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Regional environmental conditions affect microsite response in a keystone desert species

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ABSTRACT

Little is known about the environmental conditions that influence the growth rate of the keystone species *Carnegiea gigantea*. This study assesses variations in growth based on proximity to other conspecific individuals (intraspecific clumping), proximity to surface water, nurse species, and the impact of shading in an extreme desert environment. I observed that (1) at the cooler and wetter site, shading slowed growth relative to *Carnegiea* growth in the open, while at the hotter and more arid site, shaded *Carnegiea* individuals grew faster, likely related to the extremities of this site and thus more pronounced necessity of shade and a nurse. (2) Presence near runnels (concentrated drainage) did not significantly impact growth in the less extreme cooler and wetter site, but proximity to surface water drainage did increase growth rates at the more arid site. (3) Growth was faster under nurse trees than the smaller shrubs, however, not significantly so. (4) Proximity to other conspecifics (clumping) of this shallow-rooted species did not significantly change growth rates. Increased stress may be particularly crucial at the more extreme site in defining ecological responses to varying microsite conditions.

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1. Introduction

The columnar cactus, Carnegiea gigantea (Engelm.) Britt. and Rose (saguaro, Cactaceae) is a keystone species (Drezner, 2014) in the Sonoran Desert, providing ecological benefits to many species in the ecosystem. Drezner (2014) provides an extensive referenced table of over 100 species that use and depend on Carnegiea, including a wide range of birds, large and small mammals, reptiles and insects that consume pollen, nectar, and fruit, use the plant for nesting, perching and mating and a listing of a wide variety of other ecosystem services provided by Carnegiea are given. Growth rates are essential for understanding C. gigantea's basic ecology and the environmental factors that govern the survival and life cycle of individuals and demographics (Drezner, 2006a). Growth is highly variable; in southern Arizona, a 50-year old Carnegiea individual can vary in height from 90 cm to 378 cm as determined across just three sites (Steenbergh and Lowe, 1983). Growth occurs in response to summer precipitation broadly (Hastings, 1959; Drezner, 2005), though few studies have been conducted locally to ascertain which other environmental conditions influence growth.

The shade produced by common nurse plants in the desert has

http://dx.doi.org/10.1016/j.jaridenv.2015.01.013 0140-1963/© 2015 Elsevier Ltd. All rights reserved. been shown to reduce receipt of solar radiation (Lowe and Hinds, 1971; Castellanos et al., 1999). In some cases, such as for seedlings, reductions can be dramatic (Franco and Nobel, 1989). Photosynthetically active radiation (PAR) directly influences growth (e.g., Geller and Nobel, 1986; Gibson and Nobel, 1986), though aspect does not influence growth rates significantly (Pierson and Turner, 1998). Growth rates are faster on slopes than in topographically flat populations, however, likely due to soil characteristics and greater available moisture (Donnermeyer and Drezner, 2012).

C. gigantea engage in facilitative associations with so-called nurse plants (Turner et al., 1966; Drezner, 2004a). *Carnegiea* that establish under trees and shrubs benefit from the ameliorated subcanopy conditions, which include reduction of extreme summer air temperatures, soil temperatures, and desiccation (Shreve, 1931; Turner et al., 1966; Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991), and increased ambient nighttime temperatures in winter (Nobel, 1980; Drezner and Garrity, 2003; Drezner, 2007), among other benefits (e.g. Withgott, 2000; Drezner, 2004a). Ultimately, *Carnegiea* cannot establish without a nurse plant (or rock) (Turner et al., 1966). Most of the literature on nurse species focuses on these benefits to *Carnegiea*; less is known about disadvantages of these nurse associations. Reductions in soil moisture (Kropfl et al., 2002) and dew point temperatures (Drezner, 2007) have







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been documented under canopies. Although previous studies have shown that in the Sonoran Desert nurse plant morphology affects *C. gigantea*'s growth (Hutto et al., 1986; Parker, 1989; Drezner, 2006b), young *Neobuxbaumia mezcalaensis* cacti exhibit different growth rates and survival under morphologically similar nurses, possibly relating to soil nutrients and nurse–protégé interactions (Landero and Valiente-Banuet, 2010). In addition to the already slow growth associated with CAM photosynthesis, shade can dramatically reduce available photosynthetically active radiation (PAR) for *Carnegiea* (Franco and Nobel, 1989) and would presumably cause a decrease in growth rate.

Because of *Carnegiea*'s association with nurses, clumped distributions often occur locally where a nurse once stood or continues to exist (McAuliffe and Janzen, 1986). Intraspecific competition for water can ultimately result in premature mortality (McAuliffe and Janzen, 1986), though the extent of this susceptibility will vary across sites and climates. Finally, in arid environments water is a limited resource. For the very shallow-rooted (to perhaps 15 cm in depth) *Carnegiea* (McAuliffe, 1984), all water must be obtained from rainfall and subsequent runoff over their lifetimes. In the most arid reaches of their range, individuals are often limited to small ephemeral drainage channels that channelize and concentrate

rainwater (Steenbergh and Lowe, 1977). It is untested whether the additional water associated with such channels would result in significantly faster growing individuals at these microsites.

The purpose of this study is to determine whether (1) shading, (2) proximity to surface moisture, (3) clumping and (4) nurse associates influence *Carnegiea* growth rates. These will be independently tested in two different populations, one near the environmental optimum of the species (including greater rainfall), and one in the arid west where populations are more sparse, near the rain-limiting edge of their range. Understanding growth and related responses to the environment is fundamental for establishing this keystone species' age, demographics and environmental influences.

2. Materials and methods

2.1. Study sites

The Kofa site is located at 33°32′N, 114°10′W in and bordering the Kofa National Wildlife Refuge, Arizona, USA (Fig. 1) in the Lower Colorado River Valley subdivision of the Sonoran Desert (Shreve, 1951; Turner and Brown, 1994). Woody vegetation cover is about



Fig. 1. Map showing study sites (Kofa, Silverbell). Carnegiea range is modified from Turner et al. (1995).

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