Post-Dispersal Seed Predation, Germination, and Seedling Survival of Five Rare Florida Scrub Species in Intact and Degraded Habitats

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ABSTRACT.—Knowledge of seed ecology is important for the restoration of ecosystems degraded by anthropogenic activities. Current efforts to preserve and reintroduce populations of plant species endemic to Florida are hindered by a lack of information on demographic responses to human alteration. Comparisons of seed removal, germination, and establishment in both intact and degraded habitats will aid in management decisions for species in need of protection. Our objectives were to assess the impact of post-dispersal seed predation on plant populations in degraded and intact habitats, and to investigate the effects of habitat and microsite on seed germination and establishment. For five rare Florida scrub species with different seed sizes (*Liatris ohlingerae*, *Eryngium cuneifolium*, *Polygonella basiramia*, *Hypericum cumulicola*, *Paronychia chartacea* subsp. *chartacea*), we conducted a seed removal experiment with seeds exposed to insects and vertebrates, and to insects only, with a no-access control. We also planted seeds in replicated degraded and intact scrub sites (Spring Field Trial: in bare sand, Winter Field Trial: in bare sand, litter only, and under shrubs with litter), and determined background germination rates in a growth chamber. The contrasting pattern in seed removal among treatments suggested that habitat and seed size affect the likelihood of removal in Florida scrub. Species with large seeds such as *L. ohlingerae* were removed in higher frequency in degraded scrub, likely by vertebrates. Species with small seeds such as *H. cumulicola* and *P. chartacea* were removed by invertebrates and in higher frequency in intact scrub. *E. cuneifolium* had significantly more seedlings in degraded scrub and *P. chartacea* had significantly more germination in the intact scrub in the Spring Field Trial. *E. cuneifolium*, *H. cumulicola* and *P. chartacea* had higher germination in bare sand than in litter only or under shrubs. Our data indicate that scrub herbs are differentially vulnerable at particular life history stages and that this vulnerability can be context dependent. Restoration success will require a careful assessment of potential seed predators and abiotic conditions favoring germination and survival of study species in degraded habitat; efforts to increase heterogeneity in areas slated for restoration will likely promote the establishment of multiple targeted species.

INTRODUCTION

Current efforts to preserve and reintroduce populations of protected plant species are limited by lack of specific information on demographic responses to human alteration. Habitat disturbance can affect multiple life history stages of species in areas acquired for protection and restoration, including seed survival and seedling establishment. Seed predation often varies with habitat quality or type (Bossard, 1991; Holl and Lulow, 1997; Tallmon *et al.*, 2003); these patterns can be further affected by predator preferences for seed characteristics such as seed size (Booman *et al.*, 2009). Anthropogenic disturbance can either diminish (Coates *et al.*, 2006; Schleuning, 2009) or enhance seedling establishment (Schupp and Fuentes, 1995; Pugnaire and Lozano, 1997; Cole *et al.*, 2004). The direction of this influence often depends on whether disturbance historically was involved in the

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maintenance of the habitat (Hellström *et al.*, 2009) or on the growth form or functional group of the species (Zimmer *et al.*, 2010).

Habitat restoration is essential to conservation of protected species in threatened habitats such as Florida scrub (Florida Natural Areas Inventory, 2000). Florida scrub is restricted to the southeastern United States and is valuable to local and global biodiversity because it hosts a large number of rare and endemic species, several of which are endangered or threatened (Turner *et al.*, 2006). The Lake Wales Ridge of south-central peninsular Florida contains some of the best remaining examples of intact Florida scrub; this habitat is rapidly diminishing due to commercial, agricultural, and residential development (Weekley *et al.*, 2008).

There is a need to elucidate factors affecting the recruitment of native species, as goals for re-establishing scrub species are rarely achieved due to mortality of seeds, seedlings, and adults. Previous studies on the demography of Florida endemic species in their natural habitats have provided insight about critical features affecting the scrub ecosystem, such as gap dynamics and fire (Satterthwaite *et al.*, 2002; Quintana-Ascencio *et al.*, 2003; Menges and Quintana-Ascencio, 2004). These factors are important to many scrub endemics, which occur as multiple patchy populations that depend on habitat configuration and regional population dynamics for persistence (Quintana-Ascencio and Menges, 1996). Here, we focus on post-dispersal seed predation, the consumption of seeds after they have initially been dispersed from parent plants, germination, and seedling establishment. Comparing demographic responses of endemic herbs in intact and degraded Florida scrub will advance understanding of requirements for seed and seedling survival, which will suggest introduction procedures to increase plant numbers and population viability.

Our objectives were two-fold: (1) assess the impact of post-dispersal seed predation on seed germination in degraded and intact scrub habitats using a seed removal experiment, and (2) investigate the effects of habitat and microsite on seed germination and establishment using field and growth chamber experiments. We selected five scrub endemics representing a gradient of seed size for our study species. We expected seed size to influence seed predator preferences and subsequent removal from the different habitats. For our seed removal experiments, we made the assumption that removal should generally represent post-dispersal seed predation in this system because seeds of study species do not have eliasomes (lipid attachments) or fleshy fruit, giving animals little incentive to move them without consumption. We also assumed that wind movement was not responsible for seed removal, as we anchored species with pappi (modified calyx composed of bristles or featherlike hairs aiding wind dispersal) in sand. Since we did not follow seed fate after removal, and animals may sometimes drop seeds they intend to consume, our design provides a maximum estimate of predator-mediated seed mortality. Even though seed removal is not equivalent to predation, this method can reveal limitations on seed availability (Münzbergová and Herben, 2005). For one of our germination experiments, we examined the effect of single species (seeds of one species planted) and mixed species treatments (seeds of all study species planted). For a given study species, a comparison of these two treatments was expected to reveal whether seeds of other species and seeds of the same species affect germination differently.

METHODS

STUDY SPECIES

We studied five state and federally endangered herbs: *Liatris ohlingerae, Eryngium cuneifolium, Polygonella basiramia, Hypericum cumulicola,* and *Paronychia chartacea* subsp.

Table 1.—Mean seed length and width, estimated seed size (length × width), and total seeds per species used for each study. Totals for spring germination / establishment include Spring Field Trial and Spring Chamber Trial; totals for winter germination / establishment include Winter Field Trial, Winter Chamber Trial, and the gibberellic acid study (growth chamber and greenhouse germination / emergence)

Species	Seed length and width (μm)	Seed size (μm²)	Total seeds for removal study	Total seeds for spring germ / estab study	Total seeds for winter germ / estab study
L. ohlingerae	102/16	2749.5	600	222	342
E. cuneifolium	22/17	303.8	1800	606	934
P. basiramia	28/7	240.5	1200	606	910
H. cumulicola	7/4	23.8	2400	702	926
P. chartacea	6/4	22.3	1200	702	1006

chartacea. These species have distributions that are either restricted to the Lake Wales Ridge or central Florida (Wunderlin and Hansen, 2008). One of the species (*L. ohlingerae*) can occur both inside and outside of gaps, or patches of bare sand, in the scrub. The other four species are gap specialists that are concentrated inside of gaps (*E. cuneifolium, P. basiramia, H. cumulicola, P. chartacea*) (Petru and Menges, 2003; Schafer *et al.*, 2010). All five of these species are reproductive in Florida scrub from fall to early winter, and the seeds of these species represent a gradient of seed size from *L. ohlingerae* as the largest to *P. chartacea* as the smallest (Table 1). Seed size is relevant to seed predation, as this feature may determine which species' seeds appeal to seed predators, or which seeds can be easily handled (Ivan and Swihart, 2000). Invertebrates (Koprdová *et al.*, 2010; Honek *et al.*, 2011) tend to take smaller seeds than vertebrates (Reader, 1993; Howe and Brown, 2000; Perez *et al.*, 2006). We separated individual seeds from seed heads (*L. ohlingerae, E. cuneifolium*) or from fruits (*H. cumulicola*) to minimize any potential effect of seed presentation on predators' preferences.

STUDY SITES

Study sites were located in Highlands County, Florida, at Archbold Biological Station (ABS; 2104 ha), the adjacent Archbold Reserve (Reserve; 1476 ha), and the McJunkin Tract of the Lake Wales Ridge Wildlife and Environmental Area to the northwest of ABS (McJunkin; 303 ha). ABS is a globally significant natural preserve that features rosemary scrub, among other habitat types. Rosemary scrub is found in areas of locally high elevation with well drained, low nutrient soils. Several herbaceous species, many of them rare and endemic, grow in gaps of bare sand between shrubs (Abrahamson *et al.*, 1984; Menges *et al.*, 2008). The majority of these herbs recover from fire and other disturbances by seedling recruitment, whereas surrounding shrubs primarily resprout (Menges and Kohfeldt, 1995).

The Reserve includes pastureland and degraded scrub. The degraded scrub has been subject to roller chopping and light cattle grazing, with cattle on site until 2002. McJunkin is managed by the Florida Fish and Wildlife Conservation Commission. This property includes degraded scrub that was once ranchland. The ABS sites served as reference scrub sites for the degraded scrub sites within the Reserve and McJunkin; all sites were selected on Archbold and Satellite soils and share topography characteristics associated with rosemary scrub/scrubby flatwoods in the reference scrub. Species composition in the degraded scrub is similar to intact rosemary scrub sites, aside from the presence of some nonnative grasses. However, in the degraded scrub, shrubs have become overgrown, bare sand areas surrounding shrubs are more extensive, and species distributions and relative abundances

differ from intact rosemary scrub (E. Menges, pers. comm.; Navarra *et al.*, 2011). The degraded scrub sites are currently under treatments to reestablish native habitat structure and scrub species.

<div align="center">SEED COLLECTION</div>

We collected seeds at Archbold Biological Station during the reproductive season immediately before each experiment. Intact, fully pigmented seeds were separated under a dissecting microscope. Seeds were sorted into groups with forceps and sealed in foil packets for efficient field deployment (groups varied with experiment). Seeds were stored in a refrigerator (4 C) before their deployment in the field (Table 1).

<div align="center">SEED REMOVAL</div>

We evaluated the role of predators in seed fate using animal exclosures in intact and degraded Florida scrub (Jun. 2007–Apr. 2008). We exposed seeds of each species in replicated exclosure treatments (5 replicates $\times$ 3 exclosure types $\times$ 4 sites $\times$ 2 habitats; total sampling units = 120). The three exclosure types were: (1) a no access treatment (vertebrates and invertebrates excluded), a wire mesh cylinder with plastic covering that prevented access of any animals; (2) an invertebrates only treatment (vertebrates excluded), a wire mesh cage that only allowed invertebrates to access seeds; and (3) an open-access control (no animals excluded).

For the no access treatment, we constructed each exclosure from a rectangular piece of wire mesh (30.5 cm $\times$ 76.2 cm, 1.3 cm mesh, 19 gauge galvanized hardware cloth) that we shaped into an upright cylinder. A square piece of the wire mesh was attached to the top of each cylinder to prevent birds from accessing the seeds through the top. We secured the cylinder seams with wire, and then covered the outside of the cylinder with heavy duty clear plastic sheeting (up to a few centimeters from the top of the cylinder). A layer of Tangle-Trap Sticky Coating (Tanglefoot) was applied to the upper rim of the plastic sheeting to prevent access by invertebrates. For the invertebrates only treatment, we used square exclosures made from wire mesh (22.9 cm $\times$ 22.9 cm $\times$ 11.4 cm, 0.6 cm mesh) with no plastic sheeting or sticky coating. All exclosures were secured by pressing them into the sand (approximately 3 cm); each was anchored with two wire-stake flags pushed down to the ground. Additional sand was mounded up around the outside of each no access exclosure (approximately 3 cm). There were no instances of rodents digging into the exclosures in preliminary trials. The open-access control treatments had no equipment, only wire-stake flags marking treatment locations.

Experimental units were arranged in triplets (including one of each treatment type positioned within 3 m of each other). We placed a sand-filled Petri dish (100 mm diameter, 10 mm height) on the ground inside each unit and sprinkled seeds (avoiding skin contact) onto the sand-filled dish. Species with pappi were anchored by pressing the seed tips in the sand, leaving most of the seed and the pappus exposed. Petri dishes were used to easily relocate seeds and reduce displacement by wind or water. We used more seeds per unit for the smaller seeded species than for the largest seeded species (5 for *Liatris ohlingerae,* 10 seeds for *Eryngium cuneifolium, Polygonella basiramia,* and *Paronychia chartacea,* and 20 for *Hypericum cumulicola*). After 48 h, we collected the sand-filled dishes with any remaining seeds; we then counted the number of remaining seeds under a microscope. Preliminary trials and other studies suggested that this interval is well suited to assess differential removal rates (Fedriani *et al.*, 2004). We used the no access treatments to confirm that all deposited seeds could be recovered under conditions of no animal access.

To evaluate the effects of habitat and microsite on germination and establishment of the study species in intact and degraded Florida scrub, we conducted three growth chamber studies (one with a greenhouse counterpart) and two field experiments.

Germination (background laboratory trials).—Background germination rates of the five study species were observed in a growth chamber (CONVIRON CMP 4030), which served as a reference for maximum potential germination of seeds in the field. Thirty seeds per species were allocated to this study from those sorted for each of two field germination trials. These seeds were deposited in Petri dishes (10 seeds per dish) with a moist filter paper and were exposed to conditions mimicking those in the field. For our Spring Chamber Trial (May 2008, initiated simultaneously with our Spring Field Trial), the chamber was set to late spring conditions at Archbold Biological Station (daily minimum 22 and maximum 27.2 C; Archbold Biological Station Weather data, Appendix 1). For our Winter Chamber Trial (Feb. 2009, initiated simultaneously with our Winter Field Trial), winter temperatures (daily minimum 20 and maximum 22 C) were used (Appendix 1). Seeds were moistened and checked for germination daily, and trials were terminated after seeds ceased to germinate. *Liatris ohlingerae* seeds were not available for the Winter Chamber Trial.

Germination / Emergence (GA$_3$ laboratory and greenhouse trials).—Due to unknown environmental cues, a small percentage of viable seeds may not germinate in controlled conditions. To more precisely document the viability and germinability of study species, we stimulated seeds (*Liatris ohlingerae, Eryngium cuneifolium,* and *Paronychia chartacea*) with gibberellic acid (GA$_3$), a plant hormone commonly used to promote germination in growth chamber and greenhouse studies. Two hundred and sixty four seeds per species were allocated to this study from those sorted for the Winter Field Trial. Seeds were tested in two different environments: in the growth chamber (daily minimum 21 C and maximum 29 C) and in a greenhouse (hoophouse with uncontrolled temperatures, daily minimum 18 C and maximum 50 C) from May to Jul. 2008. In both environments, we used three different concentrations of GA$_3$: 100 ppm, 50 ppm, 5 ppm (PPM Calculator, http://www.supergrow.biz/PPM.jsp), and a control with no hormone applied. The solution of GA$_3$ (90% product purity) was made with powder dissolved in a small amount of 91% isopropyl alcohol and then mixed with distilled water.

We used three replicates per treatment in each environment; each GA$_3$ treatment was applied once at experiment initiation. In the growth chamber, 10 seeds were distributed to each replicate (total 120 seeds per species), and Petri dishes were arranged randomly into the growth chamber. In the greenhouse, we planted 36 seeds per treatment per species (12 seeds per flat). Seeds were buried to a depth no greater than 5 mm with forceps. Substrate sand was collected from Archbold Biological Station and sterilized at 90 C in a Fisher Scientific oven for 8 h. Flats were arranged randomly in the greenhouse, watered with ambient water, and checked daily for seedlings.

Seedling Emergence / Establishment (Spring Field Trial).—In our Spring Field Trial (initiated May 2008), all seeds were planted in open areas away from shrubs in each habitat (to focus on differences between intact and degraded habitats), and in our Winter Field Trial (initiated Feb. 2009) seeds were planted in replicated microsites within each habitat. All seeds were planted within PVC rings of 10.2 cm diameter and 7.6 cm depth, which were partially buried in the sand to keep the seeds in place. The seeds were then covered with sand, protected with a wire mesh vertebrate exclosure to reduce removal, and marked with wire-stake flags.

The Spring Field Trial included four degraded scrub sites (two Reserve, two McJunkin) and two reference scrub sites, with four subsample plots per site (6 sites ×

4 plots = 24 total plots). Six treatments were employed in each plot, with a separate PVC ring for each treatment: seeds of *Liatris ohlingerae* only (6 seeds planted), *Eryngium cuneifolium* only (20 seeds), *Polygonella basiramia* only (20 seeds), *Hypericum cumulicola* only (20 seeds per unit), *Paronychia chartacea* only (20 seeds), a mixture of all of the above species (2 *L. ohlingerae* seeds, 4 *E. cuneifolium,* 4 *P. basiramia,* 8 *H. cumulicola*, 8 *P. chartacea*) and a control with no seeds planted, to detect any seed arrival from extant adult plants (Turnbull *et al.*, 2000; Clark *et al.*, 2007). We randomly assigned planting locations for each treatment in each plot. Every planting location was visited once a week from May to Aug. and then once a month from Sept. to Feb. 2009 to evaluate seedling recruitment. Seedlings that survived to the end of the experiment were considered to be established.

Seedling Emergence / Establishment (Winter Field Trial).—In the Winter Field Trial, transects were set up in four sites: two degraded scrub (one Reserve, one McJunkin) and two reference scrub sites. Each site had two transects (2 transects × 4 sites = 8 total transects). We randomly assigned locations along the transect, species planted, and microsite type (bare sand, litter only/no shrub, or underneath shrub with litter) to each experimental unit. After a random point was located along the meter tape marking the transect, a right angle to the tape was followed until the assigned microsite type was encountered. We used three treatments: single species (seeds of one species), mixed species (seeds of the five study species), and a control (no planted seeds), all of which had PVC collars and exclosures. Twenty seeds were planted in single species treatments, and mixed species treatments included 2 *Liatris ohlingerae*, 4 *Eryngium cuneifolium*, 4 *Polygonella basiramia*, 8 *Hypericum cumulicola,* and 8 *Paronychia chartacea* seeds. Overall, there were 144 total planting locations (26 *E. cuneifolium,* 26 *P. basiramia*, 22 *H. cumulicola*, 26 *P. chartacea*, 24 mixed species, 20 controls) and 2624 seeds planted. Due to limitations in seed availability, we reduced the number of planted *H. cumulicola* units and we only included *L. ohlingerae* in mixed species units. Sites were monitored for seedlings once a month after planting, until Feb. 2010. Seedlings that survived to the end of the experiment were considered to be established.

<div align="center">ANALYTICAL METHODS</div>

For our seed removal experiment, the difference between the number of seeds removed from the no access treatments and from the invertebrates only treatments was used as an index of seed removal by invertebrates. The difference between the number of seeds removed from the invertebrates only and the open-access control was used as an index of seed removal by vertebrates. These indices represented maximum seed mortality due to predation, as seed predators may have inadvertently dropped seeds. We used logistic regression to test the hypothesis that the independent variables seed size, habitat type, and exclosure treatment influenced the dependent variable seed recovery, and to test whether habitat type and microsite influenced the dependent variables seedling emergence and seedling establishment. Logistic regression is appropriate for these analyses because the dependent variable is categorical in each. We coded PVC rings in the seed removal study as either loss of seeds ($\geq$1 seed removed) or all seeds recovered. In the seedling emergence trials, we coded each PVC ring as having emergence / establishment ($\geq$1 seedling) or no emergence / establishment. In some cases, the occurrence of too many zero entries precluded the use of logistic regression; in these cases we conducted Kruskal-Wallis analyses using total counts of germinants or seeds removed. We used a Monte Carlo computation to compare germination between years.
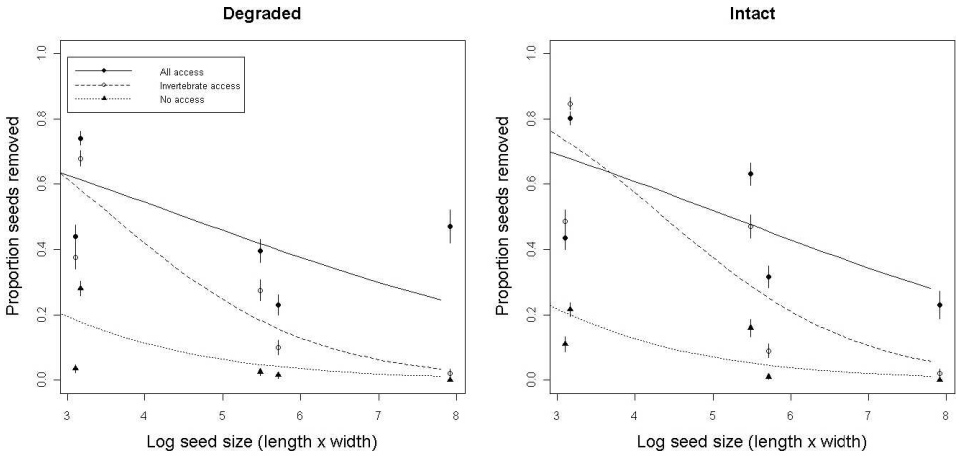
Fig. 1.—Observed (symbols) and estimated (lines) proportion of seeds removed from different exclosure treatments in degraded and intact habitats. Each point represents the data for one species undergoing one treatment (black circles = open-access controls (no animals excluded), white circles = invertebrate only access (vertebrates excluded), black triangles = no access (invertebrates and vertebrates excluded)). Corresponding trend lines depict predicted values from the logistic regression analysis. Seed size values are in μm^2

RESULTS

SEED REMOVAL

Liatris ohlingerae seeds (largest seed size) were removed the least frequently, and *Hypericum cumulicola* seeds (small seed size) were removed the most frequently (Fig. 1). In total, from largest to smallest seed size, 79 of 600 (13.2%) *L. onlingerae* seeds were removed, 354 of 1800 (19.7%) *Eryngium cuneifolium*, 391 of 1200 (32.6%) *Polygonella basiramia*, 1421 of 2380 (59.7%) *H. cumulicola*, and 376 of 1200 (31.3%) *Paronychia chartacea* seeds were removed. We found weak evidence of higher seed removal of *P. basiramia* (P = 0.052, B = 1.335, SE = 0.686, Wald = 3.785, DF = 1) and *H. cumulicola* (P = 0.047, B = 0.911, SE = 0.459, Wald = 3.943, DF = 1) in the intact scrub than in the degraded scrub. Seed removal of the other species (*L. ohlingerae, E. cuneifolium, P. chartacea*) was not significantly different between habitats.

A joint analysis of all species indicated different removal rates for seeds with different sizes and among exclosure treatments and interactive effects of seed size and habitat and of seed size and treatment (Table 2, Fig. 1). Species with large seeds tended to be removed more frequently in degraded scrub by vertebrates [(number seeds removed from ''open-access control'') – (removed from ''invertebrate only access'')], whereas smaller seeds tended to be removed more frequently in intact scrub by invertebrates [(number seeds removed from ''invertebrate only access'') – (removed from ''no access'')] (Fig. 1). For the smallest seeds (*Hypericum cumulicola, Paronychia chartacea*), we did not have complete seed recovery from the no access treatments. We also observed that the smallest seeds adhered more to organic matter than the other species and were the most difficult to locate.

GERMINATION AND ESTABLISHMENT

Germination (laboratory and greenhouse).—Our Spring Chamber Trial demonstrated substantial viability for the seeds of each species. *Hypericum cumulicola* and *Polygonella*

TABLE 2.—Logistic regression of seed recovery (yes / no) by seed size, habitat (degraded vs. intact), and treatment [open-access control (O), invertebrate access only (I), and no access (N)]. B = slope from logistic regression, SE = standard error, DF = degrees of freedom. Significant P values (<0.05) are marked with an asterisk

	B	SE	DF	Sig.
Seed size	0.006	0.001	1	<.001*
Habitat	0.169	0.135	1	0.211
Treatment			2	<.001*
O vs. I	−1.709	0.125	1	<.001*
O vs. N	−2.205	0.135	1	<.001*
Seed size * Habitat	−0.001	<0.001	1	<.0001*
Seed size O vs. I	−0.006	0.001	1	<.001*
Seed size O vs. N	<0.001	0.001	1	0.894
Habitat * Treatment			2	0.015*
Habitat O vs. I	0.233	0.164	1	0.154
Habitat O vs. N	0.471	0.166	1	0.005*
Intercept	1.214	0.105	1	<.001*

basiramia (each 86.7%) had the highest germination, *Eryngium cuneifolium* and *Liatris ohlingerae* had the next highest (each 83.3%), and *Paronychia chartacea* had the lowest germination (56.7%). In the Winter Chamber Trial (without *L. ohlingerae*), *P. chartacea* had the highest germination (86.0%), *P. basiramia* had the next highest (57.5%), *H. cumulicola* had low germination (33.3%), and *E. cuneifolium* had no germination. There was no significant overall difference in germination between seasonal conditions (tail probability of the null hypothesis P = 0.141). In the GA_3 growth chamber study, we observed little to no stimulatory effect of the hormone treatments, as there was no significant difference in number of germinants among treatments (Fig. 2). There was no germination in the greenhouse for any of the treatments.

Emergence (Spring Field Trial).—We found significant differences in emergence between habitats for one of our study species. For the Spring Field Trial (Fig. 3A, Table 3), in which all seeds were planted in bare sand, *Liatris ohlingerae* had no significant difference in emergence between habitat types (P = 0.528, B = −0.395, SE = 0.626, Wald = 0.398, DF = 1). Logistic regression analyses revealed significantly greater emergence in degraded than in intact habitat for *Eryngium cuneifolium* (P = 0.026, B = 1.449, SE = 0.649, Wald = 4.985, DF = 1). *Polygonella basiramia* had only one seedling in the intact scrub, and few in the degraded scrub (Fig. 3A, Table 3), and *Hypericum cumulicola* had only one seedling in the intact scrub, and no seedlings in the degraded scrub (Fig. 3A, Table 3). Low sample size precluded tests for these last two species.

We did not find a significant difference in emergence of *Paronychia chartacea* seeds planted in intact and degraded scrub (P = 0.372, B = 0.588, SE = 0.658, Wald = 0.797, DF = 1). However, we observed many *P. chartacea* seedlings in plots of other study species and controls, more so in the intact scrub than in the degraded scrub (P < 0.001, chi square = 32.250, DF = 1). We analyzed this observational data in order to develop further hypotheses about the seed availability of *P. chartacea* in intact and degraded scrub.

Establishment (Spring Field Trial).—Only *Liatris ohlingerae*, *Eryngium cuneifolium*, and *Polygonella basiramia* had established seedlings that survived to the end of the study (Fig. 3B). At this time, *Paronychia chartacea* seedlings had emerged too recently to be
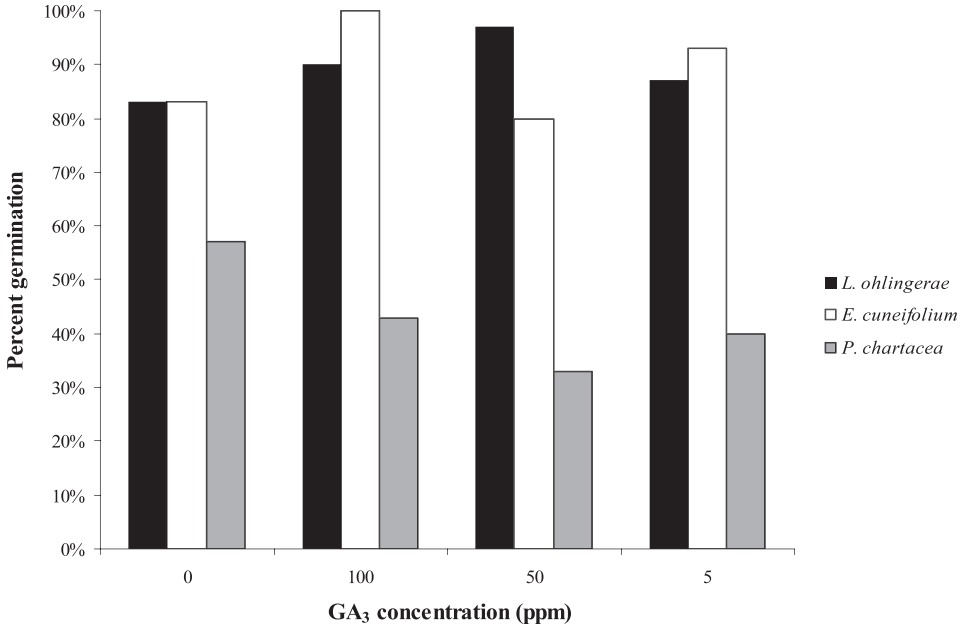
FIG. 2.—Percentage germination per species in GA₃ (gibberelic acid) growth chamber trial. *Hypericum cumulicola* and *Polygonella basiramia* were not available for this study

considered established. Logistic regression analyses of establishment for the Spring Field Trial indicated no significant differences between the two habitats, either for individual species (*L. ohlingerae*, P = 0.831, B = 0.136, SE = 0.637, Wald = 0.046, DF = 1; *E. cuneifolium*, P = 0.998, B = −19.516, SE = 10048.243, Wald = 3.772E-06, DF = 1; *P. basiramia* P = 0.998,

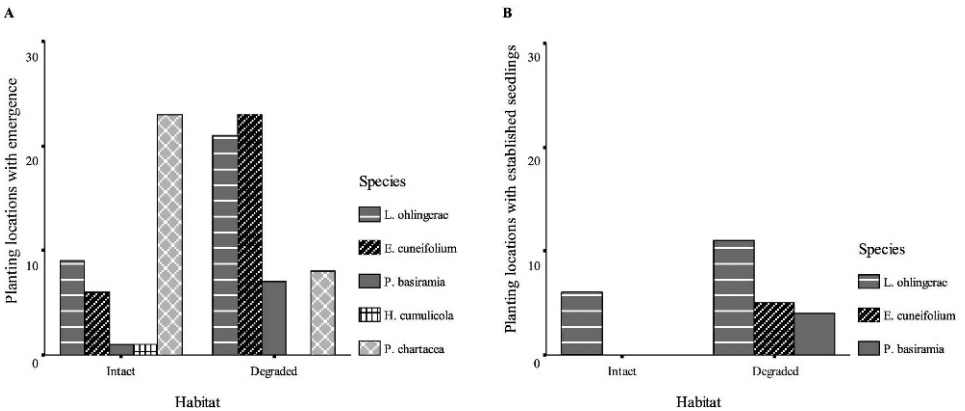FIG. 3.—Number of planting locations (PVCs) with emergence (A) and established seedlings (B) by 2/28/09 in intact and degraded scrub habitats from Spring Field Trial. There were significantly more *Paronychia chartacea* seedlings in intact than degraded scrub; these bars represent both background emergence and seedlings from planted seeds. All *P. chartacea* were newly emerged seedlings at this sampling date

TABLE 3.—Percentage emergence of total seeds planted for each species (single and mixed species treatments combined) in Spring and Winter Field Trials. Percentages were calculated by dividing the total number of seedlings within intact scrub, degraded McJunkin scrub (degraded 1) or degraded Reserve scrub (degraded 2) by the total number of seeds planted there. In Winter Field Trial, data for degraded scrub represents the Reserve only

Species	Spring Field Trial			Winter Field Trial	
	Intact	Degraded 1	Degraded 2	Intact	Degraded 2
L. ohlingerae	20.3%	51.6%	23.4%	29.2%	38%
E. cuneifolium	7.8%	18.8%	18.8%	3.9%	4.2%
P. chartacea	25.0%	8.9%	3.1%	0.9%	2.8%
H. cumulicola	0.5%	0%	0%	0%	0.3%
P. basiramia	0.5%	4.7%	5.7%	21.3%	1.8%

B = −19.257, SE = 10048.243, Wald = 3.673E-06, DF = 1) or across species (P = 0.225, B = −0.611, SE = 0.504, Wald = 1.471, DF = 1).

Emergence (Winter Field Trial).—The total number of seedlings per species per site, whether from a single or a mixed species treatment, were used for analysis due to low overall numbers of seedlings (Table 3, Fig. 4A). There were no significant differences in emergence between habitat types for any study species (*Liatris ohlingerae;* P = 0.190, B = 1.273, SE = 0.971, Wald = 1.719, DF = 1, *Eryngium cuneifolium;* P = 0.874, B = −0.105, SE = 0.662, Wald = 0.025, DF = 1, *Hypericum cumulicola;* P = 0.998, B = 18.067, SE = 8569.170, Wald = 4.445E-06, DF = 1), although our data were insufficient to conclude on the difference between habitat types for *Polygonella basiramia* (P = 0.064, B = −1.598, SE = 0.862, Wald = 3.434, DF = 1) and the planted seeds of *Paronychia chartacea* (P = 0.064, B = 2.507, SE = 0.786, Wald = 10.176, DF = 1). We again found many *P. chartacea* seedlings in plots of other study species and controls, more so in the intact scrub than in the degraded scrub (P = 0.001, B = 2.507, SE = 0.786, Wald = 10.176, DF = 1).
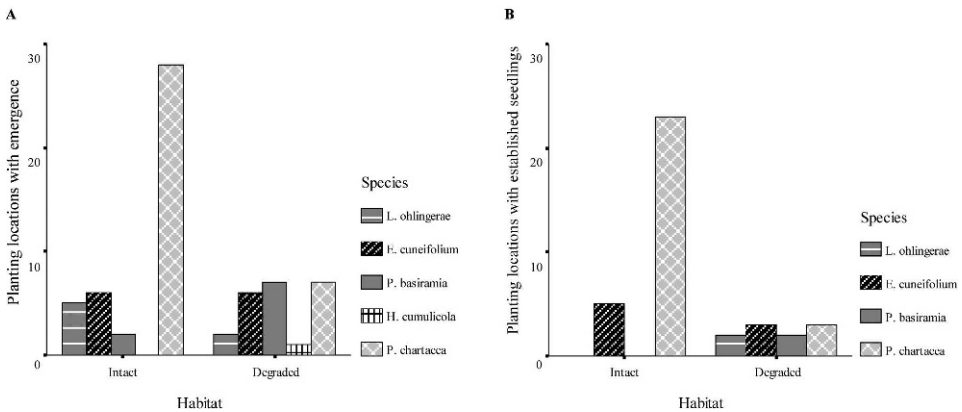

FIG. 4.—Number of planting locations (PVCs) with emergence (A) and established seedlings (B) in intact and degraded scrub habitats by 2/24/2010 from Winter Field Trial. There were significantly more *Paronychia chartacea* seedlings in intact than degraded scrub; these bars represent both background emergence and seedlings from planted seeds

TABLE 4.—Logistic regression of emergence (yes / no) by habitat (degraded vs. intact) and microsite (shrub/litter, litter only, bare sand) from Winter Field Trial. B = slope from logistic regression, SE = standard error, DF = degrees of freedom. Significant P values (alpha = 0.025 with Bonferroni adjustment) are marked with an asterisk. Litter vs. shrub: B = 0.125, SE = 0.665, DF = 1, P = 0.851. Multiple comparisons were conducted with dummy variables

	B	SE	DF	Sig.
Habitat	0.671	0.425	1	0.114
Microsite			2	0.032
Shrub vs. bare sand	−1.151	0.571	1	0.044
Litter vs. bare sand	−1.276	0.569	1	0.025*
Habitat * Microsite			2	0.356
Intact habitat by shrub	0.788	0.733	1	0.282
Intact habitat by litter	−0.397	0.736	1	0.590
Intercept	−1.046	0.322	1	0.001

When all species from the Winter Field Trial were analyzed together, we did not find a significant difference in emergence between the two habitats; but we did find differences in emergence among microsite types (Table 4, Appendix 2). Significantly more planting points in bare sand had seedlings than those in litter only, and there was weak evidence that more planting points in bare sand had seedlings than those under shrubs. In microsite analyses for individual species, this was particularly notable for *Paronychia chartacea*, which had significantly greater emergence in bare sand than in litter only for points where we planted seeds (P = 0.004, B = −2.708, SE = 0.931, Wald = 8.462, DF = 1). For points where we did not plant seeds, *P. chartacea* emergence was significantly higher in bare sand (P = 0.014, B = −2.035, SE = 0.831, Wald = 5.995, DF = 1) and in litter only (P = 0.046, B = 1.688, SE = 0.847, Wald = 3.970, DF = 1) than under shrubs with litter. There was also weak evidence of *Eryngium cuneifolium* emerging most in bare sand regardless of habitat, and *Hypericum cumulicola* seeds only emerged in bare sand (Appendix 2).

Establishment (Winter Field Trial).—*Paronychia chartacea* had significantly more establishment in intact vs. degraded scrub (P < 0.001, B = 2.379, SE = 0.642, Wald = 13.749, DF = 1). An analysis of all species together indicated significantly more established seedlings in intact scrub than in degraded scrub (P = 0.003, B = 1.145, SE = 0.388, Wald = 8.736, DF = 1), with most of those seedlings in the bare sand and second most in the litter only (bare sand vs. shrub P = 0.033, B = −0.930, SE = 0.437, Wald = 4.525, DF = 1; bare sand vs. litter only P = 0.001, B = −1.587, SE = 0.478, Wald = 11.020, DF = 1; shrub vs. litter P = 0.001, B = −1.587, SE = 0.478, Wald = 11.020, DF = 1) (Fig. 4B).

DISCUSSION

We present evidence that habitat, microsite, and seed characteristics affect seed predation and recruitment. Our data also indicate that plant species are differentially vulnerable at particular life history stages and that this relative vulnerability changes with habitat and microsite conditions. Microsite conditions favorable to seed survival may not be the same conditions required for seedling establishment, a contrast described as ''seed-seedling conflict'' (Schupp, 1995; Smit *et al.*, 2006). Studies of seed removal and establishment in different microsites are necessary to predict which sites are most likely to be occupied by adult plants.

Liatris ohlingerae appeared more limited in degraded scrub than in intact scrub due to increased seed removal. In some cases seed predators preferentially forage in degraded

areas. For example, birds consumed more seeds in degraded areas than in intact habitats of the Sierra Nevada foothills (Bossard, 1991). Harvesting of seeds by vertebrates (including rodents) was greater in treefall gaps than in undisturbed understory in Costa Rica and Panama (Schupp, 1988; Schupp and Frost, 1989). Seed removal was greater at the edges of old fields than in intact forest of New York (Ostfeld *et al.*, 1997). *Polygonella basiramia* and *Hypericum cumulicola* appeared less limited in degraded scrub than in intact scrub due to decreased seed removal. Studies on *Prunus avium* have also found lower seed removal in disturbed than in intact habitat, likely due to the reduced protective cover in gaps (Webb and Willson, 1985). A better understanding of factors affecting the local behavior and food and habitat preferences of seed predators will help to predict seed survival and recruitment.

Contrasting effects of disturbance on seed removal are likely related to which animal species consume the seeds and how disturbance shapes their habitat conditions. For instance, predators of *Polygonella basiramia* and *Hypericum cumulicola* seeds, mostly invertebrates, may use low shrub cover and associated litter to hide from carnivorous predators. These animals would be less likely to forage in degraded scrub due to the more open vegetation structure. Seed predators of *Liatris ohlingerae*, likely vertebrates, may benefit from increased visibility in foraging due to the decreased shrub cover in degraded scrub. Habitats with more contrasting disturbance regimes (Webb and Willson, 1985), like abandoned pastures, may have a more significant impact on the seed predators of *Paronychia chartacea* and *Eryngium cuneifolium*.

Level of disturbance also affected emergence. *Eryngium cuneifolium* had greater emergence in degraded scrub. Research in grasslands (Eriksson and Eriksson, 1997; Lepš, 1999; Hellstrom *et al.*, 2009; Schleuning *et al.*, 2009) and forests (Flory and Clay, 2009; Munier *et al.*, 2010) has similarly demonstrated that habitat disturbance can promote germination. *Paronychia chartacea* had greater emergence in intact scrub. Higher *P. chartacea* germination may be due to higher seed density in the seed bank in intact scrub (Navarra, 2010), which could also explain the difference between our experimental and observational data for this species. Soil disturbance also inhibits seedling establishment: seedling recruitment was reduced by mechanical disturbance for some focal species in the Czech Republic (Leps, 1999), and suppression of anthropogenic degradation resulted in higher adult tree recruitment in protected plots in the Monte Desert (Aschero and Vasquez, 2009).

Habitat disturbance often affects the establishment of particular species in an assemblage more than others (Leps, 1999). Roller chopping and cattle grazing in the Reserve may have tilled and broken the soil structure in a way that provided aeration and facilitated the penetration of developing roots for certain species (Sauer and Struik, 1964; Ehlers *et al.*, 1983). However, some species like *Paronychia chartacea* may depend on delicate microbiotic associations with the soil, such as soil crusts, that may be destroyed by animal-induced disturbance (Hawkes and Flechtner, 2002). Species dependent on fire may germinate poorly in the Reserve due to fire suppression. Fire has been shown to promote seedling recruitment (Carrington, 1999; Hartnett and Richardson, 1989; Menges and Gordon, 2010; Menges and Kimmich, 1996; Quintana-Ascencio *et al.*, 2003).

Microsite type was influential for the emergence/establishment of several study species as well: emergence in bare sand was highest for *Hypericum cumulicola* and *Paronychia chartacea,* and slightly less limiting for *Eryngium cuneifolium* than the other microsites; litter emergence was highest for *Liatris ohlingerae*. Shrub microsites limited establishment the most, although seedlings of *L. ohlingerae* and *E. cuneifolium* were sometimes able to grow under shrubs. Previous data indicate that litter can prevent recruitment and persistence of many rare plant

species (Hawkes and Menges, 1996; Menges and Kimmich, 1996; Quintana-Ascencio *et al.*, 2003; Rickey *et al.*, 2007). Thick litter depressed establishment of a perennial grassland plant in Germany while bare soil promoted establishment (Schleuning *et al.*, 2009), and quaking aspen seedlings established on bare soil instead of intact forest floor microsites in the Canadian Rocky Mountains (Landhäusser *et al.*, 2010). Further studies of seed removal in different microsites will be necessary to discern seed-seedling conflicts.

Our results have implications for effective habitat restoration and preservation of biodiversity in Florida scrub. Successful translocation of Florida scrub endemics in native and degraded habitat can be affected by both protection of seeds and location of introduction. Vertebrate exclosures are best employed for species with relatively larger seeds such as *Liatris ohlingerae*, *Eryngium cuneifolium*, and *Polygonella basiramia* that are most vulnerable during the seed to germinant transition. For those species most limited in emergence and seedling survival (*P. basiramia, Hypericum cumulicola*), it could be more beneficial to transplant adult individuals reared in greenhouse conditions than to plant seeds. *H. cumulicola* transplants have been successful in intact scrub at Archbold Biological Station (Quintana-Ascencio and Menges, 1996; C. Oakley, pers. comm.).

Certain species will require more intervention than others. Species challenged by synergism of high seed removal and low emergence may depend on a greater investment of time and resources. For example, it may take several attempts to successfully establish *H. cumulicola* in scrub undergoing restoration, using both planted seeds and transplants. On the other hand, species such as *L. ohlingerae,* which have relatively low seed removal and high germination, may require fewer total introduced seeds and trials. Species that appear less limited in degraded scrub than in intact scrub (*E. cuneifolium, P. basiramia, H. cumulicola*) may only require an initial input of seeds if adult individuals are absent or in very low abundances.

Our results emphasize the need for creating a variety of microsite types in habitat undergoing restoration. Only heterogeneous habitats with different microsites will be able to accommodate multiple species with individual requirements for establishment. Patchy burns can contribute to creation of these heterogeneous habitats (Rocca, 2009; Russell-Smith, 2002), especially in landscapes that are naturally patchy.

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APPENDIX 1.—Temperature and light schedule for Spring and Winter Chamber Trials. Fluorescent and incandescent indicate number of bulbs of each type illuminated each hour

Time	Spring C	Winter C	Fluorescent	Incandescent
0:00	22.0	20.0	0	0
1:00	22.0	20.0	0	0
2:00	22.5	20.0	0	0
3:00	23.0	20.0	0	0
4:00	23.5	20.0	0	0
5:00	24.0	20.0	0	0
6:00	24.5	20.5	0	1
7:00	25.0	20.5	1	1
8:00	25.5	21.0	1	1
9:00	26.0	21.0	1	2
10:00	26.5	21.5	1	2
11:00	27.0	22.0	2	2
12:00	27.2	22.0	2	2
13:00	27.0	22.0	2	2
14:00	26.5	21.5	1	2
15:00	26.0	21.0	1	2
16:00	25.5	21.0	1	1
17:00	25.0	20.5	1	1
18:00	24.5	20.5	0	1
19:00	24.0	20.0	0	0
20:00	23.5	20.0	0	0
21:00	23.0	20.0	0	0
22:00	22.0	20.0	0	0
23:00	22.0	20.0	0	0
23:59	22.0	20.0	0	0

APPENDIX 2.—Percentage emergence of planted seeds (and number of seedlings) per species and microsite. IBS = intact scrub, bare sand; ILT = intact scrub, litter only; ISH = intact scrub, under shrubs with litter; DBS = degraded scrub, bare sand; DLT = degraded scrub, litter only; DSH = degraded scrub, under shrubs with litter. *Paronychia chartacea* values represent both background germination and germinants from planted seeds

Species	IBS	ILT	ISH	DBS	DLT	DSH
Liatris ohlingerae	16.7%(2)	0%(0)	62.5%(5)	37.5%(3)	50.0%(4)	25.0%(2)
Eryngium cuneifolium	7.5%(18)	5.0%(5)	2.5%(7)	6.0%(13)	2.6%(4)	5.0%(10)
Polygonella basiramia	1.4%(5)	2.1%(2)	0%(0)	4.2%(9)	2.1%(5)	2.1%(5)
Hypericum cumulicola	0%(0)	0%(0)	0%(0)	0.9%(2)	0%(0)	0%(0)
Paronychia chartacea	46.4%(156)	3.6%(4)	0%(0)	5.4%(12)	0%(0)	0%(0)