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Are semiarid shrubs resilient to drought and grazing? Differences and similarities among species and habitats in a long-term study

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ABSTRACT

We assessed long-term effects of grazing cessation and drought on the shrub community of a semiarid ecosystem with a long history of grazing, located in the Mediterranean-to-desert transitional zone in Israel. Effects of grazing and drought on the cover of dominant (*Sarcopoterium spinosum*) and subdominant (*Thymelaea hirsuta*, *Noaea mucronata* and *Coridothymus capitatus*) shrubs were monitored during 12 years in four topographic habitats. With the exception of the toxic shrub *T. hirsuta*, shrub cover increased by a few (at most five) percentage points soon after the establishment of fenced plots to prevent grazing, but the difference in cover between protected and grazed plots did not increase subsequently. Response of the woody vegetation cover to the drought pulse was more complex because it was affected by both species and habitat; it showed patterns of steady decrease, transient decrease, and transient increase. Recovery after the drought pulse was relatively slow, and total shrub cover did not return to its predrought level within 7 years. Varied responses to drought and grazing preclude consideration of shrubs as a single response group. The findings heighten concern for the stability of the ecosystem in light of the increasing frequency of dry seasons predicted by climate-change models.

1. Introduction

Semiarid ecosystems are frequently characterized by a two-phase mosaic of woody patches and open herbaceous patches (Aguiar and Sala, 1999; Schlesinger et al., 1990; Shachak et al., 2008). Water controls most of the biological processes in these ecosystems (Noy-Meir, 1973), and grazing is the most common form of land use (Asner et al., 2004). Shrub encroachment occurs widely in arid and semiarid ecosystems and may be caused by either overgrazing (Reynolds et al., 2007; Schlesinger et al., 1990) or cessation of grazing (Cipriotti and Aguiar, 2012; Maestre et al., 2009). These contrasting responses to grazing are generally attributed to differences in ecosystem structure (combination of abiotic and biotic components) and functioning (the way these components interact); they also depend on shrub traits (Eldridge et al., 2011).

Woody species are considered to be primary landscape modulators (Shachak et al., 2008) in that they modulate the distribution of resources and organisms in the ecosystem, especially in semiarid landscapes (Giladi et al., 2013; Reynolds et al., 2007; Schlesinger et al., 1990). Thus, understanding of long-term processes of woody vegetation dynamics in shrublands is essential for assessing changes in their functioning and in the ecosystem services they provide, especially in relation to predicted land use and climate changes (Maestre et al., 2009). The frequency and intensity of drought events have increased during recent decades in many semiarid ecosystems; a trend that probably will continue into the future (Dai, 2011). Strong effects of drought on cover and composition of woody vegetation have been observed in various regions in recent years (Adams et al., 2009; Allen et al., 2010; Breshears et al., 2008), but the recovery dynamics of the woody vegetation following drought events has been less studied, despite its importance (but see Whitford et al., 1995). Furthermore, although theoretical models predict that synergistic interactions between drought and grazing can cause rangeland degradation (Milton et al., 1994), empirical studies that focus on long-term coaction and interaction between these factors are uncommon.

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The impact of grazing on community structure and diversity depends on the productivity of the system – which is largely dictated by rainfall amount – and on the evolutionary grazing history of the ecosystem (Cingolani et al., 2005; Milchunas et al., 1988). In this context, grazing can be considered as a long-term disturbance (press disturbance), whereas drought events are short-term disturbances (pulse disturbances) (Glasby and Underwood, 1996; Smith et al., 2009). In the present study we examined the response of shrub cover to grazing cessation and to a prolonged (2-year) drought pulse in the Negev Desert of Israel – a low-productivity system with a long evolutionary history of grazing. This region has been under grazing for thousands of years and is subject to wide within-season and year-to-year variations in rainfall, including extreme dry seasons; conditions to which the extant vegetation is adapted (Noy-Meir and Seligman, 1979; Perevolotsky and Seligman, 1998). In the Negev shrublands a few dominant and sub-dominant shrub species strongly affect nitrogen and carbon fluxes, water distribution and herbaceous biomass production (Shachak et al., 2008). Furthermore, the woody cover diminishes nutrient loss via runoff and erosion (Yair and Kossovsky, 2002), and increases species richness (Wright et al., 2006); reduction of the woody cover is considered to be the main mechanism of desertification in this region (Shachak et al., 1998). In the present study we monitored the long-term effects of grazing cessation and of drought on shrub cover and composition in a set of exclosures that were established in topographic habitats that differed in growth conditions and productivity (Osem et al., 2002). We asked: (a) What are the effects of grazing cessation and of a prolonged drought event on the dynamics of shrub cover? (b) Do patterns of change differ among shrub species, or can the shrubs be considered as a homogeneous response group? and (c) Do grazing and drought act synergistically on shrub cover?

2. Materials and methods

2.1. Study site

The study was conducted from 1996 to 2007 at the Lehavim LTER (Long-Term Ecological Research) Station (31° 20′ N, 34° 45′ E), in the northern Negev Desert, Israel. The station is located in the transition zone between the Mediterranean and the semiarid climatic regions, in the Irano-Turanian phytogeographic region (Zohary, 1973). The topography is characterized by low hills and dry stream beds (wadis), with an altitude range of 350–500 m above sea level. The bedrock of Eocene limestone and chalk is covered with loess soil. The landscape is highly heterogeneous, comprising a mosaic of exposed rock, shrubs and intershrub patches, with ephemeral winter-spring herbaceous vegetation dominated by annuals and geophytes (Osem et al., 2002; Sternberg and Shoshany, 2001).

The area was grazed by flocks of about 600 Awassi sheep and 200 Mamber goats, which foraged mainly on the herbaceous vegetation, with an average stocking rate of one head/ha. Grazing management was according to traditional Bedouin practice: from January or February to May (green season) the animals grazed the rangeland, and after the vegetation dried out the flocks left the station for the duration of the summer (June–September) and grazed contracted stubble fields and agricultural aftermaths in the region. The flocks then returned to the station and grazed the remaining dry vegetation during the fall and early winter (October–January), drawing most of their nutritional requirements from supplemented feeds. While on the station, the flocks were managed from a central corral where they were kept at night. Each flock left the corral separately each morning, accompanied by a herder, followed a meandering route that varied from day to day, and returned in the afternoon, typically after 5–6 h (Arnon et al., 2011).

2.2. Climatic conditions

Climate at the Lehavim Station is typical Mediterranean, with a mild rainy winter and spring (the growth season – November through April) and a hot, dry, rain-free summer lasting about 6 months (the rest season). Average daily temperatures range from 10 °C in winter to 25 °C in summer. Fig. 1 shows the annual (1 Oct. through 30 Sept.) rainfall for the period 1952/53–2010/11, as recorded at the nearby Lahav meteorological station (source: Israel Meteorological Service). Average (±SD) annual rainfall was 295 ± 104 mm for these 59 years, and 289 ± 90 mm for the 12-year period of the study (1995/6 to 2006/7). The seasons of 1998/99 and 1999/2000 had severe droughts, with 140 and 198 mm, respectively. These were not unique climatic events; during the 59-year period for which records are available, droughts of comparable severity (<200 mm) occurred five times prior to the study period and twice subsequently (Fig. 1).

2.3. Woody vegetation

Four main shrub species are found at the Lehavim Station. *Sarcopoterium spinosum* (L.) Spach (Rosaceae), a thorny dwarf shrub 30–60 cm tall, is common in the Eastern Mediterranean region (Zohary, 1973) and is the most abundant shrub in the station, particularly on north-facing slopes (Sternberg and Shoshany, 2001). Patches of *S. spinosum* may contain more than one individual plant (Reisman-Berman et al., 2006). Although browsed by sheep and goats, it is considered tolerant to grazing (Zohary, 1973) because of its spiny morphology (Ronel et al., 2007) and its ability to regenerate vegetatively from the root-crown and to spread by rooting from layering branches (Litav and Orshan, 1971). Sub-dominant shrubs are the toxic evergreen *Thymelaea hirsuta* (L.) Endl. (Thymelaeaceae), which is the tallest shrub at the station at 50–100 cm, the spiny dwarf shrub *Noaea mucronata* (Forssk.) Ascherson et Schweinf. (Chenopodiaceae), which is 25–50 cm tall, and the 20- to 40-cm-tall dwarf shrub *Coridothymus capitatus* (L.) Reichenb. (Lamiaceae). These shrubs occur widely in overgrazed semiarid areas of the East Mediterranean region and North Africa (Louhaichi et al., 2009; Zohary, 1973).

2.4. Experiment design

The experiment was carried out in three sites within the Lehavim station, each in a different watershed. Each site included four contrasting topographically defined habitats: north- and south-facing slopes, hilltops and wadi terraces. These habitats differed in incoming solar radiation, soil depth, rock cover, and runoff amount, and consequently also differed in water availability, shrub cover and species composition (Sternberg and Shoshany, 2001), as well as herbaceous productivity (Osem et al., 2002). In each habitat four plots were established between 1994 and 1996. Each plot was divided into two adjacent subplots, each measuring 10×10 m: one fenced in order to exclude grazing and the other open to grazing. The final analysis was based on data from 37 of the original 48 plots; these were neither vandalized nor did the initial difference in woody cover between their fenced and open subplots exceed 5%. This latter criterion aimed to avoid comparisons among subplots which may have differed in their abiotic conditions. The excluded plots were distributed evenly among the habitats and sites.

Shrub cover was measured annually at the beginning of the summer from 1996 to 2007 by the point-transect method (Bonham, 1989), with fixed 10-m-long transects that were marked with