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Short communication

Density-dependent shading patterns by Sonoran saguaros

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ABSTRACT

Woody plants produce shading patterns that can alter soil evaporation rates and provide nurse-plant effects for seedling establishment. These effects depend on the density of woody plants and associated characteristics of canopy architecture such as height, and can be particularly important in deserts. The tallest stature woody plants in some desert ecosystems are columnar cacti, which have distinctly different architecture than other woody plants for which shading effects have been systematically assessed. Focusing on columnar cacti of the northern Sonoran Desert, we used hemispherical photography to evaluate the effects of saguaro cacti (*Carnegiea gigantea*) on microclimate along a gradient of increasing cactus density. Notably, incoming annual near-ground solar radiation was reduced by up to ~10% for the highest density stand (156 cacti ha^{-1}), with spatial variation in shading patterns peaking at nearly the highest stand density (133 cacti ha^{-1}). The annual near-ground solar radiation reductions were more directly related to cacti density than to density of surrounding shrubs. Our results document that at high density, saguaro columnar cacti can have substantial effects on microclimate and, more generally, our results contribute to the growing library of relationships quantifying how shading patterns vary with woody plant architecture and density.

The canopies of woody plants attenuate incoming solar radiation and produce shading patterns that can significantly reduce the amount of solar radiation reaching the near-ground microclimate below canopies (Anderson, 1964; Breshears et al., 1997; Scholes and Archer, 1997; Martens et al., 2000; Breshears, 2006). The reduction in near-ground solar radiation due to woody plant canopy attenuation can have important abiotic and biotic consequences. Of particular note is that reduced near-ground solar radiation further affects the abiotic environment through reductions in soil evaporation rate and associated ecohydrological impacts (Breshears et al., 1998; Martinez-Berdeja and Valverde, 2008), and the biotic environment through facilitation of lower stature plants, often seedlings or juveniles in arid environments (Scholes and Archer, 1997; Flores-Martinez et al., 1998; Forseth et al., 2001).

Determining the degree of spatial shading that woody plants produce is more complex than might be apparent at first. How the overstory canopy of woody plants affects shading patterns depends on numerous factors, including the amount of canopy cover, branching pattern, foliar density, and canopy height (Campbell and Norman, 1998). Because the amount of cover from woody plant canopies can be at least as important as the architecture of a given canopy type, several studies have focused on systematically assessing how near-ground solar radiation varies along gradients of woody plant canopy cover (Martens et al., 2000; Breshears, 2006). Related assessments in more mesic environments have considered the effects of coniferous (Heithecker and Halpern, 2006) and deciduous (Ricard et al., 2003) woody plants. In more arid environments, studies have specifically considered the role of the lower as well as upper height of the canopy (Breshears and Ludwig, in press) and interactive effects between canopy cover amount and site topography with respect to slope and aspect (Zou et al., 2007).

Shading by woody plant canopies might be especially important in deserts where the solar radiation is strong and the canopy cover is often low. Studies have shown that such processes have been pivotal in facilitating plant establishment in arid environments (McAuliffe, 1984; Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991; Flores et al., 2004; Suzán-Azpiri and Sosa, 2006; Drezner, 2007; López et al., 2007; Munguia-Rosas and Sosa, 2008). One key example of the importance of facilitation is for saguaro cactus (*Carnegiea gigantea*) (Flores and Jurado, 2003; Drezner, 2006a), an iconic plant for the Southwest USA. The saguaro cactus is a columnar succulent with woody structural support and is native

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Table 1
Canopy structures associated with five different Saguaro density plots.

Density	Low	Low-medium	Medium	High-medium	High
Number of saguaro cacti (ha^{-1})	44	58	89	133	156
Average height of saguaro cacti (m)	4.48 ± 2.92	4.05 ± 2.29	4.9 ± 3.16	6.32 ± 2.95	6.84 ± 2.53
Saguaro basal cover (%)	0.04	0.07	0.07	0.16	0.19
Shrub canopy cover (%)	17.61	5.18	10.70	9.06	16.60
Average height of shrubs (m)	2.44 ± 1.21	1.87 ± 1.23	2.67 ± 1.6	3.24 ± 1.28	1.51 ± 0.88
Total cover (%)	18.11	5.33	11.11	9.70	17.72

to the hot and warm Sonoran Desert (Drezner, 2006b). Where found, saguaro cacti are often the tallest vegetation structure in the landscape. Densities can exceed 150 individuals ha^{-1}, with such high density stands even being referred to as saguaro "forests". Because height and density are two key drivers of shading patterns and even small reductions in near-ground solar radiation might be important in deserts, mature saguaro at high densities could have significant effects on microclimate.

Our objective was to assess how near-ground solar radiation varied with saguaro density. We obtained field measurements in the Saguaro National Park West in southern Arizona, USA (32°15′21″N, 111°12′25″ W) between March 2006 and June 2006. We first identified five transects that spanned from low to high saguaro densities. Each transect was 30 m long and oriented East-to-West. Along each transect we took hemispheric photos every 1 m at 1 m above the ground under uniform sky conditions, immediately before sunrise or after sunset or on overcast days (consistent with methods in related studies; e.g., Zou et al., 2007). The photos were obtained using a fisheye lens (Nikkor CF-8, Japan). We calculated mean and spatial variance of annual near-ground solar radiation for each transect, expressed as the Direct Site Factor (DSF), using HemiView software (Delta-T Devices Ltd, Cambridge, UK). DSF is the proportion of direct solar radiation reaching a given location, relative to that in a location with no sky obstructions. For DSF, 1.0 corresponds to a completely open location with no shading and 0.0 corresponds to a completely shaded location. Description of vegetation surrounding each transect was based on surveys of a 900 m^2 plot (using the 30 m transect as central axis and extending it 15 m on either side to form a 30 m × 30 m plot). To estimate the basal cover of each individual saguaro cactus, we used the cross-sectional area at breast height (1.3 m from ground, which is a commonly used metric in forestry and a height similar to that hemispheric photos were taken; Table 1). Saguaro canopy cover corresponded to basal area for plants with no branching structure and for other saguaros to the maximum plant diameter accounting for branching structure, analogous to similar measurements for trees (Breshears and Ludwig, in press).

Mean DSF decreased with increasing density of saguaro cacti, culminating in nearly a 10% reduction at the highest stand density (DSF ≈ 0.9; Fig. 1A). Spatial variation in DSF was largest just below the highest density, at the medium-high density (133 cacti ha^{-1}; Fig. 1B). The total basal cover of saguaro cacti was strongly correlated with DSF (Fig. 2A). Although percentage wise, other woody plant cover was much greater than the cover of saguaro cacti, it was not strongly related to the reduction in the solar radiation (Fig. 2B). This somewhat counter-intuitive result is likely due to the overall sparse vegetation in the desert and to saguaro architecture. Because saguaros are almost twice as tall as the co-occurring woody species, their shadows can extend farther into intercanopy locations. The shadows cast by saguaros are solid and do not depend on a foliar density, as is the case for woody species like velvet mesquite (*Prosopis velutina*) and palo verde (*Cercidium microphyllum*) (Fig. 2C).

Our findings highlight the importance of both height and stature in producing shading. Additional research is needed to assess the degree to which the reduction in near-ground solar radiation that we quantified here is relevant in an abiotic context for soil evaporation and a biotic context for facilitation of understory plants. Juvenile columnar cacti have been shown to depend on reductions in solar radiation from nurse plant shrubs (McAuliffe, 1984; Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991; Drezner, 2007; Munguia-Rosas and Sosa, 2008). Interestingly we show that adult saguaros in high density stands may contribute significantly to the overall reductions in near-ground solar radiation. We focused here only on annual totals for near-ground solar radiation; the degree of shading caused by saguaros would of course be much greater at particular times associated with seasonal and daily variation. In conclusion, our results document that at high density, saguaro columnar cacti can have substantial effects on microclimate and they more generally contribute to the growing library of relationships quantifying how shading patterns vary with woody plant architecture and density.

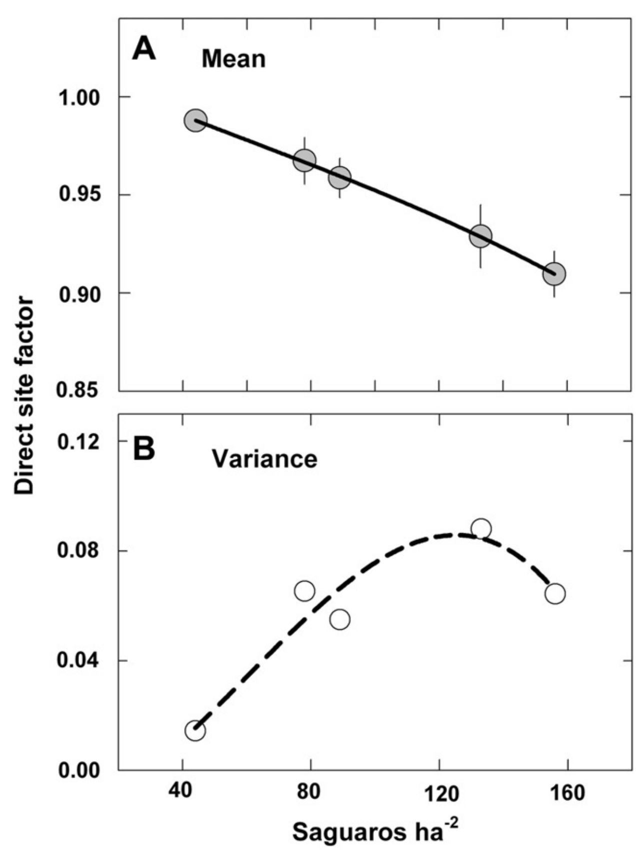

Fig. 1. Relationship between saguaro density and the annual mean (A) and the variance (B) of direct site factor (DSF).

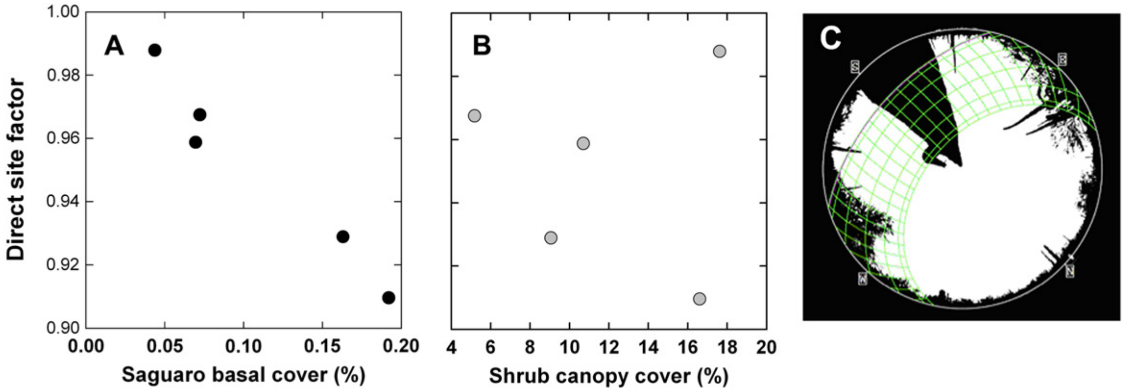

Fig. 2. Direct site factor (DSF) as related to (A) saguaro basal cover and (B) shrub canopy cover, and digitized image showing the different shading effects between high, solid Saguaro trunks and low, loose foliar structure of shrub and their relative position along the sun track (C).

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References

Anderson, M.C., 1964. Light relations of terrestrial plant communities and their measurement. Biological Reviews 39, 425–486.

Breshears, D.D., Rich, P.M., Barnes, F.J., Campbell, K., 1997. Overstory imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecological Applications 7, 1201–1215.

Breshears, D.D., 2006. The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? Frontiers in Ecology and the Environment 4, 96–104.

Breshears, D.D., Nyhan, J.H., Heil, C.E., Wilcox, B.P., 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. International Journal of Plant Science 159, 1010–1017.

Breshears, D.D., Ludwig, J.A., in press. Near-ground solar radiation along the grassland-forest continuum; tall-tree canopy architecture imposes only muted trends and heterogeneity. Austral Ecology. doi:10.1111/j.1442-9993.2009.02009.x.

Campbell, G.S., Norman, J.S., 1998. An Introduction to Environmental Biophysics. Springer, New York.

Drezner, T.D., 2006a. Plant facilitation in extreme environments: the non-random distribution of saguaro cacti (*Carnegiea gigantea*) under their nurse associates and the relationship to nurse architecture. Journal of Arid Environments 65, 46–61.

Drezner, T.D., 2006b. Saguaro (*Carnegiea gigantea*) densities and reproduction over the northern Sonoran Desert. Physical Geography 27, 505–518.

Drezner, T.D., 2007. An analysis of winter temperature and dew point under the canopy of a common Sonoran Desert nurse and the implications for positive plant interactions. Journal of Arid Environments 69, 554–568.

Flores-Martinez, A., Ezcurra, E., Sanchez-Colon, S., 1998. Water availability and the competitive effect of a columnar cactus on its nurse plant. Acta Oecologica-International Journal of Ecology 19, 1–8.

Flores, J., Jurado, E., 2003. Are nurse-protege interactions more common among plants from arid environments? Journal of Vegetation Science 14, 911–916.

Flores, J., Briones, O., Flores, A., Sánchez-Colón, S., 2004. Effect of predation and solar exposure on the emergence and survival of desert seedlings of contrasting life-forms. Journal of Arid Environments 58, 1–18.

Forseth, I.N., Wait, D.A., Casper, B.B., 2001. Shading by shrubs in a desert system reduces the physiological and demographic performance of an associated herbaceous perennial. Journal of Ecology 89, 670–680.

Franco, A.C., Nobel, P.S., 1989. Effect of nurse plants on the microhabitat and growth of cacti. Journal of Ecology 77, 870–886.

Heithecker, T.D., Halpern, C.B., 2006. Variation in microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. Forest Ecology and Management 226, 60–71.

López, R.P., Valdivia, S., Sanjinés, N., de la Quintana, D., 2007. The role of nurse plants in the establishment of shrub seedlings in the semi-arid subtropical Andes. Oecologia 152, 779–790.

Martens, S.N., Breshears, D.D., Meyer, C.W., 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. Ecological Modelling 126, 79–93.

Martinez-Berdeja, A., Valverde, T., 2008. Growth response of three globose cacti to radiation and soil moisture: an experimental test of the mechanism behind the nurse effect. Journal of Arid Environments 72, 1766–1774.

McAuliffe, J.R., 1984. Sahuaro-nurse tree associations in the Sonoran Desert – competitive effects of sahuaros. Oecologia 64, 319–321.

Munguia-Rosas, Sosa, V.J., 2008. Nurse plants vs. nurse objects: effects of woody plants and rocky cavities on the recruitment of the *Pilosocereus leucocephalus* columnar cactus. Annals of Botany 101, 175–185.

Ricard, J.P., Messier, C., Delagrange, S., Beaudet, M., 2003. Do understory sapling respond to both light and below-ground competition? A field experiment in a north-eastern American hardwood forest and a literature review. Annals of Forest Science 60, 749–756.

Scholes, R.J., Archer, S., 1997. Tree-grass interactions in savannas. Annual Review of Ecology & Systematics 28, 517–544.

Suzán-Azpiri, H., Sosa, V.J., 2006. Comparative performance of the giant cardon cactus (*Pachycereus pringlei*) seedlings under two leguminous nurse plant species. Journal of Arid Environments 65, 351–362.

Valiente-Banuet, A., Ezcurra, E., 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacan Valley, Mexico. Journal of Ecology 79, 961–971.

Zou, C.B., Barron-Gafford, G.A., Breshears, D.D., 2007. Effects of topography and woody plant canopy cover on near-ground solar radiation: relevant energy inputs for ecohydrology and hydropedology. Geophysical Research Letters 34, L24S21. doi:10.1029/2007GL031484.