TERMITE ACTIVITY ON GREEN TISSUES OF SAGUARO (*CARNEGIEA GIGANTEA*) IN THE SONORAN DESERT

Alejandro E. Castellanos, Reyna A. Castillo, Adrian Quijada

The giant saguaro (*Carnegiea gigantea*), an icon of the Sonoran Desert due to its uniqueness in the landscape, has had a role as a delimiter of the Desert's boundaries and plant communities (Shreve and Wiggins 1964). The saguaro is a long-lived perennial cactus in which many different biotic interactions have been characterized, such as its dependence on nurse plants during establishment, bird nesting and insect presence in its trunk, and bat pollination of flowers and bird dispersion of seeds (Steenbergh and Lowe 1969, 1977; Turner et al. 1969; Turner et al. 1966). Even diseased, necrotic and dead saguaro stems create habitats for insects. Given its importance in saguaro performance, biotic interactions may be the explanation for saguaro population decline and recovery at different times and places (Alcorn and May 1962; Steenbergh and Lowe 1969, 1977; Turner 1990).

Declines in saguaro forests have been noticed in different parts of the Sonoran Desert and at least one study has proposed a correlation between increased saguaro mortality and epidermal browning (Turner and Funicelli 2000). Although its causes have not been clearly identified, epidermal browning refers to a series of symptoms in saguaros, the most conspicuous being changes in color of aboveground tissues over time from green to yellow and brown (Duriscoe and Graban 1992; Evans et al. 1995; Turner and Funicelli 2000), decreasing UV-B protection, photosynthesis and gas exchange (Evans et al. 1994b; Lajtha et al. 1997). As the saguaro is a dominant and keystone species of the Sonoran Desert, changes in its population dynamics will likely have an effect on the functioning of this desert ecosystem.

Termites are important components in desert ecosystem function. Their role in cellulose decomposition and nutrient recycling has been well studied in North American deserts (Schaefer and Whitford 1981; Whitford 2002). In most cases, it has been shown that desert termites are restricted to underground nesting and feeding on woody and dead plant materials. Most of the forty species in the Sonoran Desert are specialists to particular plant species (Smith 2000), and those limited to saguaro, were found only on its lignified base (Olson 2000).

In the past, termite activity on live tissues has been reported anecdotally, and mostly in urban settings (Jones and Nutting 1989). There are no reports or studies of termite activity on living tissues of saguaro and most other desert plants. Population density and/or control procedures of *Heterotermes aureus*, *Gnathamitermes tubiformans* (subterranean termites), and other termite species have been reported in live tissue of several grass and desert plants, but without any quantification of damage (Allen et al. 1980; Bodine and Ueckert 1975; Spears et al. 1975; Ueckert et al. 1976).

In this paper, we report for the first time the presence of termites on aboveground living green tissues of saguaro. We studied termite presence on a number of sites and over several years in order to increase our understanding

about the role and causes of this previously undocumented phenomena as well as its contribution to the ecology of saguaro populations throughout the Sonoran Desert.

METHODS

Saguaro populations were sampled from Mesquite–Palo Verde plant communities within the Central Gulf Coast subdivision of the Sonoran Desert (Brown 1982; Shreve and Wiggins 1964) in Sonora, Mexico. The sites were located at 29°22'15" lat N and 112°00'29" long W (Figure 1). The associated natural vegetation showed little evidence of disturbance, and consisted of a mixture of trees (*Prosopis glandulosa*, *Cercidium microphyllum*, *Bursera microphylla, Olneya tesota, Pachycereus pringlei*) and shrubs (*Fouquieria splendens*, *Lophocereus schotti, Stenocereus thurberi, Larrea tridentata, Ambrosia dumosa*, *Encelia farinosa* (species name follows Shreve and Wiggins 1964). The nearest climatological records available were obtained from Puerto Libertad, Sonora, a coastal town, approximately 60 km from the farthest site. Puerto Libertad has a mean annual temperature of 19° C and average annual precipitation of 83.8 mm (14-year average). Winter rainfall is an important and significant percentage (40.9 %) of total annual rainfall.

Fieldwork was performed in December 1989, March 1990, January 2001, and May and August 2003. Saguaro populations were sampled using point-centered quarter transects of 700-1500 m length. Sampled points were taken every 50 m, and at each point, the four nearest saguaros were measured for height, diameter, vigor, presence or absence of termite activity (nesting tubes) along their ribs, number of ribs with such activity, and height of termite tubes on saguaro living tissues. We reported saguaro vigor based on tissue color; green tissue was considered healthy, yellow was intermediate, and brownish color unhealthy. For most analyses, saguaros were grouped in three size classes: saplings (up to 1 m), juveniles (1 to 2.5 m) and adults (above 2.5 m). In January 2001, as it was evident that termites were notoriously present on aboveground tissues of a diverse number of desert species, we sampled saguaros and other plant species in the same community for termite activity on living tissues.

At each date, we sampled aboveground nesting tubes for species identification. Although a number of other insect and arthropod species were found along the exfoliating bark tissues at the base of saguaros, we sampled only those found inhabiting the aerial nest remains on saguaro green tissues. Specimens identified as *Heterotermes aureus* (Paul Baker, pers. com.) were collected in August 2003 from aerial nesting tubes on affected green epidermal tissues of saguaro.

We used χ^2 statistical tests to identify the relationship between termite presence and vigor (or browning) in the sampled saguaro populations. Here we report only those analyses performed on data from 1989, 1990 and 2001. We used statistical software to perform our analyses (SPSS, SAS Institute) with a significance level of $p <= 0.05$ (Sokal and Rohlf 1995).

RESULTS

Presence of Termites on Aboveground Green Tissues of Saguaro

Our analysis at the study site focused on saguaros because at our first sampling dates (1989 and 1990) this was the species that conspicuously showed a presence of termites on aboveground living tissues (Figure 2). Presence of termite nesting — tubes were found most frequently in adult and juvenile saguaros and less in saplings, although the height of affected individuals went from a few centimeters to 8 to 10 m (Figure 3). Presence of termites on juvenile saguaros was most frequent in 1989, but not in 1990 when frequency was higher on mature individuals. A comparison between year and age group (Figure 2) resulted in highly significant statistical differences for presence of termites on adult saguaros in each year (1989, $\chi^2 = 15.29$; 1990, $\chi^2 = 27.55$; 2001, $\chi^2 = 25.12$; all significantly different $\chi^2 <= 0.001$).

Termite nesting tubes started at the bottom of saguaros and went, in most cases, up to the

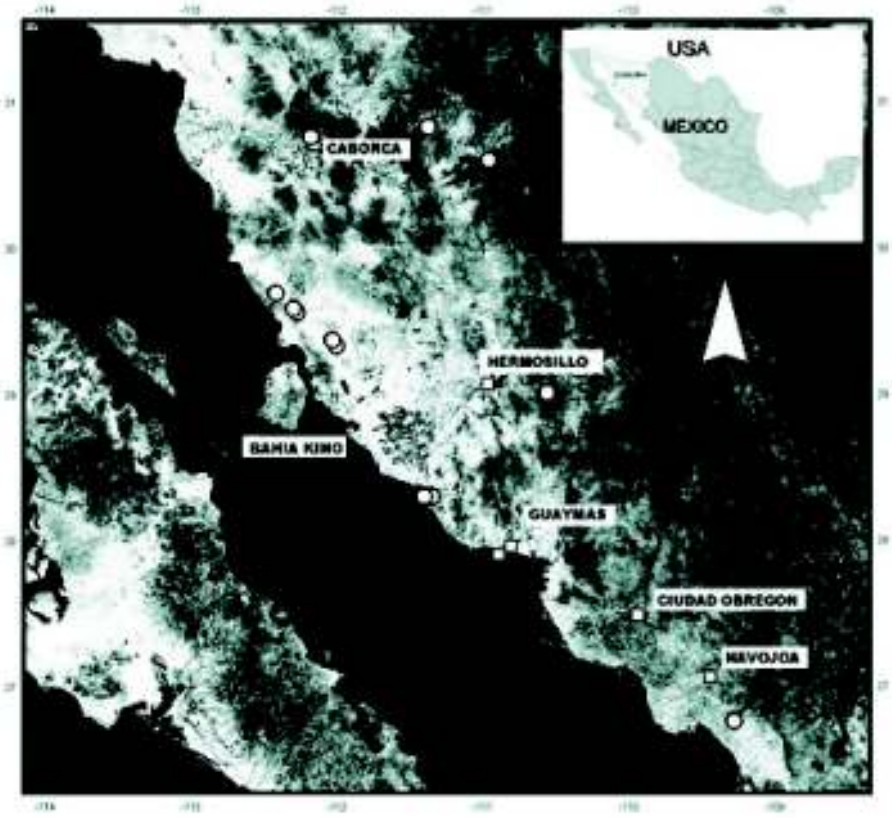

Figure 1. Location of sampled saguaro sites in Sonora (dots). Other locations in Baja California (near La Paz), Mexico and Arizona (east of Casas Grandes), USA, are not shown.

green epidermal tissues. Most adult individuals with termite presence had either some sort of epidermal damage or different degrees of epidermal browning from previous years. In saguaros, height of termite tubes was statistically and significantly correlated with height of browning surface area ($\chi = 0.8041$, $p < = 0.0001$; Table 1), although not all saguaros with browning in their tissues had termite nesting tubes on them, and some healthy saguaros had termites present only in their green living tissues. Healthy saguaros, apparently colonized for the first time by termites, had the shortest height of termite tubes along their ribs. Height of termite tubes was also positively correlated with number of affected ribs ($\chi = 0.7957$, $p < = 0.0001$), and height of saguaro ($\chi = 0.6668$, $p < = 0.0001$).

We did not notice a strong directional component on saguaro termite nesting tubes, although a formal geostatistical analysis was not performed. At our sites about 51% of all sampled individuals were affected by termite activity in 75% or more of their ribs, and a smaller percentage of saguaros had every one of their ribs affected to different degrees (data not shown).

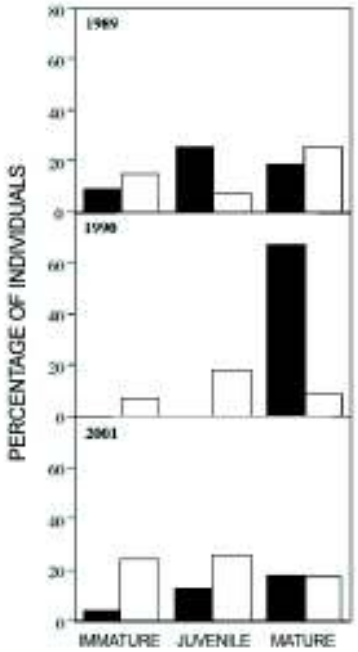

Figure 2. Percentage of saguaros with (black columns) and without (white) termite nesting tubes on aboveground green tissues. Data grouped for three age categories (see text) were significantly different $\chi^2 < 0.001$ in all years (1989, $\chi^2 = 15.29$; 1990, $\chi^2 = 27.55$; 2001, $\chi^2 = 25.12$).

Presence of Termites on Aboveground Tissues of Sonoran Desert Plant Species

We found widespread termite presence on saguaros over a large portion of their distributions in the Sonoran Desert (Figures 1 and 3a, b, c). as well as on *Pachycereus pringlei* (Figure 3d). During the 2001 field season, we also found termites in aboveground tissues of cacti such as cholla (*Opuntia fulgida*; Figure 3e), senita cactus (*Lophocereus schotti*) and pitahaya (*Stenocereus thurberi*; Figure 3f) as well as herbaceous and woody species such as *Fouquieria splendens*, *Ambrosia deltoidea*, *Ambrosia dumosa* and *Encelia farinosa* to name the most conspicuous in our sample (Table 2). In 2001, termites were found as high as 7–8 m in saguaro and cardon (Figures 3c and d).

DISCUSSION

Our study is the first to describe termite presence on aboveground green epidermal tissues of live saguaros. Previous descriptions of termite ecology in North American deserts have been restricted to underground nesting and feeding habits with decayed wood and dead plant materials (Schaefer and Whitford 1981). Termite presence on aboveground live tissue in Sonoran Desert plants has only incidentally been mentioned for species in urban and agricultural environments (Jones and Nutting 1989). There is only anecdotal references for native desert plants like *Opuntia*, *Acacia gregii*, *Dalea* and *Atriplex* (Jones and Nutting, 1989) from other North American deserts. Jones and Nutting (1989) mention that *Paraneotermes simplicicornis* was found on

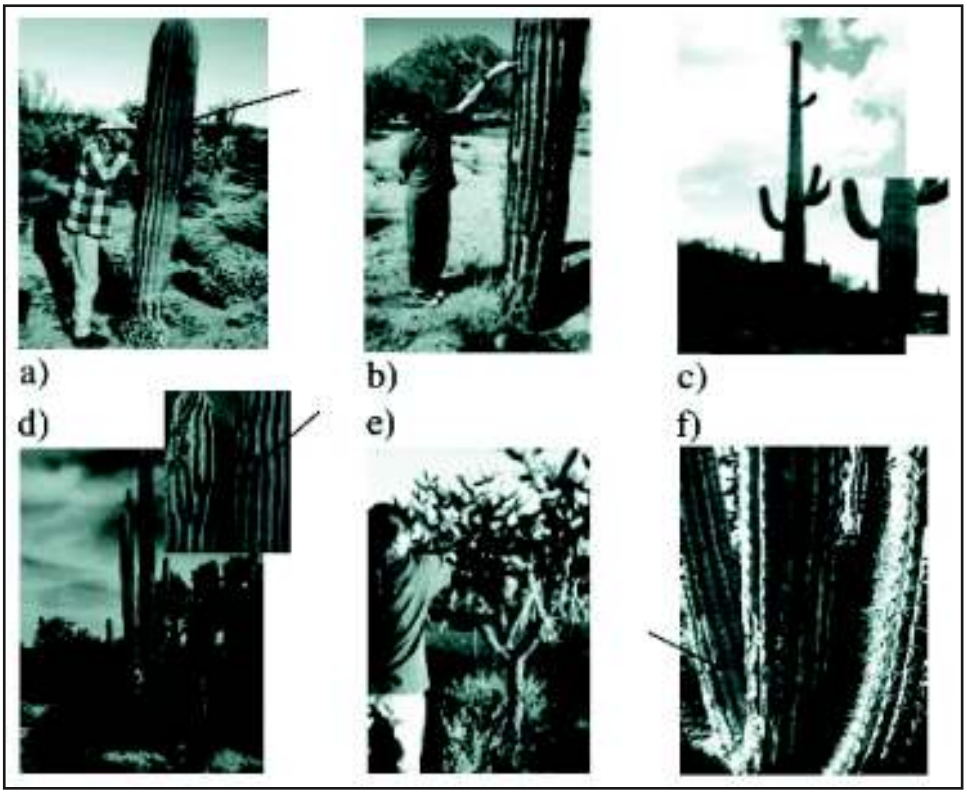

Figure 3. a) Termites along ribs in a young saguaro individual (study site); b) Adult saguaro with termites only on ribs (Organ Pipe Cactus National Monument); Termites can reach considerable heights in saguaro (c) and cardon (d), and have been found in cholla (e) and pitahaya (f) at different localities within the Sonoran Desert.

Table 1. Spearman non-parametric test for Height of termite tubes in live tissues as they correlated with Saguaro height, diameter, number of damaged ribs and height of browning in tissues. Highly statistical significance for $p <= 0.0001$.

Saguaro		ρ	p
Height of termite tubes	Height	0.6668	< .0001
	Diameter	0.2958	0.0206
	Damaged ribs	0.7957	< .0001
	Browning height	0.8041	< .0001

Table 2. Number and presence percent of termite tubes on live tissue of trees, shrub and sub-shrub species at the study site. Data are from three transects (900 * 2 m each) made in 2001.

Species	Termite presence %	Sample n
Trees		
Cercidium microphyllum	25.0	4
Olneya tesota	0	6
Shrubs		
Fouquieria splendens	54.4	54
Ambrosia dumosa	33.3	57
Lippia palmeri	28.6	14
Ambrosia deltoidea	23.3	129
Condalia globosa	16.7	12
Encelia farinosa	15.4	78
Hyptis emoryi	9.5	21
Krameria parvifolia	5.1	39
Larrea tridentata	0	33
Lycium spp	0	5
Jatropha cinerea	0	8
Cacti		
Ferocactus wislizenii	90.0	10
Pachycereus pringlei	68.5	89
Lophocereus schotti	49.1	57
Stenocereus thurberi	42.4	59
Carnegiea gigantea	33.5	243
Opuntia fulgida	25.9	27
Opuntia leptocaulis	46.7	15

cactus skeletons of chollas and *Carnegiea gigantea* (saguaro), but not on their live tissues.

Termites and Disturbance

Termite presence on living saguaro and aboveground tissues of desert species may be increasing within the Sonoran Desert. At our site in 1989, termites were noticed only on saguaro, but by 2003, they were present on shrubs and other cactus species (Table 2). Termites may not have been previously noticed on saguaro because termite tubes persist for only a short period of time during fall and early winter, they are washed away with light winter rains. Although termite activity typically ceases when temperatures are cooler than 9° C (Ueckert et al. 1976), we have no data on the physiological constraints of the species we found in our study. Given the large variability in the amount and distribution of termite presence in aboveground tissues in different years, it is possible that soil moisture and air temperature are factors that influence termite nesting tube presence.

There are a number of possible causes that may be influencing the increase of termite presence in aboveground tissues of plant species from Sonoran Desert ecosystems. Change in temperature and rainfall patterns either human (land-use change) or climatically (global change) induced may be important factors for increased termite activity aboveground. Termite activity increases during wet

years (Bodine and Ueckert 1975) and with anthropogenic disturbance. Increased abundance of certain termite functional types has been noticed in deserts and the tropics after vegetation disturbance (Black and Okwakol 1997; Davies et al. 2003). In the tropics, disturbance has lead to termites nesting in the stems of live plants (Hegh 1922), often associated with sites with poor soil nutrient conditions (Black and Okwakol 1997).

Human disturbance is increasingly widespread in the Sonoran Desert. The plant communities at the sites we studied have been increasingly decimated in their populations of keystone species such as *Prosopis* spp (mesquite) and *Olneya tesota* (ironwood), which have been selectively and heavily harvested for fencing, firewood, charcoal, and crafts. Over the last 15-20 years, charcoal has dramatically increased as a profitable domestic and export business. The statistics on wood and charcoal production from our study region are unreliable, however there is evidence that extraction levels are considerable (Taylor 2006). Given the low rate of establishment and slow growth of desert trees, overexploitation of these key species is to be expected after a few years (Suzán et al. 1997), as shown in the absence or almost complete absence of these species from our vegetation sampling (Table 2). We think that as wood removal increases to meet demand, physical and biotic processes affected by diminished litter and dead material, such as termite dynamics, may become disrupted. Wood extraction may affect primary productivity, availability and seasonality of wood litter presence, alter decomposition dynamics (Nash et al. 1999), and indirectly alter termite behavior, perhaps triggering increased aboveground presence in saguaro and other desert plants. If this is the case, we should be seeing increased termite activity in areas where land-use patterns cause impoverished litter and dead root biomass input to the soil. We know very little about the causes and ecological and functional implications of aboveground termite activities.

Other natural or human-induced changes in rainfall and land cover may be responsible for increasing aboveground termite presence on other desert species (Table 2). Increased variability in temporal rainfall patterns and increasing temperatures will occur as global change progresses. Climate models for Sonoran Desert predict an increase in rainfall and temperatures during the autumn-winter season (SRAG 2000). Because termite activity increases with late summer and fall precipitation at our sites, a change in rainfall patterns and increased temperatures during fall and winter seasons could be already happening and help explain the increased presence of termites on live plant tissues over the years, and on saguaro and cardon from many distant locations from Baja California, Arizona (Castellanos, pers. obs.), and islands of the Gulf of California (Castillo, pers. obs.) in the Sonoran Desert.

Termites and Saguaro Browning

Presence of termites on living saguaro epidermal tissues has not been described and the consequences of their presence on saguaro physiology and population dynamics is yet unknown. We found however, important similarities between our observations of termite visible effects to living epidermal tissues of saguaro with those described as first occurring for epidermal browning (Turner and Funicelli 2000). We propose that termite effects on saguaro green epidermal tissues and epidermal browning may be related phenomena. At our study site, termite presence was correlated with some of the characteristics of tissue damage that had been ascribed to epidermal browning (Table 1). Compared to healthy saguaros with no spine damage (Figure 4a), spines with termite nesting tubes (Figure 4b) showed signs of loosening first the middle spine and damage at the base of the spine areole and along the rib (Figures 4b and c), with total spine loss apparently after several events. Spine loosening and fall is a first sign of saguaro browning (Turner and Funicelli 2000).

We observed other similarities between termite effects on saguaro epidermal tissues and saguaro browning. Browning spreads from ribs to adjacent epidermal tissues, a pattern

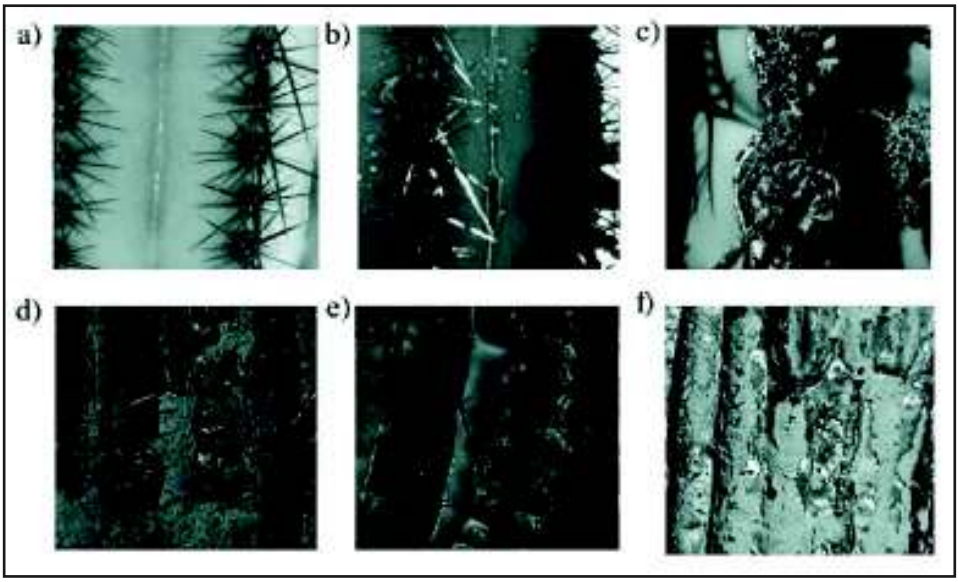

Figure 4. Saguaro browning correlates with termite activity. Healthy saguaro ribs and spines (a); Termite tubes along spines (b); Spine damage after termite presence (c); Termite damage spread to green tissue (d) (tubes were removed from region in the center of the photography to expose the kind of termite damage); Spread of termite tubes to all saguaro ridges and aerial tissues (e); Saguaro epidermal browning (f). Photographs were taken in 2001

similar to that found with termites initially climbing only along ribs and progressively spreading to adjacent green tissues (Figure 4d). Damage induced each year, either physically or possibly as a wounding response, will allow termites to spread further from lignified spines over the next years (Figure 4d). Progressive effects spreading from spine ribs to epidermal tissues (Figures 4c, d, and e) were associated with termites, with symptoms very similar to what has been reported for epidermal browning (Figure 1 in Turner and Funicelli 2000). During years with high termite aboveground activity, browning and termites were related phenomena as found in browned saguaros with termites spread all over them (Figure 4f). Since aboveground termite presence on epidermal tissues of saguaros differs from year to year (Figure 2), spread and damage may take decades.

Epidermal browning in saguaro does not yet have a known definitive causal agent. Several physical variables such as freezing (Steenbergh and Lowe 1977), air pollution (Stolte 1992), heat and UV-B load (Evans et al. 1994b; Evans et al. 1992; Turner and Funicelli 2000) have been proposed as causes of saguaro epidermal browning. Increased heat and UV-load on southern exposure saguaro stems seem to be related to the directional effects of browning found in some saguaro populations of the northern Sonoran Desert region (Evans et al. 1994a; Evans et al. 1992; Turner and Funicelli 2000). Termite effects on saguaros were visually well correlated with most previously described symptoms of saguaro browning. The symptoms we uncovered under termite nesting tubes on spines (Figure 4b), and scars left on epidermal tissues (Figure 4e), were similar to those previously associated with browning

(Turner and Funicelli 2000) and tissue hardening and lignifications of saguaro epidermal tissue (Evans et al. 1994b; Olson 2000). Although we did not specifically measure directional effects, at our sites there were no obvious directional patterns in the epidermal browning on saguaro tissues, since more than 75% of ribs were affected in at least 51% of affected adult saguaros. Some of the studied sites are at more southern, non-freezing latitudes and in regions with warmer temperatures than the locations where directional effects have been reported (McAuliffe 1993). If directional effects are present at more northern latitudes of saguaro distribution, that wouldn't cancel the possibility that increasing heat loads may benefit termite activity and aboveground growing conditions or that both effects could be related. Spine loss may diminish the cooling effects on epidermal tissues, and increase heat load, but this should be tested. As an end result, saguaro browning decreases photosynthetic carbon gain, and induces a positive feedback loop of diminishing physiological performance (Lajtha et al. 1997), inducing an early senescence process.

Termites and Sonoran Desert Ecosystem

In this paper we have described a previously undocumented and seemingly increasing phenomena of termite presence on aboveground plant species in the Sonoran Desert. We think that presence of termites aboveground may be an early warning signal that important changes are happening in Sonoran Desert ecosystems, and here we bring some evidence that such phenomena will be playing an increasingly important role in shaping the structure and function of species and ecosystems in this North American desert.

It is of outmost importance to determine the ecological and environmental factors that have enabled termites to spread aboveground, and to understand the ecological consequences of this increased termite activity. As a small glimpse of what could happen, we are amazed that such a sturdy plant as saguaro, a plant that can withstand years and possibly centuries of stressful physical conditions, may be so greatly affected by a small, almost inconspicuous insect.

ACKNOWLEDGMENTS

AECV acknowledges support from CONACYT in the form of research and sabbatical grants and David Williams and SAHRA at the University of Arizona for providing a stimulating atmosphere while on sabbatical. Iván Parra and José Llano helped with fieldwork. Paul Baker, University of Arizona, helped with taxonomic identification of termites. Alejandro Nava helped with Figure 1. Francisco Molina-Freaner, Richard Felger and other anonymous reviewers provided helpful comments on earlier drafts. We thank Laura Hoffman for greatly improving our English.

LITERATURE CITED

Alcorn, S. M., C. May, 1962. Attrition of a saguaro forest. Plant Disease Reporter 46: 156–158.

Allen, C. T., D. E. Foster, and D. N. Ueckert, 1980. Seasonal food habits of a desert termite, *Gnathamitermes tubiformans* in West Texas. Environmental Entomology 9: 461–466.

Black, H. I. J., and M. J. N. Okwakol, 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: The role of termites. Applied Soil Ecology 6: 37–53.

Bodine, M. C., and D. N. Ueckert, 1975. Effect of desert termites on herbage and litter in a shortgrass ecosystem in West Texas. Journal of Range Management 28: 353–358.

Brown, D. E., 1982. Biotic communities of the American Southwest—United States and Mexico. Desert Plants 4: 1–342.

Davies, R. G., L. M. Hernández, P. Eggleton, R. K. Didham, L. L. Fagan, and N. N. Winchester, 2003. Environmental and spatial influences upon species composition of a termite assemblage across neotropical forest islands. Journal of Tropical Ecology 19: 509–524.

Duriscoe, D. M. and S. L. Graban. 1992. Epidermal browning and population dynamics of giant saguaros in long-term monitoring plots. In Proceedings of the symposium on research in Saguaro National Monument, edited by C. P. Stone and E. S. Bellantoni, pp. 237–257. National Park Service Cooperative National Park Resources Studies Unit, School of Renewable Natural Resources, University of Arizona, Tucson, AZ.

Evans, L. S., V. A. Cantarella, L. Kaszczak, S. M. Krempasky, and K. H. Thompson, 1994a. Epidermal browning of saguaro cacti (*Carnegiea*

gigantea): Physiological effects, rates of browning and relation to sun/shade conditions. Environmental and Experimental Botany 34: 107–115.

Evans, L. S., V. A. Cantarella, K. W. Stolte, and K. H. Thompson, 1994b. Epidermal browning of saguaro cacti (*Carnegiea gigantea*): Surface and internal characteristics associated with browning. Environmental and Experimental Botany 34: 9–17.

Evans, L. S., K. A. Howard, and E. J. Stolze, 1992. Epidermal browning of saguaro cacti (*Carnegiea gigantea*): Is it new or related to direction? Environmental and Experimental Botany 32: 357–363.

Evans, L.S., V. Sahi, and S. Ghersini, 1995. Epidermal browning of saguaro cacti (*Carnegiea gigantea*): Relative health and rates of surficial injuries of a population. Environmental and Experimental Botany 35: 557–562.

Hegh, E., 1922. Les Termites, partie générale. Description.—Distribution géographique.—Classification.—Biologie.—Vie sociale.—Alimentation.—Constructions.—Rapports avec le monde extérieur. Impr. industrielle & financiére, Bruxelles.

Jones, S. C., and W. L. Nutting, 1989. Foraging ecology of subterranean termites in the Sonoran Desert. In Special biotic relationships in the arid southwest, edited by J. O. Schmidt, pp. 79–106. University of New Mexico Press, Albuquerque, NM.

Lajtha, K., K. Kolberg, and J. Getz, 1997. Ecophysiology of the saguaro cactus (*Carnegiea gigantea*) in the Saguaro National Monument: Relationship to symptoms of decline. Journal of Arid Environments 36: 579–590.

McAuliffe, J. R., 1993. Case study of research, monitoring, and management programs associated with saguaro cactus (*Carnegiea gigantea*) at Saguaro National Monument. Technical Report NPS/ WRUA/NRTR-93-01. National Park Service Cooperative National Park Resources Studies Unit, School of Renewable Natural Resources, University of Arizona, Tucson, AZ.

Nash, M. S., J. P. Anderson, and W. G. Whitford, 1999. Spatial and temporal variability in relative abundance and foraging behavior of subterranean termites in desertified and relatively intact Chihuahuan Desert ecosystems. Applied Soil Ecology 12: 149–157.

Olson, C. A., 2000. Insects and the saguaro. In A natural history of the Sonoran Desert, edited by Arizona-Sonora Desert Museum, pp. 353–356. University of California Press.

Schaefer, D., and W. G. Whitford, 1981. Nutrient cycling by the subterranean termite *Gnathamitermes tubiformis* in a Chihuahuan desert ecosystem. Oecologia 48: 277–283.

Shreve, F., and I. L. Wiggins, 1964. Vegetation and Flora of the Sonoran Desert. Stanford University Press.

Smith, R. L., 2000. Termites. In A natural history of the Sonoran Desert, edited by Arizona-Sonora Desert Museum, pp. 316–319. University of California Press.

Sokal, R. R., F. J. Rohlf, 1995. Biometry. W. H. Freeman, New York.

Spears, B. M., D. N. Ueckert, T. L. Whigham, 1975. Desert termite control in a shortgrass prairie: Effect on soil physical properties. Environmental Entomology 4: 899–904.

SRAG (Space Radiation Analysis Group), 2000. Preparing for a changing climate. The potential consequences of climate variability and change. In Preparing for a changing climate: The potential consequences of climate variability and change, edited by NOAA, ISPE, and USGS, p. 60. Tucson, AZ.

Steenbergh, W. F., and C. H. Lowe, 1969. Critical factors during the first years of life of the saguaro (*Carnegiea gigantea*) at Saguaro National Monument, Arizona. Ecology 50: 825–834.

Steenbergh, W. F., and C. H. Lowe, 1977. Ecology of the saguaro. II. Reproduction, germination, establishment, growth and survival of young plant, p. 242. U.S. Government Printing Office, Washington, D.C.

Stolte, K.W., 1992. Air pollution threats to biological resources in Saguaro National Monument. In Air pollution threats to biological resources in Saguaro National Monument, edited by C. P. Stone, and E. S. Bellantoni, pp. 217–222. Southwest Parks and Monuments Association, Tucson, AZ.

Suzán, H., D. T. Patten, and G. P. Nabhan, 1997. Exploitation and conservation of ironwood (*Olneya tesota*) in the Sonoran Desert. Ecological Applications 7: 948–957.

Taylor, M. J., 2006. Biomass in the borderlands: Charcoal and firewood production in Sonoran ejidos. Journal of the Southwest 48: 63–90.

Turner, D. S., and C. S. Funicelli, 2000. Ten-year resurvey of epidermal browning and population structure of saguaro cactus (*Carnegiea gigantea*) in Saguaro National Park. Technical Report 69, U.S. Geological Survey, Sonoran Desert Field Station, University of Arizona, Tucson,AZ.

Turner, R. M., 1990. Long-term vegetation change at a fully protected Sonoran Desert site. Ecology 71: 464–477.

Turner, R. M., S. M. Alcorn, and G. Olin, 1969. Mortality of transplanted saguaro seedlings. Ecology 50: 834–844.

Turner, R. M., S. M. Alcorn, G. Olin, and J. A. Booth, 1966. The influence of shade, soil and water on saguaro seedlings establishment. Botanical Gazette 127: 95-102.

Ueckert, D. N., M. C. Bodine, and B. M. Spears, 1976. Population density and bio-mass of the desert termite *Gnathamitermes tubiformans* (Isoptera: Termitidae) in a shortgrass prairie: Relationship to temperature and moisture. Ecology 57: 1273–1280.

Whitford, W. G., 2002. Ecology of Desert Systems. Academic Press, San Diego, CA.