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Restoration of Native Plants Is Reduced by Rodent-Caused Soil Disturbance and Seed Removal☆,☆☆

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ABSTRACT

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Granivory and soil disturbance are two modes by which burrowing rodents may limit the success of native plant restoration in rangelands. This guild of animals has prolific effects on plant community composition and structure, yet surprisingly little research has quantified the impact of rodents on plant restoration efforts. In this study, we examined the effects of seed removal and soil disturbance by the giant kangaroo rat *(Dipodomys ingens)* on native plant restoration in a California rangeland. Using experimental exclosures and stratifying restoration plots on and off rodent-disturbed soil, we assessed the individual and combined effects of seed removal and soil disturbance on seedling establishment of four native plant species. Across all species, biotic soil disturbance by kangaroo rats reduced seedling establishment by 19.5% (range = 1–43%), whereas seed removal reduced seedling establishment by only 6.7% (range = 4–12%). Rates of seed removal across species weakly paralleled kangaroo rat dietary preferences. These results indicate the indirect effects of burrowing rodents such as kangaroo rats on native seedling establishment via changes in soil properties may rival or exceed the direct effects of seed removal.

Introduction

Native grasslands are among the most critically endangered ecosystems in the United States (Noss et al., 1995), making native grassland restoration a priority for many conservation land managers. However, grassland restoration success has been limited by a lack of knowledge about the factors that affect restoration outcomes and how these factors can be manipulated to improve success (Aronson, 2013). Rodents are common in grassland ecosystems, and disturbance by rodent populations may therefore be an important factor affecting restoration success.

As burrowers, herbivores, and granivores, small mammals can have considerable effects on plant community composition and structure (e.g., Brown and Heske, 1990; Schiffman, 1994; Brock and Kelt, 2004). In extreme cases, rodents can remove up to 90% of local annual seed production (Chew and Chew, 1970; Soholt, 1973), clear vegetation from up to 32% of the landscape (Schiffman, 1994), and turn over the entire soil surface every 3 to 15 years (Hobbs and Mooney, 1995). Researchers and restoration practitioners have acknowledged that rodents may strongly impact restoration projects (e.g., Longland and Bateman, 1998; Watts, 2010; Longland and Ostoja, 2013). However, relatively few studies have examined the mechanisms by which rodents affect plant restoration, and these studies have focused primarily on the effects of granivory (e.g., Hoffmann et al., 1995; Orrock et al., 2009; Orrock and Witter, 2010). The effects of other rodent interactions (e.g., biotic soil disturbance) on restoration success remain largely unknown.

Rodent-disturbed microsites often have soil characteristics that differ markedly from less disturbed areas just meters away (Grinnell, 1923). As central place foragers, burrowing rodents tend to concentrate nutrients and organic matter from larger areas into smaller areas (Mun and Whitford, 1990). Rodents can also transport material vertically through the soil profile surface (Whitford and Kay, 1999). Collectively, these actions can cause significant changes in a variety of soil properties including bulk density, soil temperature, infiltration, soil moisture, pH, and soil nutrient levels (Whitford and Kay, 1999). These indirect effects of rodents on soil properties have been proposed as possible mechanisms explaining the keystone effects of kangaroo rats (Brown and Heske, 1990; Guo, 1996).

Rodent burrowing may be particularly important in nonequilibrium systems such as arid and semiarid rangelands, where productivity is moisture limited and there is a positive relationship between aridity and interannual variability of rainfall (Sullivan and Rohde, 2002). In nonequilibrium systems, theory suggests that abiotic factors such as soil properties, site characteristics, and weather generally have more influence on plant community structure than direct biotic interactions

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such as herbivory and granivory (Jackson and Bartolome, 2002). Consequently, a number of recent restoration studies have focused on the effects of abiotic variables such as site preparation techniques or soil amendments (e.g., Bonebrake et al., 2011; Doll et al., 2011; Kulmatiski, 2011). Rodent-caused changes in the physical and chemical properties of soil could function similarly to soil amendments, by acting as ecological filters that favor the assembly of certain species over others, independent of rodent seed preferences and seed removal.

In California's Carrizo Plain, *Dipodomys ingens* (giant kangaroo rat, hereafter GKR) dominates the rodent community and is thought to be a "keystone species" and "ecosystem engineer," as it has a disproportionately large impact on the grassland community and physically transforms the landscape (Prugh and Brashares, 2012a). Like other kangaroo rats, GKRs are primarily seed eaters (granivores) and consume vast amounts of both native and exotic plant seeds (Shaw, 1934; Williams et al., 1993). GKRs typically cut the ripening seed heads of grasses and forbs and sun-dry the seeds in either buried pit caches or in stacks on the soil surface (Shaw, 1934; Williams et al., 1993). GKRs later relocate buried caches and transfer the contents into long-term storage chambers in their burrow mounds (Shaw, 1934; Williams et al., 1993). GKR burrow mounds are established over many generations, and long-term occupancy results in mima-mound topography (Williams and Kilburn, 1991; Fig. 1).

Here, we sought to identify the individual effects of GKR seed removal and soil modification on the success of rangeland restoration efforts. We first assessed GKR seed preferences using cafeteria-style diet trials. We then quantified and compared the effects of seed removal, biotic soil disturbance, and soil chemistry on the seedling recruitment of four native plant species selected from our diet trials. These four species were selected to include a variety of growth forms and span a range of GKR seed preferences. Using experimental exclosures, we established small-scale restoration plots in areas that were accessible and inaccessible to kangaroo rats and stratified plot locations on and off GKR burrow mounds.

Methods

Study Area

We conducted this study from 2008-2011 in a semiarid annual rangeland within the Carrizo Plain National Monument, in southeastern San Luis Obispo County, California (Fig. 2). This study was a component of a larger long-term study initiated in 2007 to experimentally examine interactions among cattle, plants, and wildlife in the Carrizo Plain (Prugh and Brashares, 2012b). Parts of the monument were grazed by sheep and cattle when vegetation levels exceeded thresholds (U.S. Bureau of Land Management, 2010). The Carrizo Plain is the largest contiguous grassland in California, and it is among the last refuges for many species endemic to the San Joaquin Valley ecoregion (Germano et al., 2011). Precipitation in the Carrizo Plain is highly variable (annual CV = 47%), averages 209 mm per year, and falls primarily as rain during the winter months (MesoWest, 2011). Rainfall was nearly 50% above average when restoration plots were established, totaling 302 mm in the 2010 water year (MesoWest, 2011). The above-average rainfall likely resulted in better growing conditions and improved seedling establishment rates relative to normal conditions for some plants. Perennial bunchgrasses, most notably *Poa secunda* (Sandberg's bluegrass), may have once dominated the southern San Joaquin Valley region alongside native annual forbs (Germano et al., 2001). Exotic annual species including *Bromus madritensis ssp. rubens* (red brome), *Erodium cicutarium* (red-stem filaree), and *Hordeum murinum* (foxtail barley) are now abundant in the Carrizo Plain, and native plant cover has declined (Schiffman, 1994; Germano et al., 2001).

Our study area was located within the core habitat of the GKR, on flat terrain with no shrub cover (Fig. 2). The GKR is a state and federally listed endangered species that has experienced severe habitat loss but is locally abundant within the Carrizo Plain (Williams and Kilburn, 1991). The GKR is the most abundant member of the rodent guild in the Carrizo Plain and was the only primarily granivorous rodent species present in our study area (Prugh and Brashares, 2012a). Extensive trapping of GKR was conducted twice annually on our study sites beginning in 2007. From 2007–2012, average densities of GKR never fell below 25 ha^{-1} and peaked at more than 50 ha^{-1} (Prugh and Brashares, 2012b). GKR burrow mounds covered roughly 20% of the landscape (Bean et al., 2012). The high densities of GKR observed within the study area are fairly typical during years without extended droughts (Williams et al., 1993).

Fig. 1. Mima-mound topography that dominates the landscape in the study area within the Carrizo Plain National Monument, California. Photo credit: Don Johnson.

Diet Trials

We conducted cafeteria-style diet trials to assess the dietary preferences of GKRs. We collected ripe seed heads of the 12 most common plant species found on our plots in April 2008. We randomly chose 30 GKR mounds spread throughout our study area for diet trials, which were conducted 14 July 2008 to 28 July 2008. On each selected mound, we dug a shallow trench (approximately 1 m long, 6 cm wide, and 1 cm deep) and placed 0.5 g of seeds from each of the 12 plant species in separate piles along the trench. The order of species along the trench was randomized in each trial. We returned at dawn the next day to collect and weigh remaining seeds. Motion-trigger cameras were used to ensure GKRs visited each trench. Additionally, controls with wire mesh cages that were accessible to ants but not GKRs were initially used to assess whether seeds were being removed by ants. These controls resulted in only negligible amounts of seed removal (mean of 3% removal). For each trial, selection ratios (SR) were calculated as the proportion of each species removed relative to proportions available:

$$SR = \frac{U_i}{P_i * \sum U_i} \quad (1)$$

Where U_i = weight of seeds of species i removed and P_i = proportion of available seed (based on weight) composed of species i (Manly et al., 2002). Selection ratios > 1 indicated preference and ratios < 1 indicated avoidance. Mean selection ratios for each species were calculated across the 30 trials, along with standard errors and confidence intervals. Results of diet trials were used to select plant species for seeding in restoration plots.

Experimental Design

To examine effects of seed removal and soil disturbance on native seeding efforts, we used a randomized split-plot experimental design with two factorial treatments: kangaroo rat presence and burrow presence. In 2007, stratified randomization was used to place 10 experimental

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