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Shrub seedling survival under climate change – Comparing natural and experimental rainfall gradients

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ABSTRACT

Predicting responses of plant communities to environmental changes is a key challenge in ecology. Here we examined climate-related mechanisms regulating seedling dynamics of a common Mediterranean shrub. Our objective was to analyze effects of water availability on seedling survival and to determine whether geographical gradients can serve as proxy for predicting local climate change effects. We conducted a field experiment along a natural rainfall gradient with additional long-term rainfall manipulations at a Mediterranean site, enabling the investigation of the relative importance of biotic and abiotic factors on seedling dynamics. Along the natural and artificial rainfall gradient seedling survival increased with increasing soil water availability. However, seedling survival at the Mediterranean site yielded a clear trend of decreasing seedling survival with artificially increasing aridity whereas at the dry end of the geographical gradient seedling survival was relatively high. We attribute this pattern to biotic interactions, which appeared less negative at the dry end. These findings indicate that ignoring biotic interactions is misleading when predicting shifts in the distribution of species under climate change and that because of the complex interplay between abiotic and biotic factors, environmental gradients can be poor proxies for predicting the response of plant species to climate change.

1. Introduction

Understanding and predicting the responses of plants to environmental modifications such as climate changes represents a major challenge for ecologists (Krebs, 2009). One of the practical problems encountered by researchers is the relatively long temporal scale required to observe changes in nature (Fukami and Wardle, 2005). To overcome this problem, natural gradients that vary in their climatic conditions are often used as a proxy for the temporal changes in climate (Fukami and Wardle, 2005; Sternberg et al., 2011). For example, natural rainfall gradients provide a useful framework to analyze changes in species distribution in systems driven by water availability (Holzapfel et al., 2006; Sternberg et al., 2011). However, the response of plant species growing along natural gradients may vary depending on the amount of time the community was exposed to the particular climate conditions and to the relative contribution of other local environmental factors (Dunne et al., 2004; Fukami and Wardle, 2005; Sternberg et al., 2011). These shortcomings highlight the importance of combining experimental and correlative approaches when studying the potential effects of climate change (see also Fukami and Wardle, 2005). To the best of our knowledge, only few studies compared in situ manipulations of the limiting factor with correlations along an associated environmental gradient (e.g. Dunne et al., 2004; Liancourt et al., 2012). With this study, we attempted to fill this gap by monitoring seedling responses of a dominant shrub to climate change in a water-limited system using both a steep rainfall gradient and rainfall manipulations.

Early plant life stages are considered vulnerable to environmental alterations (Fay and Schultz, 2009; Howard and Goldberg, 2001) and particularly to climate changes (Gómez-Aparicio et al., 2005). Seedling survival depends on a narrow spatial and temporal window ("safe site") created by specific environmental conditions (sensu Harper et al., 1961). Seedling survival determines plant

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population dynamics, persistence and expansion (Kitajima and Fenner, 2002) and is therefore considered a bottleneck in many ecosystems, especially those characterized by extreme climatic conditions (Leck et al., 2008). The impact of survival success in the plant's early stages is especially large for long-lived, woody plant species, because small seedlings do not yet exhibit the robustness of adult plants that may protect them from drought, high temperatures, or competition with larger or faster developing neighbors (Matías et al., 2011; Mendoza et al., 2009). In dry regions, several studies have shown that water availability was the main limiting factor for seedling establishment (e.g. Padilla and Pugnaire, 2007), while after establishment, seedlings appeared to be less affected by abiotic and biotic factors (Davis et al., 1999; van Auken, 2000).

The contribution of climatic factors to early survival of plants is not limited to direct effects on the plant's demographic processes through an impact on abiotic resources, but can also be detected through alterations of the density and biomass of the entire community (Holzapfel et al., 2006; Seifan et al., 2010; Sternberg et al., 1999). If these alterations are species-specific, climatic changes will be associated with modifications of biotic interactions, whose direction (positive *vs*. negative) and intensity depend on the abiotic environment (Bertness and Callaway, 1994; Brooker et al., 2008). In the specific case of the potential indirect effect of climate on shrub seedling dynamics in a water limited system, we need to take into account the potential effects of two groups of neighbors: the herbaceous species and the adult shrubs. Herbaceous neighbors often have a faster growth rate relative to shrub and other woody seedlings (Sánchez-Gómez et al., 2006). This may indicate that the herbaceous neighbors can utilize abiotic resources more efficiently and may intensify competition for the limiting factors (McLaren et al., 2004; Vilà and Sardans, 1999). On the other hand, because of their faster growth rate, herbaceous neighbors may ameliorate habitat conditions, e.g. by providing shade which decreases evapotranspiration and buffers high temperatures (Holmgren et al., 1997). Adult shrubs are known to play an important role in water-limited systems as well, because they may influence seedling establishment success through alterations of microclimatic conditions, including the improvement of soil moisture, soil nutrients, temperature and light availability (Gómez-Aparicio et al., 2005; Pugnaire et al., 1996, 2004). On the other hand, adult shrubs can also negatively influence seedling establishment, especially by decreasing light availability to the seedlings growing in the shrub understory (Reisman-Berman, 2007; Seligman and Henkin, 2002).

To date, it is virtually unknown how the direction and intensity of such biotic interactions will change under a new climate. However, because many studies have shown that abiotic stress (e.g. decreasing rainfall) strongly affects the nature of biotic interactions, it is highly relevant to monitor plant–plant interactions when studying climate change. Therefore, the objective of our study was to determine whether changes in the interaction between a dominant perennial shrub and its herbaceous neighbors along a natural rainfall gradient can serve as proxy for predicting in-situ climate change effects. For this purpose, we artificially manipulated rainfall availability in accordance to regional climate change scenarios and monitored the establishment success of a common shrub in relation to herbaceous neighbors and adult shrub presence. These observations were compared to the shrub establishment success along a geographical rainfall gradient which served as spatial control for climate change scenarios (Sternberg et al., 2011). We predicted that shrub seedling survival will decrease with increasing site aridity and with experimental drought. If shrub seedling survival along a natural and artificial rainfall gradient is indeed similar, it will support the use of geographical gradients as proxy for temporal change in climate. In addition, because of the potential change in biotic interactions with climatic conditions, we predicted that the presence of adult shrubs or herbaceous neighbors will have a positive effect on shrub seedling survival with either naturally or manipulative decreased rainfall.

2. Material and methods

We conducted our study within the Mediterranean shrubland in Israel. Eastern Mediterranean scrub formations are characterized by highly heterogeneous plant communities and diverse environmental conditions distributed over a small geographical area (Danin, 1992). In Israel, this vegetation formation is found along a steep rainfall gradient across a small spatial distance ranging from 900 mm mean annual precipitation in the north to 250 mm in the south (Danin, 1992), which is accompanied by an increasing temporal variability with decreasing rainfall (Nahal, 1981). This combination offered a unique possibility for investigating climate change effects on the structure and functioning of ecosystems. Our study was conducted at three sites along the natural climatic aridity gradient (183 km; see: “2.2 Geographical gradient”), and was compared to rainfall manipulation outcomes at the central site for testing potential climate change scenarios (see: “2.1 Climate change manipulations”).

2.1. Climate change manipulations

The central study site was located in the Judean Mountains (N 31°42′, E 35°03′). It is characterized by Mediterranean climate with an average annual rainfall of 540 mm. At this site we used experimental long-term rainfall manipulations (12 years) evaluating two potential scenarios that were based on predicted climatic changes for the region: 30% decrease and 30% increase in total annual rainfall. The increased rainfall scenario was achieved by adding irrigation with drizzle sprinklers at the end of each rainfall event higher of 5 mm. Decreased rainfall was simulated by fixed rainout shelters (Yahdjian and Sala, 2002). Rainout shelters were made from metal frames (2.5 m mean height), with u-shaped plastic bands intercepting 30% of rainfall. Excess water was drained into gutters leading away from the experimental plots. Wind movement was not impeded as sides of the rainout shelters were open, additionally minimizing microclimatic differences under and outside the shelter (Fay et al., 2000). This method enabled us to manipulate only rainfall amount, while maintaining natural timing, frequency and intervals of rainfall (Sternberg et al., 2011). Five plots of 10 m × 25 m were set for each treatment and randomly located at the site. From here on we will refer to the treatments as irrigation, control and drought. For more detailed description of the experimental design see Sternberg et al. (2011).

While designing the experiment, our aim was to cover the uncertainty of global climate models and thus included artificially increased and decreased rainfall, in accordance with the available models and predictions for the region (Ben-Gai et al., 1998). However, during the course of the study high-resolution models became available, predicting a decrease in annual rainfall by 10–30% in the next decades (Smiatek et al., 2011). Therefore, while both treatments provide mechanistic information about the response of shrub seedlings to changes in rainfall, the drought treatment better mimics future climate change scenarios in the region.

2.2. Geographical gradient

Two additional sites were established north (Galilee Mountains, N 33°0′, E 35°14′) and south (northern Negev desert,