

A Debt to the Past: Long-term and Current Plant Research at Tumamoc Hill (The Desert Laboratory) in Tucson, Arizona

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Introduction

Long-term research has been recognized as beneficial to our understanding of how ecosystems function and change and how natural systems may be managed, particularly in light of prognostications of long-term climate change (Webb et al. 2009). The Desert Botanical Laboratory (Fig. 1), founded in 1903 (Bowers 2010), has inspired a long history of contributions to desert plant ecology, many of which occurred long after the Carnegie Institution of Washington ceased operations in Tucson in 1940. These contributions are original research conceived by researchers working wholly or partially at Tumamoc Hill, and many involve continuation and (or) modifications of the original research designs conceived by the founders of this historic institution. In this article, we discuss selected recent research findings that had originated with scientists based on Tumamoc and working at least partially on the laboratory grounds.

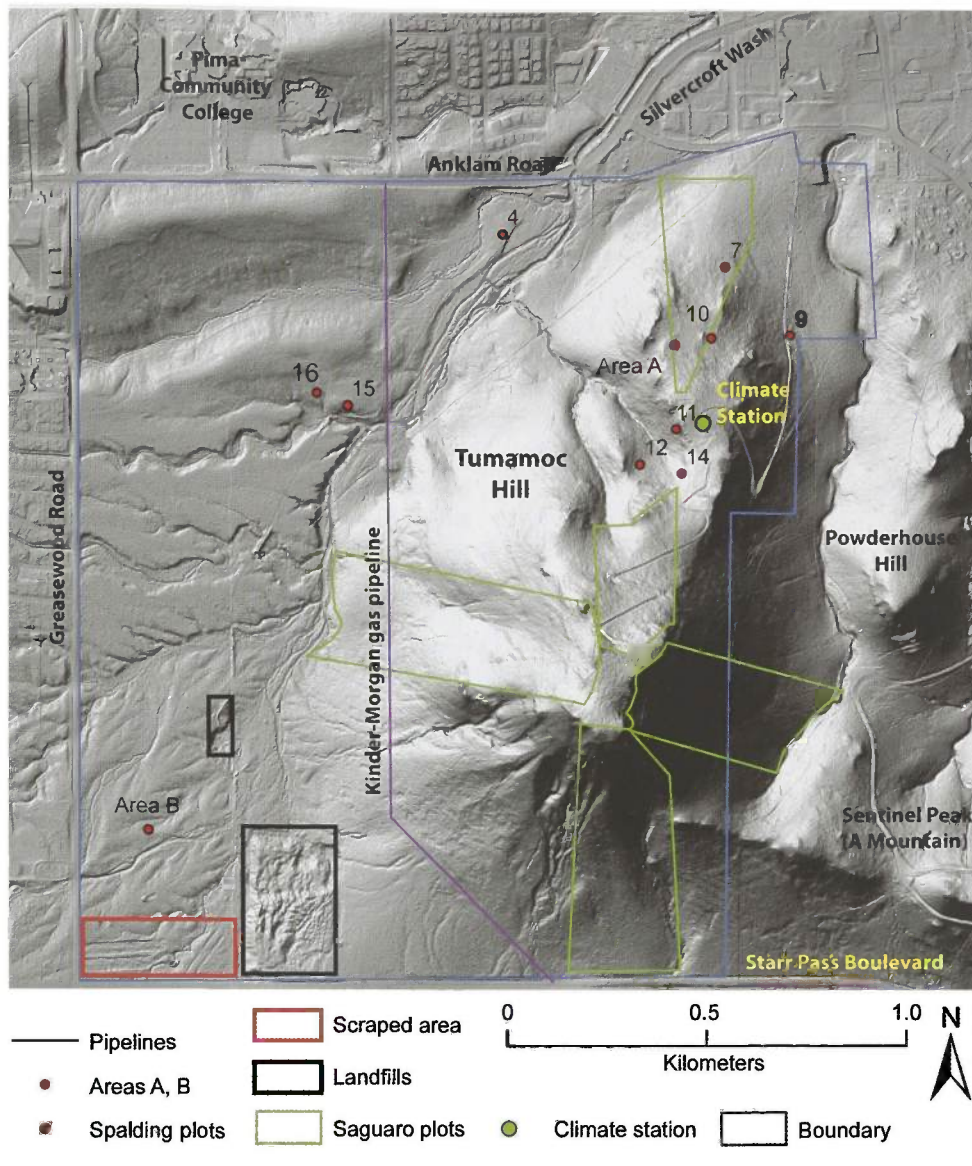
The name of the Desert Botanical Laboratory has changed over the last 100 years and is now known as Tumamoc: People & Habitats. In this paper, we will refer to this place either as the Desert Laboratory, its name over most of the last quarter century, or Tumamoc. The grounds consist of 352 hectares of land that have been fenced from livestock grazing since 1907 (Shreve 1929). Although protected from grazing, numerous other intrusions have created a mosaic of disturbances of different ages on the landscape, ranging from roads and landfills to pipeline corridors and powerlines (Fig. 1). Some of these disturbances, combined with urban development up to the Desert Laboratory boundaries, have reduced the number of long-term plots that were initially established. However, because the disturbed areas are recovering, they offer researchers new opportunities to study natural restoration in the Sonoran Desert. The research findings at this unique research station, which covers the longest period of scientific investigations of desert plants in the world, can be extrapolated to wider questions of long-term change in the Sonoran Desert.

Geology and Climate Variation

Tumamoc Hill and Sentinel Peak (A Mountain) to the east are outcrops of basaltic andesite overlying rhyolite and other volcanic rocks of Tertiary Age (Pearthree and Biggs 1999, Spence et al. 2003). A much larger area of the grounds to the west consists of colluvium and alluvium of mostly Quaternary Age dissected by washes (Fig. 1). The northwest area of the property, for example, is dominated by Pliocene-Pleistocene alluvial deposits of an age between 1 and 5 million years that are characterized by rounded ridges of eroded soils and exposed calcrete horizons developed on coarse, gravelly substrate (Pearthree and Biggs 1999). Younger deposits include alluvium of late Pleistocene and Holocene Ages associated with Silvercroft Wash and recent sediments deposited during storm runoff. Research at Tumamoc Hill has shown that edaphic (soil) conditions strongly affect plant species composition and productivity, primarily owing to effects on rooting depths and infiltration (see Edaphic Relations). The bedrock and surficial geology of the Desert Laboratory is not unique for landscapes of the Sonoran Desert, which is dominated by volcanic rocks of the types that create Tumamoc Hill and Sentinel Peak.

Tucson, which lies in the Arizona Upland subdivision of the Sonoran Desert (Turner and Brown 1982), has a mean annual precipitation of 292 mm at Tucson International Airport from February 1930 to December 2009 (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?az8820>, accessed 22 July 2010) with considerable interannual variation. The climate station at the University of Arizona, the longest record of climatic data in Arizona with initial monthly precipitation data collection beginning in 1868, has an annual precipitation of 288.4 mm (Fig. 2), of which 38% falls in the winter months of November through March and 49% falls in the summer months of June-September. Rainfall data have been collected near the laboratory buildings (Fig. 1) from 1907 until the present with the exception of 6 years when no records were kept (1940-1941, 1972-1975). This record indicates that mean annual rainfall on Tumamoc Hill is 298 mm, with 36% falling between November and March and 53% falling in June-September. The Desert Laboratory receives more than the 250 mm of precipitation, the upper climatic limit of deserts worldwide, and this area better fits the definition of a semiarid environment.

Several attempts have been made to characterize periods of southern Arizona precipitation according to hydrological or ecological effects. Turner et al. (2003) presented one definition of interdecadal climatic variability (Fig. 2, bottom). The Desert Laboratory was founded at the end of the late 19th century drought, and the first measurements of the long-term Spalding vegetation plots were made in 1906, the approximate start of the early 20th century wet period. This wet period generally extends to 1940, although drought periods occurred in southern Arizona at the end of the 1910s and during the 1930s (Fig. 2). What has variously been called the 1950s drought, began in the mid-1940s and extended into the early 1960s in southern Arizona (Fig. 2). It is referred to as the mid-century drought. The late 20th century wet period extends from the mid-1970s through at least 1995 and by many accounts to the El Niño event of 1997-1998. The last decade is known as the early 21st century drought. The early 20th century and early 21st century droughts have similar characteristics, although the early 20th century drought had far more devastating effects on pastoralists and agriculture in southern Arizona (Turner et al. 2003).



hillshade model of topography at the Desert Laboratory in Tucson, Arizona, showing the locations of permanent plots and set aside for the long-term study of perennial desert vegetation and the location of some of the disturbed sites. Landfill refers to mounds covered with material from scraped areas.

Laboratory Collection of Repeat Photography
 Hastings and Raymond M. Turner began matching old photographs in 1960 as a way of studying bioclimatology of change in the Sonoran Desert (Webb et al. 2007a), at the Desert Laboratory. Originally, their archives were at the main University of Arizona campus. The first documented camera station, was a 1960 match of a photograph taken by D.T. MacDougall, one of the founders of the Desert Laboratory, in 1960 (Webb et al. 2010a). The first publication from this collection was the classic book *Changing Mile* (Hastings and Turner 1965).

When Turner moved to Tumamoc Hill in 1976, he brought the collection with him. At the time of his retirement in 1998, the collection had about 1280 stake numbers and had grown to the largest collection of its kind in the world. By 2010, the collection, now known as the Desert Laboratory Collection of Repeat Photography, contained nearly 5000 stake numbers and photographs. Numerous publications featured photographs from this archive, including an update of the *Changing*

Mile (Turner et al. 2003), documentation of changes in the riverine and desert environments of Grand Canyon (Turner and Karpiscak 1980, Bowers et al. 1995, Webb 1996), changes in subtropical vegetation in Kenya (Turner et al. 1998), a review of changes in regional riparian vegetation (Webb et al. 2007b), and a compendium of world-wide studies using the technique of repeat photography (Webb et al. 2010b).

Hastings and Turner originally conceived their collection to evaluate long-term change in Sonoran Desert vegetation. At the Desert Laboratory, repeat photography documents a number of landscape-scale changes, including the overall increase in foothill palo verde (*Cercidium microphyllum*) (Fig. 3) and changes in saguaro (*Carnegiea gigantea*) populations (Fig. 4). In 2010, a total of 192 photographs of the Desert Laboratory and its environs have been matched, mostly by Turner and his colleagues.

Bullock and Turner (2010) summarized regional population trends in perennial vegetation of the Sonoran Desert as determined from analyses of repeat photography. Because of the long period over

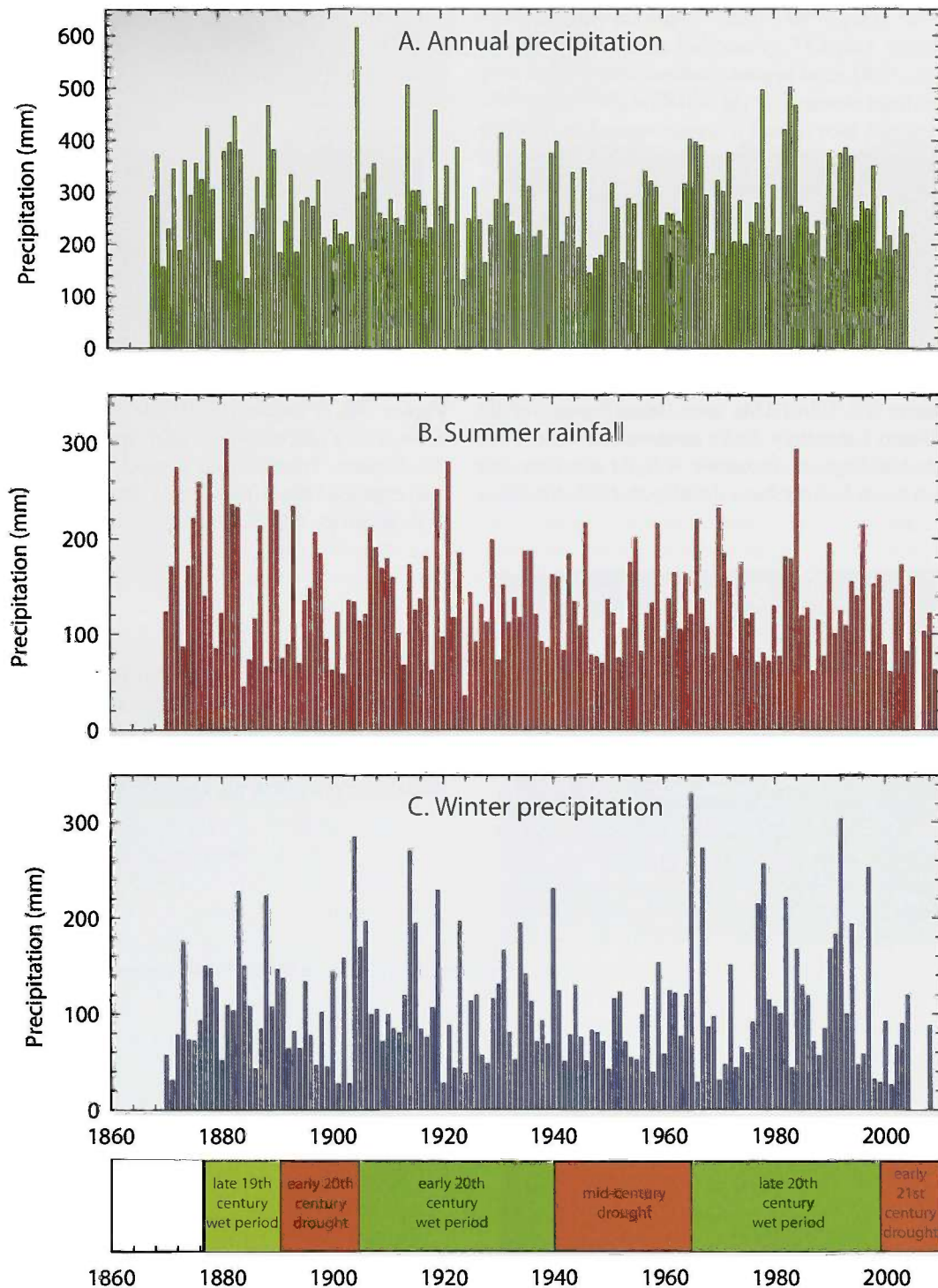


Figure 2. Annual and seasonal precipitation at the University of Arizona from 1868 to 2009. The lower panel shows generalized periods of southern Arizona climate.

which original photographs were taken and matched, age ranges were established of original photographs (1883-1959, median \approx 1900), first repeat photographs (1933-1985, median = 1962-1963), and second repeat photographs (1984-2000, median = 1994-1995). For the interval between original and first repeat photographs, or about 1900 through 1963, increases in biomass were observed for many common species, including two species of mesquite (*Prosopis* sp.), *Acacia neovernicosa*, burrobush (*Isocoma tenuisecta*), cardón (*Pachycereus pringlei*), foothill palo verde (*Cercidium microphyllum*), and ocotillo (*Fouquieria splendens*),

while decreases were observed in cirio (*Fouquieria columnaris*) in Baja California and desert spoon (*Dasyliirion wheeleri*) and Palmer's agave (*Agave palmeri*) in southeastern Arizona. For the second period, between 1963 and 1995, no changes were observed in most species studied except for noteworthy exceptions of increases in Palmer's agave, mesquite, pricklypear, cardón, and desert spoon (Turner et al. 2003). They concluded that climate was the most important reason for fluctuations in perennial vegetation, although land-use practices, particularly the intensity of livestock grazing and fire suppression, are also important factors,



Figure 3A. (January 23, 1906) This view, taken by one of the founders of the Desert Laboratory, looks northwest down a ravine to the west of the buildings on Tumamoc Hill. At this time, this part of the Tucson basin had not been developed. (D.T. MacDougal, b4-11).



Figure 3B. (February 19, 1964) Tucson has expanded into the view, with a nascent subdivision appearing on the alluvial fans in the distance. Foothill palo verde (*Cercedium microphyllum*) has also expanded blocking some of the view of the midground ravine. (J.R. Hastings, G89-3, Stake 276)

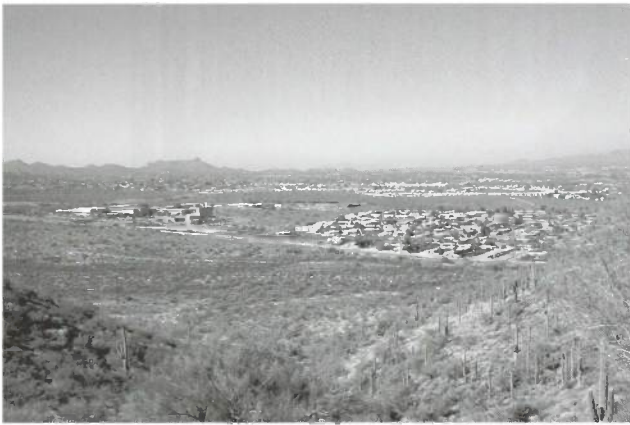


Figure 3C. (December 22, 1998) Pima Community College west campus is now prominent on the alluvial fan at midground, and the north property line of the Desert Laboratory is clearly delineated by Anklam Road. Foothill palo verde have grown and new individuals are present in the view. (R.M. Turner, Stake 276)

Figure 3. Above, repeat photographs showing increase in foothill palo verdes.



Figure 4A. (ca. 1907) This view northeast from the Desert Laboratory, shows agricultural fields in the midground and the growing city of Tucson in the distance at right. The view also shows perennial vegetation on the north slope of Tumamoc Hill (Godfrey Sykes).

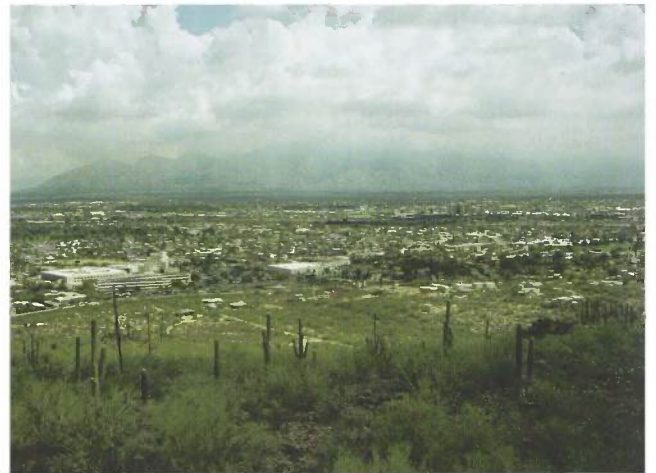


Figure 4B. (August 27, 2003) Clearly Tucson has grown; St. Mary's Hospital dominates the left midground. The number of saguaros visible from this camera station has greatly increased, particularly at right center. Overall, there is an apparent increase in biomass of perennial vegetation, notably foothill palo verde (D. Oldershaw, Stake 4678)

These regional changes are mirrored on the lands of the Desert Laboratory, although changes are related to the different geomorphic surfaces on the west side of the property. Furthermore, Bullock and Turner (2010) did not evaluate the effects of the early 21st century drought, which were devastating in some parts of the desert Southwest. The permanent plots at Tumamoc Hill chronicle the effects of this drought on desert plants in this mosaic of a landscape.

The Spalding Plots

In 1906, Volney Spalding established a number of permanent vegetation plots with the objective of recording changes in perennial and annual plants with time at the Desert Laboratory (Spalding 1909, unpublished notes 1906). At the time of its establishment, the grounds were considered to be overgrazed and Spalding could not keep the horses, goats, cattle, and burros off his new plots, prompting him to lobby for the boundary fence, which was completed in 1907. The initial measurements on these plots occurred just before the property was fenced to exclude grazing disturbance of unknown magnitude, and Tumamoc Hill became one of the world's first restoration ecology projects as those plots began to recover.

Spalding created 19 plots (Table 1), and the locations of some of these are only vaguely described (Shreve 1929; Shreve and Hinckley 1937, Goldberg and Turner 1986). Although at least two of these plots were only 1 m², most of the plots are approximate squares of 10 m × 10 m. The initial measurements used string placed at 1 m intervals to map the position of the root crown of each perennial species, allowing estimation of plant density but not cover. In 1910, Forrest Shreve remapped two of the plots and established Area A, an irregular polygon of 557 m² on which large perennial plants are counted but not mapped. On Spalding plots 11 and 15 (Table 1), Shreve mapped both the position of the root crown and the crown perimeter (Shreve 1929), allowing estimation of both density and cover as well as providing information needed to calculate survivorship and life span (Bowers 2005).

Eighteen years passed before the plots were remeasured in 1928-1929. Shreve (1929) remeasured five of the original plots, recounted the plants in Area A, and established Area B, a plot consisting of eight contiguous 10 x 10 m subplots (Shreve and Hinckley 1937). In 1936, Shreve and associates mapped the plots that had been mapped in 1928-1929, ignoring the other Spalding plots (Shreve and Hinckley 1937). The next maps were produced by two master's students, Jack M. Kaiser in 1948 and Ann V. Murray in 1957 (Murray 1959). Between 1959 and 1985, Turner and colleagues mapped four Spalding plots and Area B at irregular intervals (Table 1). In 1968-1969, Turner located and mapped five additional Spalding plots not measured since 1906 and Area A, which had not been examined since Shreve's work in 1936. Since 1969, at least one of these plots has been measured every eight years under the guidance of USGS staff at the Desert Laboratory, and during the past 105 years, the Spalding and Shreve plots have been remeasured as few as 4 and as many as 14 times (Table 1). One of the plots (17) was destroyed by road construction after the 1948 mapping and two others (plots 4 and 9) were damaged along one of their margins.

Spalding plot 16 (Figs. 5, 6) provides a good example of long-term change at the Desert Laboratory. This plot, which is 99.408 m² in area, has a total cover that changed from 28.5% in 1928 to 37.5% in 1993 and 17.2% in 2010 (Fig. 7). Creosote bush dominated this plot in 1928, and range ratany, a known root parasite (Cannon 1910), had relatively low cover (Figs. 6A, 7). By the middle of the 20th century, and during the mid-century drought, both creosote bush and range ratany had greatly decreased in cover. In 1993, when plot 16 had its highest measured total cover following the late 20th century wet period, range ratany had a higher cover than creosote bush. In 2010, creosote bush had a higher cover than range ratany, but not by much (Fig. 7) and not to the extent of 1928. Density of plants on this plot mirrors cover (Table 2), although some of the fluctuations are much larger. Total density of the most common species ranged from about 2500/ha in 1906 to about 26,000/ha in 1968 (about 6300/ha in 2010), with large changes in subshrubs. Creosotebush steadily declined through the 20th century from a high of 1610/ha in 1906 to its current density of 700/ha. Long-term change in plot 16 confirms Shreve's assertion that stability or systematic change in perennial plant assemblages in the Sonoran Desert is an illusion, a point of long-term discussion with Frederic Clements during the early days of the Desert Laboratory (Bowers 2010).

Goldberg and Turner (1986) reported many trends in desert plant species at the Desert Laboratory and noted maximum longevities, an important plant characteristic examined further by Bowers et al. (1995) using repeat photography in the Grand Canyon. Bowers (2005) used the permanent plots to examine the effects of the mid-century and early 21st century droughts on survival and longevity of 6 species of woody plants. She found that the effects of the early 21st century drought were much more pronounced than those of the mid-century drought, causing sharp declines in survival and maximum longevity for most of the species. The average life spans for creosote bush (*Larrea tridentata*), Berlandier wolfberry (*Lycium berlandieri*), white ratany (*Krameria grayi*), janusia (*Janusia gracilis*), triangle-leaf bursage (*Ambrosia deltoidea*), and brittlebush (*Encelia farinosa*) are 330, 211, 184, 53, 40, and 16 years, respectively, and reflect drought-induced high mortality during this drought.

Distribution and Expansion of Native and Non-Native Plant Species

Thornber (1909) published the first flora of the Desert Laboratory, which included three non-native species: filaree (*Erodium cicutarium*), Bermuda grass (*Cynodon dactylon*), and wall barley (*Hordeum murinum*). V.M. Spalding (1909) produced maps showing the distribution of filaree and Bermuda grass. Turner began updating the flora in 1968-1969. After a lull of almost a decade, collection resumed in 1977 and continued through 1984 (Bowers and Turner 1985). This revised flora revealed that two native species, ironwood (*Olneya tesota*) and jojoba (*Simmondsia chinensis*), had disappeared and 52 non-native species were present, including the three present in 1909. The new species were mostly annuals that were most common in disturbed habitats created after 1940, such as access roads, pipelines, and landfills (Fig. 1). Urban development had also slowly surrounded the laboratory property and many of the new plant additions undoubtedly originated from nearby residential yards.

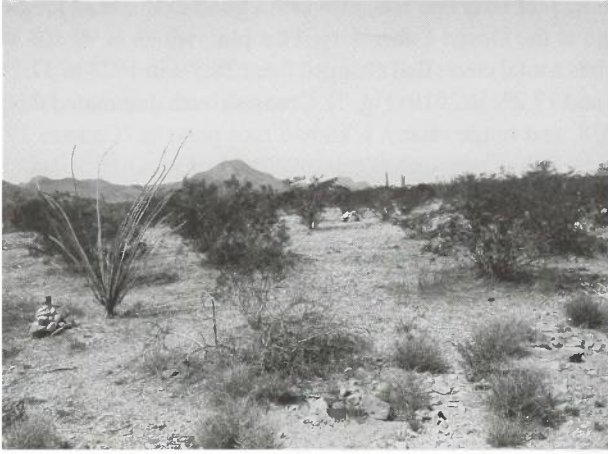


Figure 5A. (March 1906) At the time that it was established, plot 16 was dominated by large creosote bush (*Larrea tridentata*) and a prominent ocotillo (*Fouquieria splendens*), although only root-crown locations were measured in this year (Table 2). (V. Spalding, Stake 376A)



Figure 5B. (November 25, 1928). This view and the ones that follow were taken from a slightly different angle. This photograph shows plot 16 in the year that the first crown outlines were measured (see Figure 6A). The ocotillo is gone but the creosote bush remain prominent (F. Shreve, Stake 376B).



Figure 5C. (1959) This view of plot 16, taken near the end of the mid-century drought, shows an area of low cover and low plant stature (photographer not known, Stake 376B).



Figure 5D. (December 19, 1986). In the middle of the late 20th century wet period, but before the 1993 remeasurement of plot crown cover (Figure 6C), creosote bush has a large stature on plot 16 (R.M. Turner, Stake 376B).

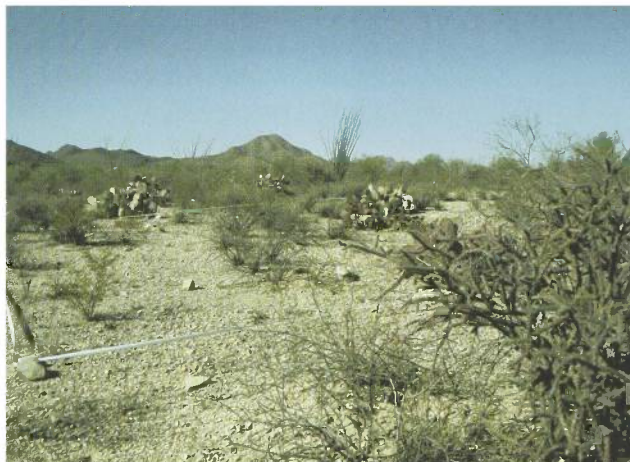


Figure 5E. (January 15, 2010) After more than a decade of the early 21st century drought, creosote bush again is diminished in size and cover is reduced. The magnitude of the changes is somewhat masked by the appearance in the foreground of a new cholla (*Cylindropuntia versicolor*) (R.M. Turner, Stake 376B).

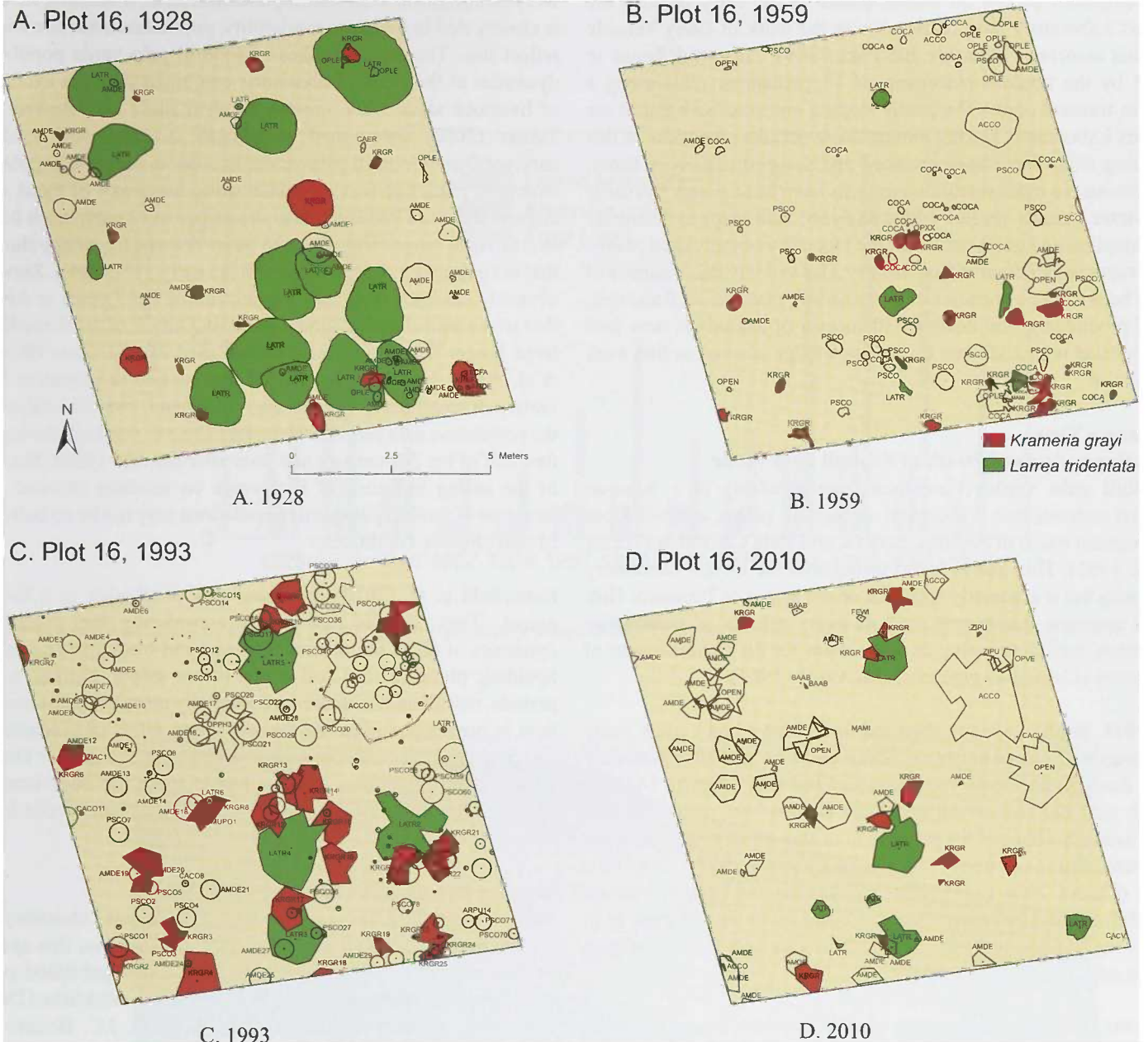


Figure 6. Maps of perennial vegetation on Spalding plot 16 at Desert Laboratory. This plot is 99.408 m² in area and was established in 1906 on alluvium west of Tumamoc Hill (Figure 1). The plants are shown as canopies and are labeled with four-letter codes. On this plot, some of the common plant codes are LATR (*Larrea tridentata*), KRGR (*Krameria grayi*), ACCO (*Acacia constricta*), and AMDE (*Ambrosia deltoidea*). In 1993, many BAAB (*Bahia absinthifolia*) plants are not labeled owing to their high density in that year.

Burgess et al. (1991) further evaluated non-native species based on a 1983 survey of these plants across the laboratory property on gridlines designed to map their location and follow their dispersal through time. The gridlines allowed 33 of the 52 species to be mapped but the remaining 19 were too rare. In 2005, Bowers et al. (2006) found 44 non-native species on the gridlines where 33 had been found previously; eight species present in 1983 were not present in 2005, and 19 species newly found in 2005 were not known in the flora previously and probably colonized the Desert Laboratory grounds in the previous 20 years. Interestingly, the non-native flora shifted from agricultural and ruderal weeds to ornamental plants as the surrounding lands shifted from farmlands to subdivisions. Ornamental species comprised 26% of non-native species in 1983 and 50% in 2005.

Several non-native annual species such as Mediterranean grass (*Schismus* spp.), London rocket (*Sisymbrium irio*) and red brome (*Bromus rubens*) had spread densely and uniformly across the property by 1983 and still held their ground in 2005. One introduced perennial grass, buffelgrass (*Pennisetum ciliare*), is a native of Africa that produces persistent, tall, coarse, standing foliage, and its increase at the laboratory is remarkable and problematic because allegedly it is linked to increase fire frequency in areas that previously rarely if ever burned (Esque et al. 2006). Between 1983 and 2005, this species greatly increased on the gridlines, representing the greatest change for any species examined (Bowers et al. 2006).

The emphasis placed on annual plants in the early days of the Desert Laboratory has continued with the work of Larry Venable and his associates (Venable and Pake 1999). This work began in 1982 by the random placement of 15 permanent plots along a 250 m transect across the gently sloping creosote bush flat at the Desert Laboratory. During almost three decades, the plots in this ongoing study have been revisited and mapped numerous times, and numerous other research questions have been posed. Focusing on winter annuals, these workers analyzed their maps to determine germination and death dates and the fecundity of individual plants. Soil cores were obtained from nearby sites to study the dynamics of seed banks. The intricacies of germination, maturation, flowering, seed production, and death of 30 species of annuals is now well understood with additions to this knowledge assured as this work continues.

A Larger View:

The Expansion and Death of Foothill Palo Verde

Foothill palo verde (*Cercidium microphyllum*) is a Sonoran Desert endemic that is abundant on bajadas, plains, and hillslopes throughout much of Arizona, Sonora, and Baja California (Turner et al. 1995). This tree is found throughout the Desert Laboratory property but is especially abundant on the slopes of Tumamoc Hill. This common desert tree controls many aspects of community function, including acting as nurse plant for the establishment of saguaros (*Carnegiea gigantea*) (McAuliffe 1984).

In 1911, Shreve (1911b) observed that "I have had a great many thousands . . . come under my observation . . . and have seen only two dead [foothill palo verde] trees of full size." A mere 14 years later, near the end of the early 20th century wet period, he had dramatically changed his perception of this tree's condition when he noted that many trees of all ages had recently died at Tumamoc Hill (Shreve 1924/1925). This reversal did not persist, because foothill palo verde appears to have increased in the 20th century in most repeat photography of the Desert Laboratory, particularly on the flanks of Tumamoc Hill (Fig. 3).

In 1995, at the beginning of the early 21st century drought, foothill palo verde dieback was again observed at Tumamoc Hill (Bowers and Turner 2001). Twelve randomly placed plots were established, with two each on the four slopes facing cardinal directions and four on the flats at the base of the hill. Altogether, 1057 living and dead trees were sampled on the 72 m × 72 m plots. Findings showed that mortality was highest among older, larger plants and was far greater on steep slopes than on level ground. The greater death rate on steep slopes was attributed to the greater aridity of these slopes where rainfall runoff is highest and soils are shallowest. The death of older plants was attributed to the greater susceptibility of older individuals to a variety of lethal forces. This natural senescence interacts with extreme drought, hastening the death of the older trees. Bowers and Turner (2001) concluded that, at the time of their study, establishment of foothill palo verde was not keeping pace with mortality and that the number of younger individuals was not great enough to maintain a stable population, but the long-term history is one of fluctuating populations, much like that of the saguaro (see next section).

The apparent influence of drought on survival of mature foothill palo verdes prompted another study that examined the effect that

wet years might have on seedling establishment. If seedling survival is closely tied to moisture availability, population structure should reflect this. The earlier studies of foothill palo verde population dynamics at the Desert Laboratory, combined with the exclusion of livestock since 1907, created an ideal study site. Bowers and Turner (2002) determined population structure and seedling survivorship of foothill palo verde. In order to measure population structure, plant age was estimated using the proxy of basal stem circumference of 980 living and dead trees in 12 plots, each 0.5 ha in size. Ages ranged from 1 to 181 years and age frequency showed that the population was in decline in the early 21st century. Survival of newly emerged seedlings was monitored for 7 years in Area A that was established by Shreve in 1910. Only 2 of 1008 seedlings lived longer than 1 year and all had died after 4 years (Bowers et al. 2004). But the low survival was related to predation by a variety of small herbivores instead of climate. Further analysis of the population data showed that establishment was high during the first half of the 20th century and poor after the mid-1950s. Because of the strong influence of herbivores on seedling survival, age structure of foothill palo verde populations may not be an indicator of past climatic conditions.

Butterfield et al. (2010) countered this conclusion to a limited extent. They showed that when considering the population dynamics of all of the perennial shrubs and trees growing on the Spalding plots, rainfall had a significant effect. During wetter periods, recruitment increased substantially more beneath canopies than in openings, indicating that the direct effect of precipitation on recruitment beneath canopies was different and greater than its effect in the open. Their work suggests again the importance of foothill palo verde in nurturing other perennial plant species in the Sonoran Desert.

Saguaro Demography and Growth Rates

The high regard that the early workers at the Desert Laboratory had for the saguaro is shown by the emphasis placed on this species in their research. It was the subject of the first published paper (E.S. Spalding 1905) emanating from the newly established Desert Botanical Laboratory (Bowers 2010). In 1908, J.C. Blumer and crew used a plane table to map all of the saguaros on the Desert Laboratory property and on Powder House Hill and Sentinel Peak (A Mountain) to the east (V. Spalding 1909, Plates 15 and 16). These maps covered more than 690 ha, showed thousands of plants, and depicted the saguaro's habitat preferences. W.A. Cannon prepared a detailed report of the root system of this cactus (E.S. Spalding 1909, p. 59-66) and E.S. Spalding described the mechanical adjustment of the pleated saguaro stem to varying amounts of precipitation over a period of almost 4 years (V. Spalding 1909, p. 59-66). Shreve analyzed the relation between height and age of the saguaro at Tumamoc Hill and then calculated its rate of establishment (Shreve 1910). He also closely examined the influence of low temperature on the plant's survival in a laboratory study where he inserted thermometers into small saguaros and then placed the plants in freezers (Shreve 1911a).

The early emphasis placed on the saguaro was not lost on later workers at Tumamoc Hill. Hastings was one of the first to study saguaros in the late 1950s, when he extended E. S. Spalding's study of the saguaro's response to rainfall (Spalding 1905). At a site on the flat to the west of Tumamoc between Spalding Plots 15

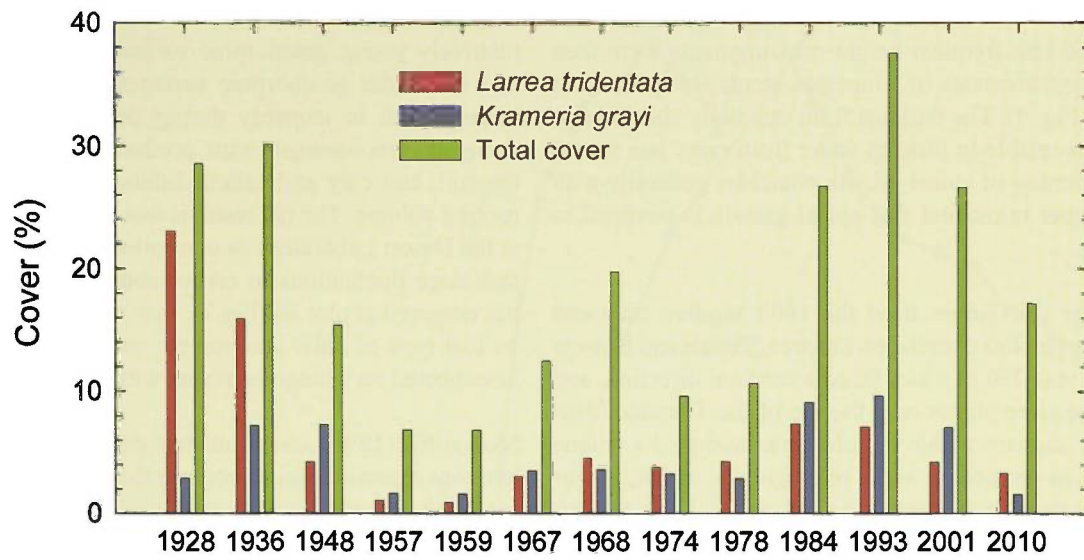


Figure 7. Trends in cover of creosote bush (*Larrea tridentata*), range ratany (*Krameria grayi*), and total cover in Spalding plot 16.



Figure 8. Photograph of the east slope of Tumamoc Hill showing the distribution of buffelgrass (*Pennisetum ciliare*), an invasive perennial grass, as the tan colored areas. Experimental work using saguaro dendrometers (inset, lower left) is being conducted mid-slope on the right side of this view.

and 16 (Fig. 1), Hastings placed spring loaded brass bands around 10 saguaros, with a wire-wound resistor attached to one end of the girdle and to the other, a contact arm (Hastings 1961). A modern illustration of this appears in Figure 8. Using photogrammetry (measurements from photographs), change in height of 11 plants was measured. The near continuous measurements of stem circumference and less frequent height measurements were then compared with measurements of temperature and precipitation at adjacent gauges (Fig. 9). The findings from this study showed that the saguaro seems unable to pick up water from rains less than 5 mm; that the beginning of apical growth coincides generally with the onset of summer rains; and that apical growth is confined to summer.

In 1964, Hastings and Turner used the 1908 saguaro map and superimposed 4 large plots over the earlier area (Turner and Bowers 1988). Each plot was 250 m wide, faced a cardinal direction, and extended from the steep slopes near the top of the Tumamoc Hill to its base. Every saguaro within the plots was assigned a unique number, its location marked on aerial photographs, its height was measured, and the number of branches was recorded. Later, the two maps were matched by superimposing the new aerial photograph over the 1908 map. The population on the 4 slopes was roughly 1.5 to 2.0 times greater in 1964 than in 1908. These 4 plots were remeasured in 1970 and 1993 (Pierson and Turner 1998). Their analysis showed that saguaro populations nearly doubled on all 4 slopes since 1908 (Fig. 4), with the greatest density of saguaros persistently occurring on south- and east-facing slopes. Their study enabled them to convert saguaro height to age, which revealed that there was an extended period of decline from about 1860 to 1908 and a surge in recruitment that began in the 1920s and peaked in the 1970s. The populations are once more in decline at the beginning of the 21st century.

Because saguaro establishment is rare, and the population is subject to boom and bust cycles, one question asked is whether those cycles are due to variation in seed production or climatic variation. Saguaros have short-lived seeds and warm temperature requirements for germination, and therefore germination and establishment must occur shortly after the seeds are dispersed. From 1967 to 1988, Bowers (1996c) studied the environmental triggers that control flowering date, raising the question as to what limits seed production. She found that flowering is controlled by cool-season rain, increasing day length, and a combination of increasing solar radiation and warming temperatures. A cool-season (November-March) rain of at least 6-9 mm is probably the initial trigger. Another study suggests a possible explanation for poor establishment rates at times in the past. Schmidt and Buchmann (1986) found that honeybees were the main pollinators of saguaro flowers. These insects are so efficient at pollen harvesting that, starting at daybreak, they will have removed virtually all of the pollen by 9 or 10 a.m. Honeybees were introduced to the region about 100 years ago and, prior to that time, the intermittent lack of native pollinators may have sporadically limited fruit set.

Edaphic Relations and Perennial Vegetation

Soils have been called the foundation of ecosystems, yet the influence of soil (edaphic) conditions on desert plant assemblages was poorly understood until the mid-1980s. Although Shreve's research on the effect of caliche (indurated soil carbonate horizons)

on paloverde root distributions was well considered, ecologists took notice when Joe McAuliffe published a paper linking the multidisciplinary concepts of geomorphology, soil hydrology, and ecosystem function (McAuliffe 1994). In a complex analysis comparing vegetation assemblages on three geomorphic surfaces at the Desert Laboratory, he showed that creosotebush preferred relatively young geomorphic surfaces with less pedogenic clay, and that older geomorphic surfaces underlain by caliche place creosotebush in jeopardy during droughts. To survive periodic droughts, creosotebush must produce roots at multiple levels in the soil, and clay and caliche inhibit root elongation, restricting rooting volume. The net result is that creosotebush varies spatially at the Desert Laboratory as controlled by the geomorphology, and that large fluctuations in creosotebush cover and density, which has occurred at plot 16 (Fig. 7), may represent merely what occurs on that type of older geomorphic surface. Less fluctuation might be expected on younger surfaces with higher infiltration capacity.

McAuliffe (1994) observed that development of clay (argillic) horizons exerts strong control over the plant species that can survive extended drought periods on those surfaces. He also observed that maximum plant diversity may occur on surfaces undergoing erosion because of the reduced infiltration effects of increased clay and caliche. Species that can persist on seasonal moisture, particularly summer rainfall with limited soil penetration, may be at an advantage on older geomorphic surfaces. This may help explain why many succulent species, particularly cacti, are more common on older geomorphic surfaces than on young ones at the Desert Laboratory.

Species-Specific Research

Numerous studies have been conducted at the Desert Laboratory concerning physiological ecology, germination and establishment, and phenology and reproduction of individual desert plant species. Shreve Plot Area A, established in 1910, has been used for several studies in recent years. In an eight year study, Bowers used this plot to evaluate the conditions controlling the seedling emergence of three prominent Sonoran Desert species (Bowers 1994). Both minimum rainfall triggers and the appropriate minimum temperatures for emergence were described for foothill palo verde (*Cercidium microphyllum*), ocotillo (*Fouquieria splendens*), and brittlebush (*Encelia farinosa*) from 1987 through 1992. In another study running concurrently with the previous study on Area A, Bowers described the germination behavior and seed bank persistence of triangle-leaf bursage (*Ambrosia deltoidea*) from 1987 to 2000 (Bowers 2002). Bowers et al. (2004) studied the timing and spatial pattern of seedling emergence and early survival for 15 species from 1987 to 1993 on Area A and found that few species emerged in all years of the study, the first-year survival averaged across all 15 species was 3.7%, and only 0.1% of seedlings lived as long as 4 years.

In 1956 and 1957, Turner (1963) measured the seasonal growth and flowering of trees found at the Desert Laboratory. He used a dendrometer to measure slight changes in the stem radius of velvet mesquite (*Prosopis velutina*) and blue palo verde (*Cercidium floridum*) growing along a water course on the west side of the property and ironwood (*Olneya tesota*) and foothill palo verde growing several kilometers to the west on a hillslope. The use of dendrometers was pioneered by MacDougal (1936, 1938) at the

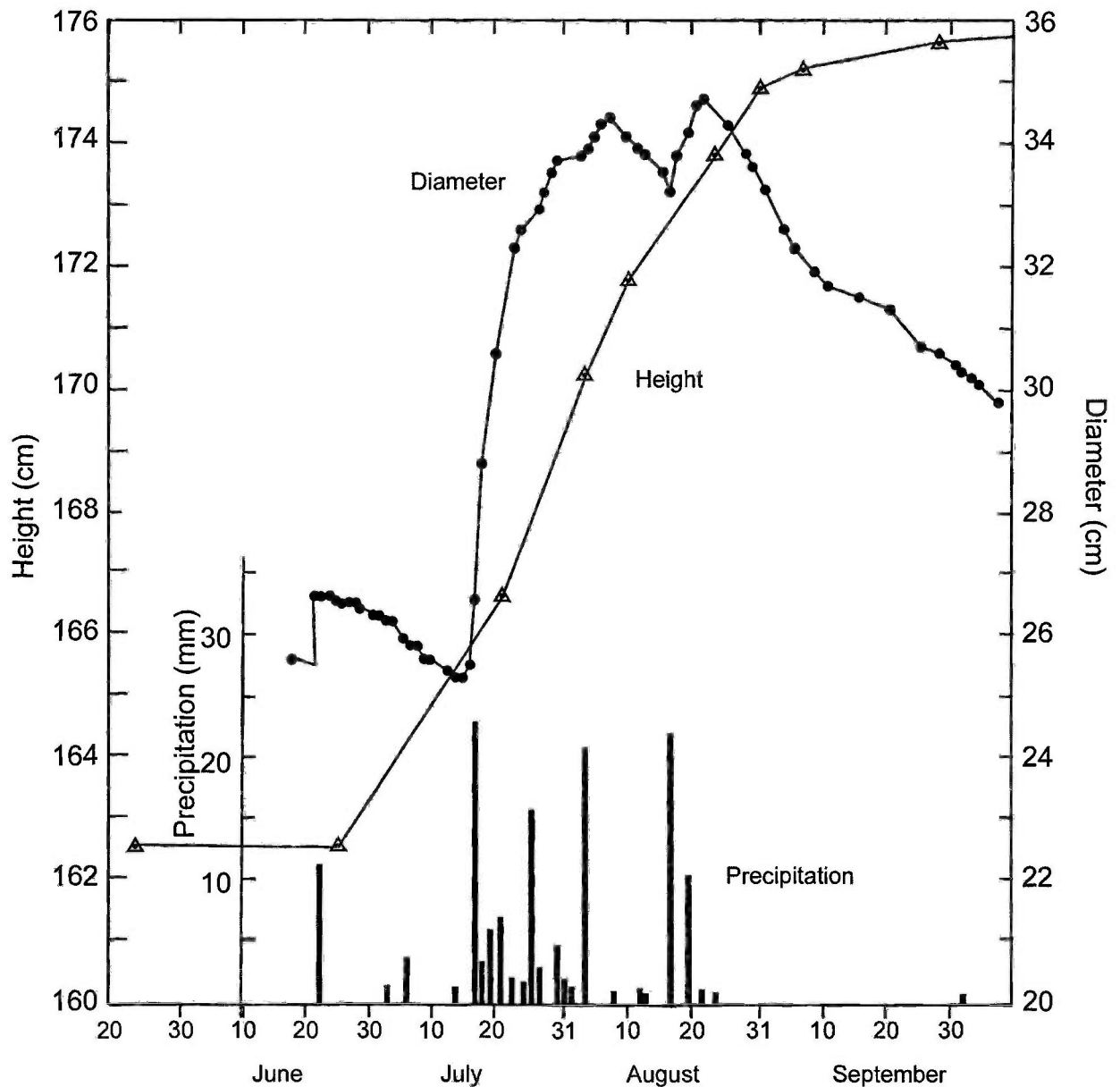


Figure 9. Graph showing growth of saguaro 4A in relation to summer precipitation in 1959 (Hastings 1961). This plant was at a site between Spalding plots 15 and 16 on the west side of the Desert Laboratory.

Desert Laboratory, and Turner's work seemed a natural extension of the early work. The two lowland species had a flush of radial stem growth in the spring in response to winter rains, while radial growth in the upland plants occurred after summer rains. Leaf growth followed different pathways for the trees. For example, in mesquite, initiation of leaf growth was closely timed – apparently by photoperiod – while leaf growth timing in the palo verde, with its extensive photosynthetic stems, was erratic. Timing of floral development in the four species was well defined, although no flowers appeared for foothill palo verde in the spring of 1956, a drought year.

As illustrated by research on saguaro, reproduction and phenology of cacti are favored research topics at the Desert Laboratory. Bowers (1998) studied flower, fruit, and seed production of barrel cactus

(*Ferocactus wislizeni*), and her work revealed basic characteristics of this short columnar cactus, which produces an average of 25 flowers/yr – a relatively low number for a desert species – but have a fruit set with up to 25,000 seeds per plant. Plants begin their reproduction when they reach a diameter of about 19 cm, which is relatively small for a species that regularly has mature adults with a diameter of >50 cm.

In the Sonoran Desert, prickly pear is one group of cacti that has greatly increased, presumably the result of decreasing frequency of severe frost (Turner et al. 2003). Bowers (1996a, 1996b, 1997) conducted sustained research on reproduction and phenology of Engelmann prickly pear (*Opuntia engelmannii*), one of the most common species of prickly pear in the Sonoran Desert. She found that the age of plants could be determined from the number of

pads (cladodes) (Bowers 1996a). Her work indicated a complex tradeoff of pad production versus flower production, since both are produced from the same areoles on the margins of the pads. During wet years, the plants produced flowers instead of new pads, whereas pad production appears to have increased during some drought years (Bowers 1996b, 1997). She estimated a maximum lifespan of 20-25 years for this species (Bowers 1996a) and explained the apparently longer-term persistence of up to a century (Bowers et al. 1995) by vegetative propagation of pads from seedling plants that appeared to have died.

This raises an important question: when do individuals that propagate vegetatively die? Is it when the stem of the plant that germinated and established is dead, or is it when all the remaining clonal material has disappeared? This important question extends to larger issues, such as the reported extreme longevity of creosote bush of many thousands of years (Vasek 1980, McAuliffe et al. 2007). This species persists via clonal material that expands into rings long after the center of the original plant has died.

Relevance: Global Change and Desert Vegetation

As with long-term global temperature and precipitation data, long-term plot data anchors our concepts of the influence of climate change – whether human influenced or natural fluctuations – on ecosystem properties and function. For example, without long-term data on saguaro demographics and growth rates, we would have little idea that this species undergoes boom and bust cycles of mortality and establishment, and that snapshots of this species' status at any given time can be extremely misleading in regard to its long-term population trajectory. Similarly, knowing this species' propensity for reproduction during wet periods and the current long-term prognostications of sustained drought, we might be concerned that at some point 50-100 years in the future, this species might not have its current visual stature on southern Arizona landscapes. We now know this simply can be attributed to its known lifespan and rare germination and establishment of new individuals. Drought may be the best explanation for changes in some parts of Saguaro National Park, where landscapes once visually dominated by saguaro now appear to be a sea of foothill palo verde (Turner et al. 2003, Plate 60).

Although geologists developed the technique of repeat photography in the late 19th century, researchers at the Desert Laboratory systematically applied this technique to regional vegetation change. Sustained application of repeat photography, especially in concert with other remote-sensing techniques, could be a cost-effective technique for addressing spatial variability of long-term change in the Sonoran Desert and other arid regions that cannot be obtained from permanent plots alone. While data collection from permanent vegetation plots, such as the Spalding and Shreve plots at the Desert Laboratory, might be the ideal way for assessing long-term landscape changes, regional establishment of permanent plots is costly and unfeasible. As Bullock and Turner (2010) demonstrate, assessments of change in species abundance using repeat photography can provide a reasonable means for evaluating regional change.

Abiotic control of desert vegetation has long been a theme of research at the Desert Laboratory. Research results from the Desert Laboratory have shaped modern ecological thought on

how long-term changes in vegetation are driven by soils, substrate lithology, and climate. We now know that geomorphic and soil characteristics can control ecosystem function and vegetation response to climate change. Researchers who develop monitoring programs that stratify desert ecosystems according to geology and geomorphology owe a debt to the pioneering research of scientists at the Desert Laboratory.

Tumamoc Hill is the premier site in the Sonoran Desert for long-term documentation of establishment and spread of invasive species. Repeated mapping of the grounds shows the rate of expansion of non-natives, especially buffelgrass, which some consider to be the largest threat at present to ecosystem function in this region (<http://216.104.181.187/drupal-6.16/index.php>, accessed 30 August 2010). At the same time, the mapping shows that some non-native species either have disappeared or have not significantly expanded or increased in abundance. Moreover, increases in ornamental species underscore that the urban-wildland interface is the front line of the effort to control expansion of non-native species into the desert environment.

Land use in the Sonoran Desert continues to exert a strong pressure on desert ecosystems, and future climate change will exacerbate recovery. The Desert Laboratory provides many examples of natural recovery from disturbances, in some cases repeated disturbances (Fig. 10). If severely disturbed areas, such as the pipeline corridor depicted in Figure 10, are not restored by active measures, such as reseeding or planting of shrubs and trees, then climate will play a role in the course of natural recovery. As shown in Figure 10, the pipeline corridor disturbed in the 1950s had substantial revegetation of trees and shrubs by 2003, following about a half century of recovery with no additional disturbance. Will the scene depicted in 2004 follow the same trajectory, or will, in the face of long-term climate change, this newly denuded surface require much longer times to recovery? This is one of the many research questions that could be addressed from the foundation of long-term research that started at the Desert Laboratory in 1903 and continues to this day.

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Figure 10A. (September 1958) Southerly view of a newly installed pipeline for transporting gasoline from El Paso, Texas to Tucson and Phoenix. It crosses the western edge of Tumamoc Hill on an easement through the Desert Laboratory property. The vegetation present is mostly annual forbs and grasses (R.R. Humphrey).



Figure 10B. (February 21, 1978) By 1978, the beginning of the late 20th century wet period, subshrubs had become established in the pipeline corridor (R.M. Turner, Stake 905A).



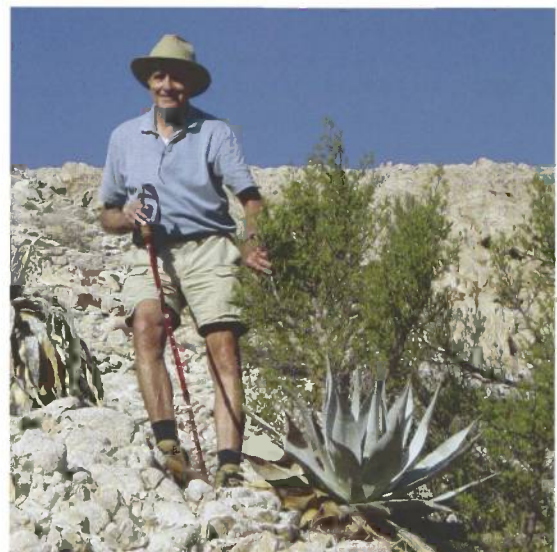
Figure 10C. (October 27, 2003) What appears to be a mature Sonoran Desert plant assemblage, albeit without saguaros, had become established in the pipeline corridor more than 45 years after disturbance (R.M. Turner, Stake 905A).



Figure 10D. (June 3, 2004) The new pipeline was installed a few months before this match. The ocotillo in the right foreground was one of several of these plants that were salvaged and planted along the pipeline corridor (R.M. Turner, Stake 905A).



Figure 10E. (April 25, 2010) In nearly 7 years after the new disturbance, many new subshrubs have become established in the pipeline corridor. The transplanted ocotillo has tilted to the west (R.M. Turner, Stake 905A).



Ray Turner with *Agave turneri* and *Bursera microphylla*, Sierra Cucapá, Mountains, south of Mexicali, Baja, California

Table 1. Measurement years of the Spalding permanent perennial vegetation plots at the Desert Laboratory, Tucson, Arizona

Plot	Size (m)	1906	1910	1928	1929	1936	1948	1957	1959	1960	1967	1968	1969	1974	1975	1978	1984	1985	1993	2001	2010	Total maps
1	10 x 10	x																				1
2	10 x 10	x																				1
3	10 x 10	x																				1
4	10 x 10	x										x				x					x	6
5	10 x 10	x																			x	1
6	10 x 10	x																				1
7	10 x 10	x										x				x					x	5
8	10 x 10	x																				1
9	10 x 10	x										x				x					x	5
10	10 x 10	x										x				x					x	4
11	10 x 10	x	x							x		x				x				x	x	13
12	10 x 10	x									x					x				x	x	10
13	1 x 1 ?																					1
14	10 x 10	x											x			x					x	5
15	10 x 10	x	x									x				x					x	12
16	10 x 10	x										x				x					x	14
17	10 x 10	x		x												x					x	4
18	10 x 10	x																				1
19	1 x 1	x																				1
Area A	about 557 m ²		[x]	[x]		[x]										[x]					[x]	1
Area B	20 x 40			8		8	8	8				8				8					8	9
Total plots measured		18	2	12	1	13	13	9	2	2	1	16	1	1	1	17	12	4	2	17	14	97

Table 2. Density (plants/ha) of selected perennial species in Spalding plot 16 at the Desert Laboratory, Tucson, Arizona

SPECIES	DENSITY (plants/ha)													
	1906	1928	1936	1948	1957	1959	1967	1968	1974	1978	1984	1993	2001	2010
All chollas	100	400	500	900	1310	1110	700	700	0	100	100	100	200	200
All perennial grasses	0	0	0	0	100	0	1210	700	0	100	400	6540	400	0
<i>Acacia constricta</i>	200	0	0	100	300	200	200	200	300	200	200	200	200	300
<i>Ambrosia dumosa</i>	0	3620	4730	3220	700	600	1010	1410	1410	1310	2110	2520	3520	3220
<i>Bahia absinthefolia</i>	0	0	0	0	0	0	7850	13,280	3620	5030	1710	4120	300	400
<i>Cercidium microphyllum</i>	0	0	100	0	0	0	100	100	400	100	100	0	0	0
<i>Krameria grayi</i>	500	1510	8150	6340	2520	2520	2720	2620	1910	2210	2210	2210	2210	1210
<i>Larrea tridentata</i>	1610	1410	1310	1010	700	600	700	805	500	500	500	604	700	700
<i>Opuntia engelmannii</i>	0	0	0	100	200	300	300	400	200	200	200	300	300	300
<i>Psilostrophe cooperi</i>	0	0	3220	600	1910	1710	2110	5530	200	500	1610	7850	1710	0
<i>Senna covesii</i>	0	0	0	0	0	0	1210	1107	18,610	200	0	1110	1310	200
<i>Tiquilia canescens</i>	200	0	3720	1410	1210	2720	400	500	200	0	0	0	0	0
Total Density ¹	2620	6940	21,700	13,700	8950	9760	18,500	27,400	27,400	10,500	9150	25,600	10,900	6540

¹ Total density only refers to the species in the table. Other plants were found at different times on this plot.