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IMPORTANCE OF EARLY LIFE STAGE LIMITATIONS ON RECOVERING POPULATIONS OF *LEPTOSYNE GIGANTEA,* SAN MIGUEL ISLAND, CALIFORNIA

Catherin A. Schwemm[1]

ABSTRACT.—Plant communities dominated by *Leptosyne gigantea* (tickseed, formerly giant coreopsis) are distributed widely across the California Islands and provide critical habitat for understory plants and vertebrates, especially in landscapes where trees are absent. *Leptosyne gigantea* populations were severely impacted by nonnative herbivores and by grazing and ranching practices during the last century. Although these impacts have been absent from most of the islands for over 2 decades, extensive spatial heterogeneity exists both within and across the islands in relation to population growth. Many sites support very dense stands of *L. gigantea* that established postgrazing; whereas others, particularly on Santa Barbara Island, have experienced relatively minimal increases in *L. gigantea* abundance and are still dominated by alien annual grasses. To determine the factors that most affect *L. gigantea* establishment and survival, I conducted seed amendment experiments across populations of variable density and age structure on San Miguel Island. These experiments tested the relative effects of seed predation, seed density, microhabitat conditions, stand density, and competition on germination and seedling survival. Postdispersal seed predation by deer mice reduced germination rates only in the highest density stands. Reduced soil moisture and interspecific competition with alien annual grasses had the strongest negative effects on both germination and seedling survival. The results suggest extreme spatial variability in regulating factors for *L. gigantea* that include rainfall, the abundance of annual grasses, consumer abundance, and intraspecific density dependence. The presence or absence of these influences on existing site conditions will determine succession following loss of the oldest-aged stands, which will likely occur soon.

RESUMEN.—Las comunidades de plantas dominadas por la *Leptosyne gigantea* (botón de oro, anteriormente coriopsis gigante) están distribuidas ampliamente por todas las Islas de California y proporcionan un hábitat crítico para plantas y vertebrados del monte bajo, especialmente en paisajes donde no hay árboles. Las poblaciones de *L. gigantea* se vieron impactadas de gran manera por los herbívoros no autóctonos y por las prácticas de pastoreo y ganadería durante el último siglo. Aunque estos impactos no se produjeron en la mayoría de las islas durante más de dos décadas, existe hetereogeneidad espacial extensiva tanto dentro como a través de las islas en relación al crecimiento de la población; muchos lugares tienen gradas muy densas de *L. gigantea* que se establecieron antes del pastoreo, mientras que otros, particularmente en la Isla Santa Bárbara, han experimentado aumentos relativamente mínimos en la abundancia de *L. gigantea* y aún los dominan hierbas anuales no autóctonas. Para determinar los factores que más afectan al establecimiento y la supervivencia de la *L. gigantea,* conduje experimentos de acondicionamiento de semillas entre poblaciones de densidad variable y estructura de edad en la Isla San Miguel para comprobar los efectos relativos de la depredación de semillas, la densidad de semillas, las condiciones de microhábitat, la densidad del grupo y la competencia por la supervivencia de las semillas y la germinación. La depredación de semillas después de la dispersión causada por los ratones de campo redujo los niveles de germinación sólo en las gradas de la densidad más alta. La reducida humedad del terreno y la competencia interespecífica con hierbas anuales no autóctonas tenían los efectos negativos más fuertes tanto para la germinación como para la supervivencia de las semillas. Los resultados sugieren variabilidad espacial extrema al regular factores de la *L. gigantea* relacionados con las lluvias tropicales, la abundancia de hierbas anuales, abundancia de consumidores y dependencia de densidad intraespecífica. La sucesión tras la pérdida de las gradas más antiguas, la cual probablemente ocurrirá pronto, se determinará por las condiciones actuales del lugar relacionadas con esos factores.

Populations of plants and animals are limited by factors that either prevent new individuals from establishing or cause mortality to those already living (Louda 1989, Gotelli and Ellison 2004, Fenner and Thompson 2005, Barbera et al. 2006). Because strong limitations often occur at very early life stages, organisms have responded by adopting particular strategies aimed at increasing productivity and juvenile survival (Pianka 1974, Fenner and Thompson 2005). In flowering plants, the transition from seed to seedling is rarely successful, and life history characteristics include traits that help facilitate seed survival, germination, and

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seedling growth (Naylor 1985, Fenner 2000, Fenner and Thompson 2005). However, given the rapid ecological changes caused by human disturbance, species' adaptations such as these may not be sufficient to maintain population growth in altered systems (Kearns and Inouye 1997, McClure et al. 2003, Fish et al. 2005). Identifying the early life stage factors that can potentially limit population growth, particularly those to which target species are not naturally adapted, will greatly improve the likelihood of success in conservation and restoration programs (Seabloom et al. 2003).

Leptosyne gigantea (giant coreopsis, or tickseed) is a dominant shrub found in several Mediterranean-type coastal plant communities on the California Channel Islands (Junak et al. 2007). Large stands of *L. gigantea* create important habitat for vertebrates and associated understory plant species, especially in island communities where trees are often absent. Populations of *L. gigantea* on the islands were severely reduced in size, and in some cases eliminated, as a result of grazing and land management practices beginning in the 1850s (Hochberg et al. 1979). From the 1850s to the 1980s, Euro-Americans and grazing livestock had both immediate and long-term impacts on island ecosystems. Domestic sheep (*Ovis aries*) were first transported to San Miguel around 1850, and there were nearly 6000 on the island by 1860 (Ellison 1937). A severe drought in 1863–1864 caused most of the sheep to starve, but not before they had eaten nearly every accessible, palatable plant (Roberts 1991). Without the plants to hold the sandy soil in place, the prevailing winds blew away much of the topsoil, leaving deposits of sand over nearly 80% of the 14.9 mi^2 of the island (NPS unpublished GIS data). Reduced numbers of sheep remained until 1950; and burros (*Equus asinus*), another exotic species destructive to vegetation, were finally removed in the late 1970s.

Recovery of *L. gigantea* populations in the decades following the cessation of grazing has varied. In some areas, *L. gigantea* has successfully recolonized historic sites; while in others, it is still mostly absent and exotic plant species, especially exotic annual grasses, dominate (Junak et al. 1993, Halvorson 1994, Corry 2006). There are few if any mortality factors (other than old age) that act on enough mature individuals of *L. gigantea* to regulate population abundance at that stage (e.g., disease, herbivory; personal observation, Salas 1990). Therefore in this study, I investigated factors that might be acting on very early life stages of *L. gigantea* to limit seed bank abundance, germination success, and seedling survival. I was especially interested in the strength of seed consumption by native deer mice (*Peromyscus maniculatus*) and the relative importance of anthropogenic limitations.

Seed Ecology

Leptosyne gigantea begins flowering in January or February depending on winter rains, and following pollination, seeds require approximately 10–12 weeks to mature. Seed set commences in late spring and continues through midsummer. Seeds enclosed in their fruit (achenes) are 2–5 mm in length, oblong and somewhat flattened, and have a very small pappus (wing). (Herein, "seed" will be used to refer to the achene as it is dispersed from the flower.) *Leptosyne gigantea* seeds are not adapted to wind dispersal (Schiffman 1997) despite the high winds that dominate island weather conditions, and seed dispersal is likely facilitated by rodents and passerine birds. The maximum number of *L. gigantea* seeds produced in a given year that will eventually establish as seedlings is some subset of the seeds present in the soil prior to winter rains (Leck et al. 1989), and herein I refer to these seeds as the prewinter seed bank (Simpson et al. 1989, Montiel and Montana 2003).

Seed Predation

The consumption of seeds by animals is often termed seed predation, and the process is usually described according to whether the seed is consumed while still on the plant or after it has dispersed. If a seed is consumed or damaged by herbivores while still on the parent plant, the process is known as predispersal seed predation and includes not only the direct consumption of seeds, but also all interspecific processes that kill or damage seeds such that they never mature (Fenner 2000, Kolb et al. 2007). A related study identified the 2 primary predispersal seed predators of *L. gigantea* as insect larvae and deer mice and found that while a substantial number of seeds can be lost to predispersal predation (>20%), this factor did not contribute to corresponding differences in seed bank abundance between populations (Schwemm 2008).

Postdispersal seed predation, particularly by rodents, is a substantial source of seed loss for many plant populations (Crawley 1983, Hulme 1998, Howe and Brown 2000). Specifically, studies have demonstrated the ability of several *Peromyscus* species to consume large portions of available seeds (Mittelbach and Gross 1984) and to regulate plant abundance under certain conditions (Boyd 1991, Cabin et al. 2000, Maron and Simms 2001, Bricker et al. 2010). Because deer mice are extremely abundant and widespread on the Channel Islands (Drost and Fellers 1991, Schwemm and Coonan 2001, Schwemm 2008), I was particularly interested in studying the influence of *P. maniculatus* on *L. gigantea* abundance via seed predation.

Microsites and Resource Competition

The physical and environmental parameters of a seed's final resting location are cumulatively termed its microsite. If these conditions facilitate establishment (i.e., they protect the seed from mortality and support germination), the location is also termed a safe site (Fenner and Thompson 2005). Microsite conditions are critical regulating factors for nearly all flowering plants (Barbera et al. 2006), and the likelihood of an individual seed within a population actually arriving at a safe site is extremely low (Naylor 1985).

The presence of exotic annual grasses can alter microhabitat conditions near the ground, often substantially reducing the availability of safe sites (Williams and Hobbs 1989, Eliason and Allen 1997). The dominance of annual grasses on the islands, particularly *Avena* and *Bromus* species, increased dramatically with the introduction of grazing practices to the islands' habitats; and in many locations, the abundance of these species has not declined in response to the absence of the grazers themselves. My investigation into factors that could be limiting *L. gigantea* therefore includes the possibility that exotic annual grasses, both living individuals and the litter layer that accumulates in the absence of disturbance, reduce safe-site availability.

METHODS

Study Sites

The study was conducted on San Miguel Island (SMI), the westernmost of the 8 California Channel Islands and one of 5 islands within Channel Islands National Park. Annual weather patterns on the Channel Islands are characteristic of Mediterranean climates throughout the world, with winter rainfall followed by summer drought (Keeley and Swift 1995). However, the dry season on the islands is moderated somewhat by fog and coastal humidity that provide additional moisture (Dorman and Winant 2000). The absence of land masses to the west of SMI results in a windier and moister climate than is found on the other Channel Islands (Dorman and Winant 2000). The average precipitation on SMI is 39.15 cm (1993–2008), with much of that coming as fog drip (Estberg 1996), and there is a nearly constant northwest wind of 20–40 km $\cdot$ h^{-1}.

Three sites on SMI were selected for study. At each site, an area of habitat 50 × 40 m (2000 m^2) was identified within which all of the sampling described below was conducted. Each site was centered within the community type described (i.e., no edge or ecotone was included). The sites differed in growth dynamics of *L. gigantea* but were all located on the north portion of the island within 1 km of each other, were without differences in slope or aspect, and were exposed to identical weather and local climate conditions. While it is not known with certainty what the sites were like when grazers were removed, all historic reports suggest that the island was nearly completely grazed with very little herbaceous vegetation remaining other than on inaccessible, steep slopes.

The first site (Grassland) was a homogenous annual grassland dominated by *Avena, Bromus,* and *Hordeum* species, with additional invasive annuals such as *Sonchus oleraceus* and *Medicago polymorpha*. *Leptosyne gigantea* density here was very low (0.01 individuals m^{-2}) and all of the individuals were 8–10 years old, aged by counting annual growth rings (Schwemm 2008). This site was representative of the ubiquitous nonnative annual grasslands that now exist in California as a result of European grazing practices over the last 2 centuries (D'Antonio et al. 2007). The presence of reproductive *L. gigantea* individuals here, albeit at very low densities, indicates that environmental conditions at the site are conducive to growth and that population limits are instead imposed by the absence of a seed source and/or factors that prevent establishment of juvenile plants. The ground at the Grassland site is covered by a thick (1–5 cm) layer of dead grass litter which has accumulated over time. Unlike most mainland systems, few disturbance processes (e.g., gopher activity, fires) exist within island systems to remove or reduce this layer or to facilitate the reestablishment of native species (D'Antonio 1993).

The second site (Transition) was a mixed community where native shrubs (*L. gigantea* at densities of 4.7 m^{-2}, *Lupinus albifrons, Isocoma menziesii,* and *Eriogonum grande* var. *rubescens*) occupied approximately a quarter (26.8%) of the area, and annual grasses, other herbaceous species, and bare ground the remainder. The understory was diverse and included annual grasses, exotic perennials such as *Carpobrotus edulis* (exotic iceplant), native herbaceous perennials (*Marah macrocarpa*), and native annuals such as *Eschscholzia californica* and *Dudleya greenei*. The age structure of the *L. gigantea* population was highly skewed toward young individuals, with few individuals older than 10 years (Schwemm 2008). The abundance of young plants suggests that at present there are few limitations on *L. gigantea* recruitment and growth at this site. Ground cover at the Transition site is much more diverse than at the Grassland site, with a low-growing vegetation layer that includes small annuals (*E. californica, Gnaphalium* sp.), low-growing and spreading perennials (*Achillea millefolium, Dudleya greenei, Marah macrocarpus, Carpobrotus chilensis*), and exotic annual grasses. While the relative amount of litter cover here was not significantly different from that at the Grassland site, the composition was much more diverse and the layer substantially thinner overall (Schwemm unpublished data). Demographic sampling of *L. gigantea* indicated canopy cover of these shrubs was approximately 30% of the area, and other shrub species provided additional cover of about 5%–10% (Schwemm 2008).

The third site (Mature) was a highly dense stand of *L. gigantea* (9.3 m^{-2}), where many individuals were unbranched and per capita flower production was much lower than in the Transition population (Schwemm 2008). Postgrazing establishment apparently occurred rapidly here with high adult survival, such that at the time of this study, density-dependent mechanisms were strongly limiting further recruitment and the population was at carrying capacity (Schwemm 2008). Most individuals were over 15 years old; and in contrast to the Transition site, young *L. gigantea* plants at the Mature site occurred only in gaps where dead individuals created openings in the canopy (Schwemm 2008). The understory, where present, was a mix of native and exotic annuals and low-growing native perennials (*E. californica, D. greenei*). Understory plants were absent from much of the site, owing to the unbroken canopy that prevented direct sunlight from reaching the ground in most places. Much of the ground surface was exposed mineral soil, with occasional soil crusts and mosses.

Study Design

SEED BANK.—To quantify the *L. gigantea* and annual grass seed banks, soil samples from each site were collected prior to winter rains in November 2006 and in October 2007. Six samples of approximately 340 mL of soil (113 cm^2 of surface area to 3 cm deep) were collected at 10-m intervals along a transect through the center of each site. A subsample of 250 mL was moistened and placed in a refrigerator (5 °C) for 2 weeks to accelerate seed development. These samples were then spread on plastic trays filled with 3:1 potting soil and perlite. The trays were maintained under greenhouse conditions with daily watering and were sampled weekly. All emerging seedlings were identified to genus (and in most cases species) and removed after counting. The samples were maintained for approximately 3 months or until no new seedlings were noted for 2 weeks. The number of *L. gigantea* seedlings emerging from the 6 samples was averaged for each site, and this number was multiplied by the proportion of the site represented by one sample (2000 m^2 /0.113 m^2).

LIMITATIONS ON GERMINATION—A factorial seed-addition experiment utilizing small mouse-proof cages was used to cross 3 treatments testing the effects of seed predation, ground cover, and seed density on seedling establishment. Cages (30 × 30 × 10 cm) were constructed of small-mesh (1/4-inch) hardware cloth. Each set of 8 cages (2 levels of mouse accessibility × 2 levels of ground cover × 2 seed densities) was replicated 6 times at 10-m intervals along transects centered in each of the 2000-m^2 study plots described above (8 cages × 6 replicates = 48 cages at each site).

Treatments were assigned randomly to cages within a replicate.

To test for rodent effects, a small opening was cut on one side of half of the cages to allow mouse access (treatment levels of "open" and "closed"). The openings allowed mice access to the seeds prior to and during the winter germination period. (Other groups that likely consume *L. gigantea* seeds are ants and ground-feeding passerines; both the open and closed cages allowed access by invertebrates but likely prevented all access by birds.) To test the effects of ground cover, half of the treatments were hand-cleared of all material that overlaid bare soil prior to seed addition. This layer included all living and dead vegetation (litter) as well as obvious nonvascular material (soil crusts) and *L. gigantea* seeds. Though most seeds of all species were likely removed in this process, a small number of seeds certainly remained on the surface and possibly below the top layer of soil. The treatment levels were then identified as "cleared" and "uncleared."

To test whether seed abundance affected seed predation impacts or whether there were density-dependent effects on germination, 2 seed densities were used (treatment levels of "high" and "low"). The densities were selected to span the range from the high limit of the natural seed bank (approx. 670 m^{-2}; 60/cage) to what might be used for a restoration seeding application (1500 m^{-2}; 135/cage).

Cages were fixed to the ground in November 2006 and seeds (collected on-island during the prior summer) scattered randomly through the top of the cage. A small amount of adjacent in situ soil was used to lightly cover the seeds. Cages were checked 3 times between January and April 2007. During each check, all *L. gigantea* seedlings were counted and marked with colored toothpicks and mortality was calculated by subtraction between observations. By January, all of the sites were already dry due to the lack of rain. Because I was interested in seedling survival between sites in addition to germination rates and it was possible that rain would return within a few weeks, I applied water equivalent to 1 cm of rainfall to all sites in an attempt to support the seedlings through the dry period. Seedling abundance increased from January to February; but after February, no additional seedlings were observed and mortality increased, so I used seedling counts from February only. The fully crossed, 3-factor randomized block design was analyzed using 3-way ANOVA in SAS (SAS Institute, Inc.), testing the effects of rodent access, ground cover, and seed density on the proportion of seeds germinated (Gotelli and Ellison 2004). Percentage results were arcsine transformed to normalize data prior to analysis.

MOUSE DENSITIES—Deer mouse abundance was compared between sites via mark-recapture trapping during 2 sessions in November 2006 just prior to and after establishing the cage experiments described above. To obtain an index of population size, each trapping session included 2 nights of trapping, with 12 or 18 traps each night. The number of traps used was consistent within a session, but the maximum number of traps was not available for all sessions. Two or 3 transects of six 12-inch Sherman live traps (H.B. Sherman Co., Tallahasee, FL.) were placed in the center of each site. Traps were baited with dry oats and checked early each morning; captured animals were identified to sex and age, marked with eartags, and released. Traps were then closed for the day and reopened at dusk. All sampling was conducted in accordance with the American Society of Mammalogists guidelines for the use of wild animals in research and teaching (Sikes et al. 2011).

RESULTS

Seed Bank

There were more *L. gigantea* seeds in the prewinter seed bank at the Transition than at the Mature site in both 2006 and 2007. Estimated mean seed density was 457.3 m^{-2} (SE 20.6) at the Transition site and 29.5 m^{-2} (SE 5.4) at the Mature site in 2006, and 413.0 m^{-2} (SE 99.0) and 162.3 m^{-2} (SE 100.0) respectively in 2007. Densities of annual grass seeds (all *Avena, Bromus,* and *Hordeum* species pooled) were substantially higher at the Transition than at the Mature site in both years sampled (Fig. 1). No *L. gigantea* seeds ever germinated from the Grassland soil samples, though if soil samples had been collected nonrandomly from directly beneath the existing adult plants, seeds would likely have been detected, albeit in low numbers.

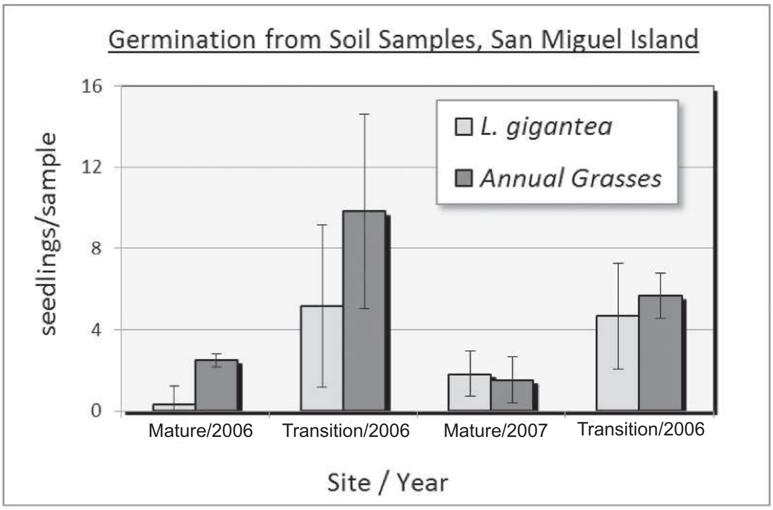

Fig. 1. Mean number of annual grass and *L. gigantea* seeds from soil samples at 2 sites, 2006 and 2007.

TABLE 1. Three-way ANOVA for the effects of rodent access, ground clearing, and variable seed density on germination success. *P* values in bold are significantly different ($\alpha = 0.05$) within habitat type.

		Grassland		Transition		Mature	
Source of variation	df	*F*	*P*	*F*	*P*	*F*	*P*
Rodent access (A)	1	1.45	0.24	2.07	**0.0452**	6.53	**<0.0001**
Ground cover (C)	1	37.6	**<0.0001**	3.58	**0.0009**	6.14	**<0.0001**
A × C	1	1.90	0.17	1.59	0.12	3.29	**0.002**

TABLE 2. Total number of germinated seeds and percent seed germination by treatment. Number in parentheses is the total number of seeds. Italicized entries indicate significantly less germination, and bolded entries indicate significantly more germination than other treatments.

	Overall		Grassland		Transition		Mature	
Treatment	Total (7202)	%	Total (2340)	%	Total (2340)	%	Total (2340)	%
Rodent access								
Open	*292*	*4.16*	89	3.80	*140*	*5.98*	*63*	*2.69*
Closed	**551**	**7.85**	106	4.53	**208**	**8.89**	**237**	**10.13**
Ground cover								
Cleared	347	4.94	**159**	**6.79**	*117*	*5.0*	*71*	*3.03*
Uncleared	496	7.07	*36*	*1.54*	**231**	**9.87**	**229**	**9.79**

Germination Success

The effects of each of the treatments—rodent access, ground cover, and seed density—on germination success differed strongly between sites. Rodents significantly reduced germination in the Mature population ($F = 6.53$, $P < 0.0001$), had a weaker but significant effect in the Transition population ($F = 2.07$, $P = 0.045$), and had no effect in the Grassland (Table 1). Of the 2340 seeds placed in both open and closed treatments at each site, 237 (10%), 208 (9%), and 106 (5%) germinated in the cages protected from mice in the Mature, Transition, and Grassland communities, respectively, compared to 63 (3%), 140 (6%), and 89 (4%) in the open treatments. The impacts of ground cover on germination were strongly site dependent. In the Grassland, the ground cover consisted almost exclusively of thick grass litter, and germination increased significantly when this

TABLE 3. Deer mouse sampling results at 3 *Leptosyne gigantea* study sites, San Miguel Island, November 2006.

Site	Date	Trap nights	Individuals	Total captures	Trap success
Grassland	5–7 Nov 2006	24	7	7	0.29
	28–30 Nov 2006	36	16	16	0.44
Transition	5–7 Nov 2006	24	9	11	0.46
	28–30 Nov 2006	36	18	26	0.72
Mature	5–7 Nov 2006	24	22	28	1.17
	28–30 Nov 2006	36	19	22	0.61

material was removed ($F = 37.6$, $P < 0.0001$). In contrast, in the Transition and Mature populations, there was a strong but negative effect of removing ground cover. The effect was greater at the Mature site ($F = 6.14$, $P < 0.0001$) than at the Transition site ($F = 3.58$, $P = 0.0009$), even though the existing ground cover layer at the Mature site was quite thin. There was a small positive effect of seed density on germination at the Mature site ($F = 3.11$, $P = 0.003$) and no effect at the other sites. Interaction effects explained very little of the additional variation in germination success, except in the Mature population, where there was a small negative effect in the interaction of ground clearing and rodent access ($F = 3.29$, $P = 0.002$).

Seedling Survival

Seedling abundance varied between treatments and sites, with a total of 838 seedlings alive across all sites in February 2007 (Table 2). By this date, however, all of the sites were becoming quite dry due to the lack of rain. Despite the application of supplemental water in January equivalent to 1 cm of rainfall, by early April there was nearly 100% mortality of seedlings at both the Mature and Transition sites and similar results in the Grassland a few weeks later. Seedling mortality was almost completely due to physiological stress of desiccation, and there was very little if any observed herbivory on live seedlings from either mice or invertebrates.

Mouse Densities

Results of mouse population sampling concurrent with the introduction of the experimental seeds in the fall of 2006 indicated that levels of mouse abundance were highest at the Mature site and lower but similar to each other at the Grassland and Transition sites (Table 3). Index values of capture success ranged from 0.29 in the Grassland to 1.17 in the Mature site (values >1.0 mean there were more captures than there were trap-nights, indicating very high population densities in a sampled population; Efford 2004). Populations were high in all cases compared to published estimates from other systems (Schwemm 2008). Due to low sample size, statistical analysis of trapping results was not possible. However, concurrent sampling by the National Park Service on SMI using established mark-recapture methods (Schwemm 2008) showed similar patterns between vegetation types.

DISCUSSION

Consumer Effects

Results presented here indicate that the impacts of deer mice on *L. gigantea* populations are related to mouse abundance under certain conditions but that more often mouse effects are weaker than or are moderated by other limiting factors. Estimated mouse abundance at the Grassland site in November 2006, when the experimental seeds were introduced, was higher than the average fall abundance estimated by NPS for their SMI grassland sampling site over the prior decade (350+ mice $\cdot$ ha^{-1}; Schwemm 2008). However, allowing mice access to seeds in the grassland did not decrease *L. gigantea* germination rates, likely because mice were feeding primarily on grass seeds. Many studies have demonstrated that granivores select seeds based on food value, which is often directly related to seed size (Reichman 1979, Mittelbach and Gross 1984, DeSimone and Zedler 1999, Howe and Brown 2001). Exotic annual grass seeds are much larger than *L. gigantea* and most other native herbaceous seeds in SMI plant communities. In contrast, the highest levels of seed predation (reduced germination when mice had access to seeds) occurred at the Mature site, where adult and seedling densities of *L. gigantea* were very high (Schwemm 2008). Mouse densities here were higher than at the other sites, and it is unclear whether increased seed predation at the Mature site was due primarily to more mice or to the absence of grass seeds as a preferred food that led to density-dependent foraging behavior by mice in treatments where *L. gigantea* seeds were more abundant (Davidson and Morris 2001). However, because consumer effects on *L. gigantea* were inversely related to grass seed abundance (i.e., strongest impacts at the Mature site, less but still significant at the Transition, and none in the Grassland), these results strongly suggest that regardless of mouse densities, the presence of annual grasses diverts granivory away from *L. gigantea* seeds.

Competition, Microsite Effects, and Soil Moisture

Germination success was reduced in the Grassland site when the litter layer was left in place compared to when it was removed; whereas the opposite effect occurred at the other 2 sites. Many studies have demonstrated the negative impacts of an existing grass litter layer on seedling emergence and survival of native species (Williams and Hobbs 1989, Martinez and Fuentes 1993, Eliason and Allen 1997, Maret and Wilson 2005). I suggest that the negative effects of annual grasses on *L. gigantea* were caused by 2 primary mechanisms: the physical impacts of grass litter that limit resource availability to *L. gigantea* seeds and the biotic competition from grass seedlings.

First, the presence of a deep grass litter layer can limit the availability of both light and water to seeds on the soil surface, reducing seed germination and seedling survival (Fenner and Thompson 2005). Changes in light regimes are often the cue that ends seed dormancy (Fenner and Thompson 2005), and the presence of litter blocks light that would otherwise reach seeds, reducing the strength of this stimulus. Increased moisture can also be a cue to end dormancy, and the presence of a thick litter layer likewise impedes the transport of water from the atmosphere to the soil surface. Because so much of the moisture available to seeds and seedlings on SMI results from fog drip (Estberg 1996), a thick grass litter layer may have a particularly strong negative effect on seeds adapted to a foggy climate. Fog drip does not have the force of rainfall to move the water through the litter to the soil, so the moisture simply remains on the litter surface, unavailable to seeds until it evaporates (Corbin et al. 2005). The presence of litter may also alter microsite conditions (e.g., temperature and humidity) such that the near-ground environment is less supportive of native seed survival and germination (Chambers and MacMahon 1994, Fenner and Thompson 2005).

Secondly, annual grass seeds emerge sooner and grow more quickly than do native seeds, making them stronger competitors for available soil moisture (Williams and Hobbs 1989, D'Antonio and Vitousek 1992, Martinez and Fuentes 1993, Coleman and Levine 2007) and light (Williams and Hobbs (1989). The inability of *L. gigantea* seeds to germinate and establish in the presence of litter and dominant grass seedlings is therefore the most likely explanation for the very low densities of adult *L. gigantea* in the Grassland; poor microsite conditions are strong limiting factors, and in exotic annual grasslands may be nearly insurmountable obstacles for native seeds (Etherington 1982, Fenner and Thompson 2005, Barbera et al. 2006, Corbin et al. 2007).

In contrast to the positive effect on germination of removing the ground cover in the Grassland, the loss of a litter layer at the other sites had a significant negative impact. The ground cover layer at these 2 sites consisted of dead material from live native annuals and low-growing perennials, some soil crusts, and little or no cover by exotic annual grasses. Any inhibitory effects that the accumulation of litter at the Mature and Transition sites had on either changing the physical environment or producing competing seedlings for *L. gigantea* were apparently countered by the facilitative conditions created by the material (Kirkman et al. 2004). Not only were fewer seedlings present in the cleared treatments, but desiccation effects of low rainfall were noted sooner in the cleared areas than in the uncleared ones (Schwemm 2008). Variable interactions between soils and ground cover across the 3 sites may also have contributed to differences in seedling survival. Soils at the Grassland site, though not directly measured, had a visibly higher clay content and retained more moisture than did the more sandy soils at the Transition and Mature sites. The cleared treatments at all sites dried out more quickly after rains than the uncleared treatments (personal observation), but seedlings at the cleared sites in the

Grassland survived longer than did seedlings at the sites with sandy, nonclay soils.

Finally, to connect early life stage limitations with population growth, observations of treatment responses should be followed by measurements of survival of the treatment cohort through to adult stages (Crawley 1997, Bricker et al. 2010). In spite of supplemental watering, physiological stress on seedlings from low rainfall in late winter 2007 resulted in the death of all the seedlings by the end of spring. While this outcome was unanticipated, it provided important information on *L. gigantea* dynamics at early stages: in some years, water limitation at the seedling stage is a much stronger population-regulating factor than anything that acts earlier (Fenner and Thompson 2005, Corbin et al. 2007).

CONCLUSIONS

Population Regulation and Succession in *L. gigantea*

Limiting factors for *L. gigantea* on SMI include both naturally evolved and human-altered processes, and the relative strengths of these factors vary across communities. For example in the Grassland, the 2 primary impediments to population growth of *L. gigantea* are the nearly complete absence of safe sites and seed limitation—both of which are directly due to the abundance of exotic annual grasses, an anthropogenic ecosystem alteration. Alternatively, factors that currently limit *L. gigantea* population growth in the Mature stand are associated with natural succession, where the high proportion of older *L. gigantea* individuals (apparently caused by self-thinning; Schwemm 2008) suggests that this population is at or near carrying capacity (Crawley 1997). Late successional communities are normally subject to strong density-dependent processes, in particular, high consumer densities (in response to structural characteristics) and low seedling survival (Barbour et al. 1999); and both of these conditions appear to exist in the mature *L. gigantea* population.

The observation of high seedling production in the Mature stand in 2007, 2008, and 2012 (personal observation) is therefore surprising but can be explained if *L. gigantea* employs a strategy that assures seedling resources in the event of a major disturbance (for example, a blowdown). Seedling recruitment of shrub species in mature Mediterranean communities is rare and usually happens on a large scale only when gaps are created by the death of older individuals (Etherington 1982, Parker and Kelly 1989). High production of seeds by *L. gigantea* may be a natural adaptation to periodic disturbances (Barbour et al. 1999).

Implications for Shrub Community Recovery and Restoration

Results from this study suggest that relatively high soil moisture conditions and moderate levels of consumer pressure were important contributing factors to *L. gigantea* population growth on SMI. A similar process of recovery has not occurred on Santa Barbara Island (SBI), however, where annual grasslands still dominate much of the island and shrub community expansion has been slower (Corry 2006). I suggest that interactions of multiple strong limiting factors—including microsite limitation on SBI (due to expansive grasslands and fairly intense pressure on vegetation and soils by nesting seabirds; Johnson and Rodriguez 2001, Corry 2006, Maesako 1999, Schwemm 2008), drier soil moisture, and periods of extremely high deer mouse densities—are responsible for the absence of substantial population growth of *L. gigantea* and other shrub species on the island. Without human intervention on SBI and in the grasslands on SMI to mitigate the factors that currently limit *L. gigantea* establishment and survival, it is unlikely that shrub community recovery will occur naturally in these systems. Understanding the relative importance of limiting factors on *L. gigantea* dynamics will allow managers to focus on addressing the important factors regulating growth, both to aid in the recovery of this species and to protect larger island shrub communities.

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