

**Long-term vegetation monitoring at
Saguaro National Park:
a decade of change**

Carianne S. Funicelli

Pamela J. Anning

Dale S. Turner

Technical Report _____

November 2000

United States Department of the Interior
National Park Service
Saguaro National Park
3693 South Old Spanish Trail
Tucson, Arizona 85730

Authors

Carianne S. Funicelli
Pamela J. Anning
Dale S. Turner
Saguaro National Park
3693 South Old Spanish Trail
Tucson, Arizona 85730

Contents

List of Figures.....	v
List of Tables.....	vi
Acknowledgements.....	vii
Abstract.....	viii
Introduction.....	1
Study Area.....	2
Methods.....	3
Results.....	9
Discussion.....	21
Recommendations.....	25
Literature Cited.....	26
Appendix 1. Corrections to 1990 Data.....	29
Appendix 2. Vegetation Map Examples	
a. 1990.....	34
b. 2000.....	35
Appendix 3. Summary Statistics for Canopy Cover of Species on all Plots at RMD in 1990.....	36
Appendix 4. Summary Statistics for Species Density on all Plots at RMD in 1990.....	38
Appendix 5. Summary Statistics for Canopy Cover of Species on all Plots at TMD in 1990.....	40
Appendix 6. Summary Statistics for Species Density on all Plots at TMD in 1990.....	42
Appendix 7. Summary Statistics for Canopy Cover of Species on all Plots at RMD in 2000.....	44

Appendix 8. Summary Statistics for Species Density on all Plots at RMD in 2000.....	46
Appendix 9. Summary Statistics for Canopy Cover of Species on all Plots at TMD in 2000.....	48
Appendix 10. Summary Statistics for Species Density on all Plots at TMD in 2000.....	50
Appendix 11. Total Change in Species Cover 1990 to 2000.....	52
Appendix 12. Total Change in Species Density 1990 to 2000.....	54
Appendix 13. Environmental Variables Measured on all Plots.....	56

Figures

Figure 1. Saguaro National Park (TMD) seasonal precipitation 1986 to 1999.....	2
Figure 2. Plot locations.....	4
Figure 3. Cover trend by species at RMD 1990 to 2000.....	12
Figure 4. Cover trend by species at TMD 1990 to 2000.....	13
Figure 5. Density trend by species at RMD 1990 to 2000.....	14
Figure 6. Density trend by species at TMD 1990 to 2000.....	15

Tables

Table 1. Summary of diversity, cover, and density by district for 1990 and 2000.....	10
Table 2. District-wide species change in density and cover 1990 to 2000.....	16
Table 3. Species that changed more on a given plot than the mean change for the district.....	18
Table 4. Grass species encountered in 2000.....	19

Acknowledgements

This project was made possible by a generous grant from Canon USA, Inc., through the National Park Foundation. Mark Holden and Pam Anning were responsible for writing the successful grant proposal. Additional support was provided by the Friends of Saguaro National Park, Southwest Parks and Monuments Association, and Earth Friends.

Many people contributed to the gathering, entering, and checking of data. From Saguaro National Park, these included: Austin Aslan, Lisa Carder, Louise Conrad, Andrew Farkas, Danielle Foster, Mark Holden, Donna King, Natasha Kline, Janis Koscielniak, Paula Nasiatka, Pamela Nicola, Katie Pencke, Keshari Thakali, Cris Trotter, and Meg Weesner.

Mohamad Chakaki, a volunteer with the Student Conservation Association, added tremendously to this effort. Other volunteers included: Devon Biggs, George Daher, and Al Mezzano.

Special thanks to Kathy Schon, for the use of her ARC/INFO workstation and office space. Also to Ron Beckwith at The Western Archaeological Conservation Center for training in the use of the plane table and alidade, as well as equipment for the project. Meg Weesner helped with the last minute conversion of files into a compatible format for analysis. Our data analysis benefited greatly from discussions with Dave Anning, Tom Orum, Nancy Ferguson, Ray Turner, and Qinfeng Guo. This report was improved by reviews by Tom Orum and Ray Turner.

Abstract

Permanent vegetation subplots allow a variety of insights into long-term community dynamics. This project at Saguaro National Park involved revisiting vegetation plots established ten years ago. All perennial species were mapped on each of 45 small plots, 10x10 m, randomly located throughout the Sonoran desertscrub vegetation community of both districts of the park. Vegetation maps were analyzed for differences in species composition, density, and cover during the past decade. *Calliandra eriophylla* and *Janusia gracilis* increased significantly at both the Rincon Mountain District (RMD) and the Tucson Mountain District (TMD) in cover and density values. The only species showing significant decline in cover and density was *Menodora scabra* (RMD only). Total mean cover and density values increased dramatically over the past decade at both districts. Non-native grass invasion increased from 2 species on 14% of the vegetation subplots to 5 species (*Bromus rubens*, *Eragrostis lehmanniana*, *Pennisetum ciliare*, *Rhynchelytrum repens*, and *Schismus arabicus*) on 18% of the vegetation subplots surveyed. Similar vegetation plots have been maintained for most of the past century at the University of Arizona's Desert Laboratory on nearby Tumamoc Hill; our effort will greatly expand the sample size and distribution for this work.

Introduction

Vegetation communities are dynamic entities, but for long-lived species, changes may not be perceptible for many years. Thus, long-term monitoring may be required to understand the responses of some plants to various disturbances and changing climatic conditions. This is certainly the case in the Arizona Upland subdivision of the Sonoran Desert (Brown 1994), where the defining species, the saguaro (*Carnegiea gigantea*), can live up to 200 years. The most informative way to capture such responses is to repeatedly map and analyze communities on permanent vegetation plots. Kuchler (1967) recognized the value of this approach several decades ago: “The appearance and spread of some species or the disappearance of others can be observed and followed, and measured with a degree of accuracy that would be unthinkable without such vegetation maps...The recognition of the dynamic features of the vegetation is very useful. It not only permits an appreciation of what is going on in the landscape and where a situation is headed; it also permits [the ecologist] to avoid mistakes that might have serious consequences if applied to some aspects of land use.”

Despite the irrefutable value of long-term monitoring of vegetation dynamics, studies of this kind have been few and far between in the Sonoran Desert. In the notable exception, Goldberg and Turner (1986) report vegetation change on 9 permanent plots at Tumamoc Hill in Tucson, Arizona, that have been mapped at irregular intervals over the course of 72 years. This sort of long-term monitoring requires cooperation and commitment between researchers over decades, a considerable undertaking. Long-term vegetation monitoring at Saguaro National Park will build upon the data collected at Tumamoc Hill in several ways: many more permanent vegetation subplots (45 in all) have been installed, representing a wider variety of microhabitats and vegetation communities and, because these vegetation subplots are to be maintained indefinitely by the National Park Service, the mapping interval is intended to remain consistent, every 10 years.

The baseline data for this study were collected in 1989 and 1990 in conjunction with a study that the National Park Service initiated to quantify the health and population structure of the park's saguaro cacti. The objective for the establishment of permanent “ecological plots” was to monitor community dynamics by mapping perennial plant species (Duriscoe and Graban 1991, 1992). This study examines the changes that have occurred in the first decade since the original maps were made. Specific variables investigated include: species composition, canopy cover, and plant density. This study will yield information about the recruitment and mortality of native species, invasion of non-native species, and potential effects of wildfire.

Study Area

The study area was within Saguaro National Park, which consists of two districts separated by the city of Tucson, Arizona. The Rincon Mountain District (RMD) is located to the east of

Tucson, and the Tucson Mountain District (TMD) is located to the west. Vegetation subplots were located within the Arizona Upland subdivision of the Sonoran Desert, which comprises about 20% of the area at RMD and 90% of TMD (the remaining 10% is desert grassland) (Martin et al. 1998). This Subdivision is characterized by a diversity of cacti associated with leguminous trees, with a variety of shrubs in the understory (Brown 1994). RMD ranges in elevation from 820 – 2,640 meters and contains many other vegetation types besides the lower-elevation desertscrub to which this study is limited. TMD ranges in elevation from 670 – 1,428 meters (Martin et al. 1998).

Annual rainfall at RMD and TMD averages 30 – 35 cm. Most of the precipitation occurs in 2 distinct wet seasons: a summer wet (“monsoon”) season from July to September, and a winter wet season from November to April (Rondeau et al. 1996). Figure 1 presents precipitation data for the past 14 years at TMD; summarized data were unavailable for RMD at low elevation.

Precipitation patterns during the year just prior to both mapping events are very similar, with moderately high summer precipitation followed by relatively low winter precipitation. However, during the mapping events, conditions in 1999-2000 were the inverse of those in 1989 – 1990. Ten years ago, the mapping event spanned a period with low summer precipitation and moderate precipitation in the winters; but during the current study, there was moderate-high summer precipitation and low winter precipitation.

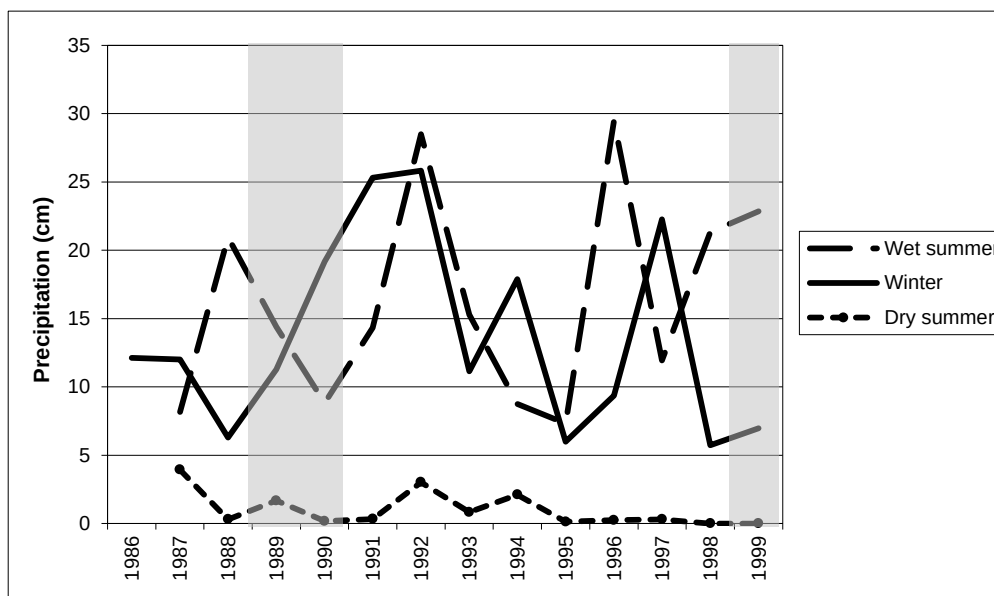


Figure 1. Seasonal precipitation at TMD 1986 through 1999. Shaded areas represent the mapping events.

Methods

Data were obtained from 45 long-term monitoring vegetation plots (including 25 vegetation plots at RMD and 20 at TMD; Fig. 2), each 10 x 10 m. These vegetation plots are embedded within the larger 4-ha plots that were randomly placed in 1989 to measure saguaro population demographics (Duriscoe and Graban 1991,1992). Within each of the 4-ha plots, 30 saguaros

were tagged for long-term study, one of which was randomly selected in 1989 to become the fixed center of a vegetation plot (hereafter referred to as “plot”).

Monitoring photographs were taken of the center saguaros, including surrounding vegetation in the plots, from the south side with Kodachrome 64 color transparency film in 35mm format, using a 28-70 mm zoom lens. These photographs were part of the 10-year follow-up of the saguaro population study and were archived at the Western Archeological Conservation Center (WACC) along with all materials associated with that study (Turner and Funicelli 2000).

All perennial vegetation (excluding grasses, ferns and fern allies) with any canopy cover located within the plot was mapped in the field using a plane table and alidade, with an empirically estimated accuracy of ± 10 cm. Nomenclature follows Bowers and McLaughlin (1987) and Rondeau et al. (1996). The plane table was usually located along the plot border on the flattest piece of ground offering the most unobstructed view of the vegetation in the plot. Plants were plotted on each field map using the alidade and a meter tape to obtain azimuth and distance values in relation to a set datum point. When necessary, multiple datum points were employed to ensure a clear view of the vegetation being mapped.

Plants with irregularly shaped canopies were mapped by recording a series of points representing the vertices of the canopy, which were then connected to form a polygon. Points were also mapped to represent plant stems. Many of the common Sonoran Desert shrubs have a very regular, rounded growth form; these plants were mapped by recording the stem location and measuring the canopy radius. Later, canopy cover was obtained using the circle generated by the radius measurements. We also made visual estimates of canopy cover for all perennial grass species, as well as ferns and fern allies over the plot as a whole.

The resulting field maps were digitized and analyzed using ArcInfo 8.0 and Arcview 3.1 Geographic Information System (GIS) software. Polygons representing plant cover were digitized and merged with the circles generated from the radius measurements to form a complete picture of canopy cover. The total cover of each species was summed for each plot. Areas of same-species overlap were counted only once. Polygons were also counted to determine species density.

In order to assess regional changes in cover per species over the past decade, each species was assigned a trend value (1, 0, or -1) per plot to indicate the direction

Figure 2

(increase, no change, or decrease, respectively) of change. For example, on plot 20, the cover of *Abutilon incanum* was 0.115 m² in 1990, and increased to 5.985 m² in 2000. *Abutilon incanum* was therefore assigned a trend value of “1” for plot 20, to indicate a net increase in cover. These values were summed for all plots to calculate the overall trend in cover and density of each species at RMD and TMD. Using this system, a species would be assigned a negative trend value if its cover or density declined on more plots that it increased on. Mapping error could artificially show an increase or decrease in cover: for instance, due to the estimated accuracy of +/- 10 cm of the alidade and plane table, accumulated error on the perimeter of several individuals could result in a positive or negative trend value when no real change has occurred. To account for these possible map errors, the trend values were assigned “no change” when: 1)

the difference in cover values between 1990 and 2000 were between 0.1m^2 and -0.1m^2 or, 2) the percent of change in cover between 1990 and 2000 was less than 5%.

Species cover and density data were analyzed for significant changes between 1990 and 2000 with the Wilcoxon Signed Rank Test (JMP-IN 3.2.1.), an analog to the Paired T-Test designed for use with non-parametric data. Significance was determined at the $p < 0.10$ level, because we felt that the standard default p-value of 0.05 does not allow for enough natural variability (Yoccoz 1991).

To analyze change on a localized plot to plot basis, the difference of cover and density for each species from 1990 to 2000 on each plot was expressed in standard deviations from the mean performance of the species over all plots in the district. For example, the following equation was used to determine if the change for an individual species was within 1, 2 or greater than 2 standard deviations from the mean. This pinpointed plots that exhibited more change than others based on the mean change per district. Plots with changes for a species greater than 2 standard deviations from the mean were considered “extreme,” and received further analysis. This was repeated for species richness to compare which plots may be gaining or losing species.

$$\frac{\text{difference} - \text{mean difference}}{\text{standard deviation}}$$

difference = species A (2000) – species A (1990)

mean difference = the mean of differences for species A for all plots where
species was present within each district

standard deviation = the standard deviation of species A for all plots where
..... specie
s was present within each district

To explore the relationship and influence of environmental variables on species distribution, a principle components analysis (JMP-IN 3.2.1) was conducted for both species cover and density. The environmental variables tested include: slope, aspect, elevation, microsite, and topography.

Deviations from original study and challenges encountered

We strove to replicate the methods of Duriscoe and Graban (1991) in order to acquire data that were comparable. However, to ensure that future iterations of this long-term monitoring project remain consistent, we felt it necessary to make some changes and clarify protocols that were previously vague or problematic.

Plot Boundaries

When the plots were installed ten years ago, the corners of most plots were not permanently marked for future reference. It is imperative that the boundaries of long-term monitoring plots be

permanently marked for ease of relocation and, more importantly, consistency of the area surveyed. We placed rebar stakes with aluminum caps labeled “subplot” at the corners of the plots as accurately as possible based on measurements from the center saguaro and interpolation from the vegetation on previous plot maps. Location data were obtained for the corner locations using a Trimble GeoExplorer II GPS unit at the high accuracy (carrier phase) setting, which generates locations to sub-meter accuracy. These 4 positions were used to register the field maps to real-world coordinates for GIS analysis. GPS location data were also obtained for the center saguaros of all vegetation subplots, but this was done using Coarse/Acquisition Code (1 – 4 m accuracy).

Slope is a confounding factor in creating square plots exactly 100 square meters and amplifies the necessity of permanent corner markers. When slope is extreme, or plot topography diverse, 10 meters as measured with a horizontal tape corresponds to greater than 10 meters on the ground. For this reason the edges of the vegetation subplot may be unequal in true ground distance resulting in a permanent plot that is not perfectly square and greater than 100 square meters in total surface area. Topography and extreme slope also push the limits of the alidade and plane table method, affecting the accuracy of mapping and compounding the asymmetric shape of many of the plots. This is a departure from the approach of Duriscoe and Graban (1991, 1992), whose final maps show the plots to be exactly square. The final maps generated in this survey were not adjusted in that manner. The plot corners are located precisely as shown on the field maps, and although the resulting boundaries of the plots are not square, they are consistent with the actual boundaries as defined in the field.

Any error generated from boundary movement between the 1990 and current iteration of this study should not be repeated in subsequent mapping events now that the corners are fixed and permanent.

Cover Calculations

Canopy cover is the vertical projection of the crown area of a species to the ground, as visualized by considering a bird’s-eye view of the vegetation (Elzinga et al. 1998, Mueller-Dombois and Ellenberg 1974). During field mapping, we often used this definition to justify specific mapping decisions. In most instances, each individual plant canopy was mapped. However, it was sometimes more efficient to group overlapping individuals of the same species. For example, if multiple individuals of *Celtis pallida* were growing together in such a way that part of their individual canopies overlapped, it is likely that we mapped one perimeter and several stems, if that would be more efficient than mapping each canopy individually. This was justifiable, because in calculating species cover values, we would be removing the same-species overlap.

However, upon close examination of the 1990 maps it became apparent that Duriscoe and Graban (1991, 1992) had calculated cover values *including* same-species overlap. In order for our data to be comparable, we retrieved their AutoCad (.dwg) files, converted them to ARC/INFO 8.0 format, and recalculated the 1990 cover values with the same-species overlap removed. In addition, we encountered several errors in the maps of the original study, both while in the field and in the conversion of the AutoCad files to ArcView and ARC/INFO files. We corrected all errors that we encountered, and used the corrected information for comparisons in this report.

Species Density

The species density values that we report represent our best interpretation of the number of individual plants per species, per plot, and are consistent with the densities generated by Duriscoe and Graban (1991, 1992). These values do not necessarily correspond to the number of stems or the number of polygons per species, per plot, for many reasons. First, many species can produce multiple stems per individual (i.e. *Larrea tridentata*, *Calliandra eriophylla*). It is often difficult in the field to determine what constitutes an individual plant; we followed the methodology of Goldberg and Turner (1986) in this case, treating a clump of vegetation with closely clustered stems as an individual. In these cases, the number of polygons represents the number of individuals of a species.

On the other hand, some species, such as *Janusia gracilis*, tend to grow in same-species clumps of well-defined individuals. These situations were usually most efficiently mapped with one canopy and many stems, and therefore the number of stems represents the number of individuals.

Plants along the plot boundaries illustrate another discrepancy between stem density and actual number of individuals. Often, the plant would be rooted outside of the plot, but the canopy would extend into the plot. In this case, the polygon would be counted as an individual.

Newly Included Species

We report on several species that were not included in Duriscoe and Graban (1991, 1992) due to absence or differences in the degree of mapping. One major addition was the inclusion of ferns and *Selaginella arizonica* in the visual estimates of cover (same as perennial grass protocol). These non-seed plants are a significant component of the flora and important indicators of microsite conditions, especially on the rocky slopes of RMD.

Ayenia filiformis and *A. microcarpa* were included on a few of the 1990 maps; however, it seems that the Duriscoe and Graban (1991, 1992) documentation of these sometimes inconspicuous perennial forbs was inconsistent. We observed one or both of these plants on several plots in high density where the 1990 map showed absence; it seems unlikely that *Ayenia* spp. were completely absent in 1990, and made such a vigorous invasion in the past decade. We made a very thorough effort to get accurate coverage and density values for these species in every plot in which they were present. Future iterations of this study should clarify recruitment and mortality patterns, as well as density and cover fluctuations.

There are a few perennial species that were present, but intentionally not mapped either in 1990 or 2000. These include *Phoradendron californicum*, *Euphorbia polycarpa*, *Allionia incarnata*, *Marina parryi* and *Evolvulus arizonicus*. As a parasitic plant hosting on desert tree species, *Phoradendron californicum* does not root itself in the ground, and thus presents a mapping challenge. The other above-mentioned species fluctuate widely by season in regard to size and growth form.

Results

1990

All analyses presented here use re-calculated cover values (with same-species overlap removed); the corrected values for the 1990 maps are listed in Appendix 1. The following summary statistics for cover and density at RMD and TMD in 1990 are presented in Appendices 3 – 6: N, mean, standard deviation, coefficient of variation (std. dev./mean), minimum, maximum, and range.

2000

An example of a vegetation map generated in 2000 as well as the matching 1990 vegetation map is presented in Appendix 2. Summary statistics for cover and density at RMD and TMD in 2000 are presented in Appendices 7 – 10.

The Decade of Change

District-wide Responses

The total number of species recorded from both districts increased from 68 in 1990 to 73 in 2000; likewise, there was an increase in the number of plant families represented, from 22 to 25 (Table 1). These increases are due at least in part to differences in the degree of mapping (see Methods) and the inclusion of new species. Species previously not encountered/mapped are: *Bahia absinthifolia*, *Baileya multiradiata*, *Carlowrightia arizonica*, *Commicarpus scandens*, *Matelea* sp., and *Stephanomeria pauciflora*. Some of these species can be annuals or perennials, depending upon rainfall patterns; therefore they may have been present in 1990 but not mapped.

Mean total cover per plot increased from 42.04 to 58.83 m² at RMD in the past decade; at TMD from 41.88 to 52.93 m². Mean density per plot increased at both districts: from 113.64 to 139.40 plants per 100 m² at RMD, and from 145.00 to 174.45 plants per 100 m² at TMD.

Several species showed increase or decrease in either cover or density at RMD and TMD over the past decade. Figures 3 – 6 present the trends in cover and density by species at RMD and TMD. Species that were mapped inconsistently or were newly included in 2000 are not included in the analysis. Cover and density trends tended to be stronger and more dynamic at RMD.

At RMD, 44 species showed an increasing cover trend, with 9 species increasing on 25% or more of the plots (Fig. 3). Of those 9 species, 6 increased on 40% or more of the plots, 2 increased on 60% or more of the plots, and 1 increased on more than 80% of the plots. Of the 6 species that showed a decreasing cover trend at RMD, only 1 species decreased on 20% of the plots. At TMD, 36 species showed an increasing cover trend, with 11 species increasing on 25% or more of the plots (Fig. 4). Of those

Table 1. Summary of diversity, cover, and density by district for 1990 and 2000. These data do not include grasses, ferns and fern allies. Species that were mapped inconsistently or not included in the 1990 maps (*Ayenia filiformis*, *Ayenia microphylla*, *Bahia absinthifolia*, *Baileya multiradiata*, and *Carlowrightia arizonica*,

Commicarpus scandens, and *Matelea* sp.) are included in the 2000 calculations. Values reported in parentheses do not include these 7 species, to allow direct comparison with 1990 data.

	Number of species	Number of species Occurring only at one district	Number of families	Mean cover per plot (m ²)	Mean density (plants per 100 square meters) per plot
RMD 1990	54	16	20	42.04	113.64
TMD 1990	53	12	19	41.88	145.00
TOTAL 1990	68		22		
RMD 2000	57 (54)	11 (10)	21 (20)	59.56 (58.83)	153.64 (139.40)
TMD 2000	59 (53)	16 (13)	23	53.27 (52.93)	183.90 (174.45)
TOTAL 2000	73 (66)		25		

11 species, 3 increased on 40% or more plots, and of those, only 1 species increased on 60% or more of the plots. At TMD, although the number of species showing a decreasing cover trend was high (17), the declining trend was relatively weak, with all of those species declining on 12% or less of the plots.

At RMD, 29 species showed an increasing density trend, while 21 species showed a decreasing trend (Fig. 5). At TMD, 32 species showed an increasing density trend, and 15 species showed a decreasing density trend (Fig. 6). More species showed a strong increasing density trend at RMD, with 6 species increasing on 25% or more of the plots, as opposed to only 4 species with similar increase at TMD. Strong decreases in species density were also greater at RMD, where density declined for 5 species on at least 20% of the plots. At TMD, the strongest declining trend (decrease on 8.3% of the plots) was demonstrated by only 2 species. Appendices 11 and 12 report the actual difference in cover and density for each species from 1990 and 2000.

Table 2 presents the species that showed significant district-wide changes. Cover values for *Fouquieria splendens* and *Opuntia phaeacantha* should be interpreted cautiously, however. The mapping techniques used in the current study may have produced higher cover values than the techniques used by Duriscoe and Graban (1991, 1992), because we tended to interpret cover more coarsely in dealing with such intricately branched species.

Species with significant increases in both cover and density at RMD in the past decade include *Abutilon incanum*, *Calliandra eriophylla*, *Encelia farinosa*, *Janusia gracilis*, *Opuntia phaeacantha*, *Porophyllum gracile*, and *Siphonoglossa longiflora*. Fewer species showed this pattern at TMD: *Calliandra eriophylla*, *Janusia gracilis*, and *Krameria grayi*. Only two species, *Calliandra eriophylla* and *Janusia gracilis* increased at both districts in cover and density.

Many species increased significantly in cover, but not density. This indicates an increase in plant size but no recruitment in the past decade. At RMD, these species are *Acacia constricta*, *Fouquieria splendens*, *Jatropha cardiophylla*, and *Lycium berlianderi*. Plants at TMD exhibiting that same pattern are *Abutilon incanum*, *Acacia constricta*, *Encelia farinosa*, *Jatropha cardiophylla*, *Opuntia acanthocarpa*, *O. fulgida*, *O. phaeacantha*, and *Trixis californica*.

Conversely, at RMD, some species showed significant decreases in density, but no significant changes in cover, indicating mortality of some plants but increase in size of the surviving plants. These are *Echinocereus* sp., *Ericameria laricifolia*, *Isocoma tenuisecta*, and *Psilostrophe cooperi* (Table 2). There were no species that increased significantly in density but not cover.

Menodora scabra is the only plant that showed significant decreases in both cover and density at RMD during the past decade, where the loss of 9 plants accounted for a 73% decline in cover. There were no significant decreases in cover or count at TMD (Table 2).

Localized changes

Table 3 presents the species on each plot that exhibited “extreme” change in density and/or cover, meaning each species that increased or decreased on a particular plot more (>2 std. dev. from the mean) than the average change of that species throughout the district. If all species behaved about the same on all plots in 1990 and 2000, we would expect no extreme changes, and we would assume that species abundance was not heavily influenced by microhabitat. However, if certain species and/or plots showed several extreme changes, then localized variables may play a significant role in their abundance and distribution.

Several species exhibited localized change from 1990 to 2000. *Carnegiea gigantea* had extreme gain or loss on 4 plots at RMD and 3 plots at TMD. Many other species exhibited similar gains and losses, but with changes limited to 1 and 2 plots. *Calliandra eriophylla* and *Carnegiea gigantea* were the only two species to show extreme differences at both RMD and TMD.

At RMD, 3 plots (11, 23, and 25) had 3 species with extreme variation in density and/or cover, while TMD had 1 plot (32) with 5 species exhibiting extreme change. Only plot 11 exhibited extreme negative change, with 2 species declining in density and 1 in cover. The Principle Components Analysis revealed that none of the environmental variables measured (slope, aspect, elevation, microsite, and topography) accounted for more

Figure 3

Figure 4

Figure 5

Figure 6

Table 2

than 10% of the variation in cover or density of species. Appendix 13 lists the environmental variables for each plot.

Species richness, not summarized in Table 3, changed extremely for only 1 plot. In 1990, plot 45 (TMD) had 11 species. In 2000, species present more than doubled to 26 for a total increase of 15 species. The average change in species richness per plot was 1.96 species (std. dev. = 2.95).

Table 3. Species that changed more on a given plot than the mean change for the district. (RMD = plots 1 – 25, TMD = plots 26 – 45). This only includes information for species that were present on more than one plot and in both study years. Mean cover and density difference is mean for a species for a given district.

Plot	Species	Cover Difference (m ²)	Mean Cover Difference	St Dev	Density Difference (# plants)	Mean Density Difference	St Dev
1	<i>Encelia farinosa</i>				175	43	53.4
4	<i>Acacia gregii</i>				-5	-0.23	1.39
6	<i>Calliandra eriophylla</i>	5.43	1.59	1.64			
9	<i>Opuntia phaeacantha</i>				-5	0.88	-0.055
10	<i>Prosopis velutina</i>	-6.76	.067	3.46			
11	<i>Acacia constricta</i> <i>Lycium berlandieri</i> <i>Ferocactus wislizenii</i>	-0.39	0.04	0.15	-2 -2	0.40 -0.08	1.17 0.9
13	<i>Prosopis velutina</i>				-4	-.22	1.11
14	<i>Ericameria laricifolia</i>	-7.15	-0.94	2.45	-59	-10.38	16.53
15	<i>Carnegiea gigantea</i> <i>Cercidium microphyllum</i>	-1.81 -34.48	0.04 -1.89	0.53 8.86	-4	-0.32	1.49
17	<i>Porophyllum gracile</i>	4.48	1.15	1.28			
18	<i>Carnegiea gigantea</i>	1.26	0.04	0.53	2	0.16	0.89
19	<i>Echinocereus</i> sp. <i>Eriogonum wrightii</i>	5.78	1.39	2.179	9	2.5	3.20
20	<i>Abutilon incanum</i>	5.87	1.33	1.78			
21	<i>Encelia farinosa</i>	17.20	5.72	5.11			
22	<i>Fouquieria splendens</i>	11.13	2.63	3.01			
23	<i>Calliandra eriophylla</i> <i>Carnegiea gigantea</i> <i>Opuntia phaeacantha</i>				27 2 9	6.26 0.16 2.17	8.35 0.89 3.18
24	<i>Janusia gracilis</i>	13.10	3.07	3.56	21	6.71	6.60
25	<i>Carnegiea gigantea</i> <i>Herissantia crispa</i> <i>Mammillaria</i> sp.	1.88 0.40	0.38 0.01	0.74 0.09	2	0.16	0.89
26	<i>Krameria grayi</i> <i>Larrea tridentata</i>	4.48 -5.4	0.95 -0.96	1.31 1.98			
27	<i>Cercidium microphyllum</i> <i>Lycium berlandieri</i>	4.72 5.34	-0.57 0.64	.066 1.55			
28	<i>Ambrosia deltoidea</i>	0.76	1.74	4.14			
29	<i>Opuntia acanthocarpa</i>				7	0.94	2.57
32	<i>Carnegiea gigantea</i> <i>Krameria grayi</i> <i>Lycium berlandieri</i> <i>Mammillaria</i> sp. <i>Opuntia acanthocarpa</i>	1.10 0.08 4.09	-0.02 0.007 0.79	0.46 .02 1.28	4 3	1.09 0.38	1.44 1.19
33	<i>Ambrosia deltoidea</i>	11.41	1.74	4.14			
36	<i>Encelia farinosa</i>				67	7.44	25.07
37	<i>Abutilon incanum</i>	9.99	1.67	3.38			
39	<i>Calliandra eriophylla</i> <i>Echinocereus</i> sp.	4.98	1.24	1.63	4	0.85	1.46
41	<i>Janusia gracilis</i>	0.55	3.06	3.17			
42	<i>Calliandra eriophylla</i>				41	7.33	13.5
44	<i>Carnegiea gigantea</i>				4	-2.0	1.96
45	<i>Carnegiea gigantea</i>				4	-2.0	1.96

Grasses

We sampled grass cover on plots by visual estimate. Duriscoe and Graban (1991) sampled grass cover on 36 plots, and we sampled all 45 plots in the current study. The total number of grass species identified increased from 21 in 1990 to 24 in 2000 (Table 4).

Table 4. Grass species encountered in 2000.

Native grass species	N (# plots)	Mean cover per plot (m ²)	Standard deviation
<i>Aristida hamulosa</i>	1	2	-
<i>Aristida purpurea</i>	9	2.5	2.1
<i>Aristida ternipes</i>	14	1.7	1.2
<i>Bouteloua aristidoides</i>	7	8.0	7.3
<i>Bouteloua chondrosoides</i>	2	18.0	24.0
<i>Bouteloua curtipendula</i>	10	5.6	6.6
<i>Bouteloua eriopoda</i>	1	1.0	-
<i>Bouteloua repens</i>	14	3.7	29.0
<i>Bothriochloa barbinodis</i>	7	1.28	0.7
<i>Brachiaria arizonica</i>	1	1.0	-
<i>Digitaria californica</i>	13	1.3	0.7
<i>Erioneuron pulchellum</i>	8	3.0	4.8
<i>Eragrostis cilianensis</i>	1	1.0	-
<i>Heteropogon contortus</i>	10	1.9	1.9
<i>Hilaria berlanderi</i>	2	2.0	1.4
<i>Leptochloa filiformis</i>	1	1.0	-
<i>Muhlenbergia porteri</i>	20	4.0	3.5
<i>Setaria macrostachya</i>	6	1.1	0.4
<i>Tridens muticus</i>	1	2.0	-
Non-native grass species			
<i>Bromus rubens</i>	1	3	-
<i>Eragrostis lehmanniana</i>	2	1	0
<i>Pennisetum ciliare</i>	1	2	-
<i>Rhynchelytrum repens</i>	3	1	0
<i>Schismus arabicus</i>	1	1	-

Duriscoe and Graban (1991) found only 2 non-native grass species of concern: *Pennisetum ciliare* (buffelgrass), and *Rhynchelytrum repens* (natal grass). In 1990 these grasses occurred on 14% of the plots surveyed and had cover values of 2% or less on each plot they were found. Five non-native species of concern were present on plots surveyed in 2000: *Bromus rubens* (red brome), *Eragrostis lehmanniana* (Lehmann lovegrass), buffelgrass, natal grass, and *Schismus arabicus* (Mediterranean grass). These species were found on 18% of the plots surveyed and had low cover values (3% or less) on all plots where they were found. Red brome and Lehmann lovegrass were found in 2000 on plot 13, an area that was burned in the Mother's Day Fire of 1994. Unfortunately, this was one of the plots for which grasses were not recorded in 1990;

therefore, we cannot determine whether these two species have invaded in the past ten years. However, Lehmann lovegrass and Mediterranean grass have both certainly invaded plots at RMD in the past ten years (plots 11 and 9, respectively). Buffelgrass remains present on plot 35, at a low density similar to that recorded ten years ago. Natal grass is present on 2 of the same plots as in 1990, has invaded 1 new vegetation plot, and is absent from 2 previously occupied plots. No clear pattern emerged regarding how non-native grass species affect native grass cover, density, or diversity.

Discussion

Cover and density increased dramatically at both districts in the past decade. These increases may be due at least in part to the different precipitation regimes experienced during the mapping events. During the 1990 study, rainfall was low in the summer and moderate in the winter, whereas during the current study, rainfall was moderate-high in the summer and relatively low in the winter.

Mean cover values were higher at both mapping events at RMD than TMD, but mean density values show the reverse pattern, with density values at TMD higher than those at RMD. This illustrates that at RMD, fewer, larger plants provide more cover than at TMD, where there are many more, smaller plants providing less cover.

Goldberg and Turner (1986) found that “fluctuations in total cover [of 3 species studied in detail] reflected changes in size of individuals more than recruitment and death of individuals. Thus, in many cases, fluctuations in cover were greater than fluctuations in density.” This pattern is echoed in our TMD plots (11 species with significant positive fluctuations in cover versus only 3 species with significant positive fluctuations in density; Table 2), but surprisingly, not as strongly at our RMD plots (11 species with significant positive fluctuation in cover versus 7 species with significant positive fluctuations in density).

The Rincon Mountains, with abundant water sources, were heavily grazed until the 1970s, with the last of the cattle being removed in 1985 (Clemenson 1987). McAuliffe (1993) noted that at RMD: “In the saguaro forest area, the composition of the vegetation resembles neither typical Sonoran desertscrub nor desert grassland. Instead, shrub species...that typically increase as a response to severe disturbances (e.g., extreme grazing pressure) form a dominant part of the understory vegetation.” Interestingly, several shrub species showed significant decline in density at RMD (but not at TMD): *Ericameria laricifolia*, *Isocoma tenuisecta*, and *Psilostrophe cooperi*. *Isocoma tenuisecta* is considered to be a serious range pest, worthless as forage; overgrazing, drought, and protection from fire promote it (Parker 1972). Perhaps these species were promoted during periods of heavy grazing, but are now in decline due to removal of that disturbance and recovery of competition with other vegetation. However, we emphasize using caution in this interpretation, because this cannot be proven without comparison with data from permanent plots in grazed areas; in addition, there may be other effects on vegetation dynamics from native grazers, such as rabbits, deer, and javelina.

Our data reinforce many of the long-term findings at Tumamoc Hill. Of the 3 species that showed significant increase in both cover and density at TMD, *Krameria grayi* and *Janusia gracilis* “have shown more or less continuous increases in density and, to a lesser extent, cover over the entire study period [of 72 years] in some or all plots” at Tumamoc Hill (Goldberg and Turner 1986). The Tumamoc Hill study also reported a decline in *Menodora scabra*; this is the only species for which we found a significant decrease in both cover and density (RMD only). Goldberg and Turner (1986) speculated that the

increase in *Krameria grayi*, a palatable grazing species, could be due to 72 years of cattle exclusion from their plots; however, they cautioned that *Menodora scabra*, another palatable species, would also be expected to increase. Our study casts further doubt upon *Krameria grayi* increases being due to grazing exclusion, because the land which became TMD escaped heavy grazing due to unavailability of water (Clemenson 1987).

Explanations as to why certain plots and species experienced extreme localized change are apparently quite complex; our PCA analysis did not highlight any one of the environmental variables explored as potential causes for such variation in cover or density. However, unique combinations of variables, perhaps including important variables that were not measured in this study (soil, temperature, precipitation, etc.) might be used to explain extreme localized variation.

At RMD, plots 11, 23, and 25 represent northern and southern extremes in the park. Plot 11, near the north boundary and bisected by a trail at 2,800 feet, was the only plot to experience extreme decline for 3 species: *Acacia constricta*, *Lycium berlianderi*, and *Ferocactus wislenzii*. Plot 11 is a flat and very accessible plot that has experienced long-term disturbance; it is unclear why the other plots in the area did not experience similar extreme declines. The other 2 RMD plots exhibiting extreme variation are located along the southern boundary of the park. Plot 23, where *Calliandra eriophylla*, *Carnegiea gigantea* and *Opuntia phaeacantha* all increased markedly in density, is unique in its combination of highest plot elevation (3,980 feet) and most extreme slope (62%) at RMD. It is located at the east-facing descent into a large canyon. Plot 25 is a south-facing plot at 3,620 feet with moderately steep slope (38%); here, *Carnegiea gigantea*, *Herissantia crispa*, and *Mammillaria* sp. all showed extreme increases.

At TMD, 5 species increased extremely in density or cover at plot 32: *Carnegiea gigantea*, *Krameria grayi*, *Lycium berlianderi*, *Mammillaria* sp., and *Opuntia acanthocarpa*. This is a relatively flat plot at 2560 feet (neither near the low nor high elevation extreme) near the intersection of Picture Rocks Road and Golden Gate Road, and we are unable to offer reasons for extreme variation at that site.

Extremely high elevation did seem to affect species richness, however. Plot 45 is the highest plot at either district, at 4,140 feet, and it experienced a doubling of the number of species present in the past decade. Perhaps the different weather patterns during this mapping event affected species presence more dramatically at extremely high elevations than at moderate or low elevations.

Livestock grazing since the 1860's has had a profound effect on the vegetation dynamics of the Arizona Upland at RMD, and to a lesser extent, TMD. Fleischner (1994) identified 3 defining ecological costs of grazing: (1) alteration of species composition of communities, (2) disruption of ecosystem functioning, and (3) alteration of ecosystem structure.

The first cost, alteration of species composition of communities, is a well-founded concern at Saguaro National Park. Many species of non-native grasses in the Tucson area

had introductions associated with cattle grazing. Five non-native grass species of concern were found during this study: red brome and Mediterranean grass (annuals), and buffelgrass, natal grass, and Lehmann lovegrass (perennials). Although these non-native grasses were found at very low densities, and have not yet affected native grass composition and density, the diversity of non-native grass species is increasing: we found 3 more species of non-native grasses than were found 10 years ago.

Although many non-native species had introductions associated with grazing, the removal of grazing pressure has not negatively impacted their success. At Tumamoc Hill, Burgess et al. (1991) found that the density and diversity of successful invasive non-native species has increased dramatically since the end of grazing there in 1907.

These aggressive species, which evolved under similar climatic regimes in Africa and the Mediterranean, are capable of out-competing native species of grasses and annuals, thus altering the composition of communities (Loope et al. 1988, Burgess et al. 1991). In comparing study plots dominated by two species of lovegrasses with undisturbed plots in southeastern Arizona, Bock et al. (1986) found significant decreases in total native herb canopy, herb species richness, shrub density and canopy, as well as significant decreases in grasshopper and bird diversity. Buffelgrass is of urgent concern: millions of acres of nearby Sonora, Mexico are cultivated fields of buffelgrass, and Mexican agricultural officials are encouraging increased buffelgrass planting in the coming decade (Nabhan and Holdsworth 1998). This species spreads readily along roadsides and poses a threat to undisturbed areas within Saguaro National Park. Buffelgrass has been observed to displace the native perennial shrub *Encelia farinosa* through root competition and allelopathy on the slopes of Tumamoc Hill (Burgess et al. 1991). Development and spread of more cold-tolerant, rhizomatous varieties of buffelgrass will likely exacerbate the problem, allowing for invasion farther north and at higher elevations (Swantek et al. 1999).

Invasion of non-native grasses may further affect ecosystem function by altering fire regimes. The natural fire recurrence interval for the Sonoran Desert has been estimated to be greater than 250 years; however, McLaughlin and Bowers (1982) showed a dramatic increase in number and size of wildfires in the 20 years prior to their study. Although summer lightning storms capable of fire ignition are common, annual and perennial production is generally not enough to sustain fire (McLaughlin and Bowers 1982). Increases in the annual fuel load and changes in its composition due to post-grazing vegetation recovery and non-native grass invasion have been blamed for this sudden increase (Swantek et al. 1999). Many of the grass species that have been introduced are fire-adapted, and their presence may increase fire frequency and size. In the Arizona Upland, the defining species, saguaros and paloverdes, are fire-intolerant; widespread fires could cause local extinctions and promote a shift in dominant vegetation to fire-tolerant species such as mesquite and acacia (Swantek et al. 1999). Certain non-native grasses not only promote fire, but also can thrive after a fire disturbance. Ruyle et al. (1988) found that Lehmann lovegrass germinates more readily after repeated burning.

Ever-increasing urban encroachment by the city of Tucson may also have an effect on vegetation dynamics at Saguaro National Park. Fountain grass (*Pennisetum setaceum*), a close relative of buffelgrass, is a popular ornamental grass in Tucson, and also an aggressive invader. For example, intense fountain grass invasion in a Hawaiian tropical dry forest protected reserve is charged with the crowding out of native tree seedlings, and hence thwarting forest restoration (Cabin et al. 2000). This species of concern, although abundant at both districts of Saguaro National Park, is not yet evident on our plots. However, fountain grass is so abundant at Organ Pipe Cactus National Monument, that it is considered to be uncontrollable (Loope et al. 1988, Felger 1990).

Clearly, the interactions of grazing and other historic disturbances, climate, and vegetation dynamics are complex, and more detailed study is needed.

This study cannot address the status of major landscape elements such as saguaros, palo verdes, mesquites, and ironwoods for several reasons. The 100 square meters plot size is not adequate to assess fluctuations in the large desert tree species; the death of just one or two mature plants on plots would dramatically affect the total cover values, possibly giving a false significant negative value (Goldberg and Turner 1986).

At the other end of the spectrum, cover values for *Mammillaria* sp. (which is commonly less than 10 cm² at maturity) should be approached with caution, because our estimated map error is equal to +/- 10 cm. Fluctuations in cover for small species require finer measurements that were impossible in the current study; density values are, however, meaningful. *Carnegiea gigantea* presents a similar challenge: the cover of individuals without arms varies so slightly over a 10-year period that we cannot detect changes with our methods.

The values reported for *Carnegiea gigantea* should be interpreted cautiously: density values are biased because the plots are centered on saguaros. For true saguaro density estimates, see Turner and Funicelli (2000). The centering of plots on saguaros also raises concern that the species encountered may be influenced by proximity to saguaros.

Recommendations

We strongly recommend that Saguaro National Park continue this study. Future iterations will greatly improve our understanding of vegetation dynamics in Saguaro National Park and in the Arizona Upland Subdivision of the Sonoran Desert. In order to ensure that future resource managers are aware of this research opportunity, re-mapping of the plots every ten years should be a priority in the park's Resource Management Plan, a document that guides staff in achieving long-term resource management goals.

Additional plots should be established in recently-acquired expansion lands in the park, especially the lands south of Tanque Verde Ridge at RMD (west of X-9 Ranch and east of the Rocking K development) and in the areas on the north and east boundaries of TMD. In keeping with the plot density used by Duriscoe and Graban (1991), 6 new plots would be required: 3 at RMD and 3 at TMD. Many of these areas were grazed by livestock until their recent acquisition, and could provide a great opportunity to monitor community-level effects of grazing; that opportunity will be missed if baseline data are not gathered soon.

Information gathered in future iterations of this study could be strengthened in several ways. It would be ideal if specific plots were remapped within a few weeks of the anniversary of the 2000 mapping so that the effect of seasonal cover fluctuations is minimized. Also, the installation of rain gauges at each plot would assist in teasing apart the relationships between rainfall and specific species responses, as would the collection and analysis of soil samples.

It is imperative that sufficient time is budgeted for the field and office work associated with this project. Many field maps were completed in single ten-hour field days with two personnel using the plane table and alidade method. However, about a third of the plots required two or more days for completion. We used 128 person-days for the field portion of this project. Once the field maps were finished, it took 18 one-person days to complete the digitizing process. Creation of final maps, data analysis, and report preparation required approximately 100 person-days. Additional time should be allotted for training in field methods, media events, and conference presentations.

Literature Cited

- Blydenstein, J., C. R. Hungerford, G. I. Day, and R. R. Humphrey. 1957. Effect of livestock exclusion on vegetation in the Sonoran Desert. *Ecology* 38: 522 – 526.
- Bock, C. E., J. H. Bock, K. L. Jepson, and J. C. Ortega. 1986. Ecological effects of planting African lovegrasses in Arizona. *National Geographic Research* 2: 456 – 463.
- Bowers, J. E. and S. P. McLaughlin. 1987. Flora and vegetation of the Rincon Mountains, Pima County, Arizona. *Desert Plants* 8: 51 – 95.
- Brown, D. E., ed. 1994. Biotic communities: southwestern United States and northwestern Mexico. University of Utah Press, Salt Lake City. 342 p.
- Burgess, T. L., J. E. Bowers, and R. M. Turner. 1991. Exotic plants at the desert Laboratory, Tucson, Arizona. *Madrono* 38(2): 96 – 114.
- Cabin, R. J., S. G. Weller, D. H. Lorence, T. W. Flynn, A. K. Sakai, D. Sanquist, and L. J. Hadway. 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. *Conservation Biology* 14: 439 – 453.
- Clemenson, A. B. 1987. Cattle, copper, and cactus: the history of Saguaro National Monument. Historic resource study, Denver Service Center, National Park Service. 272 p.
- Duriscoe, D. M. and S. L. Graban. 1991. Epidermal browning and population structure of giant saguaro cactus (*Carnegiea gigantea*) in Saguaro National Monument, Arizona. Unpublished report to USDI National Park Service, Air Quality Division, Denver, Colorado. 37 p. + attachments.
- Duriscoe, D. M. and S. L. Graban. 1992. Epidermal browning and population dynamics of giant saguaros in long-term monitoring plots. Pages 237-258 in C. P. Stone and E. S. Bellantoni, eds. Proceedings of the Symposium on Research in Saguaro National Monument, 23-24 January 1991. Southwest Parks and Monuments Association, Globe, Arizona.
- Elzinga, C. L., D. W. Salzer, and J. W. Willoughby. 1998. Measuring and Monitoring Plant Populations. BLM Technical Reference 1730-1. 477 p.
- Felger, R. S. 1990. Non-native plants of Organ Pipe Cactus National Monument, Arizona. Technical Report 31, Cooperative National Park Resources Studies Unit, University of Arizona, Tucson, 93 p.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8: 629 – 644.

- Goldberg, D. E. and R. M. Turner. 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. *Ecology* 67:695-712.
- Kuchler, A. W. 1967. Vegetation Mapping. University of Kansas: the Ronald Press Company, New York. 472 p.
- Loope, L. L., P. G. Sanchez, P. W. Tarr, W. L. Loope, and R. L. Anderson. 1988. Biological invasions of arid land nature reserves. *Biological Conservation* 44: 95 – 118.
- Martin, E. L. , P. J. Anning, M. Holden, and M. Weesner. 1998. Status of non-native plants 1999: results of the initial non-native plant inventory for the Tucson and Rincon Mountain Districts. Draft report to the National Park Service.
- McAuliffe, J. R. 1993. Case study of research, monitoring, and management programs associated with the saguaro cactus (*Carnegiea gigantea*) in Saguaro National Monument, Arizona. Technical Report NPS/WRUA/NRTR-93/01, Cooperative National Park Resources Study Unit, University of Arizona, Tucson. 50 p.
- McLaughlin, S. P. and J. E. Bowers. 1982. Effects of wildfire on a Sonoran Desert plant community. *Ecology* 62: 246 – 248.
- Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons. 547 p.
- Nabhan, G. P. and A. R. Holdsworth. 1998. State of the desert biome: uniqueness, biodiversity, threats, and the adequacy of protection in the Sonoran bioregion. The Wildlands Project.
- Parker, K. F. 1972. An illustrated guide to Arizona weeds. University of Arizona Press. 338 p.
- Rondeau, R., T. R. Van Devender, C. D. Bertelsen, P. Jenkins, R. K. Wilson, and M. A. Dimmit. 1996. Annotated Flora and Vegetation of the Tucson Mountains, Pima County, Arizona. *Desert Plants* 12: 3 – 46.
- Ruyle, G. B., B. A. Roundy, and J. R. Cox. 1988. Effects of burning on the germinability of Lehmann lovegrass. *Journal of Range Management* 41: 404 – 406.
- Swantek, P. J., W. L. Halvorson, and C. R. Schwalbe. 1999. GIS database development to analyze fire history in southern Arizona and beyond: an example from Saguaro National Park. Technical Report 61, Cooperative Park Studies Unit, University of Arizona, Tucson. 43 p.

- 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, Arizona. Report to Saguaro National Park.
- Yoccoz, N. G. 1991. Use, overuse, and misuse of significance tests in evolutionary biology and ecology. *Bulletin of the Ecological Society of America* 72: 106 – 111.