

A Century of Vegetation Change on the Santa Rita Experimental Range

Abstract: We know more about vegetation change on the Santa Rita Experimental Range since 1903 than is known about any other 20,000-ha area in the world. This record is only possible because important techniques of measuring vegetation changes were developed on the Santa Rita, such as repeat photography and the line intercept transect method, and because they were applied often and broadly. A 100-year record of experiments and systematic observations nourishes the interpretation of these changes. Together, they describe a steady increase of mesquite trees, four cycles of burroweed eruption and decline, one cholla cactus cycle, interannual and interdecadal variation in native grass composition, and the recent dominance of the nonnative Lehmann lovegrass. The most conspicuous change is the increase of mesquite, which began before 1903 when the spread of seed by livestock and cessation of fire led to the establishment of mesquite in the open grasslands. The growth of these plants and subsequent recruits transformed the grasslands into a mesquite-grass savanna, and neither the elimination of livestock grazing nor the occasional fire has reversed this change. Burroweed cycles appear to be more closely related to winter precipitation patterns and maximum plant longevity than land management activities. Similarly, the increase of Lehmann lovegrass is largely independent of livestock grazing management.

Keywords: mesquite, burroweed, cacti, perennial grasses, Lehmann lovegrass, cover, density, repeat photography

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Introduction

A century of detailed observation, repeat photography, and systematic remeasurement provide an unparalleled opportunity to reckon the past, evaluate the present, and predict the future vegetation changes on the Santa Rita Experimental Range. The long and rich history of experiments and manipulations provide valuable information for interpreting these changes. This legacy reveals that future vegetation changes will likely be contingent on the elevation and soils, future precipitation patterns, and the current condition of the vegetation.

In general, the century of vegetation change on the Santa Rita included (1) an increase in mesquite trees; (2) several cycles of burroweed and cholla cactus that persisted for several decades; (3) an initial increase in native perennial grasses following livestock removal in 1903 and subsequent seasonal and annual fluctuations; and (4) increased dominance of the nonnative Lehmann lovegrass since 1975 and the coincident decline of native grasses. However, these dynamics have not been uniformly expressed in space or time. In some cases these inconsistencies are clearly associated with unique geomorphic features such as washes and soil differences or distinct precipitation patterns, but other inconsistencies are not as easily explained.

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This paper describes the patterns of vegetation change on the Santa Rita since 1903 and reviews the research attempting to interpret the mechanisms contributing to these patterns. The information is confined to work performed on the Santa Rita in order to celebrate the richness of that legacy. The physical setting and administrative history are described first, followed by a review of the methods used to measure vegetation that were developed on the Santa Rita. The patterns and interpretations of changes in mesquite, burroweed, cactus, and perennial grasses are then reviewed. The concluding section begins by stressing that we are obliged to continue remeasuring and rephotographing these areas in order to continue this legacy. A brief description of interpretative research opportunities follows. Finally, suggestions are made for applying these data to evaluate theoretical issues of vegetation change and for developing practical management tools that are based on a large empirical body of work.

The Santa Rita

Located about 80 km south of Tucson, AZ, the 21,000-ha Santa Rita Experimental Range stretches across the western alluvial skirt of the Santa Rita Mountains. Elevation increases from about 900 to 1,400 m, and average annual precipitation increases along this gradient from 275 to 450 mm (fig. 1). Between 1,100- and 1,200-m elevation, the mean (1922 to 2003) summer and winter precipitation have been 213 and 158 mm since 1922 (fig. 2). There is striking evidence of significant interannual (CV winter = 44.7 percent and CV summer = 31.4 percent) and interdecadal variation in precipitation at these elevations, and similar

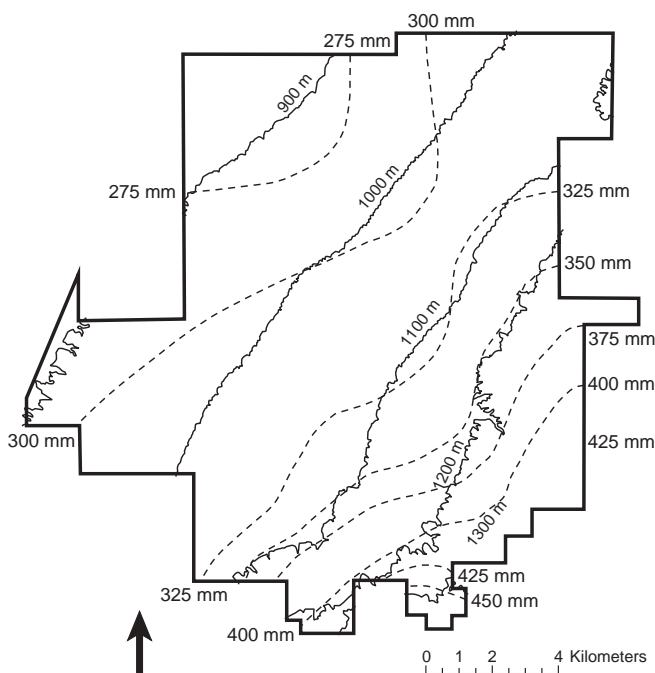


Figure 1—Elevation and annual precipitation gradients on the Santa Rita Experimental Range.

patterns occur at other elevations. Noteworthy features of the precipitation record are distinct summer and winter patterns; very wet summers in 1931 and 1984; a prolonged dry period from 1932 to the late 1950s; wet conditions in the mid 1980s; and since 1988 to 1989, high interannual variability (CV winter = 51.0 percent and CV summer = 37.6 percent).

The current vegetation is a mixture of short trees, shrubs, cacti and other succulents, perennial grasses, and other herbaceous species (table 1). The physiognomy ranges from a desert scrub at the lowest elevations to savanna woodlands at the highest. The most extensive vegetation is a mesquite-grass savanna, but Desert Grassland has become a popular moniker (McClaran 1995).

Established in 1903, the Santa Rita is the oldest continuously operating rangeland research facility in the United States (McClaran and others 2002). Until 1988, it was operated by the U.S. Department of Agriculture, first by the Bureau of Plant Industry (1903 to 1915) and later by the Forest Service (1915 to 1988). It was then transferred to the Arizona State Land Department (Medina 1996). The 38th Arizona Legislature (1987) dedicated the area for rangeland research and education, and assigned administration to the University of Arizona, College of Agriculture and Life Sciences (Arizona Senate Bill 1249).

Beginning around 1880, overgrazing of vegetation and livestock dieoff were widespread because severe droughts were common and open access to rangeland prevented control of livestock numbers (Bahre and Shelton 1996; Griffiths 1904). Fires were probably frequent prior to the intensification of livestock grazing (Humphrey 1958), and based on the survival rates of different sized plants, the average time between fires appears to have been 5 to 10 years. Since 1903, fire has been very rare. However, three arson-caused fires in June 1994 covered about 10,000 ha.

Between 1903 and 1915, livestock were excluded from all areas below about 1,200-m elevation to allow the vegetation to recover from overgrazing and to ascertain its productive potential. Since reinstatement of grazing in 1915, hundreds of experiments and manipulations have been performed to evaluate livestock grazing practices, rodent influences, methods of vegetation control, and seeding of plants (Medina 1996). A portion of this original data is available in digital form (McClaran and others 2002), but most of it resides in the paper archive at the College of Agriculture and Life Sciences, University of Arizona.

A Legacy of Documenting Vegetation Dynamics

Our well-founded understanding of vegetation change during this century is only possible because of the long record of observations, photographs, and systematic remeasurement. No other research facility has a longer and more detailed record of vegetation change. The duration and detail of vegetation change documentation at the Santa Rita is unrivaled thanks to the foresight, innovation, and initiative of early scientists. Records of their measurements and observations have been published or otherwise preserved, and there are many cases where succeeding scientists have continued these measurements. Although initial vegetation

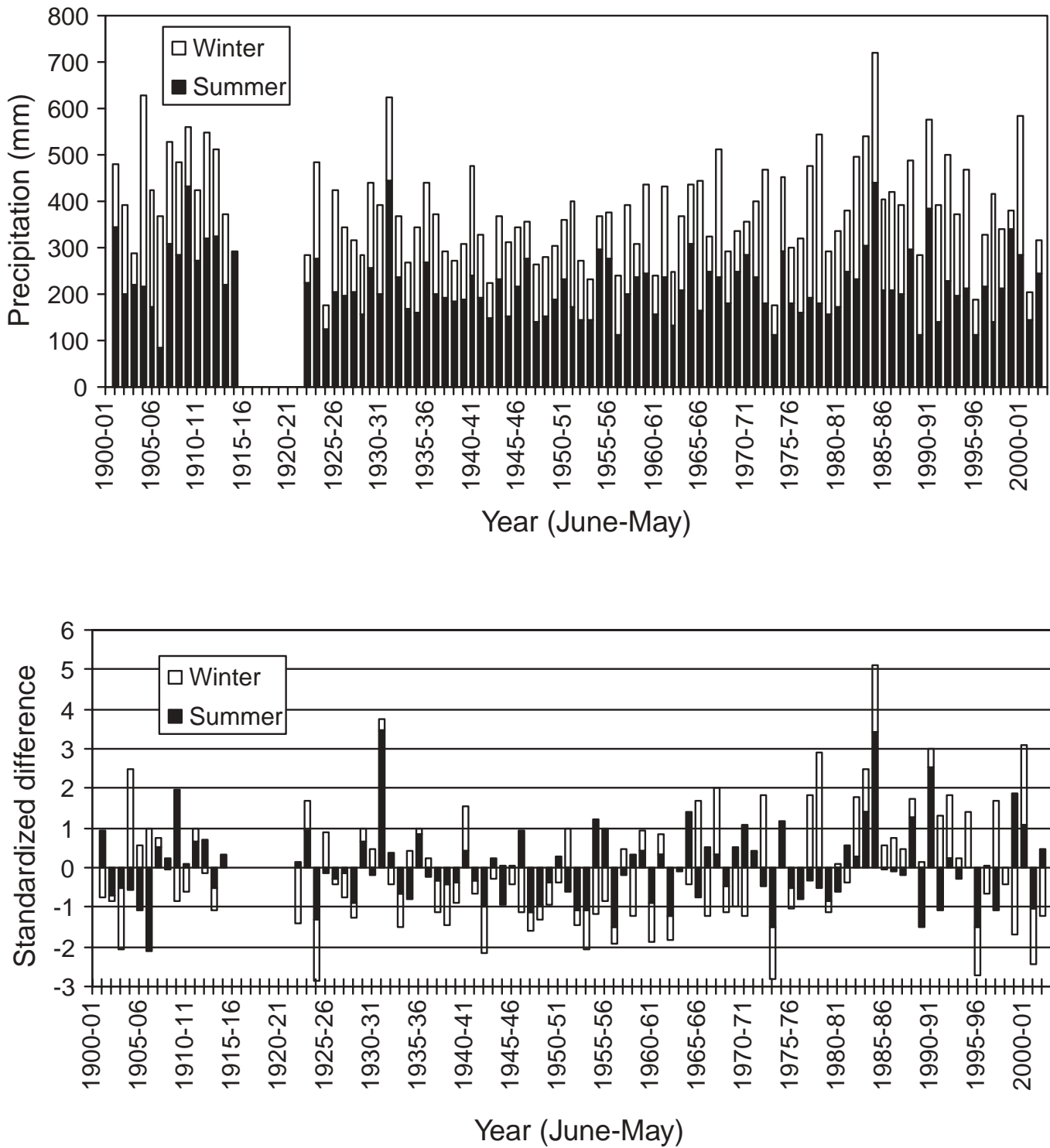


Figure 2—Seasonal and standardized difference for precipitation on the Santa Rita Experimental Range, 1901–1902 to 2002–2003. Values are from 1902–1903 to 1913–1914 for McClary Ranch, 1,200-m elevation (Thornber 1910; Wooten 1916); values since 1922 are the average of four rain gauges, Box, Eriopoda, Road, and Rodent between 1,100- and 1,200-m elevation (McClaran and others 2002). Summer months are June through September. Standardized difference is the yearly value minus the long-term average, which is divided by the standard deviation. Mean and standard deviation for McClary Ranch were calculated separately from other rain gauges.

Table 1—Common and scientific names for common shrubs and trees, cacti and succulents, and grass species on the Santa Rita Experimental Range.

| Common name | Scientific name |
|-----------------------------|--|
| Shrubs and trees | |
| Blue palo verde | <i>Cercidium floridum</i> Benth. |
| Burroweed | <i>Isocoma tenuisecta</i> Greene |
| Catclaw acacia | <i>Acacia greggii</i> Gray |
| Creosote bush | <i>Larrea tridentata</i> (Sesse & Moc.) Cov. |
| Desert hackberry | <i>Celtis pallida</i> Torr. |
| Velvet mesquite | <i>Prosopis velutina</i> (Woot.) |
| Cacti and succulents | |
| Cane cholla | <i>Opuntia spinisior</i> (Engelm.) Toumey |
| Chainfruit cholla | <i>Opuntia fulgida</i> Engelm. |
| Fishhook barrel | <i>Ferocactus wislizenii</i> (Engelm.) Britt. & Rose |
| Prickly pear | <i>Opuntia engelmanni</i> Salm-Dyck |
| Saguaro | <i>Carnegiea gigantea</i> (Engelm.) Britt. & Rose |
| Soaptree yucca | <i>Yucca elata</i> Engelm. |
| Grasses | |
| Black grama | <i>Bouteloua eriopoda</i> (Torr.) Torr. |
| Bush muhly | <i>Muhlenbergia porteri</i> Scribn. |
| Cottontop | <i>Digitaria californica</i> (Benth.) Henrard |
| Curly mesquite | <i>Hilaria belangeri</i> (Steud.) Nash |
| Fluff grass | <i>Erioneuron pulchellum</i> (Kunth) Tateoka |
| Hairy grama | <i>Bouteloua hirsuta</i> Lag. |
| Lehmann lovegrass | <i>Eragrostis lehmanniana</i> (Nees) |
| Needle grama | <i>Bouteloua barbata</i> Lag. |
| Pappus grass | <i>Pappophorum macronulatum</i> Nes |
| Rothrock grama | <i>Bouteloua rothrockii</i> (Vasey) |
| Santa Rita threeawn | <i>Aristida glabrata</i> (Vasey) Hitchc. |
| Sideoats grama | <i>Bouteloua curtipendula</i> (Michx.) Torr. |
| Six weeks grama | <i>Bouteloua aristidoides</i> (Kunth) Griseb. |
| Slender grama | <i>Bouteloua filiformis</i> (E. Fourn.) Griffiths |
| Spidergrass | <i>Aristida ternipes</i> Cav. |
| Sprucetop grama | <i>Bouteloua chondrosoides</i> (Kunth) Benth. |
| Tall threeawn | <i>Aristida hamulosa</i> Henr. |
| Tanglehead | <i>Heteropogon contortus</i> (L.) P. Beauv. |

descriptions were largely based on qualitative observations, some important systematic and quantitative measures were developed and repeatedly applied on the Santa Rita beginning in 1902.

The qualitative descriptions of the Santa Rita and nearby areas by Griffiths (1904, 1910), Thornber (1910), and Wooten (1916) are among the first systematic, professional accounts of vegetation composition and conditions in the North American arid Southwest. They provide the baseline from which to judge all subsequent vegetation changes. For example, based on Griffiths' initial descriptions (1904), Wooten (1916) was able to make the first estimates of rates of recovery for arid grasslands following exclusion of livestock grazing.

Between 1903 and 1908, Griffiths (1904, 1910) performed the first systematic and repeated measures of herbaceous biomass production in arid grasslands by clipping, drying and weighing plants in twenty-eight 0.9 by 2.1 m (3 by 7 ft) plots in the same locations. Wooten (1916) repeated those measurements between 1912 and 1914.

Griffiths's (1904, 1910) photographs in 1902 and 1903 provided the basis for the first use of repeat photography to document vegetation change in arid grasslands when Wooten (1916) used repeat photography to assess changes in burroweed abundance between 1903 and 1913. These efforts fostered the continuation of repeat photography on the Santa Rita that includes the first use to document changes in mesquite abundance (Parker and Martin 1952) and growth rates of chainfruit cholla (Tschirley and Wagley 1964). The repeat photography collection (McClaran and others 2002) is one of the largest and most accessible in the world.

Systematic and repeated mapping of individual grass plant basal area was performed on hundreds of permanent 1-m² quadrats on the Santa Rita from the late 1910s into the 1930s (Canfield 1957; Hill 1920). Although scientists at the Santa Rita developed modifications to improve the efficiency and accuracy of mapping (for example, the pantograph [Hill 1920] and the densimeter [Culley 1938]), the method was abandoned because it was too time consuming, and it did not measure the trees, shrubs, and cacti. The measurement of those nongrass species gained urgency when their abundance began to increase in the 1930s.

The line intercept transect method used to measure plant cover was developed by Canfield (1942) while working on the Santa Rita. It replaced the quadrat mapping method because it was more efficient and measured both grass and nongrass plant cover. This continues to be one of the most widely used methods of estimating plant cover in the world. Martin and Cable (1974) and Cable and Martin (1975) measured cover from 1957 to 1966 on about 200 permanent transects. By adding a width dimension to the line transect, Martin and Severson (1988) combined the measures of plant cover and density at 150 permanent located transects every 3 years from 1972 to 1984. My colleagues and I have completed the remeasurement of about 130 of those transects every 3 years between 1991 and 2003 (McClaran and others 2002). About half of those transects have a measurement history that started in 1957. This 46-year record of repeated measurement provides a unique opportunity to document long-term changes of individual species and vegetation.

Double-sampling methods of estimating herbaceous production were conducted adjacent to the permanent line intercept transects beginning in the 1950s (Cable and Martin 1975; Martin and Cable 1974). Unfortunately, the comprehensive measurement of herbaceous production was last performed on the Santa Rita in 1984 (Martin and Severson 1988).

Changes in Mesquite Abundance

Mesquite is a long-lived (greater than 200 years), leguminous tree that can grow greater than 5 m tall. The roots are both shallow and deep (0.25 to greater than 3.0 m), and some shallow roots may extend far (15 m) from the trunk (Cable 1977). Growth begins in April after a winter deciduous period (Cable 1977). Seeds can remain viable for 20 years in the soil (Martin 1970), and plants as small as 1-cm basal diameter will generally resprout from basal meristems after aboveground mass is removed (Glendening and Paulsen 1955).

Pattern

Based on observations and photographs between 1902 and 1915, mesquite trees and other woody plants such as catclaw acacia, blue palo verde, and creosote bush were most common below 1,000 m and confined to the larger washes and arroyos above that elevation (figs. 3 and 4; Griffiths 1904, 1910; Thornber 1910; Wooten 1916). However, as

early as 1902, small mesquite plants (less than 1 m tall) were scattered in the grassland areas between the washes above 1,000 m, and their increase by 1915 was noted by these observers.

Since 1930, the increase of mesquite density and cover was greatest between 1,000 and 1,150 m, the same elevations where the incipient trees mentioned earlier had been noted. Between 1934 and 1954, there was a 33-percent increase in

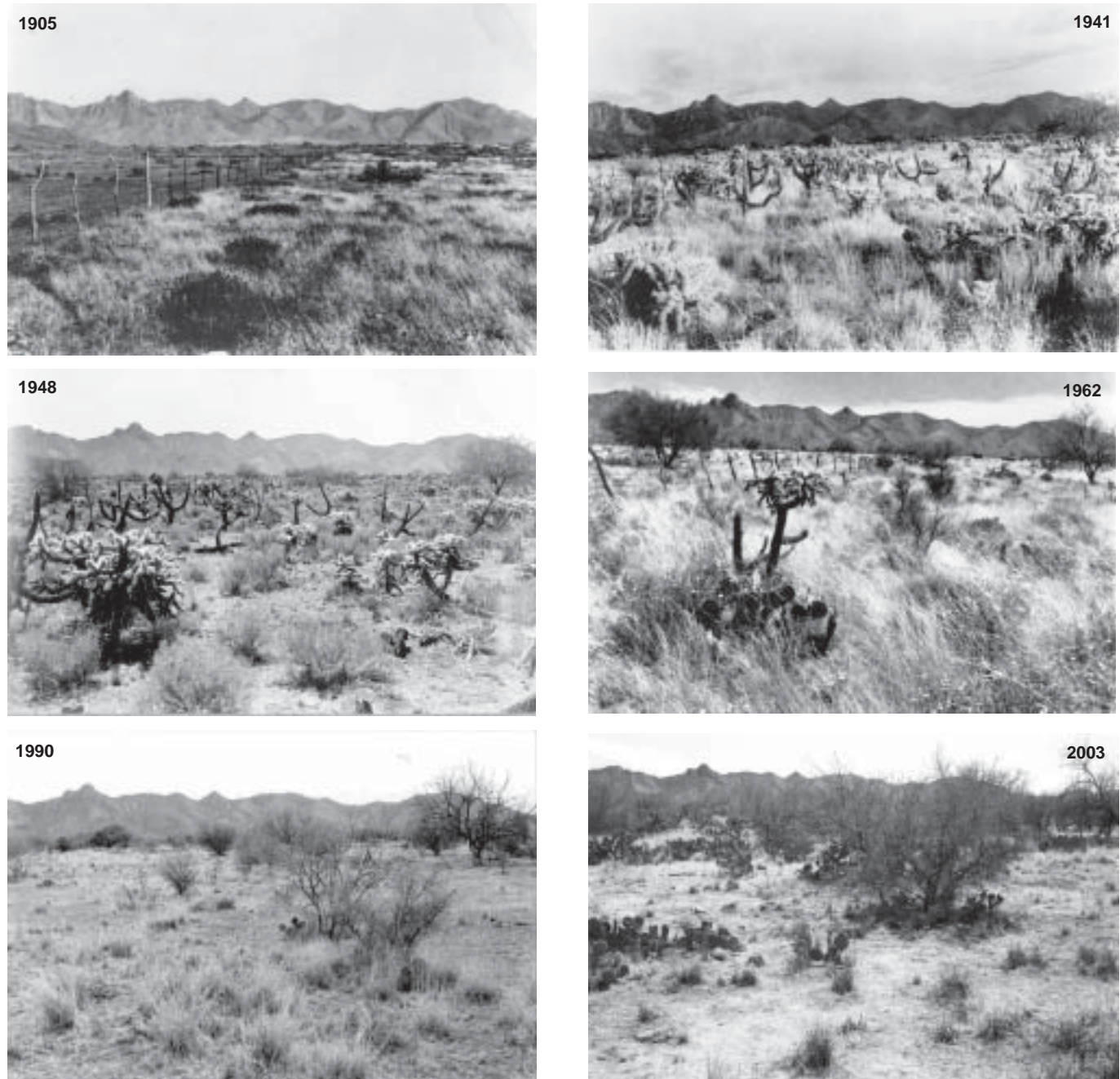


Figure 3—Repeat photography (1905 to 2003) looking east from Photo Station 231, on deep, sandy loam soil, at 1,080-m elevation (McClaran and others 2002). April 1905 shows Santa Rita boundary and ungrazed condition of vegetation, and the dark patches are probably poppy flowers in bloom. From September 1941 to June 1948 and March 1962 shows duration of cholla eruption, and seasonal variation in grass biomass. March 1990 to March 2003 shows increased size of blue palo verde, mesquite, and prickly pear cactus. The nonnative Lehmann lovegrass is not present.

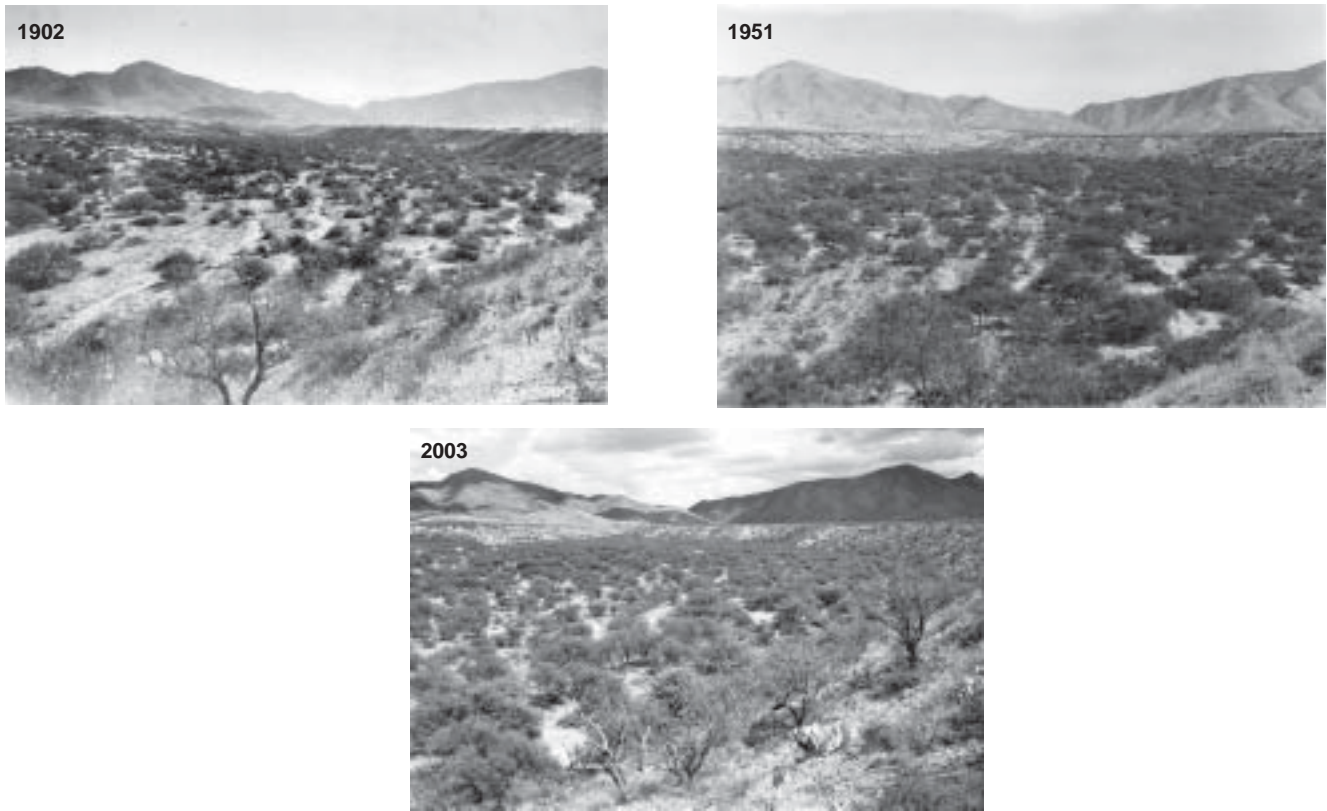


Figure 4—Repeat photography (1902 to 2003) looking east from Photo Station 222 into Box Canyon arroyo, at 1,150-m elevation (McClaran and others 2002). In 1902 mesquite are abundant in the arroyo, and a few trees are scattered on the flat grasslands above the drainage. Since 1902, there are slightly more trees in the arroyo but many new trees in the grasslands, and they appear as a dark, horizontal line above drainage.

the areal extent of the Santa Rita where mesquite density exceeded 198 plants per ha, and the occurrence of those densities spread from lower elevations to above 1,050 m (Humphrey and Mehrhoff 1958; Mehrhoff 1955). Since 1972, this density class has become the norm. Between 1972 and 1984, the average density remained about 300 plants per ha at 900 to 1,350 m elevations (Martin and Severson 1988). Over a longer time period (1972 to 2000) and slightly lower

elevation (900 to 1,250 m), density fluctuated between 200 and 450 trees per ha (fig. 5).

Mesquite canopy cover also increased after 1930, but it has not reached the maximum of 30 percent that Glendening (1952) predicted from stand-level expansion rates between 1932 and 1949. In the early 1940s, Canfield (1948) roughly estimated mesquite cover to be 4 to 8 percent throughout the Santa Rita using simple visual observations. At elevations

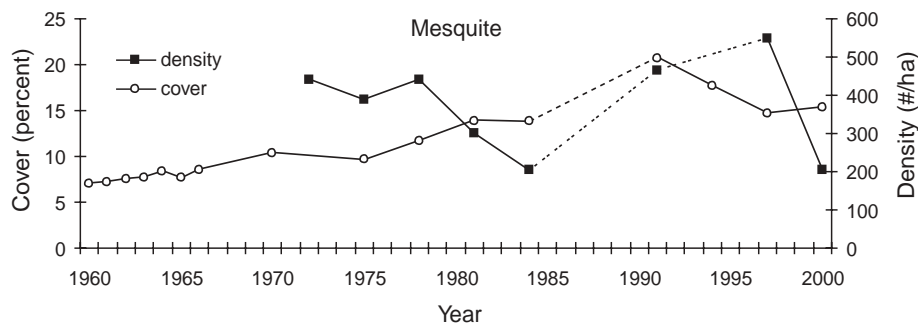


Figure 5—Change in mesquite cover and density on 74 permanent transects between 950- and 1,250-m elevation (McClaran and others 2002). No mesquite or burweed removal treatments were applied to these transects. Dashed lines indicate periods of greater than 5 years between remeasurements.

between 900 and 1,250 m, mesquite cover has increased according to systematic remeasurements of permanent line intercept transects: from 1957 to 1966, Martin and Cable (1974) estimated cover at 9.5 percent, and from 1960 to 2000, cover increased from 7 percent to a peak of 20 percent in 1991, but declined to 15 percent by 2000 (fig. 5).

Repeat photography illustrates this increase of mesquite in the grasslands (figs. 3 and 6), where increases in density have generally slowed since the 1970s, but tree cover has generally increased with the growth of individual trees. The exceptions are the washes and arroyos (for example, fig. 4) where trees were already abundant in 1902, and in areas with rocky, clay-rich soils where mesquite remains largely absent (fig. 7).

Interpretations

Numerous scientists performed experiments and controlled observations to interpret how livestock grazing, rodents, fire, and perennial grasses may have influenced mesquite dynamics.

From the early 1930s to late 1940s, the exclusion of rodents and/or cattle did not stop the increase of mesquite at elevations between 1,050 and 1,100 m. Mesquite increased from about 140 to 380 plants per ha between 1932 and 1949 (Glendening 1952) and from about 280 to 380 plants per ha (Brown 1950) across all exclusion treatments. A similar pattern emerged when yearlong and seasonally grazed pastures were compared from 1972 to 1984: the average 300 plants per ha did not differ between treatments (Martin and Severson 1988).

The likely role of cattle and rodents in dispersing mesquite seed, and the optimum burial depth by rodents for germination were revealed in the mid-1950s. Some seeds remain viable after cattle digestion, but estimates of viability vary from 58 to 73 percent (Glendening and Paulsen 1955) to only 3 percent (Cox and others 1993). Reynolds (1954) reported that kangaroo rats buried mesquite seed 1 to 3 cm, a depth optimal for germination, but they later consumed 98 percent of these seeds. He also estimated that they dispersed seeds a maximum of 32 m. Based on this, he suggested that if kangaroo rats were the sole vector of dispersal, mesquite would spread 1.6 km in 500 years, assuming a 20-year period before the newly established mesquite would produce seed.

By 1950, it was apparent that even small (1-cm basal diameter) mesquite were able to sprout from basal meristems after the aboveground portions of the plant were killed by a fire. Glendening and Paulsen (1955) and Cable (1965) reported only 11 to 60 percent mortality for 1 cm basal diameter plants, and that rate decreased to about 5 percent for plants greater than 15 cm diameter. Survival was much less likely for younger and smaller (less than 1 cm basal diameter): only one-third of 1-year mesquite survived to resprout after a fire (Cable 1961). Womack (2000) confirmed results that plants greater than 15 cm basal diameter have less than 5-percent mortality, and he noted that mortality declined as size and number of basal stems (trunks) increased. Not surprisingly, by 1965 there were no differences in the density of mesquite on unburned areas, areas burned once (1952), and areas burned twice (1952 and 1955) (Cable 1967). Similarly, 3 years after a 1975 fire, mesquite cover did not differ between burned and unburned areas (Martin 1983).

Glendening and Paulsen (1955) reported that mesquite seed germination and establishment were 16 times greater in the absence of grass than when seeds were sown within dense stands of cottontop, black grama, and bush muhly. However, they acknowledged that while grass may interfere with mesquite establishment, bare patches between grass plants were ubiquitous even in areas ungrazed by cattle.

Focusing on the seed and seedling stages of mesquite life history is helpful in understanding how the increase of mesquite has not been influenced by the manipulations of livestock, rodents, and fire. The establishment of mesquite plants in the grasslands started with the livestock dispersing undigested seeds that were produced by plants growing in the arroyos. Some of the seed in the cattle dung may have germinated and established. Kangaroo rats may have collected other seeds from the dung and buried them at optimum depths for germination. This series of events would account for the abundance of scattered small mesquite in the grasslands by 1902. The cattle vector provided the long distance dispersal that was not possible by kangaroo rats alone. By 1930, when small mesquite and caches of mesquite seed were present, the removal of rodents and/or livestock did not limit their continued recruitment or growth.

The general absence of fires between the 1880s and 1903 followed after heavy livestock grazing had reduced the mass and continuity of the grass fuel source. Consequently, the scattered, recently established seedlings in the open grasslands did not experience fires when they were most susceptible to damage (less than 5 years and less than 1 cm diameter). Griffiths (1910) and Wooten (1916) applied this scenario to interpret the increase of small mesquites in the grassy plains of the Santa Rita observed between 1903 and 1915. Although they were unfamiliar with the details of seed germination and dispersal, and seedling response to fire, they recognized that these early life history stages were key to the understanding the incipient transformation of treeless grasslands into mesquite savannas.

Changes in Burroweed Abundance

Burroweed is a short-lived (less than 40 years) shrub that can grow up to 1.3 m tall (Humphrey 1937). Roots are common at depths greater than 1 m deep but are relatively scarce at shallower (5- to 30-cm) depths (Cable 1969). The greatest period of growth occurs in spring, but some expansion of the canopy occurs in summer (Cable 1969). Seeds germinate in winter and spring (Humphrey 1937). They are toxic and not commonly eaten by livestock (Tschirley and Martin 1961).

Pattern

Four cycles of burroweed increase and decline have been reported since 1903. Their duration was about 15 to 20 years, but they have not been perfectly synchronous across the Santa Rita. Changes in abundance were a function of changes in both density (recruitment and death of plants) and cover (growth and shrinkage of plants).

The first reported cycle ended in 1914 (Wooten 1916). The beginning is harder to determine, but Griffiths (1904, 1910)

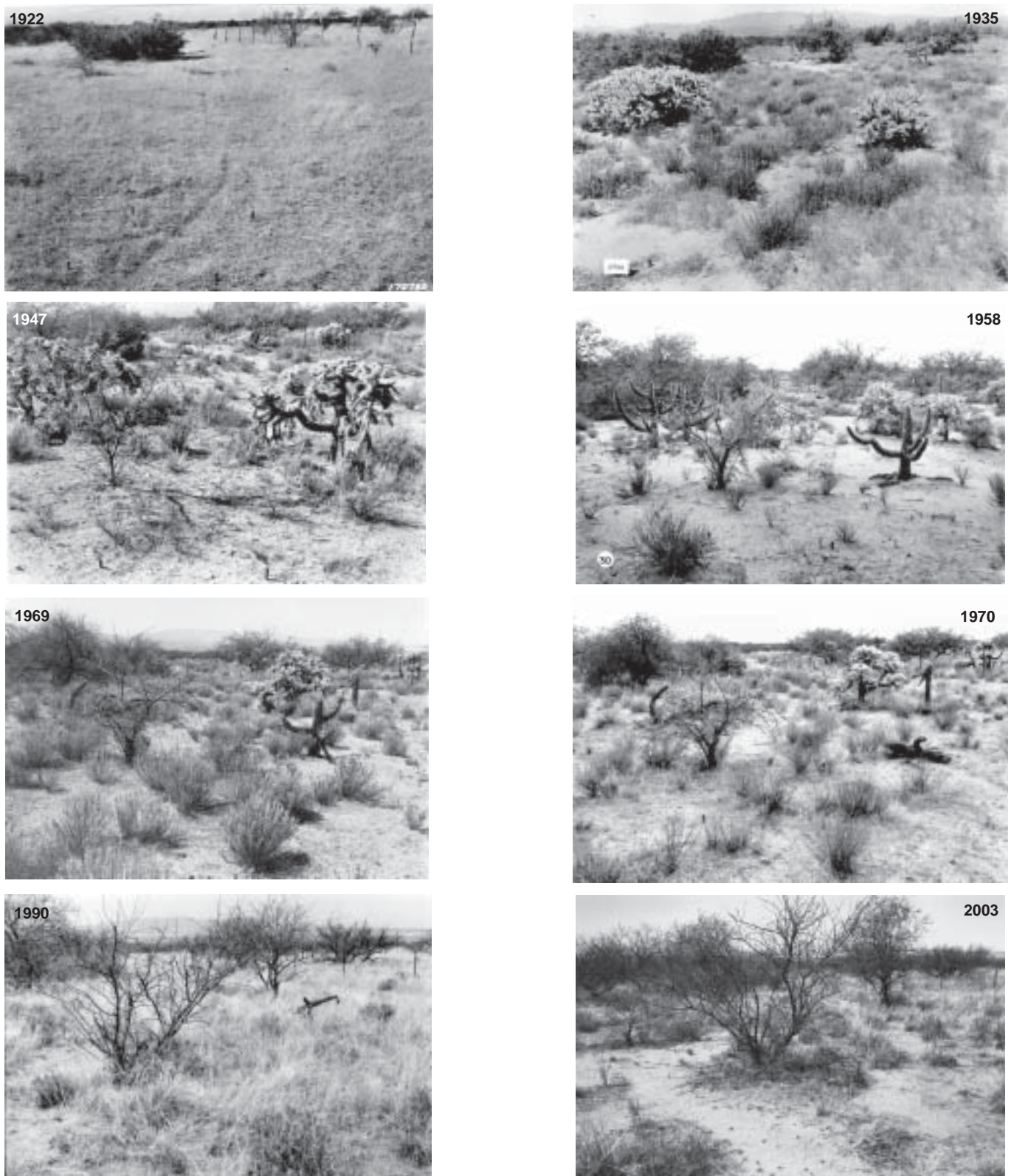


Figure 6—Repeat photography (1922 to 2003) looking west from Photo Station 111 at 1,100-m elevation (McClaran and others 2002). Area beyond fence has been excluded from livestock since 1916. December 1922 shows sparse tree presence and no shrubs in foreground. From September 1935 to October 1947 and August 1958 shows eruptions of burrowweed and cholla, a general decline of grass, and establishment of new mesquite on both sides of the enclosure fence. From March 1969 to July 1970 shows rapid death of burrowweed. March 1990 to April 2003 shows dominance of nonnative Lehmann lovegrass, and decline of burrowweed.

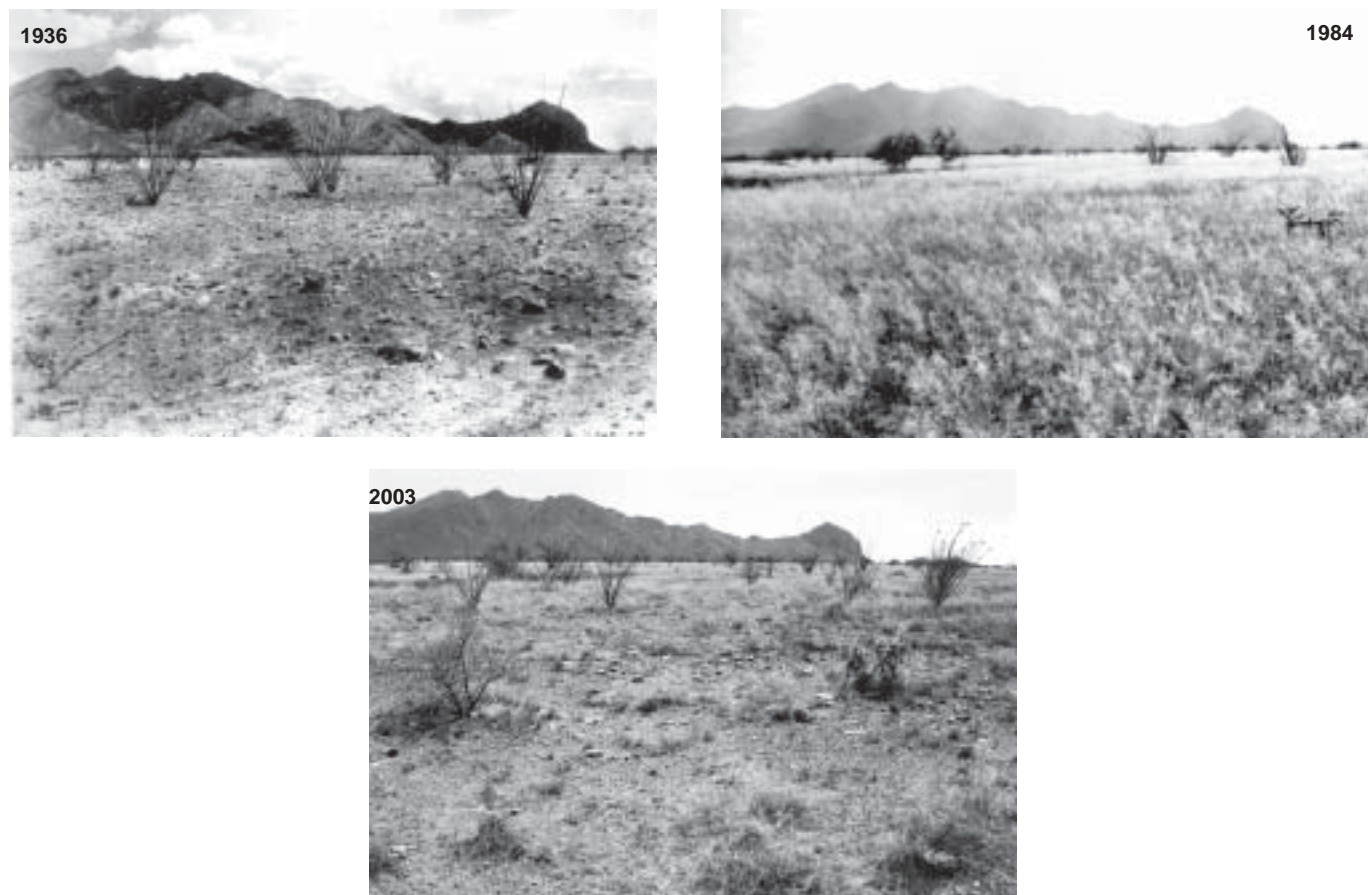


Figure 7—Repeat photography (1936 to 2003) looking east from Photo Station 45 across Madera Canyon alluvial fan at 1,100-m elevation (McClaran and others 2002). In June 1936, there is very sparse grass cover, scattered ocotillo, and three mesquite trees. From 1936 to October 1984, nonnative Lehmann lovegrass arrives and abundance reflects the wet summer in 1984. From 1984 to April 2003 there is a reduction of lovegrass, a continued ocotillo presence, a new catclaw acacia (bottom left), and the persistence of the three mesquite that were present in 1936.

first noted increases at low elevations in the northwestern portion of the Santa Rita that spread upslope to 1,100-m elevation by 1910.

The second cycle occurred in the 1930s. In 1935, Humphrey (1937) observed that large plants were conspicuous everywhere below 1,350-m elevation, and in the early 1940s, Canfield (1948) estimated cover between 4 and 9 percent below 1,250 m. The timing and extent of the subsequent decline is not clear. The extent of the highest density class (greater than 36 plants per m^2) increased only slightly from about 50 to 55 percent of the Santa Rita between 1934 and 1954 (Humphrey and Mehrhoff 1958; Mehrhoff 1955), but significant declines in burroweed by the 1950s are documented in several repeat photography comparisons (for example, fig. 6).

A third cycle peaked in the late 1960s, followed by a decline beginning in 1970 (figs. 6 and 8) over large areas of the Santa Rita. Cover on 120 permanent line intercept transects increased from 2.4 percent in 1957 to 13.5 percent in 1966, then declined to 2.5 percent in 1970 (Martin and Cable 1974). The magnitude of the increase was less on a subset of

these transects without mesquite control, but the timing was identical (fig. 8).

The most recent cycle occurred between the late 1970s and 1990s on large areas of the Santa Rita (figs. 6 and 8). Density increased from 0.6 plants per m^2 in 1972 to 2.7 plants per m^2 in 1975, then declined to 1.1 plants per m^2 in 1984 (Martin and Severson 1988). In general, the density above 1,000-m elevation was about double that below, but the timing of the cycle was synchronous. Comparing density and cover values from 1972 to 2000 (fig. 8) reveals the character of these cycles. Increases in density precedes increases in cover by about 8 to 10 years. Maximum cover mostly occurs when self-thinning reduces density and surviving plants grow larger. Near the end of the cycle, there are declines in both density and cover.

There are some locations where these cycles never materialized, and other locations where some cycles were not expressed. The cycles have not occurred in areas with rocky, clay-rich soils (fig. 7), and there is no evidence that the latest cycle occurred on deep, sandy soils (fig. 3).

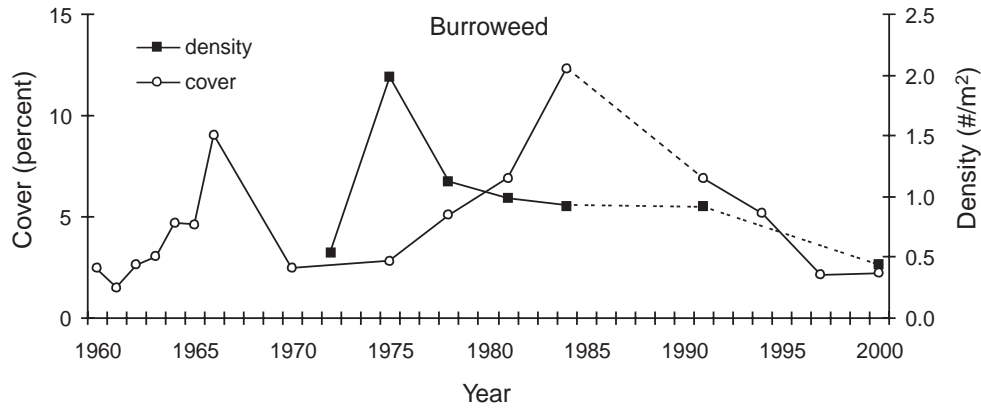


Figure 8—Change in burroweed cover and density on 74 permanent transects between 950- and 1,250-m elevation (McClaran and others 2002). No mesquite or burroweed removal treatments were applied to these transects. Dashed lines indicate periods of greater than 5 years between remeasurements.

Interpretations

The timing of the burroweed cycles appears to be independent of manipulations to livestock grazing, fire, and grass neighbors. If burroweed responded to a manipulation, it was expressed as a short-lived change in abundance that lasted only until the current cycle ended or the next cycle began. An anecdotal consensus has emerged that variation in winter precipitation is driving these cycles because of this relative indifference to livestock grazing, rodents, and fire treatments. This relationship remains anecdotal because the mechanisms have not been documented, and only one correlation analysis has been performed. Similar to mesquite, frequent fires may have limited the distribution of burroweed to lower elevations where fuels did not accumulate.

Cable (1967) placed the emphasis on winter precipitation when the immediate reduction of burroweed density following fires in 1952 and 1955 was undetectable 10 and 13 years later (fig. 9). He found a strong correlation ($r^2 = 0.91$) between burroweed density and winter precipitation between 1952 and 1958 to support his interpretation. Later, Martin (1983) applied this same interpretation (consecutive wet winters in 1977–1978 and 1978–1979) to the short-lived decline of burroweed following a fire in 1975.

The earliest assessments of livestock grazing effects on burroweed occurred near the start of the 1930s cycle. Without the benefit of replications in his study from 1931 to 1948, Brown (1950) concluded that exclusion of livestock may slow a burroweed increase, but it would not prevent one. By the time of the fourth cycle, the winter precipitation explanation was used to account for the indifference to yearlong and rotation of summer grazing from 1972 to 1984 (Martin and Severson 1988).

Between 1961 and 1964, as the third burroweed cycle began, Cable (1969) found that burroweed cover increased slightly less when growing with cottontop grass neighbors (8- to 20-percent increase) than without cottontop neighbors (8- to 27-percent increase). He applied the winter precipitation explanation to this pattern, specifically its relative importance to the two species. Cottontop was largely unresponsive to winter precipitation and, therefore, did not affect

burroweed during the time of its greatest growth. By contrast, the slight depression in burroweed growth was a function of competition for soil moisture in the summer, when cottontop is most actively growing.

There are some additional compelling coincidences of wet winters (fig. 2) and the timing of burroweed cycles. Three consecutive wet winters from 1929–1930 to 1931–1932 coincide with the beginning of the 1930s cycle. The wet winter of 1957–1958 may have initiated seedling establishment for the third cycle, and the very wet 1965–1966 and 1967–1968 winters may have contributed to an increase in plant size.

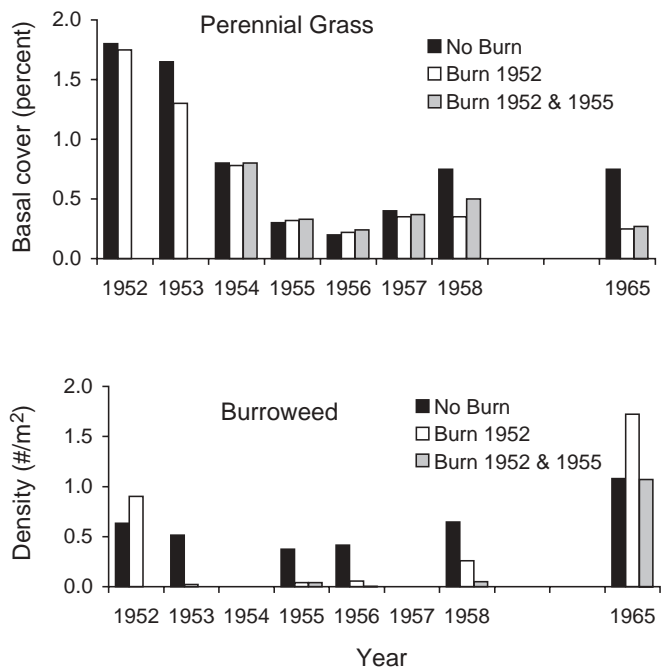


Figure 9—Changes in perennial grass cover and burroweed density in relation to two, one, and no prescribed fires (data from Cable 1967).

Finally, a similar lag between seedling establishment and increases in plant size may have contributed to the most recent cycle following consecutive wet winters in 1977–1978 and 1978–1979. The growth of plants established during this time would likely have been fostered by the extraordinary string of 13 consecutive wet winters from 1982–1983 to 1994–1995.

Changes in Cactus Abundance

The primary cacti are prickly pear, chainfruit cholla, and cane cholla, which are relatively short lived (less than 50 years). The chollas have cylindrical sections, and a growth form that is taller (less than or equal to 2 m) than broad (less than or equal to 1 m); whereas the prickly pear has flat, circular sections with a growth form that is broader (less than or equal to 2 m) than tall (less than or equal to 1 m). Both can establish new plants from seed and from fallen sections that can develop a root system when the areoles are in contact with the soil. However, vegetative reproduction is more common in the chollas than prickly pear.

Pattern

In 1903, cacti were most common below 1,000-m elevation (Griffiths 1904). An eruption of cholla at higher elevations occurred by the mid-1930s and lasted into the 1970s. Prickly pear has been the dominant cactus since 1970.

Many repeat photography series record an eruption of cholla by 1935 (for example, figs. 3 and 6). Between 1934 and 1954, the proportion of the Santa Rita supporting greater than 840 plants per ha doubled from 19 to 38 percent (Humphrey and Mehrhoff 1958; Mehrhoff 1955). The greatest increase occurred between 1,000- and 1,200-m elevation. The eruption faded by 1960, when both cholla cover and density declined (figs. 3, 6, and 10). A similar trend was

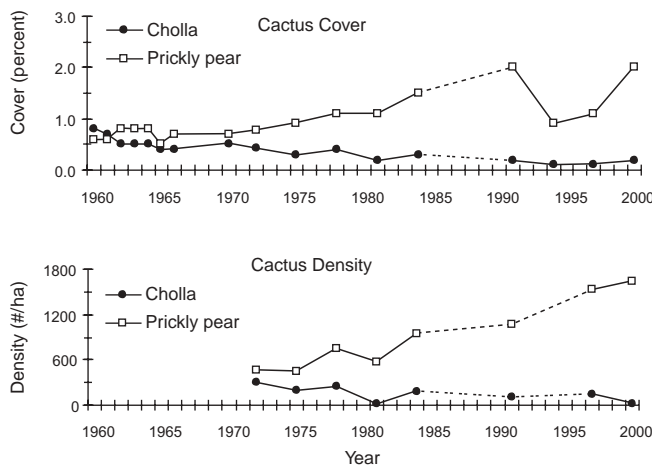


Figure 10—Cover and density changes for cholla and prickly pear cactus on 74 permanent transects between 950- and 1,250-m elevation (McClaran and others 2002). No mesquite or burroweed removal treatments were applied to these transects. Dashed lines indicate periods of greater than 5 years between remeasurements.

recorded between 1972 and 1984 at slightly higher elevations (Martin and Severson 1988). In contrast, prickly pear cover and density have increased since 1970 (figs. 3 and 10), and density of 800 plants per ha at elevations below 1,200 m was greater than the 200 to 400 plants per ha at higher elevations (Martin and Severson 1988).

These patterns have not materialized in all locations. Neither cholla nor prickly pear abundance changed markedly on rocky, clay-rich soils (fig. 7), nor did the prickly pear increase materialize everywhere (for example, fig. 6).

Interpretations

Similar to burroweed, the eruption of cholla and recent increases of prickly pear appear to be largely independent of livestock grazing and fire manipulations. The stimuli for the increases are not clear, but the rate and duration of the increases may be a function of plant growth rate, longevity, and the occurrence of a bacterium.

Combinations of cattle and rodent exclusions established as the cholla eruption commenced failed to produce any differences in cacti densities (Brown 1950; Glendening 1952). Under all treatments, densities increased from tens to hundreds of plants per ha. Similarly, the subsequent decline of cholla and increase of prickly pear between 1972 and 1984 were no different in areas with yearlong versus seasonal rotation of grazing (Martin and Severson 1988). Fire produced only a short-lived decline of cactus density, but within 10 to 13 years after fire, the cactus density exceeded that which existed prior to the fires (Cable 1965).

Tschirley and Wagle (1964) suggested that eruptions are a function of rapid growth by young plants, and that declines result from a combination of plants reaching their maximum age and the increase of bacterial infection that prevents fallen sections from establishing roots. They used repeat photography to estimate the curvilinear vertical growth rate of cholla: the rate is fastest in young plants, then slows considerably at about 15 years, and then becomes negative at about 45 years as plants disarticulate (for example, figs. 3 and 6). They suggested that recruitment of new plants from fallen sections is limited when they are infected by increasing levels of the bacteria *Erwinia carnegiea* that cause the sections to desiccate before roots can be produced.

Changes in Perennial Grass Abundance

The common perennial grass species use the C₄ photosynthetic pathway. Their seed germinates, and plants grow most vigorously in July and August after the summer rains commence. Absolute productivity is a function of both current and previous summer precipitation (Cable 1975), and there is considerable interannual and spatial variation in productivity because rainfall amounts differ greatly between years and with elevation (figs. 1, 2, 11, and 12). Productivity is about 1.6 times greater on clay-rich versus loamy soils (Subirge 1983). Plants are relatively short lived, with averages around 5 to 10 years (Cable 1979; Canfield 1957). Roots are most dense in the upper 15 cm of the soil, but some extend greater than 60 cm deep (Blydenstein 1966; Cable 1969). Several species, including cottontop and bush muhly, are

more common under mesquite trees, but others, including threeawns and Rothrock grama, are more common in open areas (Livingston and others 1997; Van Deren 1993; Yavitt and Smith 1983).

Pattern

In 1903, perennial grasses were largely absent below 1,350-m elevation except along arroyos where tanglehead, sideoats grama, and hairy grama were found (Griffiths 1904). The annual grass, six weeks grama, was dominant at lower elevations. Above 1,100 m, Rothrock grama, black grama, and bush muhly were only occasionally present, the latter primarily under shrubs. By 1909, perennial grass

abundance had increased above 1,075 m: Rothrock, black, and slender grammas between 1,075 and 1,250 m, and threeawns, sprucetop, black, and sideoats grammas above 1,250 m (Griffiths 1910; Thornber 1910).

Six years later, in 1915, perennial grasses were more common between 1,000 and 1,250 m, and under shrubs at the lower elevations when Wooten (1916) estimated the extent of different types of grass species. The annual, six weeks grama, continued as the most common grass on about 12 percent of the Santa Rita, all below 1,000 m. Bush muhly was most common on an equivalent area at those low elevations, but was largely confined beneath shrubs. Rothrock grama was the dominant grass on about 50 percent of the area, mainly between 1,000 and 1,250 m, and the common associates were threeawns, tanglehead, and slender grama. Threeawns were the dominants above 1,250-m elevation, which accounted for 17 percent of the Santa Rita.

Griffiths, and later Wooten, estimated productivity by clipping twenty-eight 0.9- by 2.1-m (3- by 7-ft) plots in the same general locations throughout the Santa Rita between 1903 and 1908, and 1912 and 1914. The average for all elevations was 845 kg per ha from 1903 to 1908 (Griffiths 1910). Wooten (1916) reported productivity by elevation between 1912 and 1914: 775 kg per ha below 1,000 m, 830 kg per ha between 1,000 and 1,250 m, and 965 kg per ha above 1,250 m.

Between 1915 and the early 1980s, similar patterns of perennial species abundance were reported in relation to elevation, and more systematic measures of plant cover, density, and productivity provided greater insights to interannual dynamics. From the 1960s to early 1980s, dominant species by elevation were similar to those reported in earlier accounts, but cottontop was more common at all elevations (Cable 1979; Martin 1966; Martin and Severson 1988). The ephemeral nature and slight stature of Rothrock grama is illustrated by its inconsistent membership in the top 5 ranking for density and consistently low ranking for cover (tables 2 and 3). Interannual variability of productivity was greater at lower elevations between 1954 and 1964 (compare figs. 11 and 12; Martin 1966). Interestingly, these estimates are about one-third to one-half the amounts reported by Griffiths (1910) and Wooten (1916). Their objective of estimating the potential productivity may have biased the location of sample areas toward the more productive sites. A decrease in grass production by 1950 is apparent at some repeat photography locations (fig. 4), but not at others (fig. 3).

The nonnative Lehmann lovegrass became the most abundant perennial grass by 1981 and 1984, based on density and basal cover, respectively (tables 2 and 3). By 1991, it was more common than all native grasses combined for both measures of abundance (fig. 13). Above about 1,100-m elevation, perennial grass productivity has more than doubled since the lovegrass gained dominance (fig. 13; Anable and others 1992; Cox and others 1990), and exceeded estimates made between 1903 and 1914 (Griffiths 1910; Wooten 1916). This was a very rapid ascent to dominance from a relatively limited area of introduction. Between about 1945 and 1975, seed was sown on about 50 areas, totaling 200 ha (less than 1 percent of the Santa Rita), but the areas were widely dispersed making the maximum distance between them less than or equal to 7 km (Anable and others 1992). This lovegrass invasion is obvious at most repeat photography

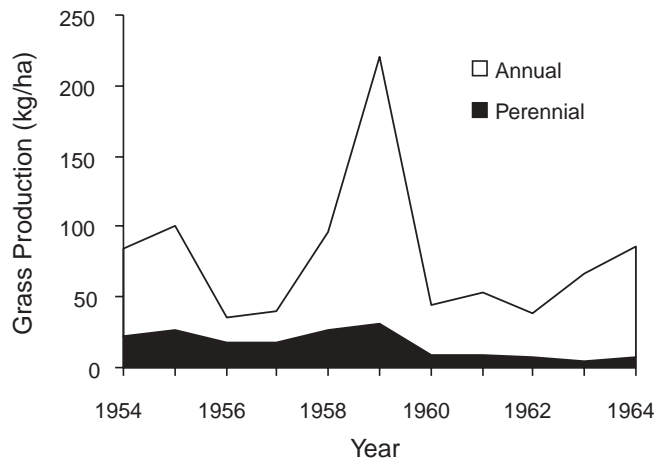


Figure 11—Interannual changes in grass production between 900- and 1,000-m elevation (data from Martin 1966).

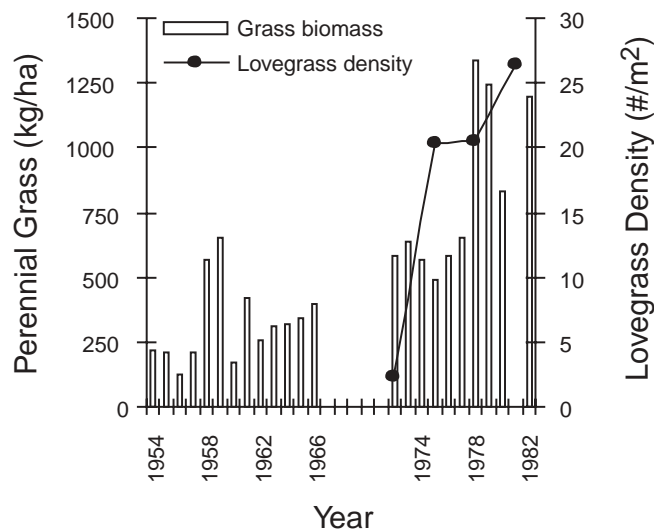


Figure 12—Interannual changes in grass production and density of nonnative Lehmann lovegrass at 1,100-m elevation (data from Cable and Martin 1975, and Martin and Severson 1988).

Table 2—Changes in the five most common perennial grass species based on density on the Santa Rita Experimental Range, 1934 to 2000. Source for 1934 and 1954 is Mehrhoff (1955). Source for other dates is from 74 permanent transects, between 950- and 1,250-m elevation, where no mesquite or burroweed removal treatments were applied (McClaran and others 2002).

| Species rank | Year | | | | | |
|--------------|----------------|---------------|-----------------|-------------------|-------------------|-------------------|
| | 1934 | 1954 | 1972 | 1981 | 1991 | 2000 |
| 1 | Rothrock grama | Fluff grass | Threeawns | Lehmann lovegrass | Lehmann lovegrass | Lehmann lovegrass |
| 2 | Threeawns | Black grama | Rothrock grama | Threeawns | Rothrock grama | Rothrock grama |
| 3 | Fluff grass | Threeawns | Cottontop | Rothrock grama | Cottontop | Threeawns |
| 4 | Slender grama | Slender grama | Black grama | Cottontop | Fluff grass | Bush muhly |
| 5 | Black grama | Cottontop | Sprucetop grama | Bush muhly | Threeawns | Cottontop |

Table 3—Changes in the five most common perennial grass species based on basal cover on the Santa Rita Experimental Range, 1960 to 2000. Source is from 74 permanent transects, between 950- and 1,250-m elevation, where no mesquite or burroweed removal treatments were applied (McClaran and others 2002).

| Species rank | Year | | | | |
|--------------|----------------|-----------------|-------------------|-------------------|-------------------|
| | 1960 | 1970 | 1984 | 1991 | 2000 |
| 1 | Threeawns | Threeawns | Lehmann lovegrass | Lehmann lovegrass | Lehmann lovegrass |
| 2 | Cottontop | Sprucetop grama | Threeawns | Cottontop | Bush muhly |
| 3 | Black grama | Cottontop | Cottontop | Bush muhly | Threeawns |
| 4 | Bush muhly | Rothrock grama | Rothrock grama | Threeawns | Rothrock grama |
| 5 | Sideoats grama | Sideoats grama | Black grama | Rothrock grama | Cottontop |

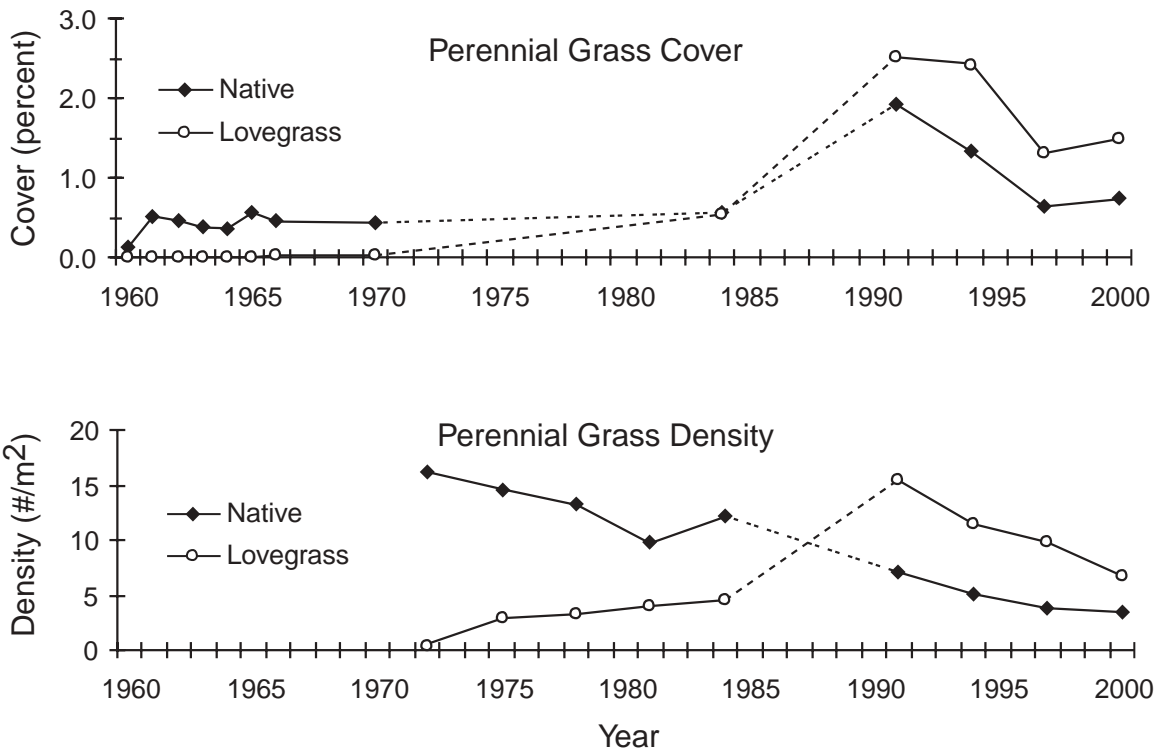


Figure 13—Cover and density changes for nonnative Lehmann lovegrass and native perennial grasses on 74 permanent transects between 950- and 1,250-m elevation (McClaran and others 2002). No mesquite or burroweed removal treatments were applied to these transects. Dashed lines indicate periods of greater than 5 years between remeasurements.

locations (for example, figs. 6 and 7), except at the lowest elevations and on deep, sandy soils (fig. 3).

Between 1984 and 1991, cover increased for both the lovegrass and native grasses, but both have declined from that maximum. In contrast, native grass density declined since 1972, whereas lovegrass density steadily increased until 1991 and then began to decline (fig. 13). These patterns suggest that the recruitment of native grasses has declined and the size of surviving plants has increased since the lovegrass gained dominance.

Interpretations

Livestock grazing, fire, neighboring mesquite and burroweed plants, and the increase of the nonnative Lehmann lovegrass have been the focus of efforts to interpret perennial grass dynamics. The results from a number of studies illustrate the important and often overriding influence of precipitation on these patterns. However, grass dynamics appear to be more sensitive to varying intensities of livestock grazing and neighboring plants than the dynamics expressed by mesquite, burroweed, and cactus.

Attention to livestock grazing has a longer and more detailed history than any other influence. It grew directly from the objectives of establishing the Santa Rita, which were to determine the potential of forage production for livestock and to develop a sustainable approach to livestock grazing. Initial efforts focused on rates of grass recovery following grazing removal, while subsequent studies addressed responses to different grazing intensities and the seasonal rotation of pastures to prevent grazing in two of three summer growing seasons.

Livestock Exclusion—The exclusion of livestock from 1903 to 1915 on all areas below 1,250-m elevation allowed Wooten (1916) to speculate on the rate of recovery to full productive potential from the degraded conditions caused by nearly two decades of overgrazing. He estimated a 3-year recovery rate for areas dominated by Rothrock grama between 1,000 to 1,250 m, and a 7- to 8-year recovery for bush muhly in areas below 1,000 m. However, subsequent comparisons with livestock exclusion are more equivocal. Total grass cover declined from about 2.0 to 0.1 percent on grazed areas as well as all combinations of rodent and/or cattle exclusion from 1932 to 1949 (Glendening 1952). Compared to adjacent grazed areas, native grass density was less and nonnative lovegrass was no different in areas that were ungrazed from 1918 to 1990 (McClaran and Anable 1992).

These contrasting results suggest that the perennial grass response to the exclusion of livestock is contingent on the condition of grass at the time of exclusion, precipitation patterns before the comparisons, and the grazing intensity outside the enclosure. Wooten may have proposed very optimistic recovery rates because the general absence of perennials in 1903 provided a degraded baseline, and the relatively verdant conditions during his observations in 1915 following six consecutive summers with above average precipitation (fig. 2). In contrast, the decline of grass cover between 1932 and 1949, which was independent of livestock exclusion, began with relatively large cover values that followed the wet summer in 1931 and declined during the subsequent, prolonged dry period (figs. 2 and 6). Finally,

grazing intensity outside enclosures is not uniform across the Santa Rita, and has changed over time since grazing was re-established in 1915. Therefore, unequivocal conclusions about grass response to livestock exclusion are not possible unless the grazing intensity outside the enclosure is documented.

Livestock Grazing Intensity—In general, grazing intensity on the Santa Rita has declined since 1915. Until 1941, the stocking rate was about 0.13 animals per ha per year. Between 1941 and 1956, it was reduced to about 0.06, which translated to a 47- to 60-percent utilization of grass production. Since 1957, stocking rates have been reduced to about 50-percent utilization (Cable and Martin 1975). A utilization rate of 40 percent was suggested in the early 1940s to prevent damage to individual plants (Parker and Glendening 1942; Reynolds and Martin 1968). However, despite repeated attempts to reduce utilization, this goal of 40 percent was never achieved (Cable and Martin 1975; Martin and Severson 1988). Across the Santa Rita, utilization varies inversely with distance from drinking water sources (Angell and McClaran 2001; Martin and Cable 1974).

Canfield (1948) made the first estimate of grass response to grazing intensity. He compared the relative cover of grass species among areas heavily grazed for 20 years, conservatively grazed for 5 years, and ungrazed for 5 and 25 years. He concluded that conservative grazing for 5 years would facilitate recovery from overgrazing to the same degree as grazing exclusion, and that dominance by cottontop indicated proper grazing intensity. Unfortunately, he provided neither descriptions of stocking rates in overgrazed and conservatively grazed areas nor estimates of absolute cover of grasses. However, his list of dominant grass species in these settings is historically significant because it provided the first quantitative approach using relative cover to identify species that indicated proper grazing and overgrazing. His work preceded by 1 year, Dyksterhuis' (1949) more widely used proposal for this approach.

Martin and Cable (1974) clearly documented the influence of grazing intensity on grass production by comparing sites where utilization decreased with increasing distance from drinking water sources. From 1954 to 1966, and between 900- and 1,250-m elevation, production of cottontop, black grama, and threeawns at 0.4 to 1 km from water was 50 percent less than at 1.6 km from water sources. Utilization decreased from around 48 to 43 percent at these increasing distances from water.

Between 1,200 and 1,300 m, Cable and Martin (1975) suggested that the recovery of grass production from drought stress would be delayed when utilization levels exceeded 50 percent. Based on responses during dry conditions (1957, 1960, and 1962) and wetter conditions (1958, 1959, and 1961), plant recovery was delayed from 1 to 2 years if utilization exceeded 50 percent.

However, differences in the response of native grass and nonnative Lehmann lovegrass density to increasing grazing intensity are less clear. Using a similar approach of increasing distance from water, McClaran and Anable (1992) reported a greater decline of native grass density from 1972 to 1990 with increasing grazing intensity, but Angell and McClaran (2001) reported no relationship with intensity from 1972 to 2000. In both studies, increased density of the

nonnative Lehmann lovegrass was unrelated to grazing intensity. These results for grazing impacts may differ because the two measures of response (biomass and density) may differ in their sensitivity to grazing. Density represents the number of plants, whereas biomass reflects their total weight. The earliest studies (Cable and Martin 1975; Martin and Cable 1974) measured biomass, while the more recent studies (Angell and McClaran 2001; McClaran and Anable 1992) measured density. In addition, McClaran and Anable (1992) relied on only a single water source.

More importantly, the intensity levels for the later studies were greater (60 percent at 0.1 km and 48 percent at 0.5 km) than the earlier studies (48 percent at 0.4 km and 43 percent at 1.6 km). There may be little difference in grass response between 50- and 60-percent utilization, but those responses will be more severe than where utilization is less than 45 percent. This observation is supported by suggestions that a 40-percent utilization rate will not damage these grasses (Parker and Glendening 1942; Reynolds and Martin 1968).

Seasonal Rotation of Grazing—Between 1972 and 1984, neither grass density nor production differed between areas experiencing yearround grazing and those where the rotation of livestock excluded summer grazing in 2 of 3 years (Martin and Severson 1988). Three pastures were used to achieve this rotation, and all animals from those pastures were confined to a single pasture for 4 to 8 consecutive months, followed by a period of 8 to 12 months of no grazing. During the study, utilization levels were 47 to 51 percent. Contrary to expectations, the provision of summer rest did not improve grass abundance. The authors suggested that at the beginning of the study, grass abundance was near maximum, and therefore was unresponsive to this treatment. Additional considerations must include the increase of lovegrass through the period, the very wet conditions through the 1980s (fig. 2), and utilization levels above the 40- to 45-percent threshold.

Effects of Fire—In general, grass abundance decreases following fire, and the recovery is dependent on subsequent growing conditions. However, seed germination of the nonnative lovegrass increases after fire.

In 1952, following the first of two prescribed fires, grass cover declined from 1.7 to 1.1 percent, but cover had already declined to 0.5 percent on both burned and unburned areas prior to the second fire in 1955 (Cable 1967). Cover declined to 0.3 percent on all three treatments in 1957, and the unburned site reached 0.8 percent cover by 1965 (fig. 9). These dynamics reflect the overriding influence of dry conditions between 1952 and 1957 (fig. 2). Cable (1965) found only lovegrass seedlings following a wildfire in June 1963, and later research revealed that lovegrass seed germination increases equally after fire and the simple removal of plant cover (Sumrall and others 1991). In both instances, seed germination is stimulated by a phytochrome response to increased red light rather than heat from the fire (Roundy and others 1992).

Effects of Mesquite—The influence of neighboring mesquite trees on perennial grass appears to be contingent on elevation, amount of mesquite, and the species of grass. Beginning in the 1940s, observations of coincident declines in grass and increases in mesquite stimulated several tree-removal studies. Fortunately, some of them had repeated

measurements performed over the following 40 years. Based on these observations, increased grass production following tree removal is most persistent at higher elevations, and is related to the tree density before removal. For example, tree removal in 1945 increased grass production during the first 5 years at all four sites, which ranged from 950- to 1,250-m elevation, but increases were greatest at 1,250 m and where initial tree density was greater than 300 plants per ha (Parker and Martin 1952). After 13 years, native grass production was greater in mesquite-cleared areas above 950 m and where initial tree density was greater than 100 plants per ha (Cable 1971). After 23 years, production was greater for native grasses only at 1,250 m and where initial tree density was greater than 300 plants per ha (Cable 1971). After 29 years, grass production was greater only at 1,250 m, but the nonnative lovegrass dominated the grass composition by that time (Williams 1976).

The relatively brief increase of grass production is probably a function of both the recruitment of new mesquite trees and the depletion of soil fertility after their removal. Tree recruitment prompted Parker and Martin (1952) to suggest that tree removal would be required every 25 years to maintain grass production. An island of soil fertility develops under mesquite. About three times more organic matter and nitrogen exists in the top 7.5 cm of soil compared to open grassland, and 13 years after tree removal there is a 30 percent decline of organic matter and nitrogen (Klemmedson and Tiedemann 1986; Tiedemann and Klemmedson 1986).

This greater soil fertility under mesquite trees may contribute to the greater likelihood of some grasses to occur under the trees. Several species, including cottontop and bush muhly are more common under mesquite than if they were randomly distributed (Livingston and others 1997; Van Deren 1993; Yavitt and Smith 1983). Tiedemann and others (1971) suggested that the greater soil fertility under mesquite might compensate for the lower light intensity for those species that are shade tolerant.

It is important to note that increases of native and nonnative lovegrass have occurred without mesquite removal, and can occur while mesquite is increasing. From 1960 to 1991, at elevations between 900 and 1,250 m, native and nonnative grass cover more than doubled, while mesquite cover increased from 7 to 20 percent (figs. 5 and 13).

The rate that Lehmann lovegrass spreads from seeded areas is not related to the abundance of mesquite. Lovegrass was seeded on the margins of the areas where mesquite trees were thinned and removed in 1945 (Parker and Martin 1952). After 13 years, it had spread 75 to 125 m regardless of mesquite treatment, and its density increased with elevation (Kincaid and others 1959). After 25 years, lovegrass productivity did not differ among mesquite treatments, but it did increase with elevation (Cable 1971). This is consistent with Van Deren's (1993) finding that the proportion of lovegrass plants under mesquite is only slightly less than would be expected randomly.

Effects of Burweed—The response of perennial grass to burweed neighbors appears to be contingent on amounts of winter and summer precipitation. In 1961, Cable (1969) removed some existing burweed plants to create cottontop plants without burweed neighbors. Cottontop production did not differ between treatments, but cover differed in the last 2 years of the study. In the very dry summer of 1962,

cottontop cover was no different between treatments, but in the following summers that had greater precipitation, cover was greater for cottontop plants without burrowweed. Cable (1969) demonstrated that basal cover was reduced because burrowweed used soil moisture during the winter when grass tillers were enlarging, rather than preemptive use of water by burrowweed in the summer. This relationship may explain why total grass cover did not respond to burrowweed removal at 1,100-m elevation in the generally dry periods between 1940 and 1946 (Parker and Martin 1952).

Native and Nonnative Grass Relationships—The inverse relationship between the increasing abundance of the nonnative Lehmann lovegrass and declining native grasses appears to be more closely related to events during seedling establishment than to interactions among adult plants. Initially, the lovegrass invasion appears to occur between existing native grasses, thus increasing total grass density and productivity, but eventually native grasses are replaced (fig. 13; Anable and others 1992; Angell and McClaran 2001; Kincaid and others 1959). The timing and magnitude of the native grass decline between 1972 and 2000 did not differ in relation to the length of time that lovegrass had been present in an area (Angell and McClaran 2001). In addition, all evidence suggests that the increase of lovegrass is as indifferent to the abundance of native grasses (Angell and McClaran 2001; McClaran and Anable 1992) as it is to the abundance of mesquite (Kincaid and others 1959). The unique response of lovegrass seed to the first summer rains may be a more important key to its highly successful recruitment. Abbott and Roundy (2003) reported that native grasses were more likely to germinate with the first summer rains than lovegrass, and therefore would suffer from the rapid soil desiccation that follows these sporadic first rains. In contrast, lovegrass germination was more likely to be delayed and follow the more regularly occurring later rains, when prolonged soil moisture and survival were more likely.

Opportunities

Continuing the systematic remeasurement and repeat photography efforts on the Santa Rita presents the greatest opportunity for improving our understanding of vegetation change because they will record the pattern and variation of future changes. The most incontestable conclusion from this century of vegetation change is that future changes can not be perceived and understood if there are no records of previous conditions. An equally important conclusion is that the response of vegetation to management practices will be contingent on past and future precipitation patterns, elevation and soils at the location, and the current mix and vigor of plant species. For example, when the next burrowweed eruption occurs, we will respond with much less anxiety than our predecessors had in the 1930s and 1950s because we understand that it is likely to be a short-lived rather than permanent change. We will not expect the eruption to occur at all locations, nor will the control of that eruption prevent future eruptions. Given the importance of this observation legacy, its continuation should be considered both an opportunity and an obligation.

In addition to continuing the ongoing remeasurements, there are several opportunities to further the documentation

and understanding of both past and future vegetation changes. Most of the areas that experienced experimental manipulations were measured for less than 5 years. Remeasuring vegetation in those areas can provide insights into the longevity of responses and the variation expressed in recent changes such as the spread of Lehmann lovegrass.

A re-evaluation of these old data sets may reveal patterns and suggest processes that were not originally apparent. These re-evaluations will certainly benefit from the application of new methods of statistical analysis such as repeated measures and mixed-effects models of analysis of variance, classification, and regression tree analysis. In addition, spatial analyses of these data sets have been facilitated by the creation of a digital archive that is available on the World Wide Web (McClaran and others 2002).

The establishment of any new experimental manipulations is given invaluable direction by these long-term records. In return, these new manipulations should be located where they will not conflict with ongoing remeasurements or opportunities to remeasure past manipulations. Finally, all efforts should be made to foster the long-term remeasurement of these new manipulations beyond the common 3 to 5 years. No message is clearer from this century of change than the certainty that the initial response to manipulations will not persist with time.

There are specific research questions that are stimulated by this legacy of observation. Given the initial focus on grass dynamics, efforts focused on the current grassland dominated by Lehmann lovegrass deserve attention. How long will the dominance persist, and will the absolute abundance (cover, density, and biomass) stabilize, increase, or decline? Will lovegrass dominance directly alter the expected patterns of mesquite seedling recruitment, and future eruptions of burrowweed and cactus? Will these patterns be altered indirectly by the lovegrass because its abundant biomass will facilitate and support more frequent fire? Does the proposed grazing intensity threshold of 45-percent utilization apply equally to lovegrass and native grasses?

Regarding mesquite, what are the maximum cover, density, and productivity per area for the species? Glendening (1952) predicted a maximum of 30-percent cover, but that mark has not been reached on the majority of the Santa Rita. The development of a soil fertility island beneath mesquite trees has been documented (Klemmedson and Tiedemann 1986; Tiedemann and Klemmedson 1986). What are the limits to this accumulation, how deep in the soil will fertility eventually increase, and how long will it last after trees are removed? These patterns are important to neighbor plants, and they are globally important because they address interests in the sequestration of atmospheric CO₂ through vegetation management.

Consulting past records, maintaining ongoing remeasurements and initiating new manipulations can advance the prediction of future burrowweed and cactus eruptions. The timing and duration of past eruptions were not entirely synchronized. The degree and spatial pattern of their asynchrony should be possible with repeat photography and the network of 30 rain gauges (McClaran and others 2002). Further investigation of the potential role of bacterial infection on cactus populations should also occur.

Finally, this accumulation of information should prove useful in evaluating both theoretical and practical issues of

rangeland vegetation ecology and management. For example, the gradients of livestock use intensity and precipitation records could be used to evaluate the theoretical propositions of equilibrium versus nonequilibrium controls on vegetation change (Illius and O'Connor 1999). Practically, the rich empirical information and documentation of contingencies such as soils, precipitation patterns, and pre-existing species composition could be used to construct a catalog of vegetation states and the events that led to transitions between those states (Westoby and others 1989).

It is obvious that the vast opportunities for future research into the patterns, mechanisms, and implications of vegetation changes are built on the rich legacy of a century of observation and research. In addition to opportunities, there are obligations to maintain and add to this legacy. Therefore, one of our goals should be that during the bicentennial celebration, our future efforts should ensure a second century of research on the Santa Rita.

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