In Situ Conservation of Wild Chiles and Their Biotic Associates

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Abstract: *Wild congeners of domesticated crops increasingly serve as sources of genes for improving crop cultivars. Although wild congeners have been included in seed collections for ex situ storage, there has been little work to protect populations of these wild species in their natural habitats for in situ conservation. We assessed the distribution of chile plants (Capsicum annuum L. var. aviculare [Dierbach] D'Arcy and Eshbaugh) relative to the dominant woody vegetation of one subpopulation in a single drainage in southern Arizona, U.S.A. Wild chiles were not found in direct sun, and the distribution of chiles under different nurse plants could be a function of random chance, microenvironmental differences under different nurse-plant species, or nonrandom dispersal by chile consumers. To examine chile distribution, we measured the association of wild chiles with nurse-plant species and compared these associations with the available cover provided by each nurse plant. We also measured the buffering capacity of each nurse-plant species, conducted mammalian and avian food-preference experiments to determine the taxa dispersing chiles, and conducted time-budget studies of potential chile dispersal agents. Wild chiles were not randomly distributed: over 75% were under the canopies of fleshy-fruited shrubs that collectively made up less than 25% of the cover. We found limited evidence that differences in buffering capacity affected chile distribution. Food-preference experiments suggested that birds are the only effective dispersal agents, and the time budgets of three common bird species were strongly correlated with chile plant distribution. These results lend support for directed dispersal by avian consumers. The distribution of chiles appears to be a function of interactions between consumers, nurse plants, and the secondary chemicals in the chiles themselves. Only through studies of in situ populations can we understand the interactions that sustain both wild-crop relatives and the genetic variability essential to future crop management.*

Conservación In Situ de Chiles Silvestres y Sus Asociados Bióticos

Resumen: *Los parientes silvestres de cultivos domesticados sirven más y más como fuente de genes para el fitomejoramiento de cultivos. A pesar de que los parientes silvestres han sido incluidos en la recolección de semillas para almacenamiento ex situ, es poco el trabajo que se ha hecho en la protección de estas especies silvestres en su hábitat natural para su conservación in situ. Ilustramos lo importante que es el mantenimiento de las interacciones de la comunidad para la conservación efectiva de chiles silvestres o chiltepines (Capsicum annuum L. var. aviculare [Dierbach] D'Arcy and Eshbaugh) in situ en el sur de Arizona, E.U.A. No se encuentran chiltepines bajo sol directo, pero la distribución de chiltepines bajo diferentes plantas nodrizas podría ser una función de suerte, diferencias microambientales debajo de distintas especies nodrizas, o dispersión no casual por consumidores de chiles. Para tratar con estas posibles causas medimos la asociación de chiltepines con nodrizas o madrinas, comparamos estas asociaciones con la cubierta disponible bajo cada nodriza. Además, medimos la capacidad de amortiguación de cada especie nodriza, condujimos experimentos de preferencia de comidas con mamíferos y aves, y condujimos estudios de presupuesto de tiempo con potenciales agentes para la dispersión de chiltepines. Los chiltepines no estaban distribuidos al azar; mas del 75% esta-*

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ban bajo la cubierta de arbustos con frutas carnosas que colectivamente constituyen menos del 25% de la cubierta. Encontramos evidencia limitada de la capacidad de amortiguamiento para afectar la distribucion de los chiltepines. Experimentos de preferencia en comidas sugieren que aves son los únicos agentes de dispersión efectivos y que los presupuestos de tiempo de tres especies comunes de aves estaban estrechamente relacionadas con la distribución de la planta de chilttepin. Estos resultados prestan soporte a dispersión dirigida por consumidores avicolas. La distribución de chiles parece ser un producto de las interacciones entre consumidores, nodrizas, y los químicos secundarios en los mismos chiltepines. Unicamente a través de estudios de poblaciones conservadas in situ podemos entender las interacciones que sostienen tanto a los parientes silvestres como a la variabilidad genética esencial al futuro manejo de cultivos.

Introduction

Wild congeners of domesticated crops are increasingly used as plant genetic resources for improving the resistance of cultivated crop varieties (cultivars) to disease, pests, and abiotic stresses (Stalker 1980). In the United States alone, genes from wild-crop relatives have been used to enhance at least 23 nontimber crops, accounting for more than 1% of the country's total annual crop production, which is worth billions of dollars annually (Prescott-Allen & Prescott-Allen 1987). The conservation of wild-crop relatives as potential genetic resources for crop improvement therefore has become a shared priority of agricultural geneticists and conservation biologists (Frankel & Soulé 1981).

Most of the funds devoted to conserving the genetic resources of crops and their wild relatives are devoted to the collection of seeds, scions, and tubers for ex situ storage (Stalker 1980; Ingram & Williams 1984). Few wild congeners are intentionally managed or even monitored in their natural habitats as a means of in situ conservation (Ingram & Williams 1984; Ingram 1990); even fewer have had protected areas explicitly designated for their conservation (e.g., Guzman-Mejia & Iltis 1991).

Although hundreds of species of wild-crop congeners occur in the world's 8500 national parks and biosphere reserves, management plans rarely address these species, and there have been virtually no attempts to conserve the current genetic variation in wild congeners or the ability of these species to evolve in their natural habitats (Food and Agriculture Organization 1996). To accomplish these goals, managers need to consider the web of interactions that enable a plant population to persist in its native habitat (Frankel & Soulé 1981; Tuxill & Nabhan 1998). Only a handful of wild-crop congeners have been subjects of detailed ecological studies in their native habitats (Nabhan & Felger 1978; Benz et al. 1990). This is unfortunate because an understanding of the adaptive strategies of wild congeners may be critical for their effective use in crop improvement (Harlan 1967; Zohary 1983). This paucity of knowledge about the ecology and management of wild-crop congeners would not be so worrisome if ex situ conservation strategies were able to obtain a greater diversity of conservation objectives (Hamilton 1994) and wild populations were not threatened with extirpation (Nabhan 1991).

To illustrate the value of detailed in situ studies of wild-crop relatives, we demonstrate their importance for understanding the ecology and advancing the conservation of "chiltepines," a form of wild chile peppers (*Capsicum annuum* L. var. *aviculare* (Dierbach) D'Arcy and Eshbaugh). We emphasize two sets of relationships upon which wild chile peppers depend: those with dispersal agents and those with nurse plants, the overstory trees and shrubs that protect vulnerable seedlings from biotic and abiotic stresses (Nabhan 1987; Valiente-Banûet & Escurra 1991). We examined these relationships in an isolated population at the northern limit of the chile's range because peripheral populations may contain unique genetic traits that allow persistence and evolution of the species at the aridmost limits of its range (Lawton 1993; Lesica & Allendorf 1995) and that may incidentally have value in crop improvement. We examined the distribution of chiles among different nurse-plant species and three possible mechanisms to explain this distribution: (1) random association, (2) microenvironmental differences leading to differential establishment and survival under various nurse plants, and (3) differential or directed dispersal to various nurse plants. Our objectives were to determine the abiotic and biotic factors that influence the distribution of chile plants and to identify the interactions on which wild chiles depend for recruitment and survival at the northern limits of their range.

Threats to Wild Chile Populations

Wild chiles are long-lived, somewhat scandent perennial shrubs that fruit in the fall. Numerous bright red fruits are produced on long pedicels and often remain on the plant through the winter if they are not consumed. The oldest wild plant we have on record is more than 30 years old, but little is known about average longevity. Wild chiles are found throughout Central America and reach the northern limits of their range in southern Arizona, U.S.A., where our investigations were conducted.

There, the species is rare enough that the U.S. Forest Service has given it "special plant" status (M. Parra-Falk, Coronado National Forest, personal communication). In southern Arizona and adjacent Sonora, Mexico, the loss of habitat, damage to plants by collectors and livestock, and overharvesting of fruit have led to local declines in wild chile population densities and, in some cases, the long-term loss of entire populations (Gentry 1942; Nabhan et al. 1990). Many populations in Sonora apparently have been overexploited during the last five decades: up to 20 metric tons of wild chiles have been harvested annually from the sierras for export as a condiment to U.S. markets (Gentry 1942; Nabhan et al. 1990). Small, isolated populations occur in at least two U.S. protected areas with International Biosphere Reserve status from the United Nations Educational, Scientific, and Cultural Organization (Organ Pipe Cactus National Monument and Big Bend National Park), but the only known population in the United States with more than 500 plants is located in Coronado National Forest, Arizona. This population forms the northern apex of a diffuse archipelago of wild chile populations in the Sonoran Desert bioregion, and although a minimum viable population analysis has not been completed, the chiles in Coronado National Forest may represent the best opportunity for protection of a viable population for long-term in situ conservation (Frankel & Soulé 1981).

Study Site and Methods

The primary study site is in an ephemeral stream drainage on the south face of Tumacacori Peak, Santa Cruz County, Arizona (31°33′N, 111°04′W) between 990 and 1290 m in elevation, less than 25 km from the international border with Mexico. This site is within a 2500-ha proposed botanical and zoological area being developed under a Memorandum of Understanding between the U.S. Forest Service and Native Seeds/SEARCH (Nabhan 1990). Through 5 years of systematic mapping and floral surveys, more than 500 wild chile plants have been tagged and mapped, 40 other species of crop congeners have been found, and more than 220 plant species have been cataloged on the proposed reserve (G.P.N., unpublished data). The area is rich in tropically derived disjuncts when compared with other localities near the limits of Sonoran Desertscrub and Madrean Evergreen Woodlands (Brown 1982), but the vegetation is predominantly semidesert grassland and mesquite woodland (Brown 1982).

Chile Plant Distribution

To assess the distribution of chile plants relative to the dominant woody vegetation, we chose one subpopulation contained within a single side drainage at our pri-

mary field site. All chile plants in the drainage ($n = 80$) were located, and their associations with nurse plants were recorded. To determine if chile plants were randomly distributed among nurse plant species, we assessed the relative cover of all potential nurse plants in the drainage by conducting five 250-m^2 strip transects and recording the canopy cover of all woody perennial vegetation in the transects following the logarithmic plot method (McAuliffe 1990). If chile plants were distributed randomly with respect to nurse-plant species, the expected distribution of chiles among nurse plants should be proportional to the cover provided by each potential nurse-plant species in the transects. Because no chiles were found in the open, the expected number of chiles under a particular nurse plant, E_J, can be described as:

$$E_J = \left[\frac{C_J}{C_{\text{tot}}}\right] O_{\text{tot}}, \qquad (1)$$

where C_J is the cover provided by species J, C_{tot} is the total cover of all potential nurse-plant species, and O_{tot} is the total number of chiles (80 in the drainage studied).

Abiotic Stress

To determine if the distribution of chiles among potential nurse plants was related to differences in the abiotic conditions under the canopies of these plants, we surveyed light penetration and ambient temperature under the canopies of five dominant woody plant species and at analogous nearby sites lacking woody cover. The shaded leaves of domesticated chile plants are known to contribute significantly to plant photosynthesis, especially when plants are affected by other abiotic stresses (Alvino et al. 1994). To examine shade quality, we measured light-extinction profiles on 24 June 1995. We used a 1-m-long LiCor LQA line quantum sensor to measure light penetration at 30 cm above ground in each cardinal direction from the main trunk of each tree sampled. We sampled five individuals of each nurse-plant species and used the mean of the four measurements divided by the ambient unobstructed light intensity to obtain a percent light infiltration value in μmols/second for each tree.

Temperature was measured by thermocouples connected to a Wescor TH-65 Digital TC thermometer at midday in summer (24 June 1995) and in winter (20 December 1995). Summer temperature exceeded 41° C on the day of sampling, and winter temperature ranged from 2.5° to 8° C during sampling. We compared air and ground temperatures outside each nurse-plant canopy with ground temperatures at the base of a chile plant's stem under the nurse-plant canopy and at 30 cm above ground beneath the nurse plant. Because air and ground measurements gave similar results, we present only the difference between ground temperatures within and outside of canopies.

Survival

To determine the effect of different shaded environments on the survival of chile plants, a replicated transplant experiment was initiated at the Desert Botanical Gardens in Phoenix, Arizona, where we established a drip-irrigated experimental plot. Equal-aged wild chile seedlings grown from the same source population were randomly transplanted into runoff catchment basins of desert soil mixed with compost. We transplanted chiles into five treatments: under netleaf hackberry (*Celtis reticulata* Torr.), under wolfberry (*Lycium andersonii* Gray), under mesquite (*Prosopis velutina* Woot.), in artificial shade made with fiberglass mesh, and without shade. Fifteen chiles were transplanted per treatment. All plants were irrigated at least monthly for 2 years and then left to survive on local rainfall (200–250 mm) alone. We recorded survival 1, 2, and 3 years after irrigation was terminated.

Dispersal

We compared the size, shape, and color of chile fruits with fruits of other bird-dispersed shrub and tree species at our primary study site. We then compiled direct observations and video recordings at our primary study site and at the Arizona-Sonora Desert Museum, located in the Tucson Mountains 66 km north of our primary study site, to determine the primary avian consumers of chiles.

To determine dispersal patterns from primary avian consumers, we conducted time-budget studies at the study site, where we sampled vegetation along transects. Birds were located along a 50 × 200 m transect within the chile population. To minimize bias associated with conspicuous perch locations, the activities of all birds were followed for as long as each bird stayed within the transect area or until the bird was lost from view. The time spent foraging and perching on all substrates was recorded. We made a total of 233 bird-substrate observations during five mornings of field observations from 0800 to 1030 hours. We conducted all observations during the autumn fruiting season between 1 September and 15 October 1996. Assuming that the probability of birds defecating seeds onto or under a particular plant species is highly correlated with the amount of time they spend perching and foraging on these substrates during morning foraging periods, these data should provide an index of the avian dispersal patterns of chile seeds.

To further investigate chile consumption by birds and mammals, we conducted two sets of field trials of fruit preference: a diurnal set to examine avian fruit preference and a nocturnal set to examine the dietary preference of nocturnal mammals. Avian fruit preference trials were conducted at the Arizona-Sonora Desert Museum. Because both wild chiles and desert hackberries occur on the museum grounds, birds involved in preference trials previously had been exposed to all fruits presented. Fruits were presented from 0600 to 1000 hours on small paper plates on the ground; three days of trials were conducted. Fruits were placed in three treatments: 20 chiles on a plate (*n* = 13 plates over the 3 trial days), 10 chiles mixed with 10 hackberry fruits (*n* = 11), and 20 hackberry fruits (*n* = 13). Plates were checked hourly and were removed when over half the fruit was consumed.

Although all mammals tested in laboratories to date show aversion to capsaicinoids (Glinsukon et al. 1980; Kawada et al. 1986; Szolcsányi et al. 1986), we found no previously published tests of mammalian responses to wild chiles in their natural habitats. Because rats have been shown to become desensitized to capsaicinoids under laboratory conditions (Bib 1990), testing fruit preferences with mammals previously exposed to chiles was necessary for determining their potential role as seed consumers. Therefore, we conducted nocturnal fruit-preference experiments at our primary field site. After dusk, when frugivorous bird activity had ceased, we placed groups of wild chile and hackberry fruit at 10-m intervals on the ground in small areas cleared of leaf litter and in depressions on rocks. Before dawn we collected the remaining fruits and tallied the number of each fruit type removed. Although ants may have removed some fruits, we saw no ant activity around fruit groups during predawn collections. Fruit presentations were done in three treatments: 20 chiles (*n* = 5 groups), 10 chiles and 10 hackberries (*n* = 5 groups), and 20 hackberries (*n* = 5 groups) over two trial nights.

Statistical Analyses

To determine if chile plants were distributed nonrandomly under nurse plants, we used a chi-square analysis (Sokal & Rohlf 1995), comparing the observed distribution of chiles with the expected distribution. A nurse-plant association score was calculated for each species as the difference between the observed number and the expected number of chile plants under a species. Thus the nurse-plant association represents the degree of association between chiles and nurse-plant species above or below that expected by random distribution of chiles among nurse plants. This metric was then used to examine the potential relationships between light penetration, temperature-buffering capacity, and chile distribution. Light penetration was arcsine-transformed and compared by analysis of variance and linear regression (Sokal & Rohlf 1995). We used partial regression analysis to examine the relationship between the substrate use of the three primary chile consumers and the distribution of chile plants under different nurse plants, controlling for the relative cover provided by each potential nurse-plant species (SPSS, Inc. 1996). We report stan-

dardized beta coefficients (b_{st}) with this analysis (Sokal & Rohlf 1995). Nocturnal and diurnal fruit preferences were evaluated with a Mann-Whitney U test because not all data were normally distributed. Nocturnal trials were evaluated by means of a one-tailed significance level to reflect our directional hypothesis that mammals would avoid eating chiles. We used SPSS version 7 for all tests (SPSS, Inc. 1996).

Results

Chile Plant Distribution

Chiles were not found in open, unprotected areas. We found a greater than expected association of wild chile plants with particular nurse plants relative to the modest contribution of their canopies to overall vegetative cover (Fig. 1). For the 83 chile plants located within the strip transects, 63 plants (78%) were found under the canopies of fleshy-fruited shrub or tree species that collectively contributed less than a quarter of the woody plant cover (Fig. 1; $\chi^2 = 112$, df = 1,9; $p < 0.0005$). Notably, 48 of the chile plants (58%) were found under

just two species: desert hackberry (*Celtis pallida* Torr.) and netleaf hackberry (*Celtis reticulata* Torr.), although these two red-fruited trees contributed only 15% of the woody plant cover in transects. Another 15 (20%) of the wild chiles were found under three other fleshy-fruited shrubs: wolfberry (*Lycium andersonii* Gray), graythorn (*Zizyphus obtusifolia* Hook), and condalia (*Condalia correllii* Johnston.). The cover contributed by these shrubs provided less than 10% of the total plant cover.

Abiotic Stress Reduction

Hackberry canopies (of both *C. pallida* and *C. reticulata*) allowed significantly less ambient light to penetrate to the median level of chile foliage (30 cm above ground) than did the canopies of other dominant shrubs ($F = 11.6$, df = 1,24, $p = 0.001$; Fig. 2), and there was a trend for species with lower light penetration to have greater frequency of association with chiles ($F = 6.26$, $r^2 = 0.67$, $p = 0.087$, df = 1,4). This trend was entirely driven by hackberry canopies (Fig. 2), however, and light penetration was not different among other shrubs tested (Scheffe's Post-hoc test, $p > 0.06$ in all cases). Three out of six species measured had significantly warmer ground temperatures in mid-winter under their canopies, and ground temperatures in the summer were significantly cooler under the canopies of all species
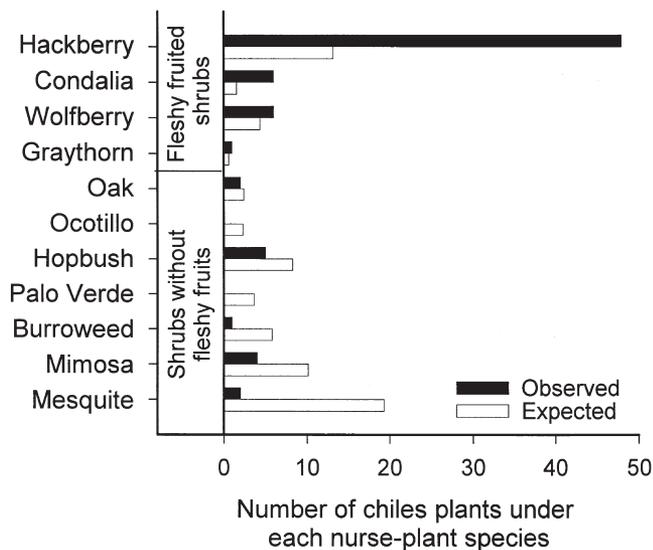

*Figure 1. Observed and expected number of chile plants under each potential nurse-plant species. The expected distribution is based on the relative abundance of each nurse plant (C_j, equation 1). The observed chile distribution is greater than expected under all nurse-plant species that bear small, bird-dispersed fleshy fruits and less than expected under the canopies of other species: oak (*Quercus oblongifolia* Torr.), ocotillo (*Fouquieria splendens Engelm.*), palo verde (*Cercidium floridum Benth.*), and burroweed (*Isocoma tenuisecta Greene*); scientific names for other species provided in Table 1.*
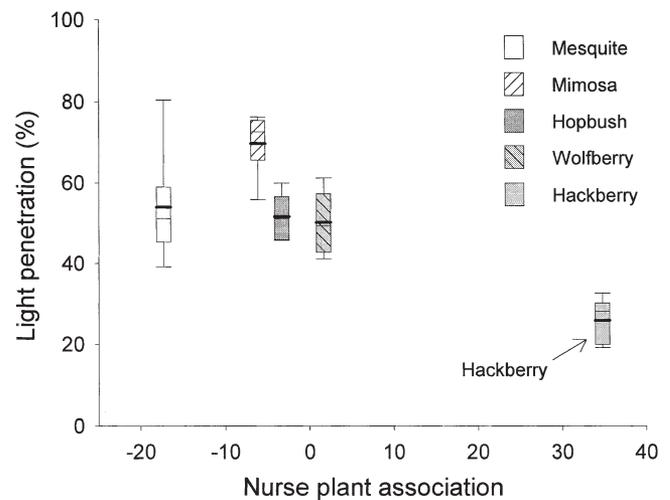

*Figure 2. Light penetration through the foliage of various nurse-plant species plotted against their nurse-plant association. Species with positive nurse-plant associations have more chiles under them than expected by chance. Boxplots represent mean (thick horizontal line), median (thin horizontal line), twenty-fifth to seventy-fifth percentile (box), and tenth to ninetieth percentile (whiskers). Data are presented for desert hackberry (*Celtis reticulata*), wolfberry (*Lycium andersonii*), mesquite (*Prosopis velutina*), mimosa (*Mimosa dysocarpa*), and hopbush (*Dodonea viscosa*).*

Table 1. Soil temperature difference (° C) under canopies of different nurse plants compared to open soil.

Species[a]	Common name	Nurse plant association	Winter buffering[b]	Summer buffering[b]
Celtis pallida Torr.	desert hackberry	34.79	$1.86 \pm .89$ (5)	14.92 ± 1.92 (8)***
Condalia globosa Johnst.	bitter condalia	4.43	$3.07 \pm .51$ (5)**	not measured
Lycium andersonii Gray	wolfberry	1.64	not measured	19.55 ± 2.19 (6)***
Zizyphus obtusifolia Hook	graythorn	0.4	$1.6 \pm .62$ (5)*	12.05 ± 1.70 (6)**
Dodonea viscosa Jacq.	hopbush	−3.28	$2.15 \pm .60$ (5)*	14.44 ± 4.24 (5)*
Mimosa biuncifera Benth.	mimosa	−6.14	-0.36 ± 1.06 (5)	10.4 ± 4.77 (5)*
Prosopis velutina Woot.	mesquite	−17.33	0.54 ± 1.11 (5)	10.73 ± 3.68 (5)*

[a] *Species are ordered by nurse-plant association score.*
[b] *Mean ± SE (number of trees sampled). Significance of temperature change under canopy compared to open soil from paired* t *tests:* *p < 0.05,* **p < 0.005, ***p < 0.0005.*

tested than in open areas (Table 1). The relative capacity of different nurse plants to buffer extremes in temperature was not correlated with these nurse plants' frequency of association with chiles (summer: $F = 0.89$, $r^2 = 0.02$, $p = 0.398$, df = 1,4; winter: $F = 1.133$, $r^2 = 0.026$, $p = 0.347$, df = 1,4). Nevertheless, the survival of chiles transplanted under hackberry may be higher than those transplanted to no-shade environments, artificial shade environments, or under mesquite or wolfberry canopies. Of the 15 replicates planted in each treatment, 5 chiles survived beneath the hackberry canopies 2 years after irrigation, and 2 survived after all other treatments were terminated (3 years after irrigation was suspended). All chiles in the other treatments died within 1 year after irrigation stopped.

Dispersal

The fruits of wild chiles are slightly larger when ripe than are other bird-dispersed fruits in the area, but generally they are similar in morphology and presentation to the other bird-dispersed fruits (Table 2). Through three seasons of observation and video analysis of bird visitations to chiles, we identified three primary chile consumers at our primary study site: Curve-billed Thrasher (*Toxistoma curvirostre*), Northern Cardinal (*Cardinalis cardinalis*), and Northern Mockingbird (*Mimus polyglottos*). All three of these species readily consumed chiles, and the Curve-billed Thrasher and Northern Mockingbird have been shown to defecate viable chile seed (G.P.N. and J.J.T., unpublished data). In 3 hours of videotaped bird activity at a large wild chile bush on Arizona-Sonora Desert Museum grounds, we observed a Northern Mockingbird take an average of 10 fruits per hour in eight different bouts. This bird was documented defending the wild chile plant from the visits of a Cactus Wren (*Campylorhynchus brunneicapillus*) and a Gila Woodpecker (*Melanerpes uropygialis*). The Gila Woodpecker was also seen consuming large quantities of chile fruit, but this species rarely occurs at our primary study site.

During 223 bird-substrate observations of the three primary avian chile consumers at the study site, we determined that all three species used plant substrates nonrandomly (all $\chi^2 > 100$, $p < 0.0005$ in all cases), exhibiting strong positive associations with desert hackberry canopies and lesser associations with other red-fruited shrubs. During our observation periods, all three species spent more than 80% of their time perching and foraging among hackberry canopies. When the substrate use of these species is compared to the distribution of chiles under their canopies, strong positive relationships occurred in all three cases (Fig. 3) (Northern Mockingbird: $R_P = 0.933$, $b_{st} = 0.949$, $p < 0.0001$; Curve-billed Thrasher: $R_P = 0.948$, $b_{st} = 1.023$, $p < 0.0001$; Northern Cardinal: $R_P = 0.953$, $b_{st} = 1.010$, $p < 0.0001$).

Table 2. Fruit characters of perennial plants bearing bird-dispersed fruit in arid subtropical and semiarid North America.

| Species	Common name	Fruit characteristics			
		Diameter (mm)	Shape	Color at maturity	Texture/taste
Capsicum annuum L.	wild chile	6–10	globose to subellipsoid	orange-red to red	pericarp thin, piquant
Celtis pallida Torr.	dessert hackberry	5–8	ovoid to ellipsoid	yellow-orange to red	pulp copious, sweet
Celtis reticulata Torr.	netleaf hackberry	6–8	globose to obovate	orange-red to brown	pulp thin, sweet
Condalia correllii Johnst.	condalia	4–8	obovoid to subglobose	bluish-black	pericarp juicy, bland
Condalia globosa Johnst.	bitter condalia	3–6	globose	blackish	thin, bitter, juicy
Lycium andersonii Gray	wolfberry	3–8	ovoid to ellipsoid	orange-red to red	pericarp juicy
Lycium berlandieri Dunal	wolfberry	4–5	spheroid to ellipsoid	red	pericarp juicy, fleshy
Solanum nigrum L.	chichiquelite	5–9	globose	purple to violet	pericarp juicy, bitter
Zizyphus obtusifolia Hook.	graythorn	4–8	ellipsoid	bluish-black to black	pericarp juicy
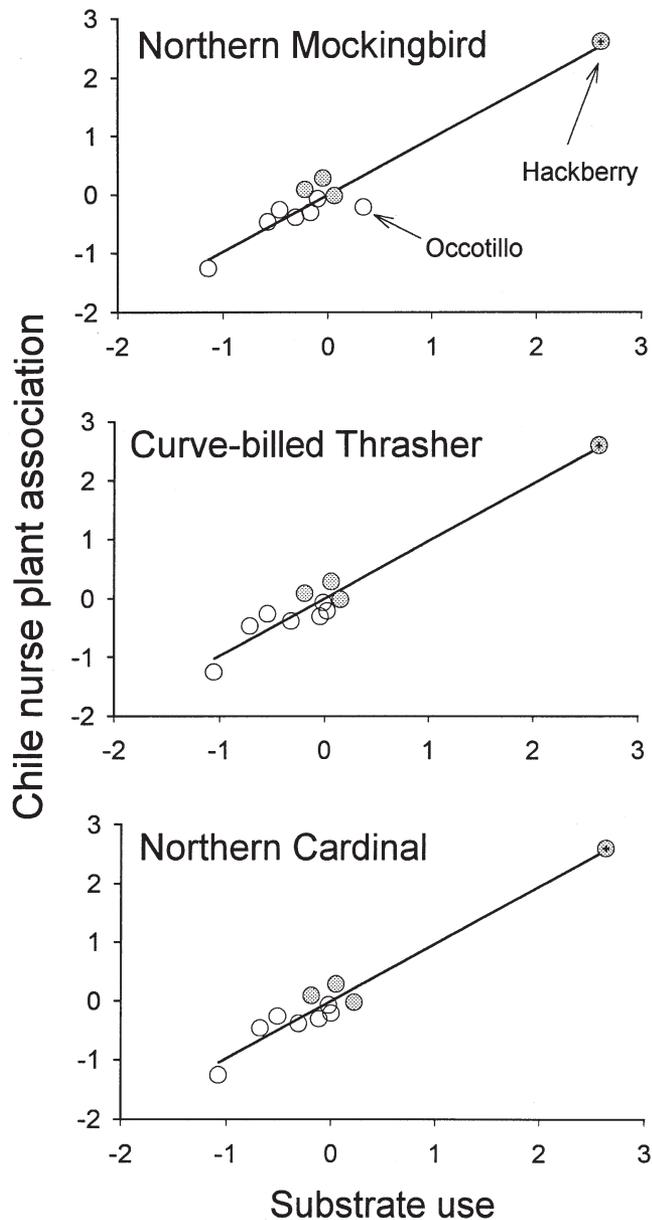
Figure 3. Partial residual plots from linear regression for nurse-plant association with chiles versus the substrate use of each chile consumer, controlling for the relative abundance of each substrate. Each point represents the association between wild chiles and a given nurse-plant species (on the y axes) plotted against the use of that species by either Northern Mockingbird, Curve-billed Thrasher, or Northern Cardinal. Open circles are species without fleshy fruits; filled circles are species bearing fleshy, bird-dispersed fruits. Hackberry (+) was the most utilized substrate by all three bird species and had by far the most chiles associated with it (Fig. 1). Ocotillo is labeled for the Northern Mockingbird because it was used substantially as a perch by mockingbirds but did not have chiles under it. Ocotillo provides almost no shade, however, because of its growth form and thus may not serve as an effective nurse plant.

In night-time trials aimed at determining the fruit consumption preferences of small nocturnal and crepuscular mammals, chiles were never consumed, whereas hackberries were readily eaten. Because our sample size is small, however, we have low power to detect differences and trends that are only marginally significant (fruits separate: $U = 5.0$, $n = 5$, $p = 0.027$; fruits mixed together: $U = 7.5$, $n = 5$, $p = 0.068$). In diurnal trials aimed at determining the fruit preference of birds, chiles and hackberry fruits were consumed in equal amounts when presented separately ($U = 58$, $n = 23$, $p = 0.645$), but when the two fruit types were mixed so that birds had to choose which if any fruit to consume, more wild chiles were consumed than were hackberry fruit ($U = 29$, $n = 11$, $p = 0.019$).

Discussion

Although wild chiles apparently depend on nurse plants for seedling survival, their distribution under nurse plants is highly nonrandom: they are much more abundant under shrub and tree species bearing fleshy fruits that ripen in summer and fall (Fig. 1; Table 2). A similar relationship has been documented in subtropical thornscrub in central Sonora, Mexico, where wild chiles were 10 times more abundant under fleshy-fruited shrub species than under other potential nurse plants (Nabhan 1987).

Our data suggest that the distribution of chiles under these nurse plants may be explained largely by the autumn roosting and foraging habitats of a particular guild of frugivorous and omnivorous birds that favor these trees and shrubs as perch sites and foraging locations, or favor their fruit as nutritional resources (Fig. 3). Our field observations indicate that Northern Mockingbirds and Curve-billed Thrashers disperse chile seeds to sites favorable for germination and survival, especially those beneath hackberry canopies. Although Cardinals follow a similar pattern of substrate use, they may be less effective at dispersing seeds due to their bill morphology and propensity to break fruits open while they eat (G.P.N. and J.J.T., unpublished data). Thus, results from this study suggest that fruiting nurse plants and chile-dispersing bird species are both involved in ecological interactions critical to the establishment of wild chiles in the few areas where they can survive.

Although the capacity of different nurse plants to temper damaging heat and freezing-cold temperatures was not correlated with their relative frequency of association with chiles, all nurse plants reduced summer ground temperatures more than 10° C (Table 1). This habitat amelioration may allow chiles to persist in an environment that is otherwise inhospitable. Also, hackberry canopies permitted less light penetration than did other species (Fig. 2), and the survival of transplanted

chile plants under hackberry canopies was also high, potentially reinforcing the pattern of greater chile abundance under hackberry canopies. Separating the effects of habitat amelioration from the strong effects of nonrandom dispersal by birds is not possible with the current data, however. After seeds are dispersed, rates of germination, seedling establishment, plant survival, and reproduction may all be influenced by features of the microsite, including light and heat penetration and reradiation (Turner et al. 1966; Nobel 1980, 1984; Valiente-Banũet & Escurra 1991; Callaway 1992), soil moisture-holding capacity and fertility (Patton 1978; Schmida & Whittaker 1981; Callaway et al. 1991: Chapin et al. 1994), and protection from herbivory (Atsatt & O'Dowd 1976; McAuliffe 1986). Each of these ecological factors may vary among potential nurse plants (Callaway 1995).

Our fruit-preference experiments confirm that certain birds readily consume wild chile fruits and may actively prefer them to hackberry fruits when the two are presented together. Additional support for avian acceptance of chiles comes from numerous lab experiments showing that birds are neurologically insensitive to capsaicin (Mason & Maruniak 1983; Szolcsányi et al. 1986; Mason et al. 1991; Norman et al. 1992) and from experiments demonstrating that the viability and germination rates of chile seeds are not affected by passage through the gut of some bird species (Norman et al. 1992). In contrast to avian reactions, our nocturnal preference trials and a large number of laboratory studies suggest that mammals are highly sensitive to capsaicin and will not ingest the chemical (Glinsukon et al. 1980; Kawada et al. 1986; Szolcsányi et al. 1986; Norman et al. 1992; Mason & Clark 1995). Both our field experiments and these laboratory tests are consistent with the hypothesis that birds are primarily responsible for the dispersal of chiles, and small mammals are not consuming the fruit or dispersing the seeds.

Although we have focused on the importance of birds to wild chile populations, the importance of the chile fruit to birds is less understood and is the focus of current studies. As rich sources of lipids, carotenoids, and other nutrients, chiles appear to be a valuable nutritional resource for several bird species, and some of these species appear important to ensuring the successful dispersal of chiles to sites under nurse plants. Thus, the importance of certain birds as dispersal agents and the fact that some of these same birds forage on the fruits of hackberry and other nurse plants could result in selection for similar fruiting traits between chiles and dominant nurse plants and may guide diffuse coevolution in fruit morphology (sensu Fox 1981).

Conclusions and Management Implications

The in situ conservation of wild chiles will be contingent on sustaining the ecological interactions between a well-defined guild of thorny, fleshy-fruited nurse plants and a loosely defined guild of frugivorous and omnivorous birds in the diverse geographic regions where wild chiles occur. The guild of birds dispersing chiles may change (Vasquez-Davila 1997) and nurse-plant associations may differ (Nabhan 1987), but, as the species dispersing chiles changes along geographical gradients, the suite of species serving as nurse plants may be predictable based on the foraging behavior of the local chile consumers. To fully conserve the interaction diversity among these organisms, we need a broader geographic perspective so that general ecological patterns are understood in terms of the particular configuration of dispersers and nurse plants at any locality (Thompson 1996).

In our study area, neither the species responsible for dispersal nor the favored nurse plants are uncommon. Nevertheless, the management of the nurse plants must be considered by Coronado National Forest resource managers if chiles are to persist. Our assessments of fire damage to nearby populations of nurse plants suggest that hackberry resprouting and growth is favored by periodic fire but that mesquite has much higher fire mortality and lower basal sprouting (Table 3). Fire suppression may therefore alter the perennial plant community by changing the ratio of fleshy fruited to nonfleshy fruited shrubs. This in turn may affect the avian consumers of chiles, as well as the number of sites that are locally available for chile dispersal and establishment. We

Table 3. Vegetation response to a 1994 fire measured in the Santa Rita Mountains less than 20 km from our primary study site.[a]

		Wash plants			Upland plants		
Species	*Common name*	*No. individuals*	*Dead (%)*	*New basil sprouts (%)*	*No. individuals*	*Dead (%)*	*New basil sprouts (%)*
Celtis pallida Torr.	hackberry	23	0	100	6	0	100
Lycium sp.[b]	wolfberry	24	0	100	5	0	100
Zizyphus obtusifolia Hook.	graythorn	21	14	86	2	0	50
Prosopis velutina Woot.	mesquite	25	40	52	25	20	80
Acacia greggii Gray	acacia	29	3	90	2	0	100
Mimosa dysocarpa Benth.	mimosa	0	—	—	30	0	100

[a] *All vegetation was examined along two transects, one along a wash and the other in the grassland above the wash, on 11 August 1994.*
[b] L. andersonii *and* L. berlandieri *were present.*

recommend that long-term studies be undertaken to determine the links between fire suppression, nurse-plant abundance, and the health and persistence of chile populations. With more direct information, fire may be used in a management context to increase the abundance of fruiting shrubs and to produce higher-quality habitat for wild chiles and their avian dispersal agents.

An additional concern in Mexico may be the over-harvesting of wild chiles by humans, an animal perhaps unique for its combination of high chile consumption and poor chile dispersal. Although intensive wild chile branch-breaking and fruit harvesting for the spice trade is occurring in a number of locations, we have not seen any studies of the sustainability of this practice or the potential damage to nurse plants or to the longevity and reproduction of chile plants. Such studies on wild jojoba (*Simmondsia chinensis*) harvesting have found damage due to trampling and breakage of surrounding vegetation and have reduced jojoba seedling survival beneath nurse plants (Turner 1978). We have seen no evidence of chile plant damage by traditional Hispanic-American harvesters at our primary study site during our 20 years of sporadic observations, but we regularly hear complaints from them that outsiders damage the plants. Although reserve designation for formal in situ protection of chile populations and other wild-crop relatives will be an important step in long-term preservation, the development of protocols and techniques for the sustainable harvesting of wild-crop relatives will also be necessary if we are to preserve both the heritage and the genetic diversity of our crops (Tuxill & Nabhan 1998).

We believe that the web of ecological interactions that shape the distribution of wild chiles illustrates the role of in situ conservation in preserving diffusely coevolved relationships as well as species; the former cannot be easily conserved within ex situ repositories. Studying these relationships in protected areas may hold some spicy surprises for economic botanists and crop breeders. For instance, a systematic examination of the range of animals deterred by capsaicinoids could guide integrated pest management schemes. Analyzing these ecological interactions in the field may also suggest to crop geneticists, agronomists, and agroecologists novel ways to breed or manage commercial chile crops (Nabhan et al. 1990). By safeguarding the opportunity to understand ecological conditions similar to those under which wild chiles evolved, crop scientists may be able to more reasonably guide future chile crop evolution.

Acknowledgments

Literature Cited

Alvino, A., M. Centrito, and F. DeLores. 1994. Photosynthesis response of sunlight and shade pepper (*Capsicum annuum*) leaves at different positions in the canopy under two water regimes. Australian Journal of Plant Physiology **21:**377–391.

Atsatt, P. R., and D. J. O'Dowd. 1976. Plant defense guilds. Science **193:**24–29.

Benz, B. F., L. R. Velazquez-Sanchez, and F. J. Santana-Michel. 1990. Ecology and ethnobotany of *Zea diplopenennis*: preliminary results. Maydica **35:**85–94.

Bib, B. 1990. After two weeks habituation to capsaicinized food, rats prefer this to plain food. Pharmacology, Biochemistry and Behavior **37:**649–653.

Brown, D. E. 1982. Biotic communities of the American Southwest—United States and Mexico. Desert Plants **4:**1–342.

Callaway, R. M. 1992. Effects of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. Ecology **73:**2118–2128.

Callaway, R. M. 1995. Positive interactions among plants. Botanical Review **61:**306–349.

Callaway, R. M., N. M. Nadkarni, and B. E. Mahall. 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in Central California. Ecology **72:**1484–1499.

Chapin, F. S., III, L. R. Waker, C. L. Fastie, and L. C. Sharman. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs **64:**149–175.

Food and Agriculture Organization of the United Nations. 1996. Draft global plan of action for the conservation and sustainable utilization of plant genetic resources for food and agriculture. Rome.

Fox, L. R. 1981. Defense and dynamics in plant-herbivore systems. American Zoology **21:**853–863.

Frankel, O. H., and M. E. Soulé. 1981. Conservation and evolution. Cambridge University Press, Cambridge, United Kingdom.

Gentry, H. S. 1942. Rio Mayo plants. No. 257. Carnegie Institution, Washington, D.C.

Glinsukon, T., V. Stitmunnathum, C. Toskulkao, T. Buranawuti, and V. Tangkrisanavinont. 1980. Acute toxicity of capsaicin in several animal species. Toxicon **18:**215–220.

Guzman-Mejia, R., and H. H. Iltis. 1991. Biosphere reserve established in Mexico to protect rare maize relative. Diversity **7:**82–84.

Hamilton, M. B. 1994. Ex situ conservation of wild plant species: time to reassess the genetic assumptions and implications. Conservation Biology **8:**39–49.

Harlan, J. 1967. A wild wheat harvest in Turkey. Archaeology **20:**197–201.

Ingram, G. B. 1990. Multi-gene-pool surveys in areas with rapid genetic erosion: an example from the Air Mountains, Northern Niger. Conservation Biology **4:**78–90.

Ingram, G. B., and J. T. Williams. 1984. *In situ* conservation of wild relatives of crops. Pages 163–179 in J. H. W. Holden and J. T. Williams, editors. Crop genetic resources: conservation and evaluation. Allen and Unwin, London.

Kawada, T., K. Hagihara, and K. Iwai. 1986. Effects of capsaicin on lipid metabolism in rats fed a high fat diet. Journal of Nutrition **116:** 1272-1278.

Lawton, J. H. 1993. Range population abundance and conservation. Trends in Ecology and Evolution **8:**409–413.

Lesica, P., and F. W. Allendorf. 1995. When are peripheral populations valuable for conservation? Conservation Biology **9:**753–760.

Mason, J. R., M. L. Avery, J. F. Glahn, D. L. Otis, R. E. Matteson, and C. O. Nelms. 1991. Evaluation of methyl anthranilate and starch-plated dimethyl anthranilate as bird repellant feed additives. Journal of Wildlife Management **55:**182–187.

Mason, J. R., and L. Clark. 1995. Mammalian irritants as chemical stimuli for birds: the importance of training. Auk **112:**511–514.

Mason, J. R., and J. A. Maruniak. 1983. Behavioral and physiological effects of capsaicin in Red-winged Blackbirds. Pharmacology, Biochemistry and Behavior **19:**857–862.

McAuliffe, J. R. 1986. Herbivore-limited establishment of a Sonoran Desert tree: *Cercidium microphyllum.* Ecology **67:**267–280.

McAuliffe, J. R. 1990. A rapid survey method for the estimation of density and cover in desert plant communities. Journal of Vegetation Science **1:**653–656.

Nabhan, G. P. 1987. Nurse-plant ecology of threatened plants in the U.S./Mexico borderlands. Pages 377–383 in T. S. Elias and J. Nelson, editors. Conservation and management of rare and endangered plants: proceedings of a California conference on the conservation and management of rare and endangered plants. California Native Plant Society, Sacramento.

Nabhan, G. P. 1990. Conservationists and Forest Service join forces to save wild chiles. Diversity **6:**47–48.

Nabhan, G. P. 1991. Genetic resources of the U.S./Mexican borderlands: wild relatives of crops, their uses and conservation. Pages 345–360 in P. Ganster and H. Walter, editors. Environmental hazards and bioresource management in the U.S./Mexico borderlands. University of California Los Angeles, Latin American Center Publications, Los Angeles.

Nabhan, G. P., and R. S. Felger. 1978. Teparies in southwestern North America. Economic Botany **32:**2–19.

Nabhan, G. P., M. Slater, and L. Yarger. 1990. New crops for small farmers in marginal lands? Wild chiles as a case study. Pages 17–23

in M. Altieri and S. Hecht, editors. Agroecology and small farm development. CRC Press, Boca Raton, Florida.

Nobel, P. S. 1980. Morphology, surface temperatures, and northern limits of columnar cacti in the Sonoran desert. Ecology **61:**1–7.

Nobel, P. S. 1984. Extreme temperatures and thermal tolerances for seedlings of desert succulents. Oecologia **62:**310–317.

Norman, D. M., J. R. Mason, and L. Clark. 1992. Capsaicin effects on consumption of food by Cedar Waxwings and House Finches. Wilson Bulletin **104:**549–551.

Patton, D. T. 1978. Productivity and production efficiency of an Upper Sonoran Desert ephemeral community. American Journal of Botany **65:**891–895.

Prescott-Allen, C., and R. Prescott-Allen. 1987. The first resource: wild species in North America. Yale University Press, New Haven, Connecticut.

Schmida, A., and R. H. Whittaker. 1981. Pattern and biological microsite effects in two shrub communities in southern California. Ecology **62:**234–251.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practices of statistics in biological research. W. H. Freeman, New York.

SPSS, Inc. 1996. SPSS. Version 7.0 Base system for windows users guide. Chicago.

Stalker, H. T. 1980. Utilization of wild species for crop improvement. Advances in Agronomy **33:**11–147.

Szolcsányi, J., H. Sann, and F. Pierau. 1986. Nociception in pigeons is not impaired by capsaicin. Pain **27:**247–260.

Thompson, J. N. 1996. Evolutionary ecology and the conservation of biodiversity. Trends in Ecology and Evolution **11:**300–304.

Turner, R. M., S. M. Alcorn, G. Olin, and J. A. Booth. 1966. The influence of shade, soil, and water on saguaro seedling establishment. Botanical Gazette **127:**95–102.

Turner, S. J. 1978. Environmental consequences of harvesting jojoba from natural stands. Pages 325–333 in D. M. Yermanos, editor. Proceedings of the third international conference on jojoba. University of California at Riverside, Riverside.

Tuxill, J., and G. P. Nabhan. 1998. Plants and Protected Areas. A World Wildlife Fund plants and people manual. Chapman-Hall, London.

Valiente-Banũet, A. and E. Escurra. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse-plant *Mimosa luisana* in the Tehuacan Valley, Mexico. Journal of Ecology **79:**961–971.

Vasquez-Davila, M. A. 1997. El amash y el pistoqué: un ejemplode la ethnoecologia de los chontates de Tabasco, México. Ethnoecologia **3:**59–69.

Zohary, D. 1983. Wild genetic resources of crops in Israel. Israeli Journal of Botany **32:**97–123.