ECOLOGICAL REQUIREMENTS OF THE ZAPATA BLADDERPOD *PHYSARIA THAMNOPHILA*, AN ENDANGERED TAMAULIPAN THORNSCRUB PLANT

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ABSTRACT—A significantly greater proportion of brush-cleared plots had the Zapata bladderpod *Physaria thamnophila* than did uncleared plots. However, density of *P. thamnophila*, especially density of seedlings, was correlated positively with a canopy-cover index on the four sites studied. These apparently contradictory results may have been due to facilitation of seeds and seedlings of *P. thamnophila* by litter. Litter, normally associated with shrubs, was spread across the site by brush-clearing. Beneficial effects of brush-clearing (without disruption of soil) on *P. thamnophila* suggest that fire may have been part of its environment in the past. The four populations of *P. thamnophila* that we studied fluctuated widely in size and in rates of reproduction and establishment from year to year.

RESUMEN—*Physaria thamnophila* estaba presente en un número significativamente mayor de parcelas con remoción de arbustos que en las parcelas sin remoción de arbustos. Sin embargo, la densidad de *P. thamnophila*, especialmente la de las plántulas, estuvo positivamente correlacionada con el índice de cobertura arbustiva en los cuatro sitios de estudio. Ambos resultados, aparentemente contradictorios, pueden deberse a que la broza ofrezca un efecto facilitador para las semillas y plántulas de *P. thamnophila*. La broza, normalmente acumulada bajo los arbustos, estaba esparcida a través del sitio debido a la remoción de los arbustos. El efecto positivo para *P. thamnophila* de la remoción de los arbustos (sin perturbar el suelo) sugiere que los incendios formaban parte de su ambiente en el pasado. El tamaño y las tasas de reproducción y establecimiento de las cuatro poblaciones de *P. thamnophila* incluidas en este estudio fluctuaron ampliamente año con año.

Understanding ecological requirements of an endangered species of plant often is essential to its preservation and successful recovery (Menges and Dolan, 1998; Pfab and Witkowski, 2000; Brys et al., 2004; Colling and Matthies, 2006). It is especially important when the species has become restricted or nearly restricted to suboptimal sites. For example, railroad right-of-ways are often the only habitat left for prairie species, but are not optimal for them (Harrington and Leach, 1989). When the mismatch between current and optimal habitat is not obvious, ecological requirements of the species may be misunderstood, reducing effectiveness of conservation actions. This is especially likely to be the case where grazing, suppression of fire, hunting, and other activities by humans have changed communities of plants and animals in ways that are less obvious than the conversion of prairie to cornfield. Currently occupied sites may even be completely unsuitable for long-term persistence; many species can persist in a site long after substantial changes in an ecosystem have reduced recruitment below rate of replacement (Eriksson, 1996; Hanski and Ovaskainen, 2002). For these reasons, studies of ecological requirements of endangered species of plants are highly desirable. We report results of such a study of the Zapata bladderpod *Physaria thamnophila*, an endangered perennial of Tamaulipan thornscrub.

There is an important potential side benefit of studying ecological requirements of an endangered plant; the results may shed light upon dynamics of its community. Endangered species can alert us to otherwise unrecognized changes in structure and composition of communities, especially where more traditional sources of information such as historical photographs and cores from lakes fall short. In the present study, we suspected that the Tamaulipan thornscrub occupied by *P. thamnophila* may be much denser now than it was historically, as a result of grazing and suppression of fire. We hypothesized that *P. thamnophila* is favored by a more open canopy of shrubs than its present habitat would suggest, perhaps associated with greater amounts of herbaceous cover.

An alternative hypothesis is that the effect of neighboring shrubs on *P. thamnophila* is positive. In arid and semi-arid climates, the net effect of neighboring plants often is positive rather than negative, a phenomenon usually ascribed to positive effects of reduced loss of water due to shading (Fowler, 1986; Bertness and Callaway, 1994; Brooker and Callaghan, 1998; Tielbörger and Kadmon, 2000; Flores and Jurado, 2003). However, negative effects also are common (Aguiar et al., 1992; Holzapfel and Mahall, 1999; Pugnaire and Luque, 2001; Maestre and Cortina, 2004). We tested both hypotheses, that neighboring shrubs have positive effects (facilitation) and, alternatively, that they have negative effects (competition in the broad sense) on *P. thamnophila*.

Tamaulipan thornscrub is a widespread plant community or, more accurately, a set of communities, but relatively little is known about its composition, dynamics, and history (Reid et al., 1990). In other parts of the southwestern United States, shrub-cover has become denser and more continuous in the past 100 years, probably as a result of changes in fire and grazing regimes (Van Auken, 2000; Archer et al., 2001). In some areas of southern Texas, conversion of former savannas to increasingly dense shrublands is well documented (Archer et al., 1988; Archer, 1995; Fulbright, 2001). Principal causes of encroachment of woody plants in savannas of southern Texas have been overgrazing by domestic livestock and a reduction in frequency of fire (Archer et al., 2001; Fulbright, 2001). It is likely that these factors also have altered structure and composition of established shrublands in the region. However, by one estimate ≥95% of the former extent of Tamaulipan thornscrub already has been lost (S. E. Jahrsdoerfer and D. M. Leslie, http://www.fws.gov/southwest/refuges/Plan/docs/Final Lower Rio Grande Valley & Santa Ana NWR Interim CMP & E.pdf). Poor management of rangelands, conversion of suitable habitat to irrigated agriculture or to pastures of non-native grasses, spread of these non-native grasses to other sites, oil and gas exploration and production, construction of roads, and urbanization are all continuing threats (United States Fish and Wildlife Service, 2000, 2004; Fulbright, 2001; Harveson et al., 2004; S. E. Jahrsdoerfer and D. M. Leslie, http://www.fws.gov/southwest/refuges/Plan/docs/Final Lower Rio Grande Valley & Santa Ana NWR Interim CMP & E. pdf; R. E. Unsworth and M. M.Engler, http://www.fws.gov/southwest/es/Documents/R2ES/draft_econ6.pdf). To these threats recently have been added potential effects of the United States-Mexico border fence (United States Department of Homeland Security, http://nemo.cbp.gov/sbi/rgv/pf225_rgv_esp.pdf). In addition to inferences about past composition and structure of Tamaulipan thornscrub, we also were interested in whether management for *P. thamnophila* would tend to preserve other species of plants that comprise its particular Tamaulipan thornscrub community. Therefore, we investigated the relationship between *P. thamnophila*, richness of herbaceous species, and abundance of grasses.

Ideally, when determining ecological requirements of an endangered species of plant, we would always be able to use properly designed and replicated experiments in combination with collection of data suitable for constructing demographic models (Schemske et al., 1994). However, in the absence of ideal data, we can still learn a great deal from the kinds of data that are more likely to be available to conservation biologists. In this study of an endangered perennial forb, we used three of these kinds of data. First, we used monitoring data, in this instance, intermittent censuses of existing populations. Second, we used data from a descriptive survey designed to characterize the Tamaulipan thornscrub vegetation of sites occupied by *P. thamnophila*. Third, we took advantage of a fortuitous experiment in which part of one site with a population of *P. thamnophila* was cleared of brush.

Materials and Methods—*Physaria thamnophila* (Rollins and E. A. Shaw) O'Kane and Al-Shehbaz (Brassicaceae; formerly *Lesquerella thamnophila*; common name Zapata bladderpod) is a federally listed endangered species (United States Fish and Wildlife Service, 2004). All known populations of *P. thamnophila* in the United States are in Starr and Zapata counties, Texas, between Zapata and Roma, a distance of 69 km. Most known populations occur on edges of terraces above the Rio Grande floodplain. A disjunct population in the Loreto Sand Plain of Tamaulipas, Mexico, may be a different species (A. Pepper and J. Manhart, pers. comm.).

Physaria thamnophila is a short-lived perennial. Timing of germination, growth, and flowering are dependent upon limited and irregular precipitation of this region (515 mm average annual precipitation at Falcon Dam, Starr County, 1971–2000). Flowering usually occurs sometime during February–April, but may occur as late as September (Sternberg, 2005; Poole et al., 2007). During long dry periods, plants become dormant and can survive loss of their leaves.

All known populations of *P. thamnophila* are in Tamaulipan thornscrub (Poole et al., 2007). Three of our four study sites (Arroyo Ramirez, Arroyo Morteros, and Cuellar) were in the Lower Rio Grande Valley National Wildlife Refuge. The fourth study site, Santa Margarita, was on private land. All four sites were within 18 km of each other in Starr County, Texas, and were dominated by the shrubs *Acacia rigidula* (blackbrush) and *Leucophyllum frutescens* (cenizo). For a fuller description of geology, soils, and composition of communities of the four study sites, see Price et al. (in press).

One-half of the Cuellar site was cleared by a Woodgator (roller-chopper; Terra Services, Inc., Katy, Texas) in December 2000. In February 2001, the newly cleared area had dense herbaceous cover, high diversity, and many *P. thamnophila*.

Because this was a long-term study conducted as time and resources permitted, design of censuses differed among years. Locations of plots within a site were permanently marked and did not change. In each census of a site, we recorded number of *P. thamnophila* in each plot in that site, except for a few plots that could not be relocated (one plot in Arroyo Ramirez in 2004, seven in Cuellar in 2004, and eight in Cuellar in 2006). We recorded number of plants flowering or fruiting in each plot during 2003–2007. We recorded number of identifiable seedlings in each plot in 2005, 2006, and 2007. Censuses were made in late February, March, or early April each year.

At Cuellar, 60 plots were located along a 217-m transect placed where the cleared area adjoined the uncleared area. Every 7 m along the transect, two plots were located; one at a random-integer distance 1–10 m perpendicular to the transect on the cleared side of the transect and the other at a different random-integer distance 1–10 m perpendicular to the transect on the uncleared side. Plots in this site were circles 1 m in radius. Except in 2005, censuses were made at this site each spring during 2002–2007.

At Arroyo Morteros, a total of 58 plots was located along 10 parallel transects of different lengths, reflecting the irregular area occupied by this population. Neighboring plots were 38 m apart. One plot was placed every 13.8 m along each transect. Plots in this site were 2-m-radius circles; the larger radius was a response to greater spacing between *P. thamnophila* in this site. Censuses were made at this site in 2005, 2006, and 2007.

At Arroyo Ramirez, a total of 34 circular plots of 1-m radius was located along three transects placed through the long axis of each of three patches occupied by *P. thamnophila*. Every 3 m along each of these transects, a plot was placed randomly right or left of the transect at a random distance 0–5 m perpendicular to the transect. Censuses were made at this site in 2004, 2006, and 2007.

At Santa Margarita, the population of *P. thamnophila* was discontinuous along a sandstone outcrop. We measured length of each of the nine patches that comprised the majority of this population. We summed these lengths to produce a discontinuous transect that ran through the middle (lengthwise) of each patch. Every 11 m along this discontinuous transect, a plot was located by moving randomly right or left perpendicular to the transect at a random distance of 0–3 m. Each of the 30 plots in this site was a 2-m-radius circle. Censuses were made at this site in 2004, 2006, and 2007.

Data describing the structure and composition of the community were collected in each plot. Five circular subplots, each 0.25 m in radius, were located in each plot for this purpose. Centers of these five subplots were (a) at the center of the plot, (b) on the edge of the plot at the position nearest the transect, (c–e) on the edge of the plot 90, 180, and 270° from position (b). In each subplot, presence or absence of each species was recorded in each of four height categories: 0.0–0.5, 0.5–1.0, 1.0–2.0, and 2.0–3.0 m above ground. No plant was taller than 3 m. It was not possible to collect all these data in a single year. We collected these data in Arroyo Morteros in 2007, in Arroyo Ramirez in 2003, in Cuellar in 2002 and 2007, and in Santa Margarita in 2004. Some plots in Cuellar did not have these data collected from them in one or both years and were dropped from analyses that would have used the missing data.

Data from the top three layers of the canopy (0.5–1.0, 1–2, and 2–3 m) were used to calculate an index of canopy cover. For each plot separately, number of subplots with $\geq$1 species of plant in it were summed for each layer, giving values of 0–5 for each layer. Sums of the top three layers were then summed, potentially giving values of 0–15 (maximum observed value was 14) for the canopy-cover index. An alternative canopy-cover index based on number of species per layer gave essentially identical results, which are not reported.

Species richness of the herbaceous layer also was calculated for each plot. *Physaria thamnophila* was excluded so that effects of richness on *P. thamnophila* could be tested. The 24 species that were observed in $\geq$1 of the top two layers of the subplots (i.e., were >1 m tall in at least one subplot) also were excluded, so that species richness of the herbaceous layer was statistically independent of canopy-cover index. The 24 excluded species were a mixture of shrubs, small trees, and cacti. The number of the remaining 127 species present in $\geq$1 of the subplots of a plot was referred to as species richness of the herbaceous layer. These 127 species included forbs, graminoids, a few cacti, and a few subshrubs.

Abundance of grasses also was calculated for each plot. Number of subplots per plot containing each graminoid species (mostly Poaceae, with a few Cyperaceae) was determined, and these values were then summed to obtain an index of abundance of grass for each plot.

Analyses of variance (ANOVAs) were used to compare each of the three descriptors of vegetation (index of canopy cover, species richness of herbaceous layer, and abundance of grasses) between treatments at Cuellar and among the three remaining sites. ANOVAs also were used to compare density of *P. thamnophila* and the proportion of *P. thamnophila* reproducing among sites. Because we had census data from all four sites in 2006 and 2007, an average density during these 2 years was calculated for each plot separately. To obtain normal residuals in analyses of density, it was necessary to drop unoccupied plots (i.e., plots where density was zero) from analyses and to log-transform density in each occupied plot. Only plots occupied in both 2006 and 2007 were used to calculate average density in those years; log transformation was done after averaging the 2 years plot by plot. To obtain normal residuals in analyses of the average proportion of plants reproducing in each plot, it was necessary to drop unoccupied plots from analyses, but no transformation was required.

Logistic regressions were used to test the effect on presence-absence of *P. thamnophila* in a plot in a given year for each descriptor of vegetation. These analyses included site as a dependent variable.

To quantify and test the relationship of each of the three descriptors of vegetation with density and reproduction of *P. thamnophila*, we used linear regressions for years that had census data from only one site, and analyses of covariance (ANCOVAs) for years with census data from >1 site. In these ANCOVAs, dependent variables initially were site, descriptor of vegetation, and their interaction; the interaction term provided a test of equality of slopes. In all instances, there was no evidence of inequality of slopes (i.e., analysis of site by descriptor of vegetation was not significant) and so the interaction term was dropped from the final analysis. As in ANOVAs that compared sites, density was log-transformed before analysis. Only plots with *P. thamnophila* were included in these analyses. Density in 2006 and 2007 was averaged before log-transformation as above. Data from the two treatments at Cuellar were pooled, and data from 2007 were used to calculate descriptors of vegetation for this site. To explore the relationship between canopy-cover index and density of *P. thamnophila*, additional ANCOVAs of the effect of cover and site on density of adults and seedlings were done using data from 2007, which was the only dataset with separate counts of adults and seedlings and a significant relationship between total density and cover of *Physaria*. Because a few plots had seedlings but no adults, or vice versa in 2007, 0.1 was added to densities of adults and seedlings of each plot before log transformation.

Total precipitation for each month of the study was obtained from the National Climatic Data Center (http://www4.ncdc.noaa.gov/cgi). We used records from Falcon Dam, which was the station nearest to study sites. To examine effects of precipitation on density of *P. thamnophila*, average density in all census plots was averaged for each site in each year and these averages were log-transformed; these were the values of the dependent variable in an ANCOVA. The independent regression variable was the summed precipitation during the preceding 12 months (March–February). Site and census year were included in the analysis as independent categorical variables.

RESULTS—Species richness of the herbaceous layer was not correlated with the index of canopy cover, but was correlated positively with abundance of grass ($r_s = 0.58$, $P < 0.001$). Abundance of grass was correlated negatively with canopy-cover index ($r_s = 0.33$, $P < 0.001$).

The two treatments in Cuellar differed significantly in all three descriptors of vegetation in 2002 and 2007 (Table 1, Fig. 1). In both 2002 and 2007, cleared plots in Cuellar had, on average, lower values for canopy-cover index as expected, and greater species richness of the herbaceous layer and more grass than uncleared plots at Cuellar.

The other three sites differed significantly in all three descriptors of vegetation (Table 1, Fig. 1). Plots in Arroyo Morteros had, on average, higher values for canopy-cover index, lower values for abundance of grass, and greater species richness of the herbaceous layer than plots in Arroyo Ramirez or Santa Margarita.

In all 5 years in which census data were collected from plots in Cuellar, a higher proportion of cleared plots had *P. thamnophila* in them than did uncleared plots (Table 2). This difference between the two treatments reached significance in 3 of the 5 years (2002, $\chi^2 = 6.65$, $P = 0.010$; 2003, $\chi^2 = 4.02$, $P = 0.045$; 2006, $\chi^2 = 5.75$, $P = 0.017$).

While average density of *P. thamnophila* in cleared plots in Cuellar was greater than in uncleared plots (Fig. 2a), this was due entirely to a larger proportion of cleared plots having *P. thamnophila* in them. There was no significant difference between occupied-cleared and occupied-uncleared plots in Cuellar in density or in proportion of *P. thamnophila* that reproduced in any year. Therefore, the two treatments in Cuellar were pooled for subsequent analyses of occupied plots.

Because size of plots differed among sites, proportion of occupied plots (i.e., plots with *P. thamnophila*) was not compared statistically among sites. Arroyo Morteros, despite having 12.57-m^2 plots, had a lower proportion of occupied plots than either Santa Margarita, which also had 12.57-m^2 plots, or Arroyo

Table 1—Results of analyses of variance comparing the three descriptors of vegetation between treatments at Cuellar, Starr County, Texas, or comparing them among the other three sites in Starr County, Texas, used to assess ecological relationships of the Zapata bladderpod *Physaria thamnophila.*

Comparison	Year	Number of plots	Average canopy-cover index (P)	Species richness of the herbaceous layer (P)	Average abundance of grass (P)
Treatments at Cuellar	2002	50	<0.001	<0.001	<0.001
Treatments at Cuellar	2007	54	0.005	0.004	<0.001
Arroyo Morteros, Arroyo Ramirez and, Santa Margarita	2007/2003/2004	122	0.001	<0.001	0.003

Ramirez, which had 3.14-m² plots (Table 2). Cleared plots in Cuellar, although only 3.14 m² in area, had a proportion occupied similar to the larger plots in Arroyo Morteros. Uncleared plots in Cuellar consistently had the lowest proportion of occupied plots.

To compare densities of *P. thamnophila* in occupied plots among sites, plots in Cuellar were pooled. Sites could not be compared in 2002, 2003, or 2005, when census data were collected from only one site. Density (average number of plants/m²) of plants in occupied plots differed significantly among sites in 2004, when data were collected from Arroyo Morteros, Cuellar, and Santa Margarita, and in 2006 and 2007, when data were collected from all four sites (Table 3). Arroyo Morteros had the highest and Santa Margarita the lowest densities of *P. thamnophila* in plots occupied by this species.

The proportion of *P. thamnophila* that were reproductive differed significantly among sites in 2004 and in 2007 (Table 3). These differences were not consistent among years. There were almost no flowering or fruiting plants and no identifiable seedlings in 2006.

Effects of characteristics of vegetation on proportion of plots occupied by *P. thamnophila* were tested only on data from Arroyo Morteros, Arroyo Ramirez, and Santa Margarita. Data from Cuellar were excluded from analysis of proportion of plots occupied because both proportion of plots occupied and each descriptor of vegetation differed significantly between the two treatments in Cuellar, making analysis of effects of descriptors of vegetation on occupation of plots in Cuellar redundant with the comparison of treatments above. No significant effect of characteristics of vegetation on proportion of plots occupied by *P. thamnophila* in the other three sites in any census was detected, although differences among sites were highly significant. However, there was a non-significant trend for species richness of the herbaceous layer to be higher in plots with *P. thamnophila* than those without in 2006 (10.4 versus 9.5 species, $P = 0.144$) and in 2007 (10.3 versus 9.2 species; $P = 0.160$).

Relationships between the three descriptors of vegetation versus density and reproduction of *P. thamnophila* were each tested separately. Canopy-cover index had a significant positive relationship with density of *P. thamnophila* in 2004 and in 2006–2007 (in plots occupied by *P. thamnophila* in both of those censuses; Table 4, Fig. 3). Density of seedlings, but not density of adults, was related significantly to canopy cover in 2007. No relationship between canopy-cover index and density of *P. thamnophila* was detected in 2002 and 2003 ($n = 17$ occupied plots in Cuellar) or in 2005 ($n = 24$ occupied plots in Arroyo Morteros). No significant effect of abundance of grass or species richness of the herbaceous layer on density of *P. thamnophila* was detected.

A significant relationship between abundance of grass and proportion of *P. thamnophila* that were reproductive in 2004 was detected (ANCOVA; $n = 63$ plots, y = proportion of plants fruiting, flowering, or both; site, $df = 2$, $P = 0.036$; abundance of grass, $df = 1$, $P = 0.232$; site by abundance of grass, $df = 2$, $P = 0.049$). The significant interaction effect occurred because the relationship between abundance of grass and proportion of *P. thamnophila* reproducing was significantly positive in Cuellar ($P = 0.011$, Scheffé test) and not significantly different from zero in Arroyo Ramirez and Santa Margarita. No census data from 2004 were available from Arroyo Morteros. No significant effect of canopy

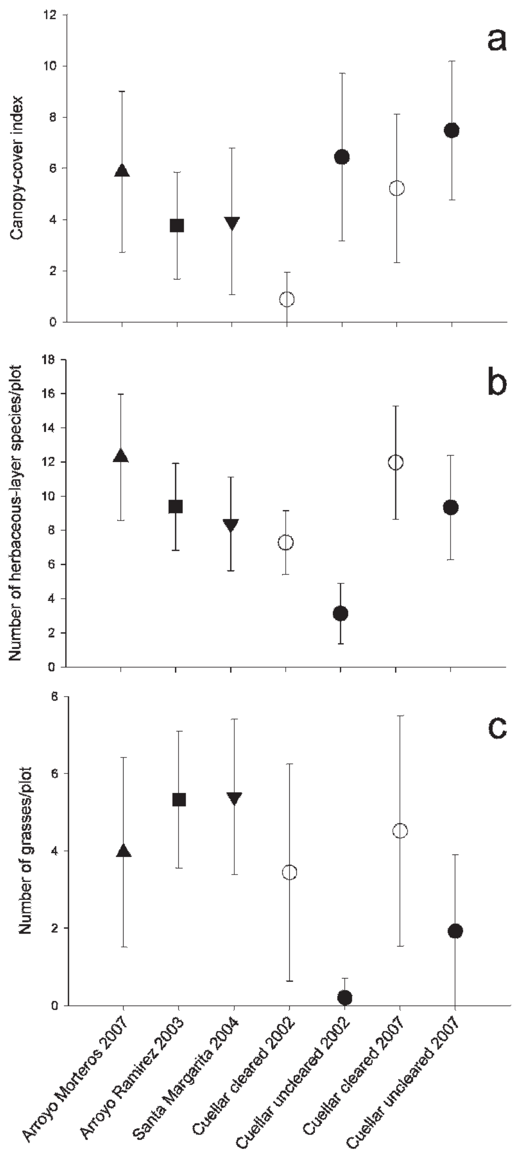

FIG. 1—Average ±1 *SD* of a) canopy-cover index, b) number of herbaceous species/plot, and c) abundance of grass used to assess ecological relationships of the Zapata bladderpod *Physaria thamnophila*, an endangered perennial of Tamaulipan thornscrub.

cover or species richness of the herbaceous layer on reproduction of *P. thamnophila* was detected.

Mean densities of *P. thamnophila* tended to be higher in years that had received more precipitation in the 12 months (March–February) preceding a census (Fig. 2b). However, precipitation only accounted for 13% of variation in mean density and was not significant. We did not have enough data to test for lags or other more complicated relationships between precipitation and density of *P. thamnophila*.

DISCUSSION—All four study sites had substantial shrub-cover, but also substantial openings in the canopy. Some open areas between shrubs were almost devoid of plants while others supported herbaceous vegetation. The two sites on edges of rocky cliffs (Arroyo Ramirez and Santa Margarita) had the least shrub-cover among the uncleared sites.

There was a complex relationship between *P. thamnophila* and shrub-cover, most likely due to a combination of positive effects (facilitation via litter) and negative effects (competition for resources) of shrubs on *P. thamnophila*. While a significantly greater proportion of cleared plots in Cuellar had *P. thamnophila* than did uncleared plots in Cuellar, density of seedlings was correlated positively with our canopy-cover index in all four sites. We observed that in undisturbed areas litter tended to be associated with shrubs, as has been reported in other arid ecosystems (Pugnaire et al., 1996; Reynolds et al., 1999). Mechanical brush clearing at Cuellar scattered litter, including woody debris, across the cleared area. Therefore, mechanical clearing may have provided favorable microsites in open areas, while in uncleared sites, favorable microsites were probably mostly under shrubs, where most of the litter was located. Because all four sites had highly erodible soil, the most likely benefit that litter provided to seedlings was a reduction in erosion. Litter may also have trapped seeds that would otherwise have washed away. However, we cannot rule out other potentially beneficial effects of litter, which might have included shading, increases in water-holding ability and nutrient content of soil, and protection from some herbivores, including trampling by domestic livestock at Santa Margarita (Flores and Jurado, 2003).

There are few comparable studies of species in Tamaulipan thornscrub. Other researchers, working in Tamaulipan thornscrub 200 and 300 km south of our populations, also elucidated complex relationships between shrub-cover and performance of seedlings. Shade-grown, potted seedlings (25% shadecloth) tended to have more leaves than open-grown ones (Flores and Jurado, 1998), there were more natural seedlings under shrubs than at the edge or in a cleared area

Table 2—Occupation of census plots by the Zapata bladderpod *Physaria thamnophila* in Starr County, Texas.

Location and variable	Year					
	2002	2003	2004	2005	2006	2007
Uncleared 1-m-radius plots at Cuellar						
Number of plots censused	30	30	27	—	29	30
Percentage of plots occupied	13	17	19	—	14	27
Cleared 1-m-radius plots at Cuellar						
Number of plots censused	30	30	26	—	23	30
Percentage of plots occupied	43	40	42	—	44	43
2-m-radius plots at Arroyo Morteros						
Number of plots censused	—	—	—	58	58	58
Percentage of plots occupied	—	—	—	41	38	59
1-m-radius plots at Arroyo Ramirez						
Number of plots censused	—	—	33	—	34	34
Percentage of plots occupied	—	—	74	—	56	94
2-m-radius plots at Santa Margarita						
Number of plots censused	—	—	30	—	30	30
Percentage of plots occupied	—	—	73	—	73	77

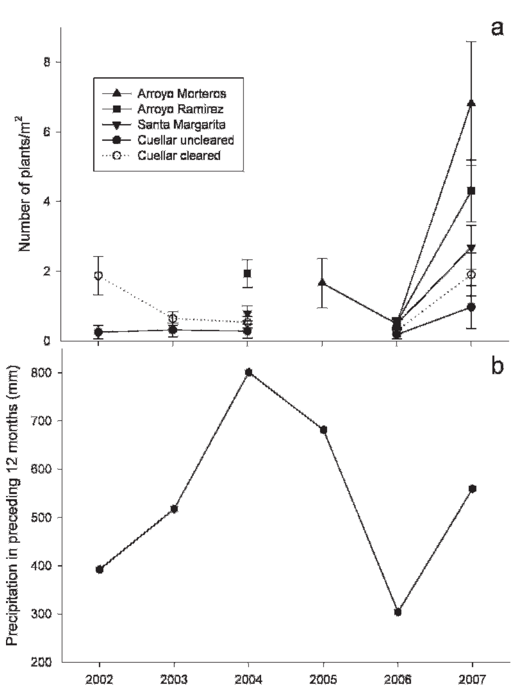

Fig. 2—a) Changes in density of the Zapata bladderpod *Physaria thamnophila* among years and b) total precipitation in the 12 months (March–February) preceding each census. Vertical bars represent ±1 *SE*.

(Garcia and Jurado, 2003), and germination, survival, and growth of sown seeds generally were greater under intact thornscrub than at the edge or in a cleared area (Jurado et al., 2006). Conversely, a site with removal of 70% of canopy had more species of forbs than an intact site (Jurado et al., 1998) and 16 of 47 species tested germinated better in direct sunlight than when shaded by thornscrub (the rest were neutral; Jurado et al., 2001). Although these researchers did not study *P. thamnophila*, their results are consistent with ours. Both sets of results suggest that presence of shrubs is neither consistently beneficial nor consistently deleterious to a seedling. Instead, the net effect depends upon additional factors such as temperature, soil moisture, and rates of erosion.

We suspect that once a seedling of *P. thamnophila* becomes established, competition from shrubs begins to outweigh facilitation. Our detection of a significant positive effect of canopy cover on density of seedlings, but not upon density of adults, is consistent with this hypothesis. We and others (Sternberg, 2005; A. Pepper, pers. comm.) have noticed that adult plants tend to be larger in open areas than they are under shrubs. However, size of plants was not measured in our study. For *P. thamnophila*, whether or not a plant reproduced is not a

TABLE 3—Selected comparisons of densities of Zapata bladderpod *Physaria thamnophila* and its reproduction among sites. Densities were log-transformed for analyses; values shown are back-transformed, least-mean-square estimates of the mean of each study site. Densities in 2006 and 2007 were averaged for each plot separately before log-transformation; only plots occupied in both years were included in this calculation. Values in a row that share letters are not significantly different.

Variable	Arroyo Morteros	Arroyo Ramirez	Cuellar	Santa Margarita	*n*	*P*
Number of plants/m^2 in 2004	—	1.71 a	0.94 ab	0.56 b	63	0.003
Percentage of plants that were reproductive in 2004	—	49 ab	42 a	66 b	63	0.045
Number of plants/m^2 in 2006 and 2007	5.96 a	2.69 b	2.60 abc	1.29 c	75	<0.001
Percentage of plants that were reproductive in 2007	60 a	33 c	60 ab	43 bc	110	0.001

surrogate for size of plant, because even small plants set some seeds. Under the hypothesis of facilitation followed by competition, *P. thamnophila* in the cleared portion of Cuellar had the best of both worlds, litter to facilitate establishment of seedlings and a reduction in competition from shrubs. Even if competition outweighs facilitation as individuals of *P. thamnophila* get older and larger, the positive spatial association with shrubs and litter created at the seedling stage may persist.

If density of the shrub-canopy remains constant over time, positive effects of shrubs on stabilization of soil and their negative competitive effects may make an intermediate density of shrub-canopy better for *P. thamnophila* than either extreme. This interpretation is compatible with the scarcity of *P. thamnophila* in the uncleared portion of Cuellar, which had higher canopy cover than any other site. It also is compatible with the observation that Arroyo Morteros, which had the highest densities of *P. thamnophila*, was intermediate in shrub-cover. However, optimal habitat of *P. thamnophila* may require temporal variation in densities of shrub-canopy. Native grasses may have been substantially more abundant before 1880 and may have supported fires that would have thinned shrub-canopies. The mechanical clearing of part of Cuellar, so beneficial to *P. thamnophila*, may have simply mimicked effects of fires. Thus, our results suggest serious consideration should be given to the possibility that fire once played a significant role in shrublands, as well as in savannas, in this region. A role for fire is compatible with, but does not depend on, effects

TABLE 4—Results of analyses of covariance (ANCOVAs) of effects of canopy cover as measured by canopy-cover index on density of the Zapata bladderpod *Physaria thamnophila* in plots occupied by this species. All measures of density were log-transformed before analysis. Slope is slope of the fitted line.

Dependent variable	Sites and years used to calculate canopy-cover index	Number of plots	Site *P*	Cover *P*	Slope
Density in 2004	Arroyo Ramirez 2003, Cuellar 2007, Santa Margarita 2004	63	0.002	0.046	0.53
Average density in 2006 and 2007	Arroyo Morteros 2007, Arroyo Ramirez 2003, Cuellar 2007, Santa Margarita 2004	75	<0.001	0.017	0.61
Density of adults in 2007	Arroyo Morteros 2007, Arroyo Ramirez 2003, Cuellar 2007, Santa Margarita 2004	110	0.316	0.294	0.25
Density of seedlings in 2007	Arroyo Morteros 2007, Arroyo Ramirez 2003, Cuellar 2007, Santa Margarita 2004	110	0.216	0.026	0.64

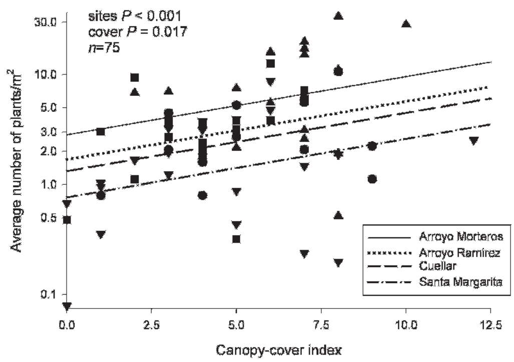

FIG. 3—Relationship between average density of the Zapata bladderpod *Physaria thamnophila* in 2006–2007 and canopy-cover index: ▲, Arroyo Morteros 2007; ■, Arroyo Ramirez 2003; ●, Cuellar 2007 (treatments pooled); ▼, Santa Margarita 2004.

of shrubs being caused by litter and competition. Regardless of causes, the positive effect of clearing brush suggests that fires that temporarily reduced shrub-canopy may have been beneficial for *P. thamnophila*. Alternatively, the difference in occupancy between cleared and uncleared plots in Cuellar might have been due to some factor not related to clearing brush. Despite the fact that many uncleared plots in Cuellar were much nearer their paired cleared plots than each other, and the same for cleared plots, cleared and uncleared plots were not intermingled randomly as would have been done in a planned experiment. Therefore, it is possible that there was some pre-existing difference between cleared and uncleared plots in Cuellar that caused the difference in occupancy by *P. thamnophila*.

Pennisetum ciliare (*Cenchrus ciliaris*; buffelgrass) was uncommon and *Dichanthium annulatum* (Kleberg bluestem) was absent from our study sites (Price et al., in press). We and others have observed that both of these non-native, invasive grasses have strong negative effects on diversity of native herbaceous vegetation (Sands et al., 2009). Both species are abundant and widely distributed in the region. Their sparseness in all four study sites probably is not a coincidence. It is more likely this sparseness has allowed *P. thamnophila* to persist in the study sites. Our results do not prove that these two grasses are major threats to *P. thamnophila* as has been suggested (United States Fish and Wildlife Service, 2004), but they certainly are compatible with that hypothesis. In contrast, presence of native grasses did not appear to inhibit *P. thamnophila*; perhaps, because native grasses are short bunchgrasses and do not form large patches.

All four sites had relatively high species richness, given their aridity. In part, this simply reflects latitude (26.5°N). Although the community is dominated by shrubs, the majority of species were herbaceous species, subshrubs, or small succulents. Only 24 of the 152 species recorded on our plots ever were >1 m tall. Richness of herbaceous species was correlated with abundance of grass. Although richness of herbaceous species was not significantly related to density of *P. thamnophila*, there was a trend for greater richness of herbaceous species in plots occupied by *P. thamnophila*, and both herbaceous richness and abundance of grass were significantly greater in cleared than in uncleared plots at Cuellar. Therefore, it is likely that many of the same factors that favor *P. thamnophila* also favor many other native herbaceous species, and management for *P. thamnophila* will maintain or enhance diversity of native herbaceous species.

The four populations of *P. thamnophila* fluctuated widely in size among years. High levels of temporal variation in sizes of populations of *P. thamnophila* also were reported by J. M. Poole (in litt.) and Sternberg (2005). We observed an even greater degree of temporal variation in proportion of plants that reproduced and in proportion of plants that appeared to be seedlings. At least some of the temporal variation we observed probably was related to variation in precipitation during months preceding each census. Absence of a statistically significant relationship between density of *P. thamnophila* and precipitation likely was due to the limited number of years of census data for all sites, and the confounding of variation in precipitation with changes in vegetation (regrowing shrubs) at Cuellar.

The high degree of temporal variation in density underscores the danger of relying upon data from populations from only one or a few years, especially for a small herbaceous species in an arid climate. Surveys conducted during dry periods likely will underestimate the size of a population and may not detect a population at all, while surveys conducted during wet years will give overly optimistic estimates of the long-term size of a population, even if the species is perennial. As a result of the high level of temporal variation in the sizes of the populations we studied, this study was not long enough to detect any trends in their sizes, although we had 3–6 years of data from each population.

Temporal variation in the sizes of these populations of *P. thamnophila* complicates determination of their sizes. Crude estimates of their sizes can be made for the two populations (Arroyo Morteros and Arroyo Ramirez) in which census plots were a sample drawn from the entire area occupied by the population. To obtain these estimates, we divided number of plants by proportion of the total area that was in census plots. A criterion for recovery is existence of 12 populations with ≥2,000 reproductive plants each (United States Fish and Wildlife Service, 2004). This criterion was met by the population in Arroyo Morteros only in 2007, when it had an estimated 78,000 reproductive plants. The criterion was never met by the population in Arroyo Ramirez. In 2007, the portion of Santa Margarita that was sampled by census plots had an estimated 1,800 reproductive plants and scattered patches of plants outside the area sampled may have brought the population up to the 2,000 minimum. At the other extreme, there was no reproductive plant in any population in 2006.

Our results are consistent with our qualitative observations in suggesting that sheet erosion is an important factor limiting establishment of seedlings of *P. thamnophila* and probably of other species. Gullying affects plants of all species and ages. Therefore, management practices that reduce sheet and gully erosion would be beneficial. These include closing areas to foot and vehicular traffic, control of erosion during construction, management of rangelands that prevents overgrazing and excessive trampling, and use of non-soil-disturbing methods to control brush. As discussed above, it is likely that management practices that favor *P. thamnophila* also will favor other native herbaceous species of the Tamaulipan thornscrub.

The positive response of *P. thamnophila* and other herbaceous species to non-soil-disturbing removal of brush suggests that thinning brush may be a useful management tool. The increase in shrub-cover in Cuellar from 2002 to 2007 suggests that recovery from roller-chopping will be relatively rapid, as Schindler and Fulbright (2003) determined elsewhere in the region. Because removal of brush may be mimicking pre-settlement fire, use of prescribed fire also should be considered. However, invasive, non-native grasses or dense brush may support fires that are more intense than pre-settlement fires, so prescribed fire should be used cautiously. A fire that is too intense could increase erosion greatly.

Although *P. thamnophila* grows well with native grasses, this species, like most other native herbaceous species, does not seem to be able to survive invasion of a site by non-native grasses. Any manipulations of habitat should be planned and monitored to ensure that they do not inadvertently encourage invasion by non-native grasses.

The wide fluctuations in the sizes of populations among years indicate that success or failure of any management practice should not be judged on results of 1–2 years. A 10-year evaluation period would be more appropriate.

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Literature Cited

Aguiar, M. R., A. Soriano, and O. Sala. 1992. Competition and facilitation in the recruitment of seedlings in the Patagonian steppe. Functional Ecology 6:66–70.

Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience 2:83–99.

Archer, S., T. W. Boutton, and K. A. Hibbard. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. Pages 115–138 in Global biogeochemical cycles in the climate system (E.-D. Schulze, S. P. Harrison, M. Heimann, E. A. Holland, J. Lloyd, I. C. Prentice, and D. Schimel, editors). Academic Press, San Diego, California.

Archer, S., C. J. Scifres, C. R. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs 58:111–127.

Bertness, M., and R. M. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191–193.

Brooker, R. W., and T. V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos 81:196–207.

Brys, R., H. Jacquemyn, P. Endels, G. De Blust, and M. Hermy. 2004. The effects of grassland management on plant performance and demography in the perennial herb *Primula veris*. Journal of Applied Ecology 41:1080–1091.

Colling, C., and D. Matthies. 2006. Effects of habitat deterioration on population dynamics and extinction risk of an endangered, long-lived perennial herb (*Scorzonera humilis*). Journal of Ecology 94: 959–972.

Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. Oikos 77:248–258.

Flores, J., and E. Jurado. 1998. Germination and early growth traits of 14 plant species native to northern Mexico. Southwestern Naturalist 43:40–46.

Flores, J., and E. Jurado. 2003. Are nurse-protégé interactions more common among plants from arid environments? Journal of Vegetation Science 14: 911–916.

Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics 17:89–110.

Fulbright, T. E. 2001. Human-induced vegetation changes in the Tamaulipan scrub of La Frontera. Pages 166–175 in Changing plant life of La Frontera; observations on vegetation in the United States/Mexico borderlands (G. L. Webster and C. J. Bahre, editors). University of New Mexico Press, Albuquerque.

García, J. F., and E. Jurado. 2003. Influence of plant cover on germination in matorral in northeastern Mexico. Forest Ecology and Management 177: 11–16.

Hanski, I., and O. Ovaskainen. 2002. Extinction debt at extinction thresholds. Conservation Biology 16: 666–673.

Harrington, J. A., and M. Leach. 1989. Impact of railroad management and abandonment on prairie relicts. Pages 153–157 in Proceedings of the eleventh North American prairie conference (T. B. Bragg and J. Stubbendieck, editors). University of Nebraska, Omaha.

Harveson, P. M., M. E. Tewes, G. L. Anderson, and L. L. Laack. 2004. Habitat use by ocelots in South Texas: implications for restoration. Wildlife Society Bulletin 32:948–954.

Holzapfel, C., and B. E. Mahall. 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. Ecology 80: 1747–1761.

Jurado, E., J. Flores, J. Navar, and J. Jiménez. 1998. Seedling establishment under native Tamaulipan thornscrub and *Leucaena leucocephala* plantation. Forest Ecology and Management 105:151–157.

Jurado, E., J. F. Garcia, J. Flores, and E. Estrada. 2006. Leguminous seedling establishment in Tamaulipan thornscrub of northeastern Mexico. Forest Ecology and Management 221:133–139.

Jurado, E., J. Navar, H. Villalón, and M. Pando. 2001. Germination associated with season and sunlight for Tamaulipan thornscrub plants in north-eastern Mexico. Journal of Arid Environments 49:833–841.

Maestre, F. T., and J. Cortina. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. Proceedings of the Royal Society of London B, Supplement 271:S331–S333.

Menges, E. S., and R. W. Dolan. 1998. Demographic viability of populations of *Silene regia* in Midwestern prairies: relationships with fire management, genetic variation, geographic location, population size and isolation. Journal of Ecology 86:63–78.

Pfab, M. F., and E. T. F. Witkowski. 2000. A simple population viability analysis of the critically endangered *Euphorbia clivicola* R. A. Dyer under four management scenarios. Biological Conservation 96: 263–270.

Poole, J. M., W. R. Carr, D. M. Price, and J. R. Singhurst. 2007. Rare plants of Texas. Texas A&M University Press, College Station.

Price, D. M., C. F. Best, N. L. Fowler, and A. Hempel. In press. ¡Viva thamnophila! Habitat and plant community of Zapata bladderpod (*Physaria thamnophila*), an endangered plant of the Texas-Mexico borderlands. Proceedings of the fifth Southwest rare plant conference. United States Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Pugnaire, F. I., and M. T. Luque. 2001. Changes in plant interactions along a gradient of environmental stress. Oikos 93:42–49.

Pugnaire, F. I., P. Haase, J. Puigdefabregas, M. Cueto, S. C. Clark, and L. D. Incoll. 1996. Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in South-east Spain. Oikos 76:455–464.

Reid, N., D. M. Stafford Smith, P. Beyer-Münzel, and J. Marroquín. 1990. Floristic and structural variation in the Tamaulipan thornscrub, northeastern Mexico. Journal of Vegetation Science 1:529–538.

Reynolds, J. F., R. A. Virginia, P. R. Kemp, A. G. de Soyza, and D. C. Tremmel. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecological Monographs 69:69–106.

Sands, J. P., L. A. Brennan, F. Hernández, W. P. Kuvlesky, J. F. Gallagher, D. C. Ruthven, and J. E. Pittman. 2009. Impacts of buffelgrass (*Pennisetum ciliare*) on a forb community in South Texas. Invasive Plant Science and Management 2:130–140.

Schemske, D. W., B. C. Husband, M. H. Ruckelhaus, C. Goodville, I. M. Parker, and J. G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584–606.

Schindler, J. R., and T. E. Fulbright. 2003. Roller chopping effects on Tamaulipan scrub community composition. Journal of Range Management 56: 585–590.

Sternberg, M. A. 2005. Zapata bladderpod (*Lesquerella thamnophila* Roll. & Shaw): its status and association with other plants. Texas Journal of Science 57: 75–86.

Tielbörger, K., and R. Kadmon. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. Ecology 81:1544–1553.

United States Fish and Wildlife Service. 2000. Final designation of critical habitat for the plant *Lesquerella thamnophila* (Zapata bladderpod); final rule. 50 CFR Part 17 RIN 1018–AG24. Federal Register 65: 81182–81212.

United States Fish and Wildlife Service. 2004. Zapata bladderpod (*Lesquerella thamnophila*) recovery plan. United States Fish and Wildlife Service, Albuquerque, New Mexico.

Van Auken, O. W. 2000. Shrub invasions of semi-arid grasslands. Annual Review of Ecology and Systematics 31:197–216.

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