

History of the Desert Lab and Cast of Characters

The Desert Lab was the brainchild of Frederick V. Coville, chief botanist of the U.S. Department of Agriculture. Inspired by his explorations of Death Valley in 1891, Coville convinced the Carnegie Institution of Washington to establish a laboratory to study adaptations of plants to aridity. In 1903, Coville and Daniel T. McDougal of the New York Botanical Garden toured the Southwest and Mexico in search of a site. They settled on Tumamoc Hill, a saguaro-studded butte overlooking what was then a small university town of ten thousand people.

From 1903 to 1940, the Desert Laboratory pioneered ecological research in deserts and played a key role in the emergence of ecology as a discipline. Desert Lab scientists were among the founders of the Ecological Society of America in 1915, and *Plant World*, a botanical journal published at the Desert Lab, was turned over to ESA in 1920 to become the journal *Ecology*. In 1940, the Carnegie Institution transferred the Desert Lab to the Forest Service, and the facility became the Southwest Forest and Range Experiment Station.

In 1956, the University of Arizona bought the Desert Lab to house the new Department of Geochronology under Terah (Ted) Smiley's direction. A young palynologist from Michigan, Paul Martin, was hired to broaden the scope of research to include the history of desert environments; he has since become well known for his work on Pleistocene extinction. During the 1950s, Ray Turner, then a professor in the Department of Botany at the University of Arizona, monitored long-established permanent vegetation plots on the Desert Laboratory grounds. After he left the university to work for the U.S. Geological Survey, he continued to track vegetation changes on the plots. In 1976 he became a full-time presence at the Desert Laboratory, moving from sterile quarters downtown to the fertile slopes of Tumamoc Hill. Both Paul and Ray retired in 1989. Their legacies include a rich paleobotanical archive now being exploited for geochemical, anatomical and genetic studies; a series of long-term vegetation plots in the Sonoran Desert; a digitized data base of plant distributions in the Sonoran Desert; and an archive of repeat photography comprising some 3000 historical views of western landscapes and one or more recent matches of each.

Jay Quade inherited Paul's position as director and injected the Desert Lab with a strong dose of geology and stable isotope geochemistry. Jay's research has spanned several continents including Asia, Africa, Australia, and the Americas. Upon Ray Turner's retirement, the USGS hired Bob Webb and Julio Betancourt as replacements. Both have broad interdisciplinary interests and skills, and have made several key contributions to our understanding of climatic effects on biological and physical processes in deserts. Bob Webb has expanded Ray Turner's repeat photography collection, has spent more than a decade studying the geomorphology and ecology of the Grand Canyon, and is extending the long-term ecological research of Janice Beatley in the Mojave Desert. Julio Betancourt has played a key role in reconstructing the long-term vegetation and climate history of the North and South American deserts. Julio and Bob were later joined by Waite Osterkamp, a USGS geomorphologist, who has done extensive work on riparian systems. Waite maintains the Vigil Network, a system of small sites and drainage basins throughout the U.S. where geomorphic, hydrologic, and biological data have been periodically collected since the 1960s. Jan Bowers, hired as Ray's research assistant, blossomed into a scientist and for the past decade has studied perennial plants on Tumamoc Hill. Betsy Pierson, who worked at the Desert Lab in the early 1990s, deserves special recognition for her efforts in resampling the saguaro population and analyzing its dynamics.

Larry Venable, a professor in the Department of Ecology and Evolutionary Biology (EEB), has conducted experimental studies on the population biology of desert annuals at Tumamoc Hill since 1982. In 2001, EEB hired two more plant ecologists, Brian Enquist and Travis Huxman. They and their students have eagerly initiated their own studies on Tumamoc Hill, becoming a welcome addition to the long tradition of ecological research at the Desert Laboratory. Other faculty from EEB (Judie Bronstein) and the School of Renewable Natural Resources (Bill Shaw) have ongoing studies on Tumamoc Hill.

In 1993, we were joined by Jack Wolfe, a retired USGS paleobotanist, who continues his research as an adjunct professor in the Department of Geosciences. M.E. Morbeck, Paul and Suzanne Fish, John Madsen and Sue Berneron keep the Desert Lab connected to the University's Anthropology Department and the Arizona State Museum. Tumamoc Hill contains an impressive array of archeological and historical features, including the original laboratory buildings, which are on the National Register of Historic Places.

Monitoring of long-term permanent plots: 1906-2003

Perennial plants on vegetation plots established in 1906 and 1928 (yellow squares and rectangles in Fig. 1) have been mapped (or, in the case of Area A, tallied) about once a decade. More than a dozen researchers have cooperated in the effort over the years, most recently by the U.S. Geological Survey group (Ray Turner and Jan Bowers). Mapping and monitoring of individual plants has made it possible to determine life spans of long-lived perennials, to follow fluctuations in establishment and mortality during wet and dry periods, and to study recovery of vegetation after a century of protection from domestic livestock.

In 1903, Volney Spalding, a retired botany professor from the University of Michigan, joined the staff of the fledgling Desert Laboratory. One of his first acts was to establish 19 plots on the Desert Laboratory grounds. Most were 100 square meters in size. He mapped the locations of all perennial plants within the plots and, when he retired from the Desert Laboratory several years later, turned the maps over to Forrest Shreve, the well-known desert ecologist. As well as mapping some of the Spalding plots in 1910, 1928, and 1936, Shreve established some new ones: Area A, a polygon about 557 square meters in size for the study of seedling survival, and Area B, a set of 8 contiguous plots, each 10 meters by 10 meters. Locations of some of the original plots were lost over the years, and one or two others were inadvertently destroyed by road construction. Ten of the Spalding plots, as well as Areas A and B, are still being monitored by Desert Laboratory researchers (yellow squares in Figure 1).

Maps made at decadal intervals have made it possible to follow changes in numbers of perennial plants as climate has fluctuated (Figure 2). The maps have revealed other kinds of changes too, some of them unexpected. The

Example of Permanent Plot data on Tumamoc Hill: Variations In Cover of Creosote Bush and White Ratany on Plot 16

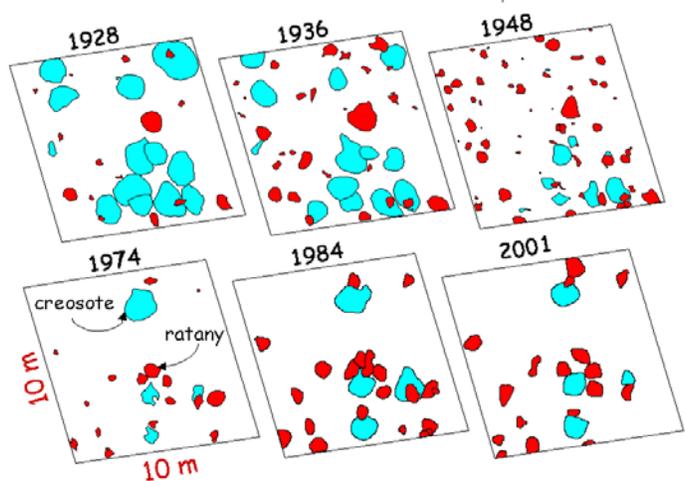


illustration shows canopies of two woody plants, creosote bush (blue) and white ratany (red), on plot 16 between 1928 and 2001. Both species are long-lived. White ratany is a root parasite on creosote bush but its demands are probably not heavy enough to kill its host under normal circumstances. On plot 16 however, creosote bush has declined and white ratany has increased, especially since 1948. The replacement of one by the other was probably promoted by a combination of severe drought in the mid-twentieth century and a type of soil that magnifies the effects of drought. This series of maps emphasizes the value of long-term research and the deep perspective it affords. If maps had been made only in 1928 and 1936, no change would be evident, and the conclusion would be that desert vegetation is inordinately stable.

Long-term saguaro plots

The exact location of all saguaros on Tumamoc Hill and adjacent Sentinel Hill was mapped with a plane table in 1908. In 1964 Raymond Turner repeated this work on a slightly smaller scale, establishing four large (~25 acre) plots on the north, south, east, and west aspects of Tumamoc Hill (yellow dotted lines in Fig. 1). He not only recorded locations of all saguaros on aerial photographs, but also their measured heights. Saguaros in these plots were mapped and measured again in 1970 and 1993. Betsy Pierson was in charge of the 1993 mapping and data analysis. These repeated censuses have made it possible to determine the relation between saguaro height and age at Tumamoc Hill, to calculate survivorship across all age classes, and to examine causes for fluctuations in population numbers during the twentieth century.

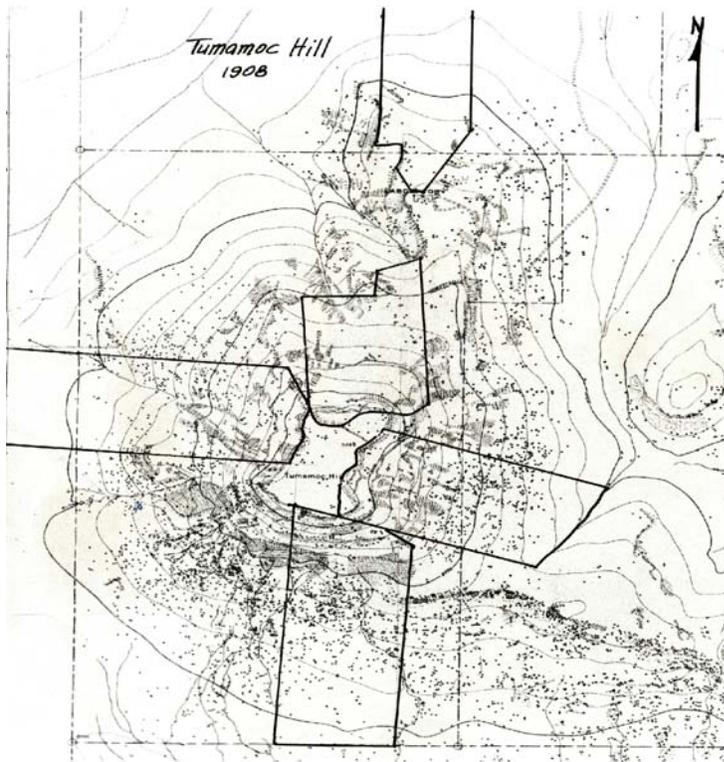
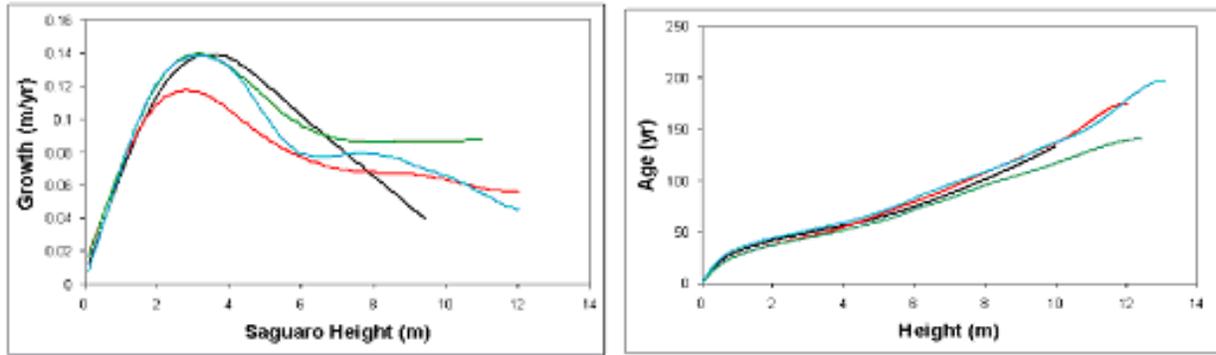
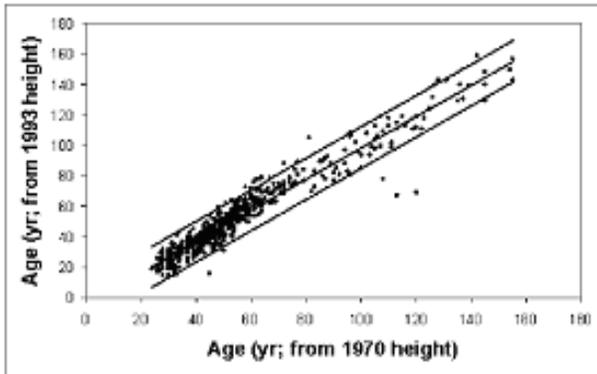


Figure 5. The first saguaro studies on Tumamoc Hill were conducted by members of the Desert Laboratory from 1908-1910 in response to observations that saguaro recruitment was not occurring in much of the Tucson vicinity. Maps were produced recording the location of all saguaros present in a 700 hectare area on Tumamoc Hill and adjacent Sentinel Hill relative to slope aspect and topography. Careful observations of growth rates were made for a subset of the population to estimate establishment date and age structure. The irregular polygons show the location of the 1964-1993 census plots on each slope, where Pierson and Turner mapped and remeasured over 4000 saguaros to develop a robust age-growth model.

In 1964, four plots (~10 ha each) were established within the 1908 mapped area on the north, south, east, and west slopes to determine the effect of slope aspect on plant growth and



demography. All saguaros were individually identified and mapped to allow repeated measurements of height and assessment of flowering and health. The plots were re-evaluated in 1970 and 1993. A model was developed for determining saguaro age, using observations of the growth rates of over 3000 uninjured plants from 1964 to 1970. Average height and annual



growth during this period were calculated for each plant and combined into 0.5 m height classes. The relationship between age and size was determined by integrating the growth rate-height relationship and then used to predict the age of all uninjured saguaros based on their height. Average annual mortality was also estimated from the frequency of deaths among individuals in 0.5 m height classes during this period. The model was verified by comparing predicted age based on size in

1993, estimated age based on 1970 height plus 23 yrs. Age and mortality data were then used to compute population age structures and survivorship curves for each census date. Changes in population sizes and the estimated age structures were then used to infer regeneration trends. Saguaro populations fluctuated substantially in size and age structure over the 85 years. During much of the last two centuries, populations were in decline due to low regeneration rates. Although some recruitment probably occurs most years, saguaro persistence is maintained by episodic surges in regeneration resulting in substantial population gains such as occurred in the mid 19th and 20th centuries.

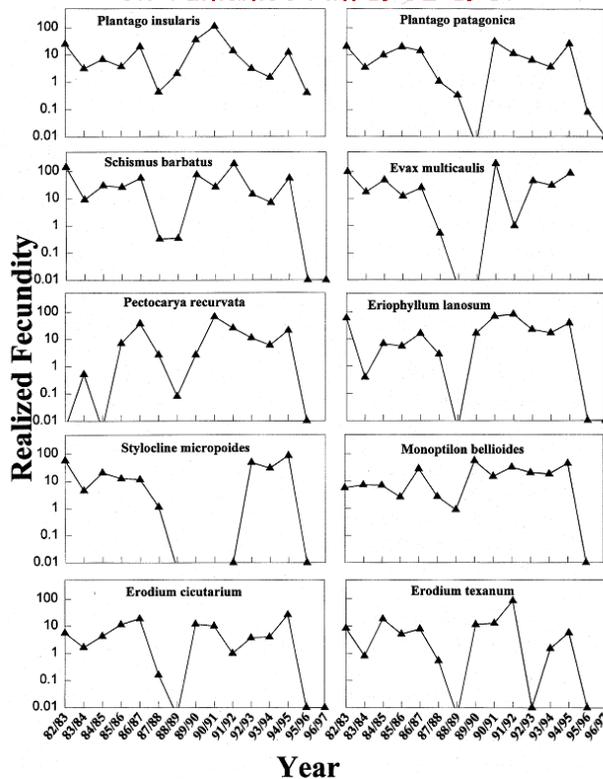
Blue paloverde riparian study

Blue lines in Figure 1 correspond not only to major drainages on the Desert Laboratory grounds, they also show the location of a long-term study of blue paloverde, a common riparian tree in the Sonoran Desert. These riparian galleys are being studied by Ray Turner and Jan Bowers of USGS. Maps made in 1907 and again in 1966 showed large losses in blue paloverde numbers, probably a response to drought and entrenchment of a major drainage channel. A third round of mapping in 1985 demonstrated a dramatic reversal of this decline. A series of wetter years promoted a substantial increase in blue paloverdes, especially along reaches where sediment accumulated, making a favorable environment for seedling establishment.

Winter Annuals permanent plots: 1982-2003

Permanent plots established for the study of winter annuals are located within the areas circumscribed by dotted white lines. These plots have been instrumental in testing theoretical predictions about the way plants behave in variable environments. In 1982, Larry Venable, Department of Ecology and Evolutionary Biology, University of Arizona, began long-term studies of winter annuals at the Desert Laboratory with particular emphasis on population ecology. Annual plant species comprise 50 percent of local floras in the Sonoran Desert, and of these about 60 percent to 80 percent are winter annuals. Seeds of winter annuals germinate during cool-season rains, and, if the seedlings survive, the plants flower between February and April and die when hot weather arrives in May. When abundant, winter annuals help sustain populations of rabbits, tortoises, and other browsing animals. In good years, after abundant winter rains, spring-blooming annuals add millions of seeds to the soil seed bank, renewing the major food source for certain species of ants, rodents, and birds. Not all years are good years, of course, and after very dry winters, winter annuals are present only as dormant seeds in the soil.

Population Fluctuations of Winter Annuals on Tumamoc Hill 1982-1987



The work of Larry Venable and his graduate students has illuminated the relation between winter annuals and climatic variability. Not all seeds germinate even in good years; rather, a fraction of seeds remains dormant, thus preventing extinction in case no seedlings survive long enough to flower and disperse seeds. As Figure 3 shows, species of winter annuals differ in their specific response to climatic variability. Those that vary greatly in reproductive success allow smaller fractions of seeds to germinate at any one time. Those that are more certain of reproductive success take greater risks and germinate a higher proportion of seeds. Differences in bet-hedging behavior allow many different species of winter annuals to co-exist by providing a mechanism for sharing the same environment through time.

Figure 3

Mapping of invasive, non-native species

Invasive exotic species constitute a large and growing threat to biodiversity and ecosystem stability in the Sonoran Desert region. Early in the twentieth century, when fields and open desert surrounded the Desert Laboratory, only three species of exotic plants grew on the

grounds. One hundred years later, suburban sprawl has nearly isolated the Desert Laboratory grounds from natural desert, and weeds and cultivated plants have invaded from nearby yards and gardens. Now 52 of the 346 species in the Desert Laboratory flora are exotic. Of these, red brome, an annual grass from the Mediterranean region, and buffelgrass, a perennial grass from southern Africa, are a major fire hazard. Most native Sonoran Desert plants do not survive wildfire. By promoting frequent burning, these exotic grasses might greatly alter the species composition and structure of natural Sonoran Desert communities. Buffelgrass poses an additional threat by depriving native shrubs and trees of soil moisture.

In 1983, Tony Burgess, Raymond Turner, and Janice Bowers surveyed the grounds of the Desert Laboratory in a regular grid, recording all species of exotic plants encountered on the gridlines. Figure 4 illustrates the distribution of six exotics in 1983. The stippled area on the map for *Erodium cicutarium* (filaree) shows where this species occurred in 1903. It has since naturalized throughout the grounds. *Bromus rubens* (red brome), not even present in 1903, was first collected on the Desert Laboratory grounds in 1968, at which time it was not common. The species has since become one of the most abundant winter annuals on the grounds. The Desert Laboratory grounds were fenced in 1907 to exclude domestic livestock. Subsequent disturbances included clearing and digging for a natural gas pipeline and a city sewer line, installation of electric utility lines, excavation of shallow clay quarries, and construction of a landfill. Although localized, these disturbances apparently gave exotics a foothold for invasion, whence they spread into undisturbed patches, perhaps after drought when deaths of native plants left open space.

Mapping of non-native plant species in 1906 & 1983

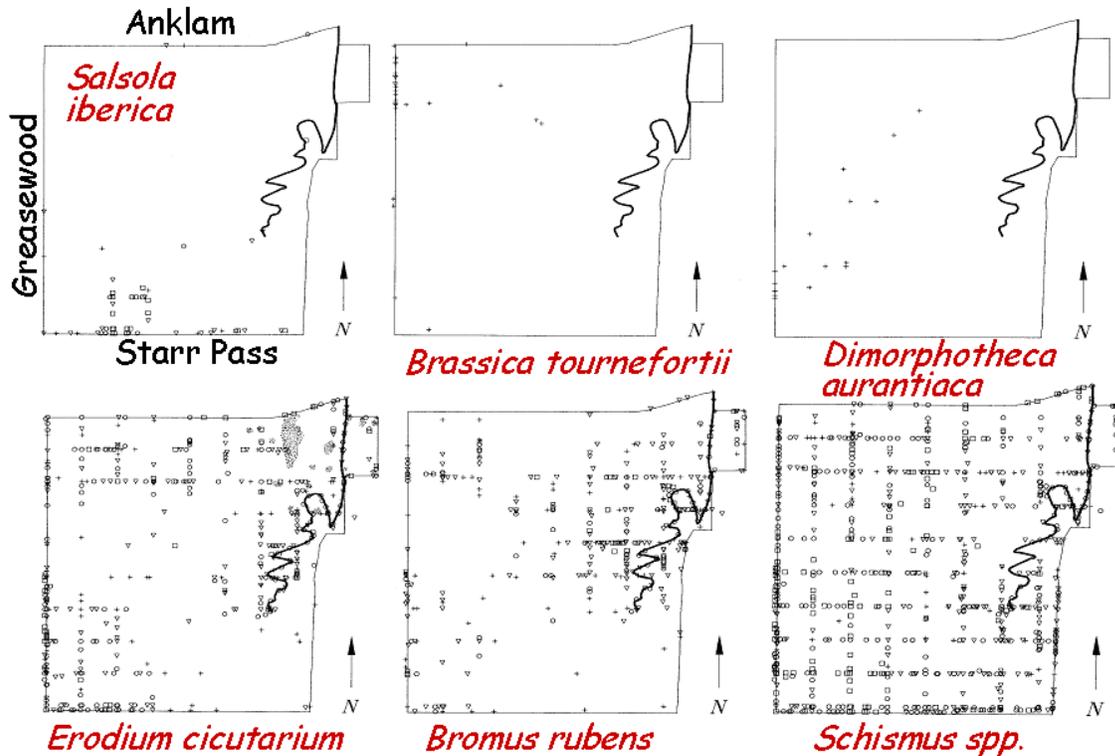


Figure 4

Phenology, reproductive and population ecology desert plants

Jan Bowers studies the effects of climatic variability on the reproduction, establishment, and survival of woody desert plants such as foothill paloverde, barrel cactus, Engelmann prickly pear, and triangle-leaf bursage. During the past decade, she has undertaken numerous investigations on Tumamoc Hill, including: (1) dieback of foothill paloverde following severe drought, (2) between-year variability in flower, fruit, and seed production of Engelmann prickly pear, fishhook cactus, and barrel cactus, (3) methods of using plant size and annual growth rates to age-date prickly pear and barrel cactus, (4) population dynamics of foothill paloverde, Engelmann prickly pear and barrel cactus, (5) rainfall patterns that trigger natural germination of common desert shrubs and cacti, and (6) longevity of seeds in the soil. In the course of her research, Jan Bowers has gathered new information on the longevity, survivorship, and fecundity of common desert plants, filling some surprising gaps in our knowledge of their life history.

Her work has demonstrated that populations of foothill paloverde are less stable than previously supposed and can experience large fluctuations in establishment over the course of a century. She has discovered that Engelmann prickly pear and fishhook cactus are remarkably sensitive to climatic variability, producing more flowers and fruits during wetter years. She has challenged other preconceived ideas about desert plants, as well, showing that seeds of barrel cactus, triangle-leaf bursage, and other woody plants can and do live in the soil for more than a year; that episodic rather than constant mortality is typical of certain species; and that seedling survival is as likely to reflect intensity of predation as seasonal drought.

The plants that Jan Bowers studies locally on Tumamoc Hill are intricately woven into the fabric of the Sonoran Desert as a whole. Some are vitally important to insects, birds, and mammals as seasonal sources of pollen, nectar, and seeds. Others function as nurse plants, hiding seeds and seedlings from hungry animals and protecting tender shoots from heat and frost. As global warming continues, knowing how these species respond to climatic variability will help us predict the future of Sonoran Desert plant and animal communities

Plant community structure and scaling studies

Brian Enquist's lab is focused on three studies. Brian is utilizing the plant diversity on the hill to measure variability of leaf functional traits associated with plants in the Sonoran Desert. He is measuring leaf level photosynthesis, leaf stoichiometry (nitrogen, phosphorus, and carbon ratios) and specific leaf area (leaf laminal area divided by dry leaf mass). Brian is combining this local leaf level database with a global database to assess physiological trade-offs on the leaf level - both at local and global scales.

One component of Brian Enquist's research on the Tumamoc Hill involves Chuck Price's dissertation research (plant productivity/scaling study in Fig. 1). This work is focused on understanding how plant size, abundance, productivity, and biotic/abiotic variation influences plant community structure and dynamics across spatial scales. Chuck is mapping the spatial positions and sizes of all individuals within a 10-20 ha plot within the boundaries of Tumamoc Hill. Patterns resulting from this mapping will then be compared to those found in tropical, subtropical, and temperate vegetation communities along a latitudinal gradient that varies greatly in

climate. This work will be conducted in conjunction with an analysis of allometric relationships in Sonoran Desert plants, particularly how various plant characteristics scale with mass.

The Enquist lab has also established several small (1.2m x 1.2m) plots in varied environments on the hill to measure variability in ecosystem (plant and soil) and soil CO₂ exchange. These measures are based on infrared gas analyzer measurements within small sealed tents. This technique allows us to accurately measure ecosystem fluxes but on a smaller scale. These measurements will be used to compare ecosystem flux measures along altitudinal gradients here in Arizona and across diverse environments in Colorado. Lastly, it bears mentioning that the Enquist group is also keenly interested in pursuing work related to maintaining and expanding the long-term monitoring vegetation plots found on the hill.

Physiological Ecology and Ecosystem Studies

Travis Huxman's research group is interested in understanding how abiotic (climate, soils, etc.) and biotic (life form diversity, species interactions, non-native species invasions, etc.) factors interact to influence physiological processes in deserts from the scale of cells to whole landscapes. The primary motivation for this research is to understand how climate variability and global change influence ecosystem processes in arid lands. The Huxman group uses Tumamoc Hill for several projects focused on understanding factors that control carbon metabolism in plant, soils and ecosystems.

First, as part of her dissertation research Danielle Ignace is looking at the effects of soil surface on the photosynthetic performance of creosotebush, which is a dominant drought tolerant species found in the deserts of the southwestern U.S. (Sonoran, Mojave, Chihuahuan Deserts). The study includes two soil surface deposits of different ages; a Pleistocene (clay rich soil that inhibits deep infiltration of precipitation) and a Holocene (sandy, coarse texture that allows deep infiltration of precipitation). Danielle has measured canopy volume, percent dieback, photosynthesis, water stress, and carbon and nitrogen isotopic content of leaf tissue. She has shown that greater allocation to rapid growth and reproduction in wet conditions on the older soil surface result in a greater productivity potential during prolonged wet periods, but also increase the probability of mortality during protracted drought.

Alex Eilts (another student in the Huxman group) is evaluating the effects of shifts in understory species composition on growth and performance of paloverde. Specifically, he is asking whether a non-native grass (bufflegrass), which displaces native shrubs and grasses, has greater competitive influence on the native tree. Theoretical consideration (based on spatial and temporal resource partitioning) suggest that the tree may perform better in the presence of the non-native species. The results to date suggest the opposite; that the presence of bufflegrass in similar densities as native understory species significantly accelerates self-thinning and pruning in paloverde, increasing the probability of mortality. It appears that bufflegrass may be influencing the translation of precipitation into biologically available water, altering seasonal water status in the tree.

Jessie Cable (another student in the Huxman group) is currently working on two projects on Tumamoc Hill, both of which focus on the role of biological soil crusts (cyanobacteria, lichen and fungi that form living mats on the soil surface) in ecosystem processes in desert systems. In small plots, she is evaluating the relative contribution of these soil microbial systems to whole-ecosystem photosynthetic and respiratory processes using gas exchange and stable isotope

technology. She has shown that the crust system responds favorably to fairly small rainfall events, while plants and the remaining microbial systems in soils require larger precipitation events to initiate function. Considering that the southwestern deserts receive considerable precipitation in event sizes that only may affect soil microbial crusts, these cyanobacteria, lichen and fungi communities may be important contributors to carbon cycling. Additionally, in collaboration with a project initiated by Jayne Belnap (USGS – Canyonlands), Jessie is using a rainfall manipulation on Tumamoc Hill to understand the importance of seasonality of precipitation on carbon exchange dynamics in soil crust systems. This study is embedded in a manipulation that is focused on nitrogen cycling and the influence of crust function on soil food webs in different climate conditions.

Finally, the Huxman group has a series of collaborations with other researcher on the Hill focused on several interdisciplinary questions. Travis is collaborating with Larry Venable to understand how variation in ecophysiological performance of desert annuals contributes to the coexistence of different groups of species in a temporally variable climate system. They are using rainfall manipulations and natural variation in performance between microsites to address this question. Additionally, the Huxman group has been periodically evaluating the large scale (100's of meters) exchanges of carbon dioxide, water and energy from desert vegetation on Tumamoc Hill by the use of micrometeorological techniques (specifically the eddy covariance technique). This work has focused on understanding how all components of a system respond together to variation in climate, and is use to make comparisons across a network of large-scale flux systems in other biomes. This work contributed significantly to a collaboration with Brian Enquist, where together we showed that a single temperature function can explain much of the variation in ecosystem metabolism across a set of diverse biomes (Enquist et al., 2003). This work suggests that differences between the carbon exchange characteristics of diverse ecosystems may be explained by the ecological and evolutionary consequences of varying time periods available for photosynthetic and respiratory activity.

Barrel cactus/ant mutualisms

Judith L. Bronstein, EEB, University of Arizona, William F. Morris, Department of Biology, Duke University, and Josua Ness, postdoc, EEB, University of Arizona, have recently established a study of the potentially mutualistic relationship between barrel cactus and ants. Barrel cacti (*Ferocactus wislizeni*) have extrafloral nectaries at the areoles. Two abundant species of ants (a *Solenopsis* and a *Crematogaster*) avidly collect the nectar. The Bronstein lab has initiated pilot studies of the two barrel cactus-ant relationships to determine (1) if they are mutualistic, specifically whether ants defend the plants from damaging herbivores (the herbivore of greatest interest is a pyralid moth that lays its eggs on the buds), (2) if there is a difference in the quality of protection afforded by the two ant species, and (3) if the competitively dominant ant species is also the better mutualist. Thus, they are extending the study of mutualism from the usual pairwise focus to a three-species perspective in which both competitive and mutualistic effects play important roles.

Desert Tortoise Disease Study

Desert tortoises are being studied on Tumamoc Hill by Bill Shaw and Cristina Jones, School of Renewable Natural Resources at the University of Arizona, Cecil Schwalbe of the USGS Sonoran Desert Field Station, and Don Swann, Saguaro National Park. Urban development adversely affects the desert tortoise, *Gopherus agassizii*, through habitat loss, illegal collection, uncontrolled domestic dogs, and roads. A less visible consequence, yet just as detrimental, is the spread of disease into free-ranging populations along urban boundaries, which can be transmitted by escaped or released captive desert tortoises. One such disease is Upper Respiratory Tract Disease (URTD), caused by the pathogen *Mycoplasma agassizii*. Though extensive studies have been conducted on the Mojave population of the desert tortoise following a catastrophic decline attributed to URTD, very little is known about the prevalence of URTD in the Sonoran population.

The research team began a study in July 2002 that examines URTD in desert tortoises on Tumamoc Hill and other sites in the Tucson Basin. The purpose of this study is to use two analyses, one that detects specific antibody in plasma present after exposure to *M. agassizii* (ELISA) and another that detects *M. agassizii* RNA gene sequences in nasal secretions (PCR), to determine the prevalence of URTD in captive and free-ranging Sonoran populations of the desert tortoise in and around the Greater Tucson area. Tumamoc Hill is one site being used to conduct searches for free-ranging tortoises; it is a prime example of tortoise habitat along the urban-wildland interface. Additional free-ranging desert tortoises are being sampled along an urban gradient from the Santa Catalina, Rincon, Tortolita, Tucson, Sierrita, and Silverbell Mountains.

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