Articles

Enhancing Quality of Desert Tortoise Habitat: Augmenting Native Forage and Cover Plants

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Abstract

Vegetation in habitat of the federally listed desert tortoise *Gopherus agassizii* in the Mojave and western Sonoran Desert is now partly or mostly dominated by nonnative annual plants. To improve forage quality and augment availability of perennial cover plants, we tested seeding (pelletized or bare seeding), watering, and fencing for increasing a native annual forage species (desert plantain *Plantago ovata*), a perennial forage species (desert globemallow *Sphaeralcea ambigua*), and two shrub species (cheesebush *Hymenoclea salsola* and winterfat *Krascheninnikovia lanata*) that provide cover in desert tortoise habitat of southern Nevada. Treatments were ineffective at establishing the perennial species, even though greenhouse assays confirmed that some bare and pelletized seeds were germinable. In contrast, pelletized seeding quadrupled the density of desert plantain compared with not seeding or seeding untreated seed by the end of the first year (autumn 2013). Fencing tripled density of desert plantain to 17 plants/m^2. Pelletized seeding plus fencing produced a desert plantain density of 39 plants/m^2, the highest average density among all treatment combinations. The positive effect of fencing persisted until at least the second year after treatment (autumn 2014). Augmenting native annual forage plants favored by desert tortoises is feasible.

Keywords: fencing; irrigation; pelletized seed; *Plantago ovata*; preferred plants; restoration

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Figure 1. A desert tortoise *Gopherus agassizii* foraging in a patch of the native annual forb desert plantain *Plantago ovata* in southern Nevada in 2004. Photo by R.J. Abella.

Introduction

When the desert tortoise *Gopherus agassizii* in the Mojave and western Sonoran Desert was listed in 1990 as threatened under the US Endangered Species Act (ESA 1973, as amended), numerous threats were perceived to have reduced populations and impeded recovery (U.S. Fish and Wildlife Service 1990). One threat was habitat degradation because of reduced native vegetation. A Revised Recovery Plan emphasized vegetation enhancement as a priority for reversing declines in desert tortoise habitat quality (U.S. Fish and Wildlife Service 2011). Specifically, the plan called for reducing nonnative plants, while increasing native annual forage plants and perennial cover plants (U.S. Fish and Wildlife Service 2011).

Native vegetation is a critical component of quality desert tortoise habitat (Jennings and Berry 2015; Figure 1). Within a southwestern Mojave Desert site, 97% of desert tortoise burrows were below native shrubs (Baxter 1988). Shrubs also form a "fertile island" spatial pattern of concentrated soil nutrients and ameliorated microclimate, important for recruitment of annual forage plants (Abella and Smith 2013; Drake et al. 2015). Certain annual and herbaceous perennial plants are forage favored by desert tortoises and supply essential nutrients and protein (Oftedal et al. 2002; Esque et al. 2014; Jennings and Berry 2015). For example, Nagy et al. (1997) reported that during their first 2 y, juvenile desert tortoises required 175 g (dry matter) of quality forage while growing from a body mass of 34 to 55 g. Years with minimal plant production have corresponded with major die-offs of desert tortoises (Longshore et al. 2003; Lovich et al. 2014) and low fecundity (Turner et al. 1984; Henen 1997).

Forage composition has changed during recent generations of desert tortoises, even within the 50-y lifetimes of individual tortoises (Beatley 1969; Brooks and Berry 2006; Averill-Murray et al. 2012). Nonnative species now dominate the annual plant flora (Jennings and Berry 2015). Desert tortoises avoid eating at least one widespread invader—the annual grass *Schismus* spp. At a central Mojave Desert site, for example, desert tortoises ate only 42 (0.02%) of the 239,000 *Schismus* plants they encountered during the spring foraging season (Oftedal et al. 2002). Conversely, desert tortoises ate 120 (35%) of 346 plants they encountered of the native annual forb desert plantain *Plantago ovata*. This made the native 3 times as important in tortoise diets, even though it was 700 times less abundant on the landscape. Several native forbs, such as desert plantain, exhibit high nutritional quality compared with nonnative annual grasses (Nagy et al. 1998; Oftedal et al. 2002; Hazard et al. 2009).

Despite the potential of vegetation enhancement in assisting desert tortoise recovery, the Revised Recovery Plan notes that vegetation enhancement is virtually unstudied for its ability to increase desert tortoise populations (U.S. Fish and Wildlife Service 2011). The science of vegetation enhancement and restoration in deserts has developed with diverse goals, such as reducing fugitive dust to improve air quality, and has not directly focused on the desert tortoise (e.g., Winkel et al. 1995; Abella and Newton 2009; DeFalco et al. 2012). Meanwhile, desert tortoise conservation efforts have rarely included attempts to actively restore or augment native vegetation for improving habitat quality. Active revegetation (e.g., seeding or planting) is distinguished from indirect approaches (e.g., reducing grazing through fencing) for increasing native vegetation, because unassisted re-establishment of desert plant composition can require decades to centuries after disturbance (Abella 2010).

A first step toward evaluating whether enhancing vegetation contributes to increasing desert tortoise populations is developing reliable techniques for establishing native plants important to tortoises. This task is not trivial. The same factors of extreme temperatures, low and variable rainfall, seed predation, and herbivory that limit natural productivity of deserts complicate active revegetation (Bainbridge 2007). Treatments, such as irrigation and fencing to deter herbivory, have potential to enhance seeding success (Brooks 2000; Suazo et al. 2013; Scoles-Sciulla et al. 2014). Pelletizing seeds, by covering them with a protective coating, may also increase plant establishment (Taylor and Harman 1990). However, pelletizing seed has sometimes reduced germination and emergence of seedlings (Jones et al. 2014).

To increase understanding of potential for vegetation enhancement in desert tortoise recovery efforts, we conducted a multifactor field experiment aimed at augmenting native forage and cover plants. We hypothesized that seeding, fencing, and watering would increase native plants relative to no treatment. We further hypothesized that pelletizing seed would enhance plant establishment.

Methods

Study area

We conducted the experiment within a 10,600-ha site, managed by the Bureau of Land Management (Southern Nevada District), where release of translocated desert tortoises is authorized. The site is in Clark County, 35 km south of Las Vegas, and 10 km southwest of Jean, Nevada. The area is in the eastern Mojave Desert, which is a hot desert that receives most of its rainfall in winter. At an elevation of 800 m, our experimental site occupied a valley between low mountain ranges and typifies the creosote bush–white bursage *Larrea tridentata–Ambrosia dumosa* valleys with high desert tortoise habitat potential (Nussear et al. 2009). Average density of mature perennial plants (>10 cm tall) included 1,700/ha for creosote bush; 5,900/ha for white bursage; and scattered occurrences of cheesebush *Hymenoclea salsola,* winterfat *Krascheninnikovia lanata*, desert globemallow *Sphaeralcea ambigua*, littleleaf ratany *Krameria erecta,* and big galleta grass *Pleuraphis rigida*. Major annual plants included the nonnative grass Arabian schismus *Schismus arabicus* and the native forbs desert plantain, shaggy fruit pepperweed *Lepidium lasiocarpum,* pebble pincushion *Chaenactis carphoclinia,* devil's spineflower *Chorizanthe rigida,* and broadfruit combseed *Pectocarya platycarpa*. Soils had parent material derived from limestone, dolomite, and sandstone and are classified as Haplocalcids and Petrocalcids within the Weiser–Oldspan–Wechech association (Lato 2006). A weather station, 5 km away, reported an average of 11 cm of rainfall/y during the 2008 through 2013 available record (Clark County 2014).

The study area has a long history of grazing by livestock and feral animals, perhaps dating back to the 1500s when Spanish expeditions passed through (Paher 1971). Commercial livestock operations and expansion of feral horse *Equus caballus* and burro *E. asinus* populations followed, peaking in the late 1800s and early 1900s for livestock and through the mid-1900s for horses and burros (Lovich and Bainbridge 1999; Abella 2008). Commercial livestock grazing does not presently occur in the study area, but some feral horses and burros inhabit the area. Effects of potentially centuries of grazing and trampling of plant communities by livestock and feral animals are poorly understood. We do know that on contemporary landscapes, livestock and feral animals eat many of the same plant species favored by desert tortoises. Some of these plants include the native annual forbs desert plantain and desert dandelion *Malacothrix glabrata* and herbaceous perennials such as desert globemallow (e.g., Avery and Neibergs 1997; Abella 2008; Jennings and Berry 2015). Our study was performed to enhance present vegetation in ways anticipated as favorable to desert tortoises, through increasing favored forage plants and perennial plant cover above levels in existing vegetation.

Field experimental design and treatments

We selected our experimental site (14 ha) because it was bisected by a little-used dirt road (~1 vehicle/d) that enabled access for implementing treatments, was typical of valley habitat in the translocation area, and was near a weather station (Figure 2). We located sampling units ≥5 m from the road to reduce potential roadside influences (Craig et al. 2010). The experimental design was a split-split plot, including the whole-plot factor of watering (present or absent), the subplot factor of seeding (none, bare seed, or pelletized seed), and the sub-subplot factor of fencing (present or absent). Each of the 12 treatment combinations was randomly assigned and replicated 5 times, totaling 60 sampling units, arranged according to Figure 2.

At the finest level of the experimental design (sub-subplot level), we constructed 30 fenced areas (each 10 m × 10 m) nested within the center of seeded and watered areas. Each fenced area had a paired unfenced area of equivalent size 4 m away. The wire fencing was 1 m tall, affixed to metal poles at the four corners, bent parallel to the ground at the base to deter burrowing animals, and had openings of 3 cm in the wire (Figure 2). We constructed the fence to deter large- and medium-sized herbivores (e.g., feral burros, jackrabbits *Lepus californicus*). No evidence existed of breaches in fences during the experiment.

At the subplot level of the experimental design, seeding was conducted in areas of 24 m × 106 m, overlapping the fenced and unfenced areas (Figure 2). Either bare or pelletized seed of four native species was broadcast by hand on the unmanipulated soil surface in January 2013. The seeded species included three native perennials, designed to augment cover (the shrubs cheesebush and winterfat) and forage (the herbaceous forb desert globemallow). We seeded the species at

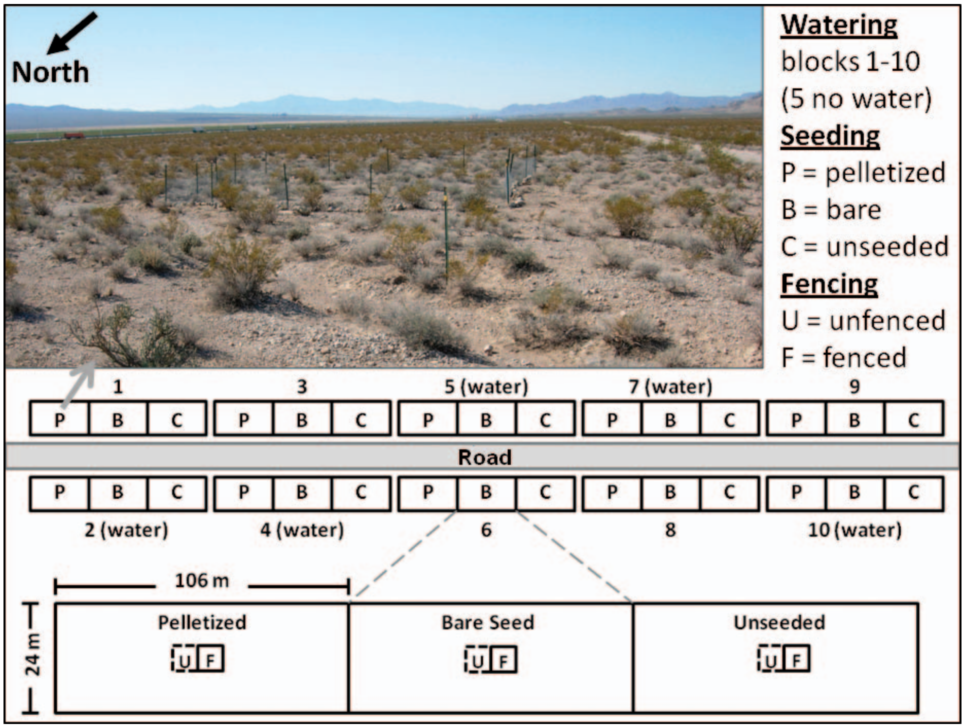

Figure 2. Experimental layout for testing forage augmentation treatments for the desert tortoise *Gopherus agassizii* in southern Nevada during 2013 and 2014. The diagram depicts treatment arrangement within the split-split plot experimental design. Watering was applied at the whole plot, seeding at the subplot, and fencing at the sub-subplot level. Five of the 10 blocks (serving as whole plots) received watering, as shown in the diagram. The photo shows a paired unfenced (foreground) and fenced plot, with the dirt road bisecting the site shown on the right. Interstate 15 is to the east of the site, and is on the top left of the photo just below the north arrow (photo by S.R. Abella, September 2014).

approximately the following densities: 5,000 seeds/m^2 for cheesebush, 1,700 seeds/m^2 for winterfat, and 13,000 seeds/m^2 for desert globemallow. The annual forage species—desert plantain—was seeded at 5,300 seeds/m^2. These seeding densities reflected the maximum density feasible from the seed we had available for each species. The seed lot was obtained by the Bureau of Land Management from an eastern Mojave Desert seed zone of Clark and southern Nye County, Nevada, and eastern San Bernardino County, California. For the pelletized seed treatment, seed was coated using Gro-Coat® (Seed Dynamics, Inc., Salinas, CA). The Gro-Coat® substance included a coating of mineral and organic material and binding (e.g., clay, starches, sugars) to hold the coating together (Figure 3). We assayed germinability of the seed lot, with methods and results presented in Figure S1, *Supplemental Material*. At least 10% of seed among species and seed types, and up to 98%, was readily germinable in a greenhouse.

At the whole-plot level of the experiment, we applied a watering treatment beginning the day after seeding (January 31, 2013) and on February 28, March 15 and 28, and April 12 and 24, 2013. We performed watering using a sprayer affixed to a tanker truck, filled with Las Vegas municipal water. Water was sprayed evenly across the five blocks assigned the watering treatment (Figure 2). On each of the first five watering dates, the treatment delivered 20,000 L of water, or 0.5 mm of water over the soil surface. With the intention of maintaining forage as green as possible, the last event (April 24, 2013) delivered 2.5 mm of water. In sum, the watering treatment delivered 0.5 cm of water, doubling the amount of natural rainfall (0.4 cm) that fell during February through April 2013 (Clark County 2014).

Data collection

Within a total of 60, 8 m × 8 m sampling units (centrally located in fenced and paired unfenced areas) corresponding to each of the 5 replicates of the 12 treatment combinations, we measured the complete vascular plant community including seeded species during the first year after treatment in 2013. We performed measurements during the spring growing season (April, 3 mo after seeding) and during autumn (November, 10 mo after seeding). In entire 64-m^2 sampling units, we visually categorized cover (to the nearest 1%) by species of all vascular plants. Cover was defined as the area of ground covered by live foliage and stems rooted in plots. A ground coverage of 0.5 m^2 in the 64-m^2 plots corresponded with 1% cover. We further counted the number of perennial plants (including seedlings). To estimate densities of annual species, we counted annual plants within 5, 1 m × 1 m quadrats evenly spaced within each sampling unit. During all measurements, we included both live and dead annual plants because desert tortoises eat senesced plants (Esque et al. 2014). Nomenclature and classification of growth forms (e.g., shrub or forb) follow NRCS (2015).

Figure 3. Pelletized seed immediately after seeding in January 2013 in desert tortoise *Gopherus agassizii* habitat in southern Nevada. Photo by E.C. Engel.

The first-year, short-term results after treatments were of greatest interest for testing reliability of augmenting forage in the context of a desert tortoise translocation occurring that year. But from a standpoint of sustainability of the one-time seeding and for perennial plant establishment, longer term results were of interest. Thus, we revisited plots 20 mo after seeding on September 24, 2014. Annual plant cover was sparse then, so we focused on categorizing cover (in 0.01% increments) of the seeded desert plantain in the 5 quadrats/sampling unit. Additionally, we counted perennial plant seedlings in sampling units.

Data analysis

For the 2013 first-year spring and autumn sampling, we analyzed the response variables of desert plantain density, native annual plant density (excluding desert plantain), and native annual species richness/m^2 (which included desert plantain, because the species did occur naturally at the site). Density of desert plantain ranged widely between 0 and 344 plants/m^2, so we conducted analyses using ranked data to improve normality and equalize variance. We analyzed nonnative Arabian schismus density only in spring and seedlings of the native perennial desert globemallow only in autumn, because visible plant stalks were sparse or absent at other times. Using the 2014 inventory, we analyzed desert plantain cover and frequency (out of 5, 1-m^2 quadrats/plot). Each of the response variables (Table S1, *Supplemental Material*) was analyzed according to the split-split plot experimental design including three main effects (watering, seeding, and fencing), all interactions therein, and block defined as a random variable in a mixed-model analysis of variance. For terms significant at $P < 0.05$, we separated least-squares means through Tukey adjustments. We performed analyses using PROC MIXED in SAS software (SAS Institute 2009).

Results

Seeded species

Seedling establishment of the three seeded perennial species was minimal during the experiment. We did not observe winterfat during any inventory. We first observed live seedlings of cheesebush and desert globemallow during the autumn 2013 inventory (10 mo after treatments). At that time, cheesebush seedlings inhabited 3 of 20 (15%) pelletized-seeded plots and 5 of 20 (20%) bare-seeded plots. The species never had > 5 seedlings/m^2 and was not analyzed statistically. Seedlings of desert globemallow were more common; they inhabited 13 of 20 pelletized (65%) and 9 of 20 (45%) bare-seeded plots in autumn 2013. In the statistical analysis of autumn 2013 globemallow seedling densities, seeding was the only significant term because only seeded plots contained seedlings (Table 1; Figure 4, bottom right). Both cheesebush and globemallow were then absent in the autumn 2014 inventory (20 mo after treatments).

The seeded native annual forage species, desert plantain, displayed greater establishment than did the perennials. In spring 2013 (3 mo posttreatment), pelletized seeding resulted in greater density of desert plantain than did bare seeding (Table 1; Figure 4, top left). The only interaction in the experiment for any 2013

Table 1. Summary of analysis of variance results for vegetation response variables during three inventories after implementation of the experimental treatments of watering, seeding, and fencing in desert tortoise *Gopherus agassizii* habitat in southern Nevada. Treatments included (1) presence or absence of watering; (2) no seeding of native plants, seeding untreated seeds, or seeding pelletized seed; and (3) presence or absence of fencing. Bold *P*-values are < 0.05 and declared significant statistically.

Response variables[a]	Experimental treatments						
	Water (W)	**Seeding (S)**	**Fencing (F)**	**W × S**	**W × F**	**S × F**	**W × S × F**
Spring 2013	*P*-values						
Plantago ovata/m^2	0.75	**0.04**	0.12	0.92	0.40	0.51	0.74
Native annuals/m^2	0.26	0.86	0.98	0.85	0.84	0.99	0.46
Native richness/m^2	**<0.01**	0.63	1.00	0.94	0.16	0.15	0.42
Schismus arabicus/m^2	0.52	0.15	0.33	0.35	0.78	0.67	0.85
Autumn 2013							
Plantago ovata/m^2	0.79	**<0.01**	**<0.01**	0.86	0.31	**0.04**	0.42
Native annuals/m^2	0.45	**<0.01**	**0.01**	0.41	0.47	0.87	0.40
Native richness/m^2	0.85	**<0.01**	**0.02**	0.13	0.31	0.46	0.51
Sphaeralcea ambigua/m^2	0.87	**0.02**	0.95	0.91	0.46	0.49	0.64
Autumn 2014							
Plantago ovata cover	0.89	0.20	**0.01**	0.87	0.51	0.36	0.79
Plantago ovata frequency	0.85	0.07	**0.03**	0.41	**0.03**	0.38	0.13

[a] Native annual plant density does not include the seeded species *Plantago ovata,* but native annual richness does include *Plantago ovata* because the species was part of the resident vegetation at the site before seeding and on nonseeded plots.

variable occurred for desert plantain in autumn 2013 (10 mo after treatments). Seeding with fencing produced the highest density of 39 ± 18 plants/m^2 (mean ± standard error of mean, $n = 10$), compared with all other treatment combinations averaging 6 ± 1 plants/m^2 ($n = 50$). Within the factor of seeding, pelletized seeding resulted in significantly greater desert plantain density than bare or no seeding (Figure 4, bottom left). Fencing also increased desert plantain, tripling its density (Figure 5, top).

In the autumn 2014 inventory (20 mo after treatments), the positive effect of fencing on desert plantain persisted (Table 1; Figure 6, top). For desert plantain frequency, a fencing × irrigation interaction occurred, where unfenced, nonwatered plots had lower frequency (27%) than did other treatment combinations (43–49%).

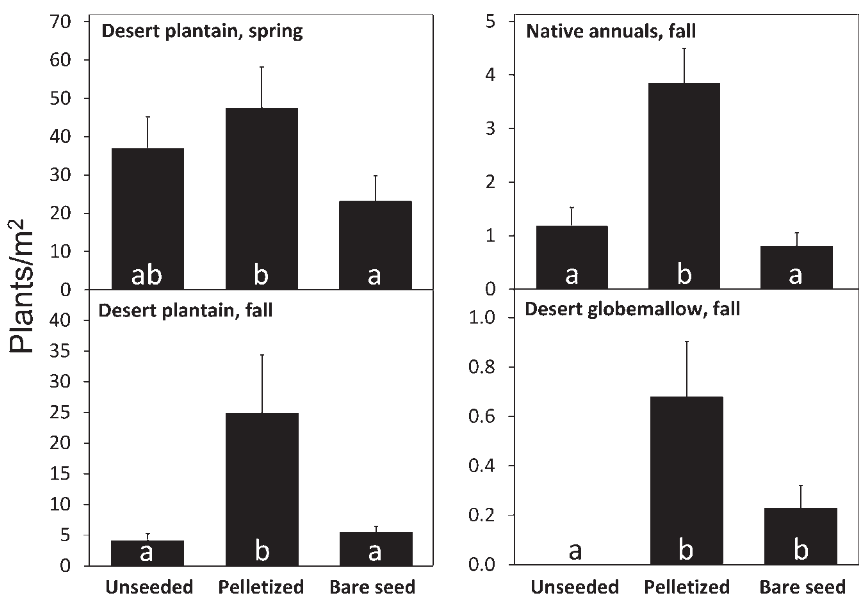

Figure 4. Average density of the native annual desert plantain *Plantago ovata* in spring and autumn, total native annual plants other than desert plantain, and the perennial desert globemallow *Sphaeralcea ambigua* across seeding treatments during 2013 in desert tortoise *Gopherus agassizii* habitat in southern Nevada. The spring inventory was 3 mo after seeding and the autumn inventory was 10 mo after seeding. Means without shared letters differ at $P < 0.05$. Error bars are one standard error of the means.

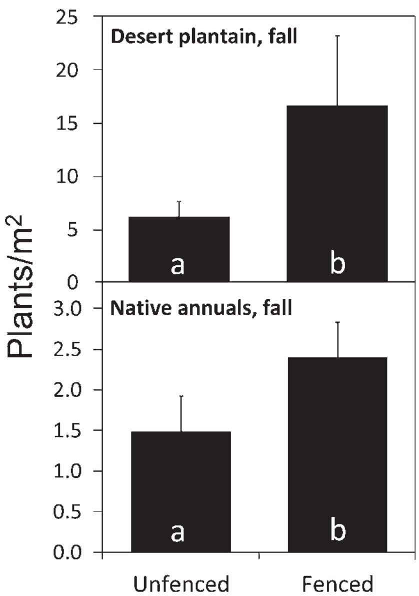

Figure 5. Average density of the native annual desert plantain *Plantago ovata* and total native annual plants other than desert plantain across a fencing treatment, in desert tortoise *Gopherus agassizii* habitat in southern Nevada. These data were collected in November 2013, 10 mo after treatments. Means without shared letters differ at $P < 0.05$. Error bars are one standard error of the means.

With triple the cover and almost double the frequency on pelletized-, compared with unseeded or bare-seeded plots, the positive effect of pelletizing also tended to persist but was not statistically significant (Figure 6, bottom).

Nonseeded species

Treatments had no statistical effect on nonnative annual plants. The nonnative grass Arabian schismus was not influenced by any treatment (Table 1). The nonnative annual red brome *Bromus rubens* infested only 6 of 60 (10%) plots in spring 2013 (3 mo after treatments) and displayed no trend with treatment. For example, red brome infested an identical 2 plots apiece (out of 20 plots) for each of the three seeding treatments. The nonnative forb redstem filaree *Erodium cicutarium* occurred in 10 of 60 (17%) plots in spring 2013 and displayed no pattern with treatments.

Treatments had neutral or positive effects on non-seeded, native annuals (Table 1). In spring 2013 (3 mo after treatments), native richness averaged 2.9 $\pm$ 0.2 species/m^2 in watered plots and 1.7 $\pm$ 0.1 species/m^2 in nonwatered plots. In autumn 2013 (10 mo after treatment), density of nonseeded, native annual plants was highest in plots that had received pelletized seed of the four focal species (Figure 4, top right) and that were fenced (Figure 5, bottom).

Discussion

Enhancing annual plant forage

Native annual forage plants for the desert tortoise can be augmented, at least for a period of a few years. A next step is evaluating whether augmenting native forage enhances health of desert tortoises and population sizes. Owing to potential interactions of forage with other factors affecting the desert tortoise (Averill-Murray et al. 2012), this question is difficult to answer but existing research provides some insight. Short-term experimental feeding trials have found that forage quality affects desert tortoise health. Hazard et al. (2009, 2010) reported that captive juvenile tortoises (0.5–1.5 y old) lost weight when fed only senesced grasses (low in nitrogen and digestibility), but gained weight when fed the native forb desert dandelion. Similarly, captive adult desert tortoises gained weight when fed a protein- and nutrient-rich native perennial forb (desert globemallow), but lost weight on a diet of *Schismus* spp. (Barboza 1995).

Field studies that have correlated plant abundance with desert tortoise populations over time also suggest that availability of quality forage may be a limiting factor.

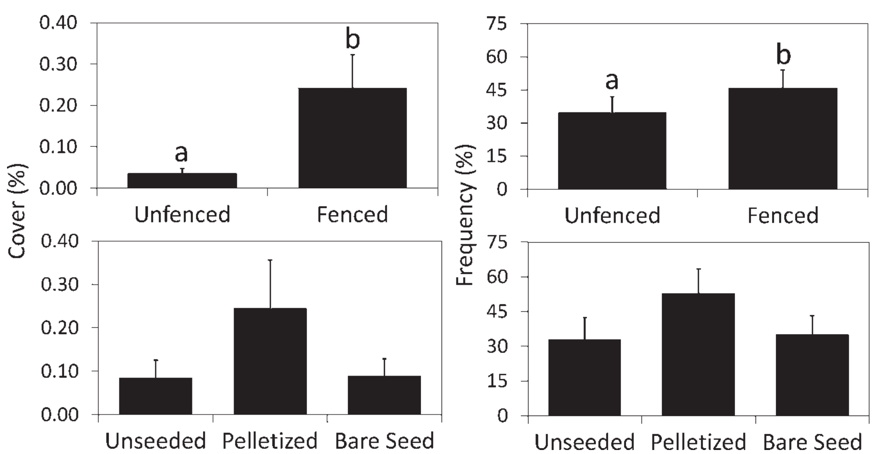

Figure 6. Average cover and frequency of the native annual desert plantain *Plantago ovata* in September 2014, 20 mo after fencing and seeding treatments in desert tortoise *Gopherus agassizii* habitat in southern Nevada. Frequency is the average percentage of 1 $\times$ 1 m quadrats in which desert plantain occurred, out of 5 quadrats/plot, and averaged among plots within treatments. Means without shared letters for the fencing treatment differ at $P < 0.05$. For descriptive purposes, means are shown for the seeding treatment that had P-values of 0.20 for cover and 0.07 for frequency. Error bars are one standard error of the means.

Over 40 y (1964–2003) in the northern Mojave Desert, average growth of individual desert tortoises in 9-ha plots was positively correlated with annual plant production per year (Medica et al. 2012). In Joshua Tree National Park, desert tortoise survival between 1991 and 2011 was positively correlated with winter rainfall (Lovich et al. 2014). Winter rainfall, in turn, related to abundance of native annual plants and herbaceous perennials (Miriti et al. 2007; Rao and Allen 2010). From 1994 to 2001 near Cottonwood Cove in Lake Mead National Recreation Area (eastern Mojave Desert), 7-y survival probability for desert tortoises was 0.27, with mortality events corresponding with years producing few or no annual plants (Longshore et al. 2003).

Augmenting forage through active management may be most beneficial in dry years and on sites containing few forage plants. Despite our experiment occurring during a dry period, the pelletized seed and fencing treatments enhanced establishment of desert plantain. Encompassing our seeding (January 2013) and up to the first inventory (April 2013), only 21% of the average precipitation (which was 5.6 cm) fell from November 2012 through March 2013 (Clark County 2014). The next hydrological year (November 2013 through March 2014), preceding our final inventory in autumn 2014, received only 4 cm of rainfall (70% of average). July plus August monsoonal rainfall in 2013 (5.4 cm, 134% of average) and 2014 (8.0 cm, 198%) both exceeded average. The high summer rainfall resulted in the 20-mo period of the experiment (January 2013 to September 2014) receiving 18.5 cm of precipitation, near average (103% of the 17.9-cm average). Summer rainfall, however, does not necessarily affect winter annuals such as desert plantain (Smith et al. 2014). These observations raise the question: could seeding have been more effective in wetter years, but be less useful to desert tortoises because moister conditions would already have stimulated naturally occurring forage? On the other hand, the most rainfall-responsive plants are now the nonpreferred, nonnative grasses (Beatley 1974; Jennings 2002; Oftedal et al. 2002). This likely makes providing native plants with advantages (such as pelletizing seed for desert plantain) important to enhance seedling establishment and replenishment of seed banks across years.

The watering treatment had minimal influence, with its only significant main effect being increased species richness of native annuals. Beatley (1974) described autumn and winter rainfall scenarios that could "trigger" germination of winter annual species in the Mojave Desert, with individual rain events exceeding 1.5 to 2.5 cm being key. The total amount of water ($\sim$1 cm) falling on watered plots during the 3 mo after seeding (February through April 2013) resulted from approximately equal proportions delivered by our watering and natural rainfall. These receipts of water were spread out in seven watering or natural rainfall events, so no single event delivered the minimum amount that Beatley (1974) suggested was required for triggering germination. Transporting water to our field site was difficult, and further research is needed to evaluate other irrigation regimes. For example, other approaches could include a single watering event that delivers $\geq$1.5 cm of water, or strategically augmenting natural rainfall events otherwise yielding $<$ 1.5 cm of water. Furthermore, seeding earlier in autumn (November–December), rather than late January, may expand the time window that seeds can experience germination-triggering rainfall, though longer exposure of seeds to granivory could be a tradeoff. Watering across large or inaccessible areas may not be practical, but effective watering regimes may still be suitable for stimulating germination in patches across the landscape.

Perennial plants

Cover sites below shrubs are key habitat features assisting desert tortoises with thermoregulation and protection from predators (Berry and Turner 1986). Our treatments failed to increase density of the two seeded shrub species. Establishing shrubs through seeding has also been difficult in other Mojave Desert studies (e.g., Ott et al. 2011). Management resources may be most effectively used through research studies determining specifically where availability of cover sites most limits desert tortoise populations. It could be hypothesized that cover sites are not limiting in mature desert shrubland, but they are limiting on disturbed sites containing few shrubs. Berry et al. (2013) provided support for this hypothesis, because disturbed areas with few shrubs in the northwestern Mojave Desert contained few desert tortoises. Similarly, desert tortoises continued using burned habitat (without shrubs) for foraging, but tortoises retreated to unburned areas to seek cover below shrubs (Drake et al. 2015).

In addition to providing cover, perennial plants may influence quality of tortoise habitat in several other ways. Perennial forbs, such as desert globemallow, can supply forage that may be critical to sustaining desert tortoises during dry years with few annual plants (Hansen et al. 1976; Jennings and Berry 2015). Different perennial species also "cultivate" different annual plant communities below their canopies, with this variety of forage important to diversifying desert tortoise nutrition (Abella and Smith 2013; Jennings and Berry 2015).

When seeking to augment or diversify perennial plant composition, planting seedlings has been more reliable than seeding in the Mojave Desert (Scoles-Sciulla et al. 2014). Use of good planting stock, combined with treatments such as protection from herbivory, has resulted in $>$ 50% survival for a variety of shrub species (Abella and Newton 2009). Although outplanting nursery-grown seedlings might be criticized for being practical only in small areas, this technique is more cost-effective and vegetates more area than seeding when no seeded species become established, such as in our experiment.

Another option warranting consideration is seeking to increase survival and growth of naturally established seedlings or mature individuals. For example, fenced plots at the Desert Tortoise Research Natural Area in the western Mojave Desert had twice the perennial plant cover after 15 y compared with nearby unfenced areas subject to livestock grazing and off-road vehicle use

(Brooks 1999). Our fencing treatment over time may have a similar influence on existing creosote bush and white bursage shrubs. In addition, covering natural, small seedlings with temporary shelters could be more cost-effective than seeding (Bainbridge 2007).

Alternative vegetation management strategies

Captive desert tortoises have subsisted on artificial diets such as commercially available kale *Brassica oleracea* (Hazard et al. 2009). Could chronically laying out such agricultural forage plants (perhaps especially in dry years) be cheaper and more effective than trying to manage natural forage plants? Disadvantages of the "agricultural" approach could include the following: the diversity of forage species potentially important for balanced desert tortoise diets is missing (Chaffee and Berry 2006), fire hazard from nonnative plants is unabated (Steers and Allen 2010), interactions are uncertain between tortoise foraging and common ravens *Corvus corax* and other predators of tortoises (Berry et al. 2013), and there is little overall benefit to the habitat or other species (Lovich and Bainbridge 1999). Providing agricultural plants for strategic augmentation of desert tortoise forage is likely to have disadvantages, but it may warrant comparison with other potential treatments in a comprehensive ecological framework.

Reducing nonnative grasses is another possible treatment for enhancing forage quality. When nonnative grasses are reduced, native annual forbs can respond positively (Brooks 2000; Steers and Allen 2010). On a burned site in the western Mojave Desert, Steers and Allen (2010) found that carefully timed applications of the herbicide Fusilade reduced nonnative grasses and the nonnative forb redstem filaree and at least doubled native annual plant abundance. Although redstem filaree appears to provide better forage than the nonnative grasses, a concern with this species is that it readily invades after disturbance and forms monocultures (Abella 2010). Effects of herbicide on the desert tortoise are unclear, but herbicide applications timed early in winter—to exploit the accelerated phenology of nonnative compared with native species (Marushia et al. 2010)—would generally be occurring when adult tortoises are inactive (Esque et al. 2014). However, juveniles can be active during this period, and adults can emerge to hydrate after rain events at any time of the year (Esque et al. 2014). These observations highlight a need to evaluate several candidate techniques for favorably changing plant community attributes within a framework including effects on health of tortoises and other species.

Conclusion

A conservative habitat-management strategy for the desert tortoise would likely include maintaining perennial plants as cover and promoting conditions for a diverse native annual plant community (Jennings 2002; Berry et al. 2013; Esque et al. 2014). Given a long history of livestock grazing, use of habitat by feral burros and horses, and invasion of competitive nonnative plants, it is unclear how anthropogenic activities have altered native annual plant composition in recent centuries. Desert plantain, for example, comprised the greatest percentage (10%) of any plant species in feral burro diets among Mojave Desert studies (Abella 2008). Although desert plantain is a favorite food plant of both feral burros and the desert tortoise, the possibility cannot be dismissed that species even more favored have already declined. Our experiment showed that seed pelleting and fencing can augment abundance of desert plantain, and potentially other annual forage plants. A next step is evaluating how desert tortoises respond to improvements in forage quality at scales of patches within home ranges and landscapes.

Supplemental Material

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Figure S1. Emergence through time of native plant species sown as bare or pelletized seed and watered daily or weekly in a greenhouse during 2013.

Found at DOI: http://dx.doi.org/10.3996/022015-JFWM-013.S1 (48 KB PDF).

Table S1. Data used to analyze effects of watering, seeding, and fencing on seeded and nonseeded forage and cover species for the desert tortoise *Gopherus agassizii*.

Found at DOI: http://dx.doi.org/10.3996/022015-JFWM-013.S2 (31 KB XLS).

Reference S1. Baxter RJ. 1988. Spatial distribution of desert tortoises (*Gopherus agassizii*) at Twentynine Palms, California: implications for relocations. Pages 180–189 in Szaro RC, Severson KE, Patton DR, technical coordinators. Management of amphibians, reptiles, and small mammals in North America: proceedings of the symposium. Fort Collins, Colorado: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. General Technical Report RM-166.

Found at DOI: http://dx.doi.org/10.3996/022015-JFWM-013.S3; also available at http://www.fs.fed.us/rm/pubs_rm/rm_gtr166.html (1404 KB PDF).

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Reference S5. U.S. Fish and Wildlife Service. 2011. Revised recovery plan for the Mojave population of the desert tortoise (*Gopherus agassizii*). Sacramento, California: U.S. Fish and Wildlife Service.

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