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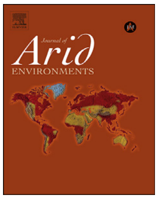

Shape and size adjustments of a cactus with rib and furrow morphology

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ABSTRACT

Hundreds of cactus species have evolved the rib and furrow morphology that aids in water storage and provides photosynthetic and thermal benefits. Limited work has been done on understanding rib spacing and furrow size in the context of a wide range of environmental variables. Data were collected in two *Carnegiea gigantea* Sonoran Desert (Northern Hemisphere) populations, that were analyzed using General Linear Models and MANOVA to assess the relationships between rib and furrow metrics, height and direction on the plants, and several environmental and plant-wide variables (e.g., intraspecific crowding, shade, branching). Furrow sides are smaller lower on the plant, but are not related to orientation suggesting adjustment with growth. Rib spacing is not related to height on the plant, but is related to direction (greater spacing to the north and west), likely due to thermal and photosynthetic differences. Intraspecific crowding and shade affect the size of furrows. This morphology offers both a long-term response to general conditions (furrow size, e.g., shade, regional factors) and short-term response (rib spacing) to seasonal variations in temperature and moisture for direct response to fluctuating conditions. These mechanisms will continue to be important with changing climate, and through range shifts associated with warming.

1. Introduction

Hundreds of species of cactus have stems with adaptations for large fluctuations in water storage, with a rib and furrow design (accordion-like in cross-section) that enables them to swell with water inputs as the furrows expand to a more open position. As water is slowly used, the stem contracts as the furrows close and rib spacing decreases. Such expansions and contractions affect not only water storage, but also receipt of photosynthetically active radiation (PAR). As the non-spined (not shaded) furrows close, direct insolation decreases, leaving proportionally more spine-shaded rib areas exposed. The ribbed morphology increases the unshaded surface area for absorbing PAR (e.g., Lewis and Nobel, 1977; Yeaton et al., 1980). Thus when rib depth increases, less PAR is received, and greater depth also causes decreases in nocturnal CO_2 uptake for these CAM (Crassulacean acid metabolism) photosynthesizing plants (Nobel, 1980). The increased surface area (compared to a smooth cylinder) increases convective heat loss while increasing the boundary layer which buffers the plant from high summer temperatures (Lewis and Nobel, 1977; Yeaton et al., 1980). Such adaptations for great fluctuations in water and thermal and photosynthetic processes have undoubtedly contributed to the success of this group in arid environments. The rib and furrow structure responds to environmental conditions, yet we have limited empirical information about such responses.

Carnegiea gigantea (Engelm.) Britt. and Rose (Cactaceae, saguaro) is a keystone species in the Sonoran Desert (Drezner, 2014) and one of several species whose rib and furrow structure has been studied. Early work done by Spalding (Spalding, 1905; MacDougal and Spalding, 1910) looked at the expansion and contraction of a few individual *Carnegiea* plants over several months to years. Observations considered expansion in the weeks following a rain event, faster and greater expansion on the south side furrows, with the delays to the north side on the order of days to weeks (MacDougal and Spalding, 1910). Maximum expansion on the north side of the plant may only be reached 1–2 months after the south side maximum (MacDougal and Spalding, 1910). They attribute the overall observed patterns of expansion and contraction on insolation with variations observed seasonally (MacDougal and Spalding, 1910). More recently, Nobel and colleagues have investigated (often through models and simulations) the rib and furrow morphologies of cacti including how this affects convection and heat loss with differences in number of ribs, and carbon dioxide uptake in

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Ferocactus acanthodes (Lewis and Nobel, 1977), PAR uptake on different ribbed forms (Nobel, 1980), as more closely spaced ribs occur where PAR interception is potentially greatest in both *Carnegiea* and *Ferocactus acanthodes* (Geller and Nobel, 1984), among other simulations on PAR, rib number and related measures on several other species of cacti such as *Lophocereus schottii* (e.g. Nobel, 1988).

Carnegiea rely on facilitative nurse associations for their survival when they are small and susceptible to extreme climatic conditions (e.g., Turner et al., 1966). Drought (Turner, 1990), severe freezes (Niering et al., 1963; Steenbergh and Lowe, 1976), trampling and browsing (Niering et al., 1963), extreme ground surface temperatures (Franco and Nobel, 1988), and a range of other conditions threaten the survival of young plants (Drezner, 2004; Drezner and Lazarus, 2008). Runoff may redistribute seeds to more xeric and exposed microsites which can affect survivorship (Drezner, 2013) and which can significantly influence individual growth rates (Drezner, 2015). *Carnegiea* grow slowly upwards from their apical meristem, sometimes reaching heights of over 10 m. Because of their establishment under the canopies of nurse plants, root competition, more commonly with other conspecifics, can ensue (McAuliffe and Janzen, 1986). The shallow but laterally extensive root systems can result in intense intraspecific competition under a shared nurse that can result in measurably thinner individuals, which in some cases has brought about the premature freezing mortality of *Carnegiea* due to the higher rates of heat loss associated with thinner stems (McAuliffe and Janzen, 1986), as well as the premature death of the nurse by the more shallow-rooted cactus (McAuliffe, 1984). As plants get larger, they become more resistant to the natural fluctuations (e.g., temperature, precipitation) in their environment (Steenbergh and Lowe, 1983; McAuliffe and Janzen, 1986). Disadvantages of nurse associations include shading that may slow growth in more mesic populations (Drezner, 2015). *Carnegiea* growth slows when the plant shifts resources from apical growth upwards to branch production (Steenbergh and Lowe, 1983; Drezner, 2003a), which serve the important function of increasing flower and fruit production that form on stem and branch apices (Steenbergh and Lowe, 1983). All of these factors play a role in *Carnegiea* ecology and survival, yet limited work has been carried out to understand these variables in the context of water storage and the plants' rib and furrow design.

The purpose of this study is to quantify furrow size and rib spacing to assess morphology, orientation, stem diameter, and close proximity of conspecifics (competition for water), among other variables. This will aid in our understanding of this adaptation in hundreds of species for water storage and structural flexibility to tolerate wide swings in water availability during wet and dry periods. I test whether the size of furrow sides and rib spacing are related to position on the plant (height and direction), in a western and an eastern population that represent opposing sides of the rainfall gradient. Nine additional variables (plant NS diameter high and low, plant EW diameter high and low, plant height, presence of competitors, shading, total number of branches and total number of branches > 5 cm) are analyzed to determine their effect on rib spacing and furrow size.

2. Methods

2.1. Study sites

Two populations were sampled (Fig. 1), one in the Usery Mountains (UM), east of Phoenix, Arizona (33.487°N, 111.612°W, about 650 m elevation), and the second at the Kofa National Wildlife Refuge (Kofa), near *Carnegiea*'s western boundary (33.534°N, 114.165°W, about 400 m elevation). These represent the Lower Colorado River Valley subdivision of the Sonoran Desert (Kofa) and the Arizona Upland (UM) subdivision (Shreve, 1951; Turner and Brown, 1994). These two sites are about 240 km apart, with Kofa near the western water-limited edge of the species' range (Turner et al., 1995), while the UM population is in the wetter northeastern portion of their range (Drezner, 2008). The Quartzsite meteorological station (#026865) is near Kofa, while data for the Bartlett Dam meteorological station (#020632) are used for the UMs (Cooperative Climatological Data Summaries, Western Regional Climate Center). Temperatures at Kofa are more extreme compared to the UMs, as seen by mean minimum January temperatures (2.7 °C at Kofa, 4.6 °C at UM) and mean maximum July temperature (42.7 °C at Kofa, 40.6 °C at UM), with differences in precipitation being even more pronounced. The dry Kofa site averages about one third of UM January rainfall (13 mm vs. 40 mm), less than half of UM's mean July rainfall (12 mm vs. 28 mm), and nearly one third of mean annual precipitation (128 mm vs. 341 mm). Vegetation coverage reflects these dramatic differences in moisture with only 7% cover at Kofa, compared to about 31% at the UM site (Drezner, 2006a). Similarly, *Carnegiea* densities are about 60 plants per hectare at the UMs compared to only 22 plants per hectare at Kofa (Drezner, 2006b).

Fig. 1. Map showing the locations of the two study sites (Kofa, Usery Mountains (UM)).

2.2. Field methods

Plants were quota sampled in each population. For each *Carnegiea* encountered, a variety of measurements were taken. Plants less than 2 m in height were not sampled. The distance between two ribs (*rib*) was measured, as well as the distance from the rib peak (excluding spines) to the bottom of the adjoining furrow (*furrow*), representing the side of the "valley" (see figure on p.65 in Spalding (1905) for a cross sectional diagram). These two measurement were done eight times each on each plant, in the four