overcome mild habitat fragmentation because of extremely poor dispersal abilities, whereas a more prolific disperser may be unaffected. "Assigning the blame" to either intrinsic or extrinsic factors can be

nearly impossible, and is certainly beyond the scope of this study. However, it is important to understand contribution of such factors to the rarity of annual plants. The ability to isolate, understand, and roughly rank the factors influencing population decline may be central to preventing future species extinctions.

Study Goals and Questions

The Santa Cruz Tarplant is facing a suite of threats from veiled and entangled sources. In recent years, many tarplant populations have disappeared without being directly developed, and all but three of the remaining populations seem to be suffering from low and declining population sizes. It was hence the goal of this study to conduct some preliminary experiments and observations that might help isolate some of the multiple environmental or genetic factors behind low population size and poor reproductive fitness. We also examine the possibility that allee effects and/or intrinsic biologic traits could also be influencing a positive relationship between plant performance and population size. To this end, our primary experimental components were:

1. *Population Size and Fitness* - Document the relationship between plant performance and population size by testing both reproductive characters (seed set, seed weight, ray/disk proportions, receptacle size, and germination) and physiological characters (plant height, branch length, total number of buds produced, flowering timing, and plant density) in 9 to 11 tarplant populations of different sizes.
2. *Common Garden Experiment* - Using seeds from populations of different sizes and characteristics, conduct a greenhouse common garden experiment, and measure the same fitness traits as those taken in the field.
3. *Habitat Measurements* – Compare indicators of habitat quality such as plant density, the presence of invasive plants, and evidence of disturbing forces in large and small populations.

4. *Self-Fertilization* - Conduct initial experiments to determine whether the tarplant is capable of self-fertilization, with the intent of making suggestions about a possible lack in pollination.
5. *Invasives Removal* - Test the effects of invasive plants on juvenile tarplant seedlings by removing invasive plants in the early spring.

Using the data gathered from these experiments, we attempted to answer the following questions, which are further addressed in the discussion section:

- Is there evidence linking environmental limitations (such as a lack in proper pollination or resources) to negative fitness consequences in small populations?
 - Do plants grown in the greenhouse exhibit the same reproductive and physiological characteristics as those grown in the field?
 - Does this data say anything about genetic diversity?
 - Could there be evidence of an allee effect?
- How do habitat traits such as the presence of exotic plants and disturbing forces relate to population size?
 - Does the removal of invasive plants aid tarplant survival?
- Are the intrinsic dispersal and dormancy abilities of the tarplant compounding extinction probability?

Methods

Population Size and Fitness

Reproductive variables of plant fitness were measured over two summers (2000 & 2001) by collecting seed heads from nine populations. The number of seed heads gathered varied between 10 and 150, depending on the size and status of the population. Ray and disk achenes were counted and weighed separately for each seed head and the receptacle diameter of each head was measured with electronic calipers. Seed head diameter measurements were used to

calculate seed head area (an estimate of the portion of the seed head accessible to non-dormant seeds) and seed head perimeter (the portion of the seed head available to dormant seeds). Three separate germination trials of non-dormant disk achenes were conducted with seeds collected in 2000. Seeds heads were removed from all nine populations in 2000, but seeds were counted in the field for three populations in 2001 due to extremely small population sizes. Seed weight data is thus missing for these three populations for 2001, but data all other variables exists for both years.

Seeds were collected from all populations within two weeks, yet plants in some populations had begun to senesce almost a month earlier than others. This introduces a small chance of error in our seed counting, since disk achenes begin falling from the plants once the seed head is dried. Therefore it is possible that some populations had lost a few disk achenes before collection. We consider this effect negligible, because care was taken to collect only what appeared to be completely intact seed heads, and our data does not reflect a trend towards lower numbers of disk achenes in those populations that were further senesced⁵.

Physical characteristics of the plant, such as plant height, longest branch length, total number of buds, ray / disk floret proportions and timing of flower production were measured in the summer of 2001. Height, leaf length and buds were measured for all plants in populations under thirty individuals, and on 30-60 individuals for populations of greater size. In large populations, random sampling was done along a transect through the center of the population area. Due to a very strong heat spell near the beginning of the flowering season, florets on two of the populations wilted before sampling, and no active flowering was observed.

Fitness variable data for 2000 and 2001 was compiled and plotted on one graph for each trait. Population size was calculated as the geometric average of the last ten years of population size measurement in order to account for some variability while assigning less weight to large shifts in population size. Paired t-tests were done to determine if there was a significant difference in trends between years. Regression analysis was conducted grouping data for 2000/

⁵ Graham Hills (n3) was partially senesced in advance, Twin Lakes (nA) and caltrans (n4) were more advanced

2001 for variables with no significant difference between years, and separately for three variables that were significantly different (total seed weight per head, seed head area, seed head perimeter).

Common Garden Experiment

Plants from nine populations were grown from seedlings in a greenhouse for almost six months. Two trials were conducted over a year and half. Data was recorded every other week for longest branch length, plant height, flowering timing, and total number of flowing heads during the growth phases, while mortality rates were closely watched. Seeds were collected, counted and weighed once plants had senesced. The morphological and seed data presented here was taken from our second common garden trial, because the first group of plants experienced a severe aphid attack. The first group of plants was used in the pollination experiment.

Habitat Measurements

Habitat quality was measured by several parameters in all 11 populations and some recently extinct populations during the summer of 2001. Three to nine vegetation plots (30 x 30 cm grid) were randomly sampled within the growth areas of the tarplant. Identifying all the species in each plot and counting the number of plants determined relative proportions of exotic/native species. Percentage bare ground and percentage tarplant cover was determined by estimating the cover of tarplants, other plants, and bare ground in 2x2 cm sub-plots within the 30x 30 cm plot. Tarplant density was estimated by counting the number of plants in each plot, although this measure does not represent the true density of tarplants over the entire growing area.

Self-Fertilization

Greenhouse plants of 9 tarplant populations (4 natural and 5 re-introduced) were grown for 12 weeks to maturity. From each of the nine populations, five individuals that had begun to flower at the same time were used. Two to four flowers on each plant were paired that were of similar size and that had begun to flower within 48 hours of each other. Using a q-tip™, one

flowering head was pollinated using pollen from its own head while the other flower was pollinated with a q-tip™ that had been brushed against 10-15 flowers produced by other plants in the same population. No intentional cross-pollination between different populations occurred and pollinated individuals were well separated on the greenhouse bench. We have allowed for the possibility of small amounts of cross-contamination due to the large amounts of pollen produced by the plants and the presence of thrips.

Invasives Removal

This experiment was conducted in only one population out of concern for harming the tarplants in the manipulation of surrounding plants. Population n4, also referred to as the Apple Hills or Caltrans population, exists on a tiny strip of hard-packed land between a highway and a housing development. The plants in this population are tiny, an average of 7 cm in height, and only the rare plant produces more than one seed head. Invasive plants were removed when they had just begun to sprout from two small (30 x 30) plots in April of 2001. Two adjacent control plots, with ± 10 plants of the removal plots, were established at the same time. The numbers of individuals in all plots were counted again in June, and select seed heads removed from plants that survived to determine seed set and weight.

Results

Population Size and Fitness

Seed Numbers: A strong significant trend was observed between the number of non-dormant seeds and population size (Figure 2), but not for the number of dormant seeds (Figure 3). However, there was a significant regression when looking at the proportion of total seeds that were dormant in a seed head (Figure 4, $p = .0059$)

Seed head sizes: The number of non-dormant seeds produced by a seed head was significantly correlated with the total area of the seed head ($R^2 = .241$, $p < .0001$, Appendix 9).

The number of dormant seeds produced was significantly correlated with the seed head perimeter ($R^2 = .193$, $p < .0001$, Appendix 9). The average seed head area and perimeter, plotted against population size, shows a somewhat of a visual trend, albeit not significant with the samples available (Table 1). Figure 5 shows a significant correlation between population size and the number of non-dormant seeds divided by head area; while Figure 6 gives the proportion of dormant seeds divided by head perimeter. These graphs indicate that the relationship between a proportional increase in dormancy and population size is not confounded by the relationship between number of seeds and head size.

Seed Weights and Germination: The weight of dormant seeds was significantly positively correlated with population size ($p < .0001$, Figure 7), while correlation of the weight of non-dormant seeds with population size was only marginally significant ($p = .0673$, Figure 8). The total seed weight produced per head was also significantly correlated to population size. Heavier seeds were produced by many of the populations in 2000 as opposed to 2001 (Figure 9). Germination rate of non-dormant seeds was not significantly correlated with seed weight, mainly due to several outlying populations with low germination. Disk achene germination was not significantly correlated with population size (Table 2).

Physiological Traits and Flower Timing: Population size was significantly correlated with median measurements of longest branch length, total seed heads, and the number of non-flowering buds in late June. It was not significantly correlated with averages of these measurements, median height, or the number of flowering or past flowering heads in June (see Table 3 and Appendix 9).

Florets: Population size was significantly correlated with the number of non-dormant florets and the number of dormant florets, but not the proportion of dormant florets per head (Table 3 and Appendix 9). Since these trends are not represented in the actual number of seeds produced per head, we conclude that the number of florets observed at a fixed point in time in the field is not a good representation of total seed production.

Common Garden Experiment

The first batch of plants experienced an aphid attack when the seedlings were six weeks old, and the aphids disproportionately attacked the plants from the native populations in Santa Cruz. The data presented here is taken from the second batch of common garden plants. Tarplants from the native populations had higher mortality early on and marginally fewer of these plants bolted and produced large branches. Of the plants that fully bolted and produced branches, there were slight non-significant differences in the height and longest branch length between the native and reintroduced populations. The numbers and weights of seeds produced per population were not significantly different between populations for either ray or disk achenes (Appendix 9). It should be noted that the reintroduced plants were all founded with seed stock from the Northern San Francisco Bay, which had likely been separated from the Santa Cruz population for some time, thus are likely to exhibit genetic differences.

Table 4 shows the statistics for many of the traits measured in the common garden experiment. Figures 15 through 17 highlight some of the most important trends found when comparing common garden and field plants. The common garden plants from smaller populations did not produce a higher proportion of dormant seeds (Figure 16) or more seed heads than plants from larger populations (Figure 17). Instead, they demonstrated a remarkable uniformity in almost every fitness-related trait. Non-dormant seed production was very low in the greenhouse plants, while dormant seed production and total seed heads per plant were quite high compared field plants.

Habitat Measurements

Tarplant density, percent bare ground, and percent invasive species were all significantly correlated with population size (Figures 10-12). Refer to Appendix 9 for the distribution of percent cover for each population.

Self – fertilization

Seed heads that received pollen from other flowers produced significantly larger numbers of non-dormant disk achenes. The number of ray achenes produced was slightly, but not significantly affected by pollination (Figure 1). This experiment was affected by the presence of large numbers of thrips on the flowers, which we assume may have spread pollen around within seed heads, but most likely did not travel between heads. Thrips were found in equal abundance on all plants; therefore we assume the control treatment is still accurate in representing how more deliberate pollination can increase seed-set. However, these background levels of thrip pollination thwarted attempts to discover whether zero self-fertilization occurred for the disk florets.

Invasives Removal

The seedlings in the removal plots experienced dramatically higher survival rates than those in the control plots (Figure 13). Dormant seed set in the removal plots was higher than the seed set in the control plots (Figure 14). No differences were seen in seed head size or seed weights between the two treatments.

Discussion

The data presented by this study strongly suggest that plants in small populations have lower individual fitness. Our data implies several environmental mechanisms that may link poor plant fitness to small populations. Disrupted insect mutualisms (pollination) may reduce the production of non-dormant seeds (and possibly the weight of seeds). Other resource limitations may also reduce the weight of dormant seeds, the size of the plants, and the total seed heads produced in smaller populations. Our data also provides direct evidence linking poor habitat quality (e.g., sparsely distributed plants, heavy cover of exotic, and a lack of disturbance) to smaller populations. This research highlights that environmental factors do not only act on a population holistically, but also can significantly affect the fitness and phenotype of individual plants. Most importantly for the tarplant, poor habitat quality may not only cause fewer plants to appear each year, but may cause a higher proportion of dormant seeds to be produced.

In the literature, genetic factors are the most commonly cited reason for observing indicators of low plant fitness in small populations, yet direct causation is extremely difficult to prove. Genetic viability was not examined directly in this experiment and thus cannot be ruled out as a factor in population decline. However, in our greenhouse experiment, plants grown from the seed of small populations did not show trends consistent with their relatives in the field (e.g., less non-dormant seeds, lighter dormant seeds, fewer seed heads, ect). Therefore, it seems logical to look for environmental sources of population decline.

Is there evidence linking environmental limitation to negative fitness consequences in small populations?

Evidence of poor reproductive fitness in small tarplant populations is seen in the increased proportion of dormant seeds, less branched plants, and fewer total seed heads.^{6,7} While the *number* of non-dormant seeds (Figure 2) and the *weight* of dormant seeds (Figure 7) produced per head was correlated with population size, no correlation was found between the *weight* of non-dormant seeds or the *number* of dormant seeds produced per head. Since greenhouse experiments showed that pollination was necessary for only the production of non-dormant seeds (Figure 1), we can speculate that field populations with low non-dormant seed production might be suffering from low pollination rates, which could be a result of fewer pollinators in the landscape and thus an environmental source for population decline (also see section on allee effects). Lower masses of dormant seeds in small populations could also be indicative of self-pollination or poor pollen selection (Vaughton, 1997 and Lipow 2000).

⁶ Other factors tested in this study that did not correlate with population size include plant height, average branch length, or average total heads (the correlation presented here refers to median branch length and median total seeds). It is likely that the extensive variability in many of the populations skewed the averages, while the median gives a more accurate representation of the most common plants.

⁷ Many studies have found that germination ability is inhibited by low population sizes, a finding not represented here. We only germinated the non-dormant seeds, most of which germinated rapidly. A high success rate may have masked any trends between populations. This could be interpreted as slight evidence that genetic sources are not inhibiting germination.

The findings that small populations tend to produce fewer non-dormant seeds and an increased proportion of dormant seeds may simply be a confounding effect of smaller, resource limited plants. We tested this possibility by dividing the number of disk achenes per head by seed head area and proportion of dormant seeds by seed head perimeter⁸. Presented in Figures 5 and 6, our data shows that these trends are significant independent of seed head size. These calculations give a “density” of achenes on the seed head. In smaller populations, the numbers of non-dormant seeds are significantly less dense, thus dormant seeds are a greater fraction of the total seeds produced on both large and small seed heads.

Limiting resources are a likely cause for the less branched plants with smaller seed heads (Table 3) and possibly the lower mass of dormant seeds produced by the smaller populations. Plants grown in the greenhouse from the seeds of small populations did not have fewer seed heads (Figure 17), lighter seeds, or less branching (Table 4). Therefore, obvious genetic limitations are not causing these effects in the field populations. It is logical to deduce that a lack of some necessary resource such as water, sunlight, or nutrients, is hindering the ability of the plants to grow and produce seeds to their full capacity. A lack in necessary resources could have originated directly from a change in resource availability (e.g., falling water tables) or indirectly through competition from exotic plants.

Allee Effects

The possibility of allee effects complicates the suggestion that the data discussed above is evidence of environmental troubles and not genetic problems. An allee effect is the *result* of small population size, which could have been *caused* by either genetic or environmental forces. For example, poor pollination does not de facto prove an environmental source of population

⁸ It was estimated that non-dormant seeds have access to the entire area of the seed head, while dormant seeds have access to the perimeter edges. While this estimate is not a completely accurate representation of the area available to both types of achenes, it accurately portrays the proportional available space. In actuality, the dormant seeds should have access to a doughnut-shaped circle slightly inside the perimeter, while the non-dormant seeds have access to most of the top of the cone-shaped receptacles.

decline. Poor pollination could be a result of fewer pollinators in the landscape, which is a habitat quality (environmental) problem; or pollinators may not be attracted to small patches of flowers, which is an allee effect⁹. Such was demonstrated by Groom (1998) who showed the presence of a population size threshold below which lack of pollination and subsequent poor reproductive success lead to extinction. In addition, lower dormant seed weight in small populations does not necessarily prove an environmental origin of population decline just because the common garden plants do not display these trends. The possibility that transparent genetic problems (such as a vulnerability to disease) resulted in a small population that could not attract pollinators, and thus did not have adequate pollen selection to produce plentiful large seeds, is a remote, but viable alternative.

Our data demonstrate that smaller tarplant populations have comparatively poor reproductive fitness (as seen by less branched plants with fewer seed heads supporting less non-dormant seeds and lighter dormant seeds). Combined, these effects will drastically affect the ability of a small population to rebound to a stable size. The impact of fewer and lighter seeds on the success of the populations, regardless of causality, may be powerful in terms of ultimate population success. In particular, the seed trends observed show a proportional increase in dormancy. This is probably not a by-product of seed head size,¹⁰ but instead a result of the significant fall in non-dormant seed number due to improper pollination. The negative relationship between population size and a proportional increase in dormancy (Figure 6) has not been found in previous studies, and the population as a whole will be seriously affected by mostly dormant seed output.

⁹ Many researchers have used other interpretations of allee effects, which may not be technically correct according to recent definitions of the allee effect (Stevens 1999). The assertion that pollen limitation is evidence of an allee effect has been used by Lamont et al (1993) and even in the classic Groom (1998) paper. However, pollen limitation could be an effect of simply fewer pollinators in the area, which has nothing to do the size of the plant population or the presence of conspecifics. Unless evidence is given that pollinators are not as heterogeneously distributed as plants, then there could be several causes of pollinator limitation.

¹⁰ As seed heads decrease in size, the perimeter to area ratio increases, therefore we might expect that smaller plants are proportionally less able to produce non-dormant seeds. This trend

How does habitat quality relate to population size?

Many published studies have implied that poor plant fitness in small populations is a result of adverse genetic effects as opposed to poor habitat quality. Alternatively, figures 10 -12 show that several indicators of habitat quality can be positively correlated with tarplant population size. While this evidence does not directly confirm that invasive plants or a lack of disturbance is causing low population size, it certainly implies that the tarplant seems to respond negatively to a lack of disturbance or the proliferation of invasive plants.

Plant density data is used simply as an indication of the available niches in the habitat for tarplant growth; a dense population might have uniformly better habitat than a sparse one. Since many (but not all) of the smaller populations experienced low density, we assume that certain small population (such as Graham Hill and the Canyon Population) might have fewer opportunities for growth than a more dense population. More reliable data can be gleaned from the removal experiment, which clearly shows that removing invasive grasses in the spring can dramatically improve survival rates of the tarplant (Figure 13) and the production of dormant seeds (Figure 14). This small-scale experiment implies that in certain populations, juvenile survival as opposed to germination is limiting population size. The experiment was conducted in the caltrans population (n4); a very dense population on a tiny strip of land in the midst of urban sprawl and agricultural lands. Removal of invasive grasses may not be as feasible or helpful in populations that have less dense concentrations of tarplants. In other populations with different conditions, recruitment sites may be more limiting than juvenile survival. However, the evidence is clear that invasive grasses inhibit population growth for populations with similar environments to site n4 as well as limiting access to resources that encourage the production of dormant seeds. In this population, almost all of the surrounding plants are exotics, thus we could not test the difference between removing just invasive plants and removing all competitive plants from around the tarplants. This is unfortunately, the reality of most of the extant tarplant populations. Before

is documented in the data taken from each individual seed head for all the populations (Appendix 9).

the invasion of European grasses, the native perennial bunchgrasses likely provided more spatial heterogeneity and less competition to the tarplants. However, the thick blanket of invasives that exists today prevents tarplant recruitment and growth.

Disturbing forces are thought to be key factors in tarplant survival. Many of the now extirpated tarplant sites disappeared rapidly after cattle were removed or annual fires were stopped (see footnote #2). These disturbances may act to help germinate dormant seeds, create recruitment sites, and reduce the presence of invasive grasses. This study used bare ground as a surrogate indicator of disturbing forces. As expected, our data suggests that smaller populations have less available bare ground. We attempt to draw a simple correlation between percent of bare ground exposed and the population size (Figure 11), applying hard numbers to a trend that many local botanists have suggested for years: that low levels of disturbance are associated with small populations.

The forces affecting the quality of tarplant habitat are not easily separated from the landscape of Northern California. The invasion of European grass species has altered the coastal prairies to a point where restoration may not be possible. Invasive grasses, which in many areas are more prevalent than native species, may inhibit native plants' access to resources and fundamentally change the grassland ecology. The intense fragmentation and urbanization of the area has also changed the natural disturbance regimes in entirety. The effects of these environmental changes are dramatic, and pervade every aspect of the tarplants ecology.

The Santa Cruz tarplant seems to be suffering from a host of adverse environmental effects such as disrupted mutualisms, poor resource access, exotic proliferation, and low levels of disturbance. In this study, these indicators of habitat quality appear to be a more obvious reason for population decline than inadequate genetic resources because of the outcome of our common garden experiment. On one side, these data can be considered "bad news " for the tarplant because the multiplicity of environmental factors may hasten extinction (i.e., low non-dormant seed production plus lack of disturbance prevents germination of both dormant and non-dormant

seeds). On the other hand, the above findings are “good news” because conservation efforts can focus on removing the environmental limitations, while it would be impossible to ‘fix’ low levels of genetic variation.

Are the intrinsic dispersal and dormancy abilities of the tarplant extinction probability?

The findings of this study shed light on the reproductive strategy of the tarplant. The proportional increase dormancy in small populations may lead to extinction under the conditions that exist today, but may have been a strategy for survival several hundred years ago under different conditions. There are several scenarios that might explain how the tarplant persisted in pre-developed California; either in stable population locations relying persistent dormancy, or in shifting metapopulations relying on high levels of dispersal. In the first scenario, frequent disturbances would cause large bursts in dormant seed germination in time to rescue a declining population with reduced fecundity. With a larger dormant seed bank, the population may be ‘buffering’ itself against what could be a prolonged period of poor conditions. Unfortunately, in today’s environment, disturbances are rare enough that a period of poor conditions may be too long for adequate recovery. Alternatively, the trends towards increasing dormancy as population falls may not be a survival strategy. Instead of relying on dormancy, the tarplant may have relied on high dispersal rates and the maintenance of a lively metapopulation in an environment of frequent extinctions and colonizations. Today, dispersal rates for *H. macradenia* is very low, as the non-dormant seeds fall directly from the plant, and the ray achenes would only be dispersed upon contact with animals.

The dispersal strategy of the tarplant is quite unusual in comparison to other members of its botanical family. The scientific literature is rife with examples of members of the Asteraceae that produce dimorphic seeds. Yet almost all documented cases show that the central disk achenes disperse more readily than the ray achenes because of pappus-like structures on the disks (which are absent in the tarplant). Therefore, many asters use the strategy by which non-dormant seeds are wind dispersed, and dormant seeds remain in the core patches. The tarplant,

however, is somewhat of an evolutionary mishap, as dispersal ability has disappeared for non-dormant seeds and dormant seeds are (in theory) animal-dispersed. Poor dispersal abilities are frequently cited as increasing the extinction risk of rare species (Thomas 2000), implying that some species are pre-disposition for extinction. This is definitely a possibility for the tarplant, yet we must consider the recent dramatic changes in the landscape. Hundreds of years ago, if the tarplant existed in shifting metapopulations, we can assume that animal herds were much more abundant, and sufficient disturbance occurred in the surrounding environment so that randomly distributed dormant seeds would germinate readily and start new populations.

These two theories for past tarplant ecology, either stable dormant populations or shifting metapopulations, have significant implications for what type of conservation strategy should be adopted. If the former is true, then efforts should be concentrated on restoring forces of disturbance and germinating the dormant seed banks. If the later is a more accurate representation, then management efforts may be more effective by relocating populations into a more frequently disturbed habitat. Examining the success of those populations that have been actively managed and those that have been relocated can test these options.

Conclusions

This study provides suggestive evidence that a host of environmental factors are causing poor reproductive viability and thus population decline in the Santa Cruz Tarplant. Small populations of *H. macradenia* place increasing more of their seed resources into making dormant seeds as population numbers decline. We have used data from a common garden experiment and hand-pollination trials to show that pollen limited plants produce fewer non-dormant seeds. While small populations might be producing less non-dormant seeds because a lack of pollen, plants in small populations are also less branched and produce fewer seed heads than their relatives in the greenhouse. Such effects likely represent resource deprivation, possibly because of competitive invasive plants or environmental changes. Genetic sources of population decline

cannot be ruled out by our study; nor can the possibility that some of the poor fitness traits observed in small populations are result of allee effects, thus the original cause of population decline may remain unknown. Our data shows that smaller populations are dominated by invasive plants and experience fewer disturbing forces. In addition, removing invasive plants in the juvenile phase has the potential to dramatically increase population size and seed production. Many Santa Cruz tarplant populations are declining as a result of negative environmental factors. Whether these forces are the only or the original cause of population decline remains to be discovered; we can be confident that alleviating adverse environmental pressures on the tarplant will aid in the survival of this species. The tarplant is unique in the Aster family by only dispersing its dormant seeds. When compared to the tactics employed by similar plants, it becomes obvious that the reproductive strategy of the tarplant does not work in the present context of highly fragmented and infrequently disturbed coastal grasslands. Without intervention and proper management this plant would rapidly proceed towards extinction.

Chapter 3: Population Trends

Local botanists and the California Department of Fish and Game have been periodically monitoring tarplant population sizes over the last twenty years. This data represents an unusually complete record for an endangered plant of the tarplant's status (see Appendix 4). Many interesting trends can be drawn from this data. Here we document and analyze population history and changes over time, attempting to draw conclusions about the population trajectories and variation.

Methods and Results

Population size data since 1978 was collected from several different sources (CNDDDB, Hayes, Bainbridge, Hillyard). No population has a complete history since 1978, out of 21 possible data entries, the total ranged from only 5 entries to a maximum of 19 (Appendix 4). In general, the reintroduced populations have a more complete record than the native populations. Rainfall data for Santa Cruz and Berkeley were taken from the National Climatic Data Center website. Population sizes over time were plotted over time with average annual precipitation for both Santa Cruz and Berkeley (Figures 19 and 20).

Next, this study investigated whether population size in the early 1990's could predict how the population size might change in a decade. An average of population size over the years 1993 and 1994 was taken to represent a complete data set of population sizes in the early 90's. This average was plotted against population size in 2001 (Figure 21) and population size change between 1993/1994 and 2001 (Figure 22). In Figure 21, the regression line falls below the line that would represent zero change, thus net population growth was negative. More importantly, most of the populations that were small in 1993/1994 (many of which were reintroduced populations) decreased in size over the next eight years. An exception is the native population 'n4', which has recently rebounded in population size with very tiny dense plants in a small area.

Two other populations have significantly increased in size, the largest natural population at the airport and the largest reintroduced population. Figure 22 further exemplifies this trend, with many of the smaller populations in 1993/4 experiencing negative growth in the later 1990s. Two of the larger populations that also show a negative trend both experienced significant habitat change.

Can variability in population size over time be correlated to the current size of the population? The coefficient of variation for the complete data set of population size (for the extant populations) was plotted against current population size (Figure 23). No significant trend was observed, but many of the smaller populations in 2001 had high coefficients of variation while most of the large populations had low coefficients of variation.

Conclusions

There seems to be a threshold of minimum viable population size from which it is difficult for tarplant populations to recover. Many populations that have fallen under 1000 individuals have gone extinct; others may experience drastic fluctuations in the following years, yet only to fall in size again. This variation in population size might all be an indicator of a 'doomed' population, as all of the larger populations in 2001 have had lower coefficients of variations over the last 20 years (Figure 6). Populations under 50 individuals have a wider range in possible coefficients of variation, which might be represent a lower limit to which the current population size / variation trend can be observed. One explanation is that once a population experiences a drop below minimum viable size, it may vary considerably for many years before falling to an extremely low size. It may then hold steady at this low size (such as 10-30 individuals) with these few remnant plants appearing for a number of years before extinction. This suggests that while a minimum viable population size of 1000 individuals may represent the size at which a population cannot recover, once a population falls below 50 individuals consistently over a number of years, it ceases to act as viable long-term population and may experience low levels of variation (such as populations represented by nA, r7, r8, r9).

Population size also seems to vary with annual precipitation. While causal observations were made over several summers that intense heat spells caused flowers to wither, long-term climatic data suggests a correlation between rainfall and the number of plants observed. Dry years may directly reduce tarplant germination, or they may simply shift the competitive balance in favor of more drought tolerant invasive grasses. Some researchers have theorized that the tarplant grows in soils with a hard clay layer several inches under the soil. This layer may trap the water that is filtered out in the surrounding sandy soils. Thus, the wet germination zones of the tarplant may exclude other invasive plants in wet years, but yield to more hardy grasses in drought years.

Chapter 4: Recommendations for Research and Management

As in the study of many scientific problems, there are many questions that remain to be asked about the tarplant. Some of the questions that would help most deducing a cause of population decline include:

1. Do disturbing forces primarily act to simulate germination, create recruitment sites, or prevent growth of exotics?
2. What causes dormant seed germination in a lab environment?
3. Can the dormant seed bank be germinated in extirpated populations?
4. How long will dormant seeds remain viable?
5. Can we prove a pollen limitation in natural populations?
6. Can pollen limitation be attributed to allee effects or a lack in pollinators?
7. Is there direct evidence of a loss in genetic variation, accumulation of deleterious mutations or inbreeding depression?
8. Can we increase the size and seed production of individual tarplants by supplementing resources (e.g. water or fertilizer) without perpetuating the growth of exotics?

In order to truly understand the dynamics of the tarplant's ecology, much more research needs to be done. Unfortunately, there is not enough commitment, funding, or time to perform such extensive studies. Proper management techniques for the tarplant need to be implemented immediately, therefore we need to use this limited information and suggest management options that might have a chance of success.

The findings of this study have major implications for the management of the Santa Cruz tarplant. All but three populations (at Watsonville airport, Porter Ranch, and the Mezue population) are in need of serious management efforts to reduce negative environmental pressures from a

lack of disturbance and invasive plants. The three large populations should be maintained as they are, with cattle grazing at porter ranch and the mezue population, and frequent mowing at the airport. Management efforts in the smaller populations should primarily focus on introducing disturbances aimed at germinating the dormant seed bank, increasing non-dormant seed production and reducing competition from invasive plants. Actions need to be carefully considered, as introducing an improper level of disturbance could easily cause extirpation.

The futures of small and nearly extirpated populations may depend entirely on the ability to germinate the dormant seed bank, and thus the implications of lighter dormant seeds may be quite significant. The most effective way to germinate the dormant seeds in natural environments is very likely controlled burning; as the heat of a fire probably helps open the hard dormant seed coat. Several populations that have experienced burns increased their size by orders of magnitude the following year. The literature representing other plants with fire-germinated seeds has shown that dormant seeds of low mass may be killed instead of germinated by the heat (Delgado, 2001). Therefore, it may be difficult to stimulate germination of the many low-mass dormant seeds produced by a small population because of the relative fragility of these seeds. Also of concern is that burning might germinate a dormant seed bank while proper management following the burn is not available. For example, a controlled burn in 1992 produced almost 10,000 plants at the Arana Gulch site; which previously produced only a handful of plants. Unfortunately, there was no program set to graze or mow this site, the offspring of those plants germinated by the fire failed to establish and reproduce. The population today is once again approaching extirpation, but with a significantly reduced seed bank. Therefore, an integrated management plan should be in place before undertaking a prescribed burn if we are to avoid 'wasting' the dormant seed bank.

The lack of non-dormant seed production in smaller populations means that without significant disturbance, germination rates will be low. Total non-dormant seed production can be very low for some of the smaller populations. For example, 50 plants were observed in population r6 in 2001, and the average non-dormant seed production per head was 8.4 disk achenes, thus the entire population likely produced less than 500 non-dormant seeds. Without

significant disturbance in this population and absent extremely high non-dormant germination rates, the population may exponentially decrease in size within several years. Attempts to increase the size of the plants or to raise levels of pollen flow could help improve non-dormant seed production. Substantial preliminary research should be conducted before intervention such as watering the tarplants while weeding exotics or hand pollinating within populations. Another method of increasing the size and seed production of the plants could be to reduce competition from invasive plants. The removal experiment in population n4 indicates that competition from invasive grasses after germination is more limiting than recruitment sites, although this does not necessarily rule out the need for creating more recruitment sites. Removing invasive grasses from around the tarplants in the spring is a simple and effective way to increase population size and possibly even individual plant fitness.

The introduction of other disturbing forces may also help keep down the invasive grasses and create more recruitment sites. In a few populations, heavy grazing seems to have a positive effect on the tarplant and a negative effect on the exotics. Yet, introducing grazing to those populations that are not currently grazed is not usually a feasible management option. Mowing is often used as a proxy for grazing, yet is not as effective in targeting the exotic plants and can also damage the native plants. Mowing can effect species composition, nutrient retention, and resource availability quite differently than other disturbing forces such as cattle or fire (Kirkman, 1998; Maron, 2001). Mowing seems to be effective in the largest tarplant population at the Watsonville airport, yet is not helping other small populations recover from population decline at the Caltrans, Graham Hill or Twin Lakes sites. Therefore, mowing may be an adequate substitute for more natural disturbances when a population is large and healthy, but mowing is not an appropriate rehabilitation technique for very small populations.

The timing of mowing may be very important even in the large populations. Mowing late in the season, once the plants have begun to bolt, can adversely affect plant growth. I conducted a small survey to show how different mowing times can dramatically change fitness traits by sampling plants in the same population that had been subjected to two different mowing treatments. One side of Watsonville airport site was mowed in early April 2001, the other end

was mowed in late May. Reproductive characteristics and morphological fitness traits described above were compared for the two areas. Plants in the treatment mowed earlier were larger, had more branches, more total heads, produced more seeds, but the seed weights were not significantly different between treatments (Figures 18). The difference in the early and late mowing of the population n1 is very significant. Overall, these plants will produce less seeds and be less successful than those in the segment of the population mowed earlier.

Increasing the level of proper disturbance should be the main goal for tarplant management. Such treatments should be aimed at helping germinate dormant seeds, encouraging the production of non-dormant seeds, and controlling exotic plants. Management techniques should not be altered for the three tarplant populations with greater than 1000 plants; but these populations should be closely monitored for changes. Despite these suggestions, the tarplant may be a good candidate for ex-situ propagation and re-introduction since tarplant populations at the watsonville airport, porter ranch, and mezue are the only independently functioning and stable populations. Within the next ten years, it is quite possible that most of the small populations will disappear regardless of management. Past efforts to rehabilitate tarplant populations that have crashed have been largely unsuccessful, and while these attempts should not be abandoned, conservationists should prepare themselves for the fact that survival of such small populations is unlikely. Ex-situ efforts need to be implemented to avoid losing the genetic resources of troubled populations.
