Hierarchical analysis of vegetation dynamics over 71 years: soil–rainfall interactions in a Chihuahuan Desert ecosystem

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Abstract. Proliferation of woody plants in grasslands and savannas is a persistent problem globally. This widely observed shift from grass to shrub dominance in rangelands worldwide has been heterogeneous in space and time largely due to cross-scale interactions among soils, climate, and land-use history. Our objective was to use a hierarchical framework to evaluate the relationship between spatial patterns in soil properties and long-term shrub dynamics in the northern Chihuahuan Desert of New Mexico, USA. To meet this objective, shrub patch dynamics from 1937 to 2008 were characterized at patch and landscape scales using historical imagery and a recent digital soils map. Effects of annual precipitation on patch dynamics on two soils revealed strong correlations between shrub growth on deep sandy soils and above-average rainfall years ($r = 0.671$, $P = 0.034$) and shrub colonization and below-average rainfall years on shallow sandy soils ($r = 0.705$, $P = 0.023$). Patch-level analysis of demographic patterns revealed significant differences between shrub patches on deep and shallow sandy soils during periods of above- and below-average rainfall. Both deep and shallow sandy soils exhibited low shrub cover in 1937 (1.0% ± 2.3% and 0.3% ± 1.3%, respectively [mean ± SD]) and were characterized by colonization or appearance of new patches until 1960. However, different demographic responses to the cessation of severe drought on the two soils and increased frequency of wet years after 1960 have resulted in very different endpoints. In 2008 a shrubland occupied the deep sandy soils with cover at 19.8% ± 9.1%, while a shrub-dominated grassland occurred on the shallow sandy soils with cover at 9.3% ± 7.2%. Present-day shrub vegetation constitutes a shifting mosaic marked by the coexistence of patches at different stages of development. Management implications of this long-term multi-scale assessment of vegetation dynamics support the notion that soil properties may constrain grassland remediation. Such efforts on sandy soils should be focused on sites characterized by near-surface water-holding capacity, as those lacking available water-holding capacity in the shallow root zone pose challenges to grass recovery and survival.

Key words: aerial photography; Chihuahuan Desert, New Mexico, USA; cross-scale linkages; ecological-state mapping; hierarchy theory; Jornada Basin LTER; object-based change detection; petrocalcic soil; Prosopis glandulosa; *shrub patch dynamics; shrub proliferation; soil depth.*

Introduction

The proliferation of woody plants in grasslands and savannas is a persistent phenomenon globally. Soil and landform properties interact with climate drivers and land use to influence the abundance and distribution of woody plants in arid and semi-arid grasslands and savannas worldwide (McAuliffe 1994, Scholes and Archer 1997). In these water-limited systems, soil and landform properties influence plant-water availability by affecting the lateral redistribution of rainfall on the soil surface, subsurface soil–water dynamics, and plant rooting depth (Tongway et al. 2001, Duniway et al. 2010). Precipitation regime (i.e., total amount and

seasonality of precipitation, intensity of precipitation events, and frequency of extreme dry or wet periods) interact with soil properties and land use to create heterogeneity in plant-available water both spatially and temporally (seasonal, annual, and decadal; Wondzell et al. 1996, Duniway et al. 2010). Interactions between these factors that operate at different spatial scales (precipitation, soils, and land use) contribute to the widely observed heterogeneity of the shrub encroachment process across space and time; few robust generalizations have emerged (House et al. 2003, Peters et al. 2004). Therefore, to disentangle the heterogeneity in processes and mechanisms governing woody-plant proliferation, we present long-term data to capture temporal dynamics at two spatial scales across different soils, holding constant precipitation and land-use history.

Previous studies have demonstrated the importance of soil properties (i.e., soil texture, depth, fertility) in determining susceptibility to shrub encroachment,
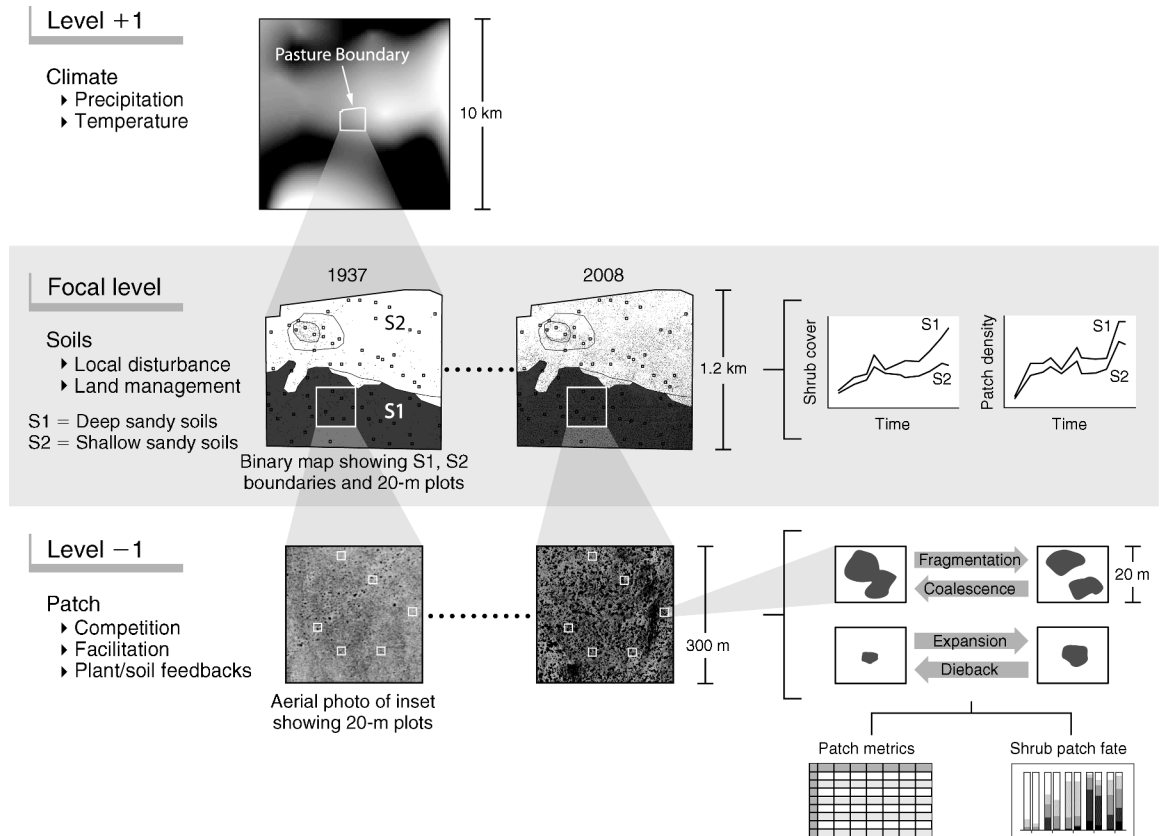
FIG. 1. Hierarchical framework for multi-scale analysis of the influence of soil properties on shrub patch dynamics derived from time-series aerial photography on the Jornada Basin LTER in southern New Mexico, USA. The hierarchical-level approach went from the broad scale of the 150-ha pasture (Level +1) to that of shrub cover and density by soil type (Focal level) to fate metrics at the level of the individual shrub patch (Level −1). Soil classes were determined using reflectance and spectral indices from a 24 Febuary 2002 Landsat ETM+ image with slope and planar curvature terrain attributes (see Browning and Duniway [2011] for details). Field characterization of soil classes identified the two dominant classes as deep (S1) and shallow (S2) sandy soils (see Table 1). Landscape attributes were calculated from binary maps of shrub cover. Patch metrics were based on shrub patches manually digitized on digital aerial photographs. The fates of shrub patches for each time interval were assigned values defined in Table 2.

broadly noting that coarse-textured soils are favored by shrubs and fine-textured soils favored by grasses (Buffington and Herbel 1965, Scholes 1990, Scholes and Archer 1997, Fravolini et al. 2005). We build upon the understanding that soils modulate trajectories of change in the shrub encroachment process by (1) integrating data derived at multiple spatial scales to characterize interactions across precipitation, soils, and patch scales, (2) identifying mechanisms by which soils modulate patch-scale dynamics, and (3) quantifying patterns for both shrub and grass growth forms over a 71-yr period.

Long-term perspectives on woody patch dynamics that capture the range of responses to biotic interactions, land treatments, and disturbance (e.g., fire, drought, grazing) are necessary to envision future landscape configurations and predict vegetation community responses to disturbance and changing climate (Peters 2010). The long-lived, slow-growing nature of many woody species requires an approach capable of discerning the net outcome of climate–soil interactions

on recruitment, mortality, and stand development. To meet this task, data must be available over long time periods (i.e., multi-decadal), collected in a consistent manner, of sufficient temporal resolution or frequency to characterize vegetation dynamics, and examined at multiple scales of observation.

Hierarchical frameworks facilitate the decomposition of complex ecological systems into component processes operating at different spatial scales (i.e., soil map unit vs. shrub or grass patch) (Allen and Starr 1982). Hierarchies comprise both vertical structure of discrete organizational levels, commonly defined by process rates and horizontal structure of constituents capable of interacting with one another (e.g., shrub patches) at a given level that are constrained by higher organizational levels (Wu 1999). For example, changes in shrub cover at a pasture scale reflect the net outcome of patch-level processes such as recruitment, canopy expansion and reduction, and mortality whereby the lowest hierarchical level reflects initial conditions upon which higher levels exert influence (see Fig. 1). In arid and semiarid ecosystems,

TABLE 1. Soil properties in the 150-ha study area for each soil class mapped using Landsat ETM+ imagery and topographic indices (see Browning and Duniway [2011] for details regarding digital soil mapping).

Soil class[†]	Area (%)	Soil class properties					No. plots
		Slope (%)	Depth <100 cm (%)[‡]	Surface sand (%)[‡]	Subsurface clay (%)[‡]	Soil depth (cm)[§]	
S1	42.8	3.4 (0.6)	0	87.1 (4.4)	9.1 (2.6)	>100.0	13
S2	47.5	1.0 (0.4)	100.0	83.5 (4.8)	13.3 (5.3)	51.1 (19.2)	26
S6	3.0	2.1 (0.3)	63.6	82.5 (4.5)	11.3 (0.3)	36.3 (27.1)	3

Notes: Data were derived from field surveys of 24 sites ($n = 8$ for each soil class) where soils were hand-augered to depth of 1 m. Shown for each soil class are the percentage of the total study area, soil class properties (SD in parentheses), and the number of 20 × 20 m plots used to characterize shrub dynamics. See Browning and Duniway (2011) for details regarding digital soil mapping.

† S1, deep sandy soil; S2, shallow sandy soil.

‡ Percentage of the soil class where depth to the petrocalcic horizon is <100 cm.

§ Mean depth to the petrocalcic horizon (where encountered within 100 cm of the soil surface).

precipitation is a broad-scale driver that influences patch-scale processes differently according to soil properties and the intervening geomorphic template (Peters et al. 2006).

Soil and landscape properties modulate both patch-scale and community-scale plant processes in water-limited ecosystems (as in Fig. 1). Landscape position, local topography, and soil surface and subsurface properties affect the efficiency with which incoming precipitation is made available for plant uptake. Contributing area, slope steepness and shape, and surface soil properties (e.g., texture, roughness) determine how much run-on water a site will receive and the fraction of precipitation and run-on water that will infiltrate into the soil profile or be lost as evaporation or run-off (e.g., Wu and Archer 2005). In arid ecosystems, sites receiving more run-on water and/or occurring on flat terrain tend to be more productive than those that do not receive run-on water or occurring on steeper slopes. Additionally, sites with coarse surface textures (within 5 or 10 cm of surface) tend to be more productive because rapid infiltration and

low water-holding capacity of surface soils reduce evaporative losses (Sala et al. 1988).

Once water has infiltrated into the soil profile, subsurface soil properties can affect whether infiltrated precipitation is retained near the surface and available to shallow-rooted species or is in deeper layers where it is only available to plants with extensive root systems, such as woody species (Walter 1973, McAuliffe 1994). Past work conducted on sandy soils indicated that grasses (e.g., *Bouteloua eriopoda*) are more resilient to drought in soils with high water holding capacity in the upper soil layers (within ~1 m of surface) and woody species (e.g., *Prosopis* species) tend to dominate on soils that promote percolation to deeper depths (Herbel et al. 1972, Gibbens et al. 2005, Yao et al. 2006). Thus, subsurface soil properties appear to be especially important for vegetation dynamics during drought on sandy soils, which are common in water limited systems globally (Fig. 2).

In addition to topo-edaphic influences on plant water availability, plant–soil feedbacks play an important role

TABLE 2. Shrub fate categories, together with definitions of fate attributes assigned to shrub objects manually delineated on co-registered digital photography.

Fate-category group[†]	Fate category[‡]	Definition
Appearance	New	First appearance of a shrub patch on a digital image.
Growth	Expan	Increase in patch size due to canopy expansion; this category corresponds to circular patches possibly corresponding to a single shrub canopy.
	ExpanP	Canopy expansion resulting in the transition of a patch depicted as a point to that of a polygon.
	Coalesc	Increase in patch size due to coalescence of the focal shrub with neighboring shrub patches, thereby increasing shape complexity.
Dieback	Dieback	Decrease in size of shrub polygon due to canopy dieback; this designation applies to circular rather than larger complex patches.
	DiebackP	Decrease in patch area resulting in transition from a polygon to a point.
	Fragment	Loss of patch area resulting from the fragmentation of conglomerate patches into constituent shrubs.
Disappearance	Disapp	Previously existing patch that is no longer discernable, representing patch mortality. Patch mortality does not imply plant mortality.
Persistence	Maintain	Shrub polygons do not change appreciably in size (15% of patch area) or shape from one image to the next.
	Persist	Shrub objects persist as points with no recognizable canopy growth.

Note: Categorical designations characterize fate between two aerial photographs.

† "Group" corresponds to the generalized grouping created to summarize shrub patch dynamics over the 71-yr period (Fig. 5).

‡ "Fate category" values were assigned to objects in building the database.

in patch- and community-scale plant dynamics (e.g., Ludwig et al. 2005), particularly during periods of drought. The spatial distribution and density of plants and associated gaps between plant canopies can greatly affect surface water redistribution and vulnerability to erosion. Plant basal cover tends to slow overland flow, promote infiltration, and reduce flow erosivity (Pierson et al. 1994, Bautista et al. 2007). Plant canopies protect the soil surface from rain-drop impact and wind erosion (Wainwright et al. 1999, Okin 2008). Loss of protective plant cover and associated increases in the size and connectivity of bare areas have been shown to greatly increase erosion by wind and water (Okin et al. 2009). Thus, the loss of protective plant cover complicates ecosystem recovery by both reducing a site's ability to capture water, either as precipitation or run-on, and increasing the susceptibility to erosion.

The relative importance of soil and landscape properties and associated plant–soil feedbacks also varies with climate. For example, plant community, landscape, and soil surface properties that affect run-on/run-off dynamics and infiltration are less important during low-intensity rain events and when evaporation demands are low (Sala et al. 1988, Bautista et al. 2007). Similarly, when erosive forces of wind and water are low (e.g., low wind speeds, low-intensity rains) plant–soil feedbacks that limit erosion potential are less important. Subsurface water-holding capacity is more important during droughts (Yao et al. 2006) than during periods when there is adequate precipitation to meet plant demands (Noy-Meir 1973). A common subsurface soil horizon in dryland ecosystems that has been demonstrated to greatly alter soil-water dynamics, particularly during drought, is a soil horizon cemented with calcium carbonate (i.e., petrocalcic horizon). Though these horizons are rock like in morphology they can have very high water-holding capacities and retain water at plant-available tensions for many months (Duniway et al. 2007, 2010).

Although there has been work documenting patterns in woody encroachment in dryland ecosystems of the southwestern United States (Goslee et al. 2003, Laliberte et al. 2004, Barger et al. 2011), there is little work analyzing temporal patch dynamics of woody-plant proliferation that accounts for the underlying soil heterogeneity (e.g., Browning et al. 2008). We build on previous work at the Jornada Basin Long-Term Ecological Research site in southern New Mexico (USA) to isolate the effects of soil properties on contributions of shrub patch demographic processes to landscape-level metrics for shrub cover and patch density (Browning et al. 2011). In addition, we explore relationships between annual rainfall and shrub patch dynamics (e.g., colonization, growth, fragmentation, and canopy dieback).

The overarching objective of this study was to examine the influence of the edaphic template on shrub dynamics quantified at two spatial scales within a nested hierarchy, those of contiguous shrub patches and the 150-ha pasture. Specifically, we sought to (1) analyze the relationships between soil properties and patch demographics associated with shrub proliferation from 1937 to 2008 using time-series aerial photography and (2) examine correlations between annual precipitation and shrub patch dynamics observed on different soils.

METHODS

Study site

The study was conducted on the Chihuahuan Desert Rangeland Research Center (CDRRC), a component of the Jornada Basin Long-Term Ecological Research site (JRN) near Las Cruces, New Mexico, USA. The JRN lies in the northern Chihuahuan Desert between the Rio Grande corridor to the west and the San Andres Mountains to the east within the southern Jornada del Muerto Basin (Southern Desertic Basins, Plains, and Mountains Major Land Resource Area; USDA-NRCS 2010).

The 150-ha study area at 1324-m elevation (UTM 13 N, 0323482E, 3601557N, NAD83) was historically dominated by grasses but has transitioned to a shrub-dominated ecosystem (Gibbens et al. 2005). A 2004 field survey of all shrubs within 20 plots (20 × 20 m) revealed that honey mesquite (Prosopis glandulosa Torr.) constituted 89.3% of shrubs, with mormon tea (Ephedra torreyana) and soap-tree yucca (Yucca elata) representing 7.0% and 2.6%, respectively. Grass cover, consisting of black grama (Bouteloua eriopoda), tobosa (Pleuraphis mutica), dropseed species (Sporobolus spp.), and bush muhly (Muhlenbergia porteri), declined precipitously between 1947 and 1960 (Laliberte et al. 2004).

Long-term (1930–2008) local average annual rainfall was 232.2 mm, with 144.9 mm occurring from July through October and 86.8 mm occurring in the remaining months. Monthly records of precipitation over the study period for Selden rain gauge, 2.3-km from the study site, were aggregated by rain year from November to include rainfall through the following October. We deviate from the standard water year (i.e., October through September) in this study because (1) long-term (18-yr) phenological records indicate that the deciduous shrub, Prosopis glandulosa (that is the focus of this study), retains its leaves through October and (2) soil moisture from October precipitation seldom carries over into subsequent months due to October evapotranspiration demands (see Fig. 5 in Duniway et al. 2010). Mean maximum monthly temperatures range from 13.5°C in January to 35.0°C in July (Wainwright 2006).

Land use and management history

Widespread degradation of grasslands in much of the western United States at the turn of the 20th century prompted governmental oversight and management of southwestern rangelands. Degradation was due, in large part, to overgrazing by sheep and livestock in the 1880s
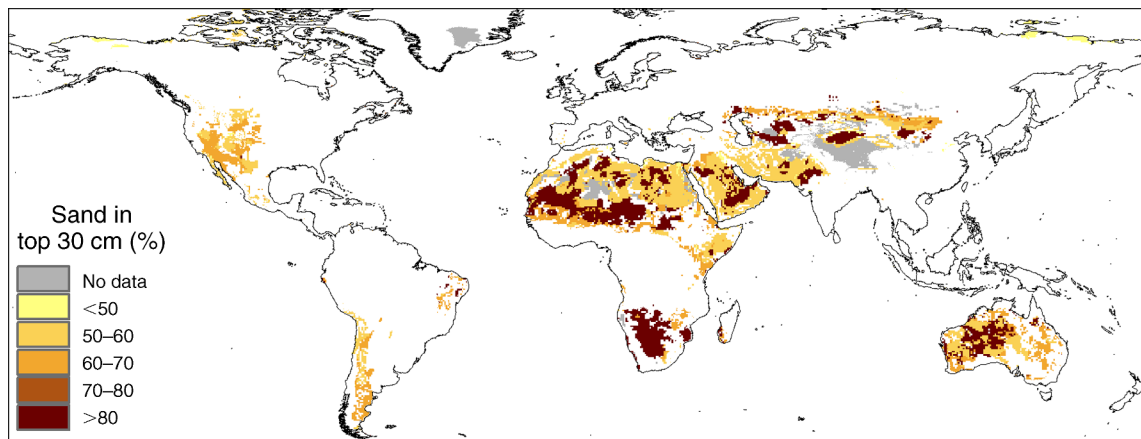
FIG. 2. Global map of surface sand content (0–30 cm, percentage by mass) in sandy soil types that occur in water-limited systems. Water-limited systems are defined as those areas where the ratio of mean annual evapotranspiration to mean annual precipitation is equal to or less than 0.5 (the Aridity Index; Trabucco and Zomer 2009). Sandy soil types included are sandy loams, loamy sands, and sands (as classified by the U.S. Department of Agriculture, mapped here as areas with >50% sand and <20% clay; Batjes 2005).

and a sequence of drought years in 1886 and the early 1890s and 1900s (Fredrickson et al. 1998). Livestock production has been a prominent economic activity in much of the Jornada Basin following the U.S. Civil War of the 1860s (Fredrickson et al. 1998, Havstad et al. 2006). Livestock grazing continues in the region, albeit with a steady reduction in stocking rates over the course of this study (1937 to 2008).

Trends in stocking rates for cattle on the CDRRC show a general decrease from 1930 to the mid-to-late 1960s (~220 mature cows [i.e., animal units, AU] to ~125 AU), an increase to levels comparable to the 1930s by ca. 1980 (~250 AU) and then a decreasing trend to considerably low rates by 2008 (~90 AU; Derek Bailey, *unpublished data*). Patterns in stocking rates track broad-scale patterns in precipitation, reflecting range management decisions based on available forage. Stocking rates in the study area that falls entirely within one pasture are presumed equal and assumed to mirror general regional trends.

An herbicide treatment was conducted in June 1973 over a portion of the shallow sandy soil class S1 (see *Soils*, below, for description). Spatially explicit records of historic land treatments were not readily available; however, Laliberte et al. (2004) reported this treatment previously. We excised the herbicide-treated area discernable on the imagery from the study region for landscape- and patch-scale analyses to avoid confounding factors in our evaluation of relationships between spatial patterns in soil properties and long-term shrub dynamics.

Soils

The study area is dominated by sandy soils that are part of the broad alluvial plain of the ancestral Rio Grande River (Mack et al. 1996). The area is now primarily a mosaic of varying sandy soil types due to post depositional geomorphic processes, primarily re-working of the sediments by wind and water (Monger et al. 2006). Three National Resources Conservation Service (NRCS) ecological sites constitute the majority of the alluvial plain as mapped by Monger (2006), and include: (1) a shallow sandy soil underlain by a petrocalcic horizon at 50 cm or less (shallow sandy [USDA NRCS Ecological Site Information System code R042XB012NM]; 8% of the alluvial plain), (2) a sandy soil with some clay and carbonate accumulation in the top 100 cm without a petrocalcic horizon within 50 cm (sandy [R042XB015NM]; 62%), and (3) a deep sandy soil with little horizon development or water-holding capacity, including no petrocalcic horizons, within 100 cm (deep sandy [R042XB011NM]; 12%) (Bulloch and Neher 1980, USDA-NRCS 2010).

To refine the existing coarse soil survey (third order; mapped at 1:48 000 scale) to represent soils at a scale commensurate with shrub patch dynamics, we completed a soil map based on digital soil mapping techniques using Landsat 7 ETM+ imagery and topographic variables from a digital terrain model (DTM) derived from airborne interferometric synthetic aperture radar (Intermap Technologies, Englewood, Colorado, USA; Browning and Duniway 2011). Soil classes were mapped at 30-m spatial resolution using a combination of unsupervised and supervised image classification methods. A spatially distinct, ephemerally flooded 2.8-ha playa characterized by heavy clay soils occurs within the study area (Monger et al. 2006) but was excluded from analyses in this study. In the upland region of the 150-ha study area, three distinct soil classes were delineated (Fig. 1, Table 1). The two dominant soil classes in the area (classes S1 and S2) constituted 90% of the study area. We focused our research effort on the two dominant sandy soils.

Field sampling by Browning and Duniway (2011) determined that soil class S1 is a deep soil with low water-holding capacity (no root-restrictive layer or clay accumulation in the top 100 cm). In contrast, S2 is a shallow soil (root restrictive layer within 100-cm) and has greater water-holding capacity in the top 100 cm than S1 due to higher clay content and presence of petrocalcic horizons (Duniway et al. 2007). There was also a slight increase in sand in the top 5 cm of 3.6% from soil class S2 (83.5%) to soil class S1 (87.1%; Table 1). We hereafter refer to soil class S1 as "deep sandy soil" to indicate the lack of a petrocalcic horizon or clay accumulation in the top 100 cm and to soil class S2 as "shallow sandy soil" to denote the presence of a petrocalcic horizon within the top 100 cm ($\sim$51.5 cm; Table 1).

Hierarchical approach to vegetation dynamics

Data were derived at three levels of organization coinciding with annual precipitation as a broadscale driver (Level +1), shrub cover and density by soil type (Focal level), and fate metrics determined at the level of individual shrub patches (Level −1; Fig. 1). We employed object-based methods to quantify vegetation dynamics at two scales of observation: the 150-ha pasture and individual shrub patches. Binary images of shrub cover were the basis for pasture level metrics for cover and shrub patch density; these analyses were conducted using automated object-based image analysis of 11 co-registered digitized photographic images to designate shrub and grass dynamics from 1937 to 2008. Patch-scale analyses were conducted by manually digitizing shrub patches (i.e., image objects) on the 11 co-registered images to quantify dynamic changes in patches on deep sandy and shallow sandy soils from 1937 to 2008 (Fig. 1); intervals between photo acquisitions ranged from 3 to 10 years (7.1 ± 2.4 yr [mean ± SD]). See Table 1 in Browning et al. (2011) for details regarding photo scale and film attributes.

Vegetation dynamics by soil type (Focal level).—We extended the long-term study of vegetation dynamics from 1937 to 2008 over the 150-ha pasture on the Chihuahuan Desert Rangeland Research Center by Browning et al. (2011) to incorporate changes in grass cover and to isolate the effects of soils on observed grass–shrub vegetation dynamics. All co-registered, geo-coded images were subjected to object-based image analysis to generate separate binary layers for shrub and grass cover. To map shrub cover, images were segmented at a fine and coarse scale (scale parameters 3 and 250, respectively); the shrub classification was performed at a finer scale (i.e., scale parameter = 3) than the grass classification using a rule-based approach with three features: mean brightness, mean difference to neighbor, and mean difference to super-object. Relating the two segmentation levels in this fashion allowed for simultaneous extraction of shrubs in both light and dark backgrounds.

Overall classification accuracies for the shrub-cover maps ranged from 89.9% to 98.0% based on manual interpretation of geo-coded imagery by an experienced image analyst. Cohen's Kappa coefficient ($\hat{K}$; Cohen 1960) for the shrub image class ranges from −1 to 1 with zero indicating no better agreement of reference data with the classified result than expected with a random classified map. The $\hat{K}$ values for the shrub image class ranged from 0.517 to 0.965 (see Browning et al. [2011] for full image accuracy assessment).

Grass cover was mapped at the coarse scale to depict large patches of grass; this was in contrast to the canopy-level mapping of shrub objects largely due to confidence in feature extraction from archive aerial photography. The coarser segmentation scale for the grass-cover mapping (i.e., scale parameter = 250) resulted in polygons larger than the largest shrub patch, and avoided confusion between shrubs and grasses with similar brightness values (Laliberte et al. 2004).

To quantify the effect of soil depth on changes in mean and variance in shrub cover, cover from binary classified images was summarized using 20 × 20 m nonoverlapping quadrat sample windows. This was achieved by intersecting a 20 × 20 m polygon feature class with co-registered binary images to derive percent shrub cover by quadrat as the percentage of 1-m^2 cells classified as "shrub." This window size was selected by calculating the variance of estimated shrub cover across window sizes from 2 to 70 m and identifying the window size at which variance stabilized (Greig-Smith 1983). Each 20 × 20 m quadrat was assigned to the intersecting soil class mapped by Browning and Duniway (2011).

Repeated-measures analysis of variance (ANOVA) was conducted on mean shrub cover for untreated S1 (deep sandy soil) and S2 (shallow sandy soil) 20 × 20 m quadrats to assess whether changes in cover on two soils were different over time. Mauchly's sphericity test was used to examine the form of the common covariance matrix and to ascertain whether univariate or multivariate interpretations were appropriate (SAS Institute 2007). Mauchly's criterion for sphericity was violated ($P < 0.0001$); therefore, we report multivariate results for repeated-measures ANOVA. To circumvent the arbitrary inflation of patch-density values by intersecting binary shrub images with 20 × 20 m quadrat boundaries, shrub patch density was calculated for each year as the number of shrub patches divided by the area mapped for soil classes S1 and S2.

Patch-level analysis (Level −1).—To enhance interpretation of pasture-scale metrics characterizing changes in shrub abundance and patch density, we devised a two-phase protocol. Using manual interpretation to monitor the fate of individual shrub patches through time, we (1) manually delineated shrub patches on each co-registered aerial image, and then (2) categorized changes in patch appearance, disappearance, shape, size, and configuration from one image to the next.

A number of factors can influence the detectability of plant canopies (e.g., image quality, photo scale, time of day, and season of image acquisition). For consistency in delineating new patches, we digitized small patches (<4 m^2 in area) as points and larger patches as polygons (Archer et al. 1988). To standardize detectability and delineation of shrub patches, the 11 geo-coded images were aggregated to a common spatial resolution of 1 m using a nearest-neighbor resampling method. Digitizing methods were designed to minimize observer error following Browning et al. (2009). Once all shrub patches were depicted (as either points or polygons), a unique identifier was assigned to individuals to track their fate from one image to the next.

The delineation and categorization of shrub patches were conducted for all patches intersecting the boundaries of 13 and 26 plots on S1 (deep sandy) and S2 (shallow sandy) soil classes, respectively. Shrub fate categories are defined in Table 2. For this analysis, we defined a *patch* as a discrete shrub canopy image object comprising one or more individual mesquite shrubs with overlapping canopies. By manually digitizing shrub patches, we circumvented misidentification of individuals due to co-registration errors and discrepancies that could arise from differences in automated image-classification accuracy.

Fate assignments were designed to quantify patch dynamics encapsulating shrub recruitment, growth, and mortality for detailed monitoring of individuals (Browning et al. 2011). Increases and decreases in canopy size for relatively small circular patches were categorized as *canopy expansion* and *canopy dieback*, respectively. Additional categories were specified to include canopy growth by coalescence with neighboring patches and dieback by fragmentation into constituent patches (Table 2, Fig. 1). Persistence and stability denote maintenance of shrub canopy size as polygons or points from one image to the next; a threshold of $<15\%$ change in shrub patch area was set to represent persistence in size.

To evaluate whether soil class influences shrub patch demographics, we calculated rates of change for specific fate categories (Table 2) and performed a nonparametric χ^2 analysis to determine whether soil class exhibited an effect on the percentage of patches in fate categories. For the χ^2 analysis, we collapsed the 10 fate categories specified above into five representing patch appearance (i.e., colonization), growth, dieback, disappearance, and stability (i.e., persistence) to avoid problems associated with small sample sizes across nine fate classes. To retain information regarding coalescence, canopy expansion, fragmentation, and canopy dieback, we calculated rates of change for all nine fate categories (see Table 2).

Rainfall and shrub demographics (Level +1 and Level −1).— Effective and robust linkages between annual or seasonal patterns in climate (i.e., temperature and rainfall) and shrub dynamics from aerial photography

TABLE 3.   Percentage of years for which annual precipitation (1 November–31 October) deviated more than 0.5 standard deviations from the long-term (1930–2008) average annual rainfall (232.2 mm).

Time period	Percentage of years >0.5 SD from long-term average	
	Drier	Wetter
1937 to 1947	30.0	10.0
1947 to 1955*	75.0	0.0
1955 to 1960	40.0	40.0
1960 to 1967*	71.4	28.6
1967 to 1977	30.0	10.0
1977 to 1980	0.0	33.3
1980 to 1989*	11.1	44.4
1989 to 1996*	28.6	14.3
1996 to 2004	25.0	25.0
2004 to 2008	0.0	50.0

Notes: Standardized differences were calculated by subtracting the long-term mean from the annual value and dividing by the standard deviation for the long-term average. Asterisks denote significant differences ($P < 0.05$) in percentages for shrub patch fate for deep and shallow sandy soils (see Fig. 5).

remain elusive. This is largely attributed to challenges associated with infrequent (and often multi-decadal) time steps between available images, slow growth rates for many shrubs, and detection limitations of older aerial photography (Browning et al. 2009). We overcame certain of these obstacles with a dense aerial photo record and manual interpretation of shrub objects that might be overlooked by an automated image-classification algorithm.

We examined the correlation between shrub patch fates (Table 2) and the frequency of years drier and wetter than the long-term average rainfall. Rainfall metrics were based on differences from the long-term average (1930–2008) that are standardized by the standard deviation. Standardized differences represent the number of standard deviations (SD) from the long-term mean. We calculated the percentage of years (for each time period ranging from 3 to 10 years) that were 0.5 SD greater (wetter) and 0.5 SD less (drier) than the long-term average (Table 3). Correlations between percent dry and percent wet years and rates of shrub colonization, growth, dieback, fragmentation, coalescence, and disappearance on two soils were evaluated using PROC CORR in SAS (SAS Institute 2007).

RESULTS

Vegetation dynamics by soil type

Shrub cover and patch density.—Repeated-measures ANOVA revealed a strong soil × year interaction ($F_{10,2707} = 183.09$, $P < 0.0001$), signifying that shrub cover on the two soils changed differently over time. Shrub cover was similarly low on both soils in 1937, $1.0\% \pm 2.3\%$ and $0.3\% \pm 1.3\%$ (mean ± SD) on deep and shallow sandy soils, respectively, and diverged significantly over time to reach $19.8\% \pm 9.1\%$ and $9.3\% \pm 7.2\%$, respectively, in 2008 (Fig. 3A). Changes in
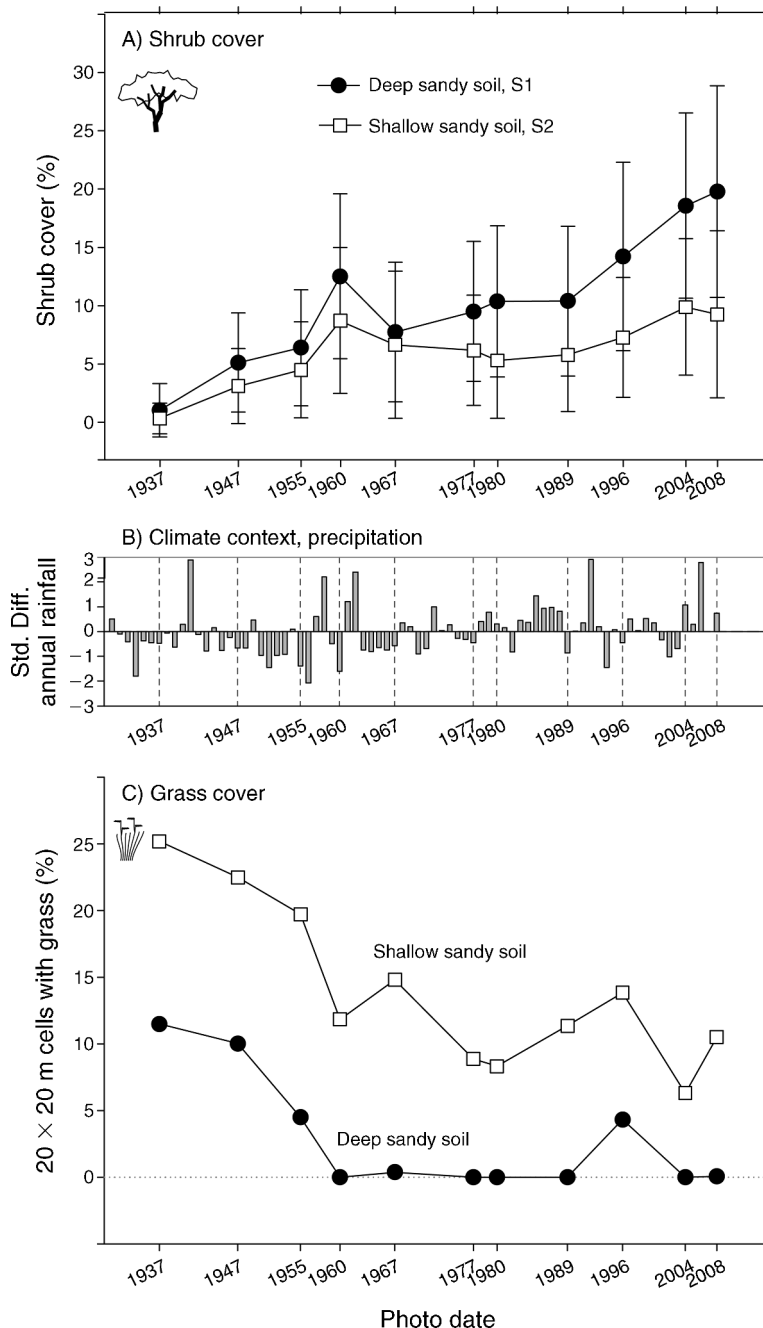
FIG. 3. (A) Percent shrub cover from 1937 to 2008 on deep and shallow sandy soils across a 150-ha landscape on the Jornada Basin LTER (New Mexico, USA). Shrub cover (mean ± SD) was calculated as the percentage of shrub (1-m) pixels within nonoverlapping 20 × 20 m quadrats. (B) The climate context for observed patterns in both shrub cover and grass cover, expressed as standardized differences, the number of SDs from long-term (1930–2008) average rainfall (232.2 mm). Values were calculated by subtracting the long-term mean and dividing by the long-term SD. (C) Grass cover was mapped following protocols from Laliberte et al. (2004). Data on the abundance of grass from 1937 to 2003 for each soil class were translated to the percentage of 20 × 20 m quadrats where grass was present.

shrub cover were dynamic across space and time (Fig. 4). Shrub cover on the shallow sandy soil (S2) was more patchily distributed across the time series and patterns in the amount and distribution of shrub cover on the two soils diverged after 1967 (Figs. 3A and 4).

The broad-scale classification of grass cover revealed a marked difference of 13.7%, with higher grass cover on shallow sandy soils in 1937 (Figs. 3C and 5). The subsequent decrease in grass cover occurred on both soils, but precipitous early declines on the deep sandy
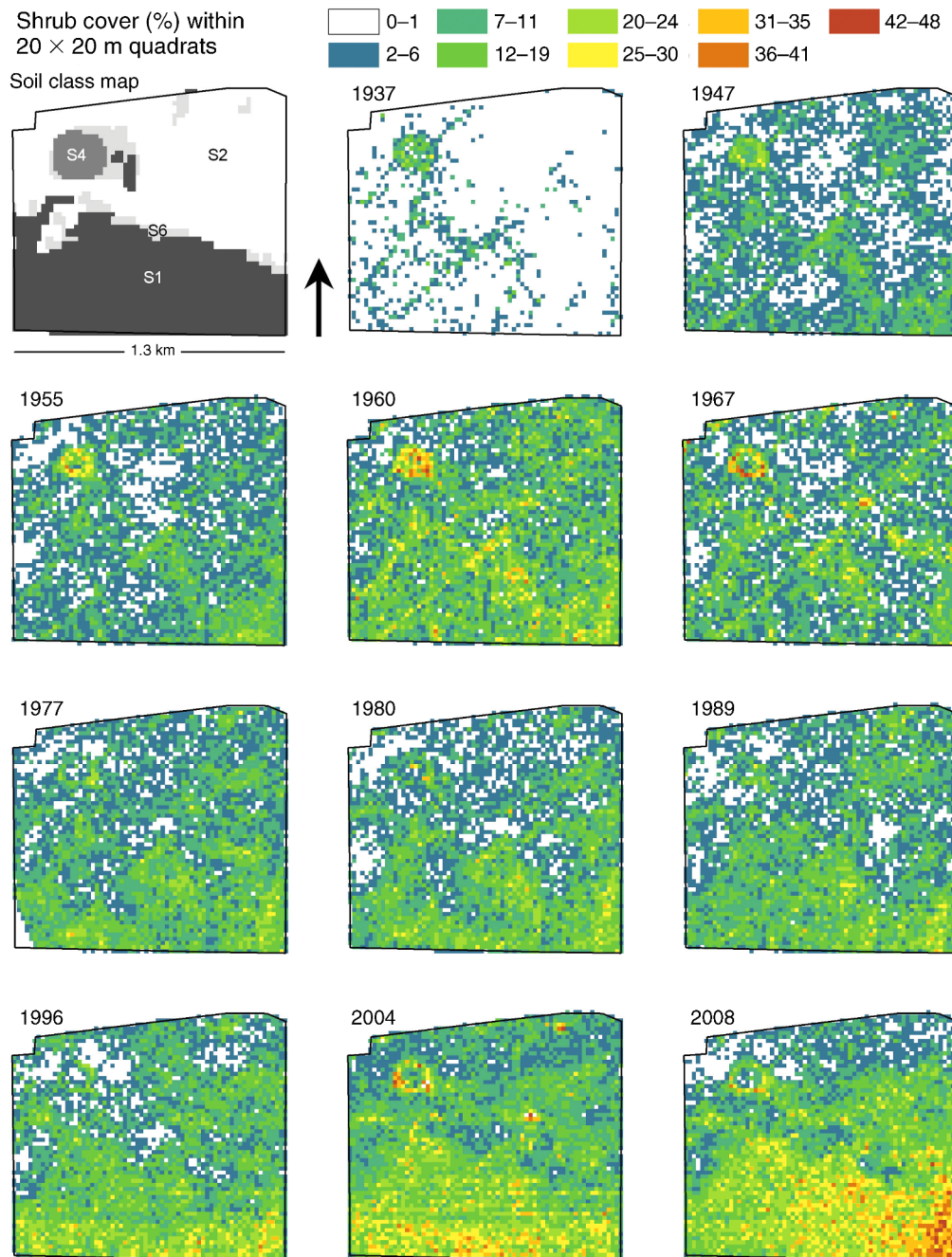
FIG. 4.   Percent shrub cover from 1937 to 2008 on deep (S1) and shallow (S2) sandy soils for a 150-ha landscape on the Jornada Basin LTER (New Mexico, USA). Shrub cover is expressed as the percentage of shrub (1-m) pixels within nonoverlapping 20 × 20 m quadrats.

soil (S1) occurred from 1947 to 1955 and from 1955 to 1960 on the shallow sandy soil. Between 1947 and 1960 10 of the 14 years experienced below-average rainfall and seven of those years were consecutive (the 1950s drought from 1950 to 1957; Fig. 3B). By 1960 grass cover disappeared on the deep sandy soil (S1), yet persisted on the shallow sandy soil (S2). The increase in 1996 grass cover on the shallow sandy soil S1 represents

growth and persistence while that on the deep sandy soil S2 was ephemeral (Fig. 5).

Shrub patch density (PD) on the deep sandy soil was consistently higher than that on the shallow sandy soil, although trends were similar for most time periods. Patterns were fairly stable, with three periods of prominent increase in PD. In 1937, PD was low on both soils (7 and 2 patches/ha on deep and shallow
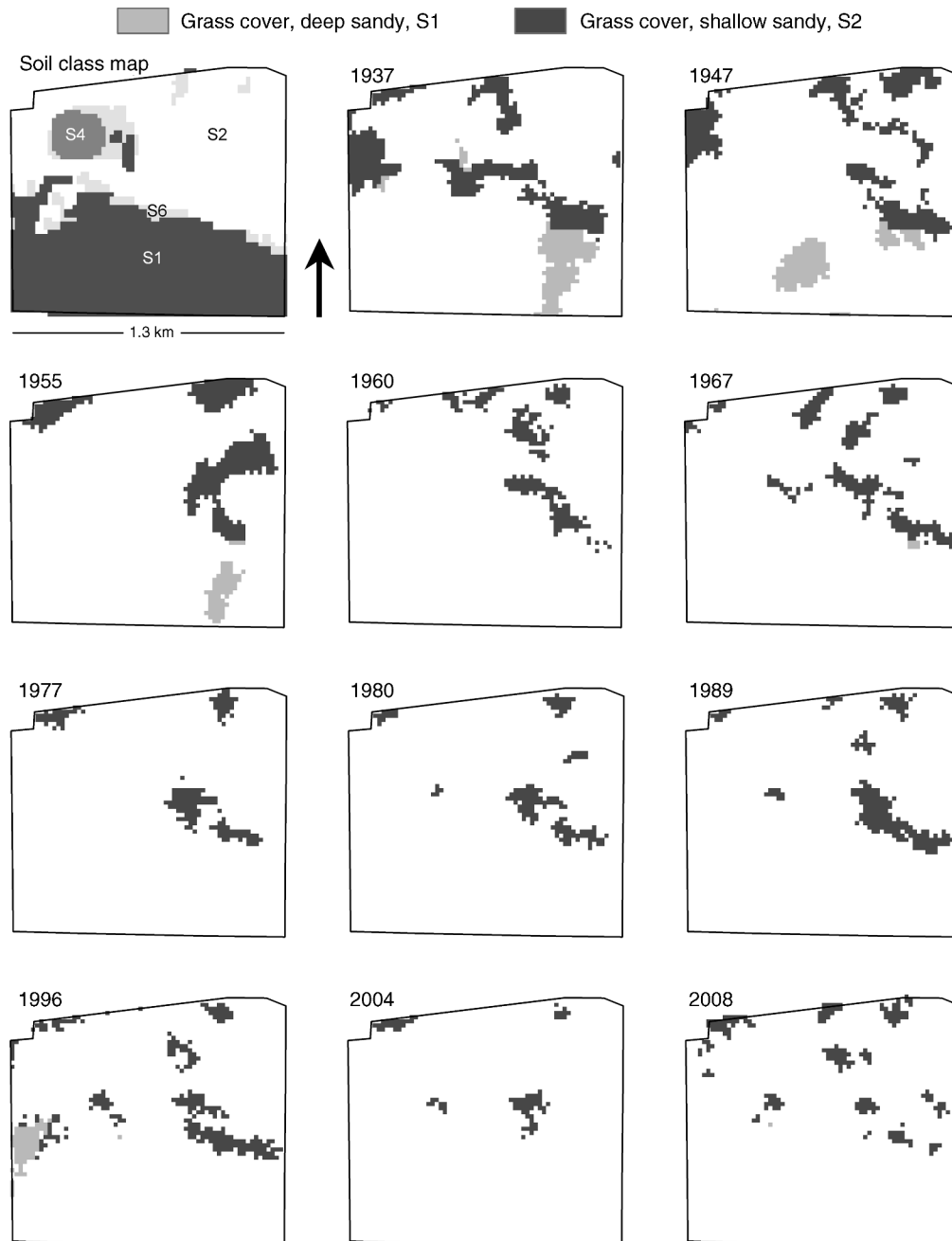
FIG. 5.   Grass cover on deep (S1) and shallow (S2) sandy soils from 1937 to 2008. Grass cover was estimated using a broad-scale object-based image classification of aerial photography. Due to the quality of earlier photographic images in the time series, the image segmentation to classify grasses was coarser than that used to delineate shrub cover. As such, grass cover might be underestimated due to the inability to distinguish small grass patches.

sandy soils, respectively) and then exhibited high rates of increase from 1937 to 1947 (Fig. 6A). Mean patch size increased on both soils during periods of stability in PD from 1947 to 1960 (Fig. 6B). The decrease in patch density from 1960 to 1967 occurred on both soils. Periods from 1967 to 1977 and 1996 to 2004 were periods of marked increases in PD on both soils (Fig. 6A). In all years after 1937, mean patch size on deep

sandy soils S1 was higher than or equal to that on shallow sandy soils S2. Mean patch size on deep sandy soils demonstrated an upward trend from 1977 to 1996 (Fig. 6B).

Patch-level analysis

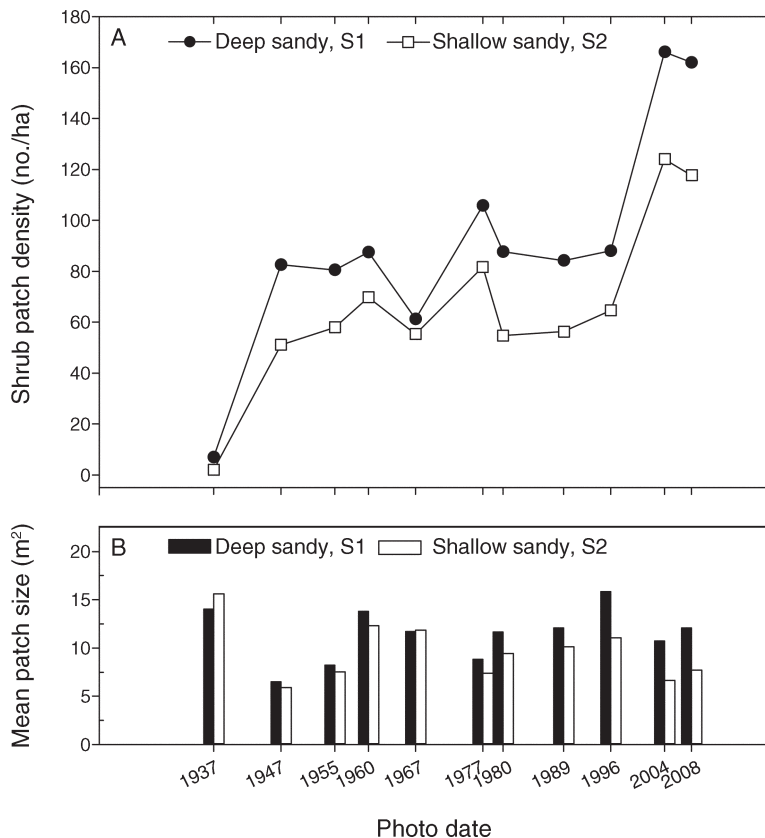*Shrub patch fate.*—Patterns in shrub patch fate on deep and shallow sandy soils demonstrated both broad

FIG. 6.   (A) Shrub patch density (total number of patches per unit area) and (B) mean patch size on deep (S1) and shallow (S2) sandy soils across a 150-ha landscape on the Jornada Basin LTER in southern New Mexico. Patches were delineated using object-oriented image analysis of time-series aerial photography.

scale consistency and fine-scale differences at different periods over the 71-year study record. From a broad perspective, shrub population dynamics on both sandy soils were characterized by shrub colonization and

growth from 1937 through 1960 (Fig. 7). Between 1960 and 1967, patch dynamics transitioned to that of a shifting mosaic where an array of demographic changes (i.e., colonization, growth, dieback, disappearance, and
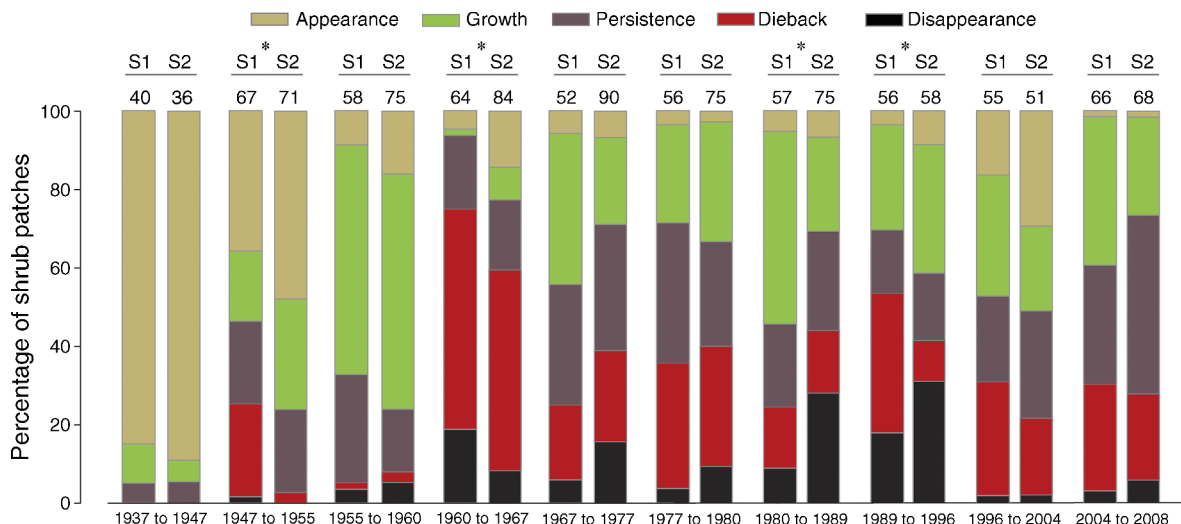

FIG. 7.   Patterns in shrub patch demography on deep (S1) and shallow (S2) sandy soils over 10 time periods spanning 71 years. Patches were manually digitized on 11 co-registered aerial photographic images. Fate categories over each time period are represented as the percentage of the total number of shrub patches for each period on each soil (numbers above bars). Fate categories are defined in Table 2. Asterisks denote significant differences (α = 0.05) in fate percentages between deep (S1) and shallow (S2) sandy soils for a given time period.

TABLE 4. Shrub patch demographics from manual interpretation of time-series aerial photography on two sandy soils of different depths.

Time period	Colonization (patches·yr⁻¹·ha⁻¹)		Canopy growth (patches·yr⁻¹·ha⁻¹)		Coalescence (patches·yr⁻¹·ha⁻¹)		Disappearance (patches·yr⁻¹·ha⁻¹)	
	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow
1937 to 1947	8.8	4.2	0.3	0.3	*0.0*	*0.0*	*0.0*	*0.0*
1947 to 1955*	7.8	5.6	3.9	3.2	*0.0*	*0.0*	*0.3*	*0.0*
1955 to 1960	2.6	3.1	13.5	10.4	*4.2*	*1.3*	*1.0*	*1.0*
1960 to 1967*	1.0	2.2	0.3	1.2	*0.0*	*0.1*	*4.4*	*1.3*
1967 to 1977	0.8	0.8	4.7	2.5	*0.5*	*0.1*	*0.8*	*1.8*
1977 to 1980	1.8	0.9	11.2	9.5	*0.8*	*0.4*	*1.8*	*3.0*
1980 to 1989*	0.8	0.8	6.2	2.6	*1.8*	*0.0*	*1.6*	*3.0*
1989 to 1996*	0.8	0.9	5.2	3.5	*0.3*	*0.0*	*3.6*	*3.4*
1996 to 2004	2.9	2.5	4.9	1.8	*0.8*	*0.0*	*0.3*	*0.1*
2004 to 2008	0.8	0.4	13.0	4.9	*3.4*	*0.6*	*1.3*	*1.3*

Notes: See Table 1 for soil properties. Shrub patch appearance (i.e., colonization), growth, coalescence, disappearance, dieback, and fragmentation are defined in Table 2. Asterisks denote significant differences ($P < 0.05$) in percentages for shrub patch fate for deep (S1) and shallow (S2) sandy soils (see Fig. 5). Patch-based metrics reflecting processes that translate to decreases in patch density (i.e., disappearance and coalescence) are italicized while those that translate to increase in patch density (i.e., colonization and fragmentation) are not.

persistence) co-occur (Bormann and Likens 1979). On both soils shrub patches were distributed across all demographic classes from 1967 to 2008. However, differences in fate contributions existed between deep and shallow sandy soils for periods marked by a high frequency of years with above- and below-average rainfall (denoted by asterisks in Fig. 7 and Table 3).

Chi-square tests were conducted for each time period to distinguish soil class differences in the percentage of shrub patches in each of five fate category groupings (i.e., appearance or colonization, growth, persistence, dieback, and disappearance; Table 4, Fig. 7). There were significant differences in percentages from 1947 to 1955 ($\chi^2_4 = 15.54$, $P = 0.004$) with greater dieback (i.e., >15% decrease in shrub patch area) on the deep (S1) than on the shallow (S2) sandy soil. Similarly, from 1960 to 1967 ($\chi^2_4 = 9.64$, $P = 0.047$) with there was higher patch disappearance, canopy dieback, and lower patch colonization on the deep sandy soil. In addition, there were significant differences in shrub fate percentages by soil class from 1980 to 1989 ($\chi^2_4 = 12.30$, $P = 0.015$) and 1989 to 1996 ($\chi^2_4 = 11.60$, $P = 0.021$). From 1980 to 1989, patches on the deep sandy soil exhibited growth (i.e., >15% increase in shrub patch area) while those on the shallow sandy soil experienced high mortality. Conversely, from 1989 to 1996, patches on the deep sandy soil were marked by higher canopy dieback and fragmentation, although patch disappearance was high on both (Table 4, Fig. 7).

Rainfall/soil effects on shrub demographics.—The 71 years documented by this study encompassed a range of climate events. The first photo date in 1937 occurred at the end of the 1930s drought which was followed by the severe drought of 1951 to 1956 across the southwestern United States (Herbel et al. 1972, Woodhouse and Overpeck 1998). The mid-1970s marked a shift to a higher frequency of single and consecutive wet years and a decreased frequency of consecutive dry years (Fig. 3B). The trend of increased precipitation later in the study

period is exemplified by extremely wet periods from 1980 to 1989 and 2004 to 2008.

Correlations between percentage of years drier or wetter than average (Table 3) and percentage of patches that increased/decreased in size, appeared, disappeared, coalesced, and fragmented (Table 4) were evaluated for each time period and soil class. For all 10 time periods (1937–2008), shrub patch growth on the deep sandy soil S1 was positively correlated with the percentage of wet years ($r = 0.671$, $P = 0.034$ and $r = 0.770$, $P = 0.009$ for growth and coalescence, respectively; Table 5). Shrub colonization on the shallow sandy soil S2 was positively correlated with the percentage of dry years ($r = 0.705$, $P = 0.023$; Table 5). Correlations between fate metrics on a given soil revealed that shrub patch growth and coalescence were strongly and positively correlated on both deep ($r = 0.844$, $P = 0.002$) and shallow ($r = 0.811$, $P = 0.004$) sandy soils, while a strong negative correlation between shrub patch colonization (i.e., appearance) and disappearance was significant on the shallow sandy soil only ($r = -0.773$, $P = 0.009$; data not shown).

To explore the relationship between rainfall and dynamic patch demographics following the colonization phase (1937 to 1960), we ran the correlation analysis using only data from 1960 to 2008. Using data from the last seven time periods, no demographic pattern on the shallow sandy soil was correlated with rainfall metrics. However, shrub patch growth and coalescence on the deep sandy soil were correlated with rainfall. Patch coalescence on deep sandy soils was positively correlated with the frequency of wet years ($r = 0.806$, $P = 0.029$) and growth was negatively correlated with the frequency of dry years ($r = -0.915$, $P = 0.004$) indicating the patch growth was positively correlated with frequency of years that were not dry (Table 5).

DISCUSSION

Our hierarchical 71-year analysis bridged manual interpretation of shrub patch demographics and auto-

TABLE 4.   Extended.

Canopy dieback (patches·yr⁻¹·ha⁻¹)		Fragmentation (patches·yr⁻¹·ha⁻¹)	
Deep	Shallow	Deep	Shallow
0.0	0.0	0.0	0.0
3.6	0.0	1.6	0.4
0.5	0.5	0.0	0.0
9.4	7.3	4.2	1.3
2.1	2.1	0.5	0.6
15.6	10.0	0.0	0.0
2.1	1.4	0.5	0.3
3.6	1.2	3.6	0.0
0.3	1.0	4.9	0.6
10.4	4.9	1.3	0.0

mated landscape depictions of percent cover and patch density using aerial photography to enrich our interpretation of the drivers (rainfall), abiotic constraints (soils), and their interactions governing processes across space and time. We combined a mechanistic perspective on soil-moisture dynamics and annual rainfall with long-term changes in vegetation at different spatial scales. From this perspective, we propose that available water holding capacity governed the response to disturbance, i.e., overgrazing and drought, that resulted in two contrasting endpoints (i.e., ecological states)—a shrubland and a shrub-invaded grassland, with distinct differences in ecological potential.

Hierarchical analysis of effects of soil properties on dynamic transitions

Our examination of long-term vegetation dynamics across three organizational levels revealed two distinct stages in the shift from a grass to a shrub-dominated system (Fig. 8). The long-term, multi-scale perspective

indicated that the dominant mechanisms and processes influencing shrub dynamics changed over time.

Early in the shrub proliferation process captured in this study, climate—specifically, precipitation—functioned as a broad-scale driver atop the topo–edaphic template with an extreme event (i.e., 1950s drought) marking a divergence in post-drought response of shrubs and grasses. Seed-bearing mesquite plants and livestock coexisted on the 1937 landscape and grass cover decreased precipitously in the early periods of the study. As shrubs established, biotic processes (i.e., competition for soil water and nutrients) likely played an increasingly important role in plant community dynamics. Similarly, abiotic (i.e., aeolian erosion, saltation [particle transport by wind or water], and deposition) processes also increased in importance as soil-stabilizing grass cover was lost.

The influence of soil properties on shrub patch dynamics was most effectively realized during periods of above- and below-average rainfall. Shrubs on the two soils (deep sandy soil and shallow sandy soil) exhibited significantly different responses to abiotic forcings during the 1950s drought. Shrub dieback and mortality were higher on deep sandy soils during the two driest periods in this study, i.e., 1947 to 1955 and 1960 to 1967. These results provide supporting evidence for the importance of soil properties in plant responses to severe drought demonstrated by Hamerlynck and McAuliffe (2008) in a Mojave desert ecosystem.

One explanation for the difference in shrub mortality can be attributed to greater sand movement by wind on the deep vs. the shallow sandy soil. Greater fluxes of saltating particles would result from the combination of early losses of grass cover, coincident increases in the distribution and connectivity of bare ground, and the

TABLE 5.   Correlations between metrics for shrub patch demographics on the two soil classes (deep sandy [S1] and shallow sandy [S2]) and frequency of wet or dry years using 1 November to 31 October rain year (Tables 3 and 4).

Fate-category group	Deep		Shallow		Deep		Shallow	
	r	P	r	P	r	P	r	P
All time periods (1937–2008)†								
Colonization	0.400	0.252	**0.705**	**0.023**	−0.599	0.067	−0.573	0.083
Patch growth	−0.562	0.091	−0.306	0.390	**0.671**	**0.034**	0.454	0.188
Coalescence	−0.390	0.266	−0.159	0.661	**0.770**	**0.009**	0.566	0.088
Disappearance	0.173	0.633	−0.480	0.160	0.199	0.582	0.333	0.347
Canopy dieback	−0.263	0.462	−0.260	0.468	0.360	0.306	0.406	0.244
Fragmentation	0.332	0.349	0.590	0.073	−0.134	0.713	−0.179	0.622
Post-colonization time periods (1960–2008)‡								
Colonization	−0.082	0.862	0.657	0.109	−0.074	0.875	−0.257	0.578
Patch growth	**−0.915**	**0.004**	−0.684	0.090	0.570	0.182	0.277	0.547
Coalescence	−0.675	0.096	−0.484	0.271	**0.806**	**0.029**	0.566	0.185
Disappearance	0.626	0.132	−0.285	0.536	−0.129	0.783	−0.040	0.932
Canopy dieback	−0.199	0.670	−0.011	0.982	0.409	0.362	0.305	0.507
Fragmentation	0.629	0.130	0.882	0.009	−0.310	0.499	−0.292	0.525

Notes: Shrub patch metrics were derived from the manual interpretation of 11 digitized aerial photographs from 1937 to 2008. Shrub patch appearance (i.e., colonization), growth, coalescence, disappearance, dieback, and fragmentation are defined in Table 2. Boldface entries denote statistically significant correlations ($P < 0.05$).

† Ten time periods; see Table 3 for the 10 specific time periods.
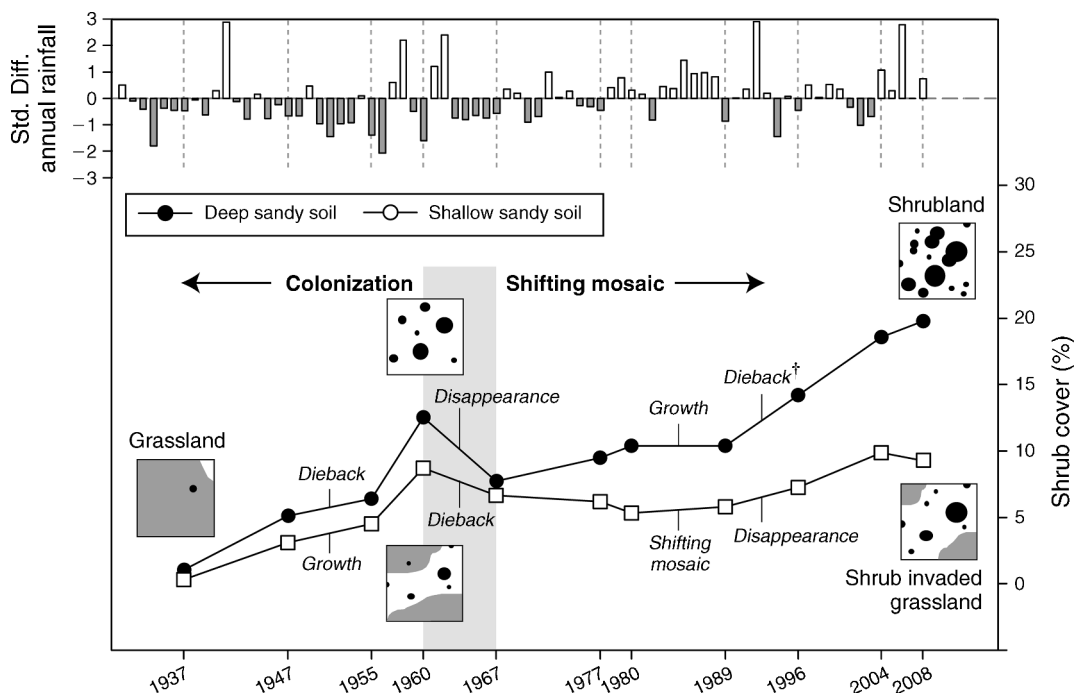
‡ Seven time periods.

FIG. 8. Conceptual synthesis of shrub patch-level dynamics and landscape depictions of shrub cover on two sandy soils over 71 years. Shrub patch demographics (italic text labels) demonstrate a high degree of dynamism during periods with no net change in cover (lines), highlighting the need for multi-scale observations. Shallow and deep sandy soils exhibited low shrub cover in 1937, with edaphic constraints governing two different endpoints. Shrub dynamics were characterized by colonization or appearance of new patches until 1960 (i.e., Colonization stage). Patch dynamics post-1960 represent a shifting mosaic whereby shrub patches at different stages of development co-occurred on shallow and deep sandy landscapes (i.e., Shifting-mosaic phase; see Fig. 7). Patch-based analysis of demographic patterns revealed significant differences ($\alpha = 0.05$) between patches on deep and shallow sandy soils in four time periods labeled with italic text to signify the dominant and distinguishing process on each soil (e.g., Growth; see Table 2 for patch fate descriptions). From 1989 to 1996 (Dieback†) more patches on the deep sandy soil exhibited dieback, although growth of existing patches also occurred (Fig. 7). Histograms provide the climate context for shrub dynamics as annual deviations from long-term average rainfall, calculated by subtracting the long-term (1930 to 2008) average and dividing by the standard deviation. Gray bars denote below-average annual rainfall while white denotes above-average annual rainfall. Patch demographic responses on soils with different water-holding capacities to the end of severe drought followed by the increased frequency of wet years (after 1960) manifest as different trajectories.

coarser surface texture of the deep sandy soil (Okin et al. 2006, Field et al. 2010). While mesquite has been shown to tolerate burial, it is reasonable that abrasion by saltating sands would adversely affect shrub growth and performance. Thus, we hypothesize that during extreme dry periods, shrubs on deep sandy soils sustained more damage from saltating sands than shrubs on the shallow sandy soils, which retained a critical level of grass cover over the same time period. Focused field assessments to document effects of saltation on the fate of shrubs in aridlands are needed.

Conversely, shrub patch growth on the deep sandy soils was strongly and positively correlated with periods of above-average rainfall, a perspective afforded with frequent aerial photo coverage. Patch growth correlated with above-average rainfall did not necessarily translate to an overall increase in shrub cover in all periods (e.g., 1980 to 1989). That periods of high shrub patch growth did not result in increases in shrub cover in all cases was

due to the roughly equal proportion of opposing demographic processes (i.e., shrub growth vs. dieback).

The shifting-mosaic phase of shrub proliferation is marked by the coexistence of shrub patches at different stages of development (Bormann and Likens 1979) and can be expanded to encompass comparable proportions of patch establishment and growth with patch dieback and mortality. Coincident demographic processes, such as patch establishment, growth, dieback, and mortality, fluctuate and can occur amid stability or directional changes in overall shrub cover. We integrated metrics for shrub patch demographics and shrub cover at the pasture scale to evaluate whether observed vegetation dynamics fit the shifting-mosaic model. The shrub fate metric is calculated as the ratio of colonization and growth to disappearance and dieback of shrub patches for a given time frame; values near 1 denote roughly equal proportions corresponding to a shifting mosaic. When placed in the context of net changes in landscape shrub cover, distinct colonization and shifting-mosaic
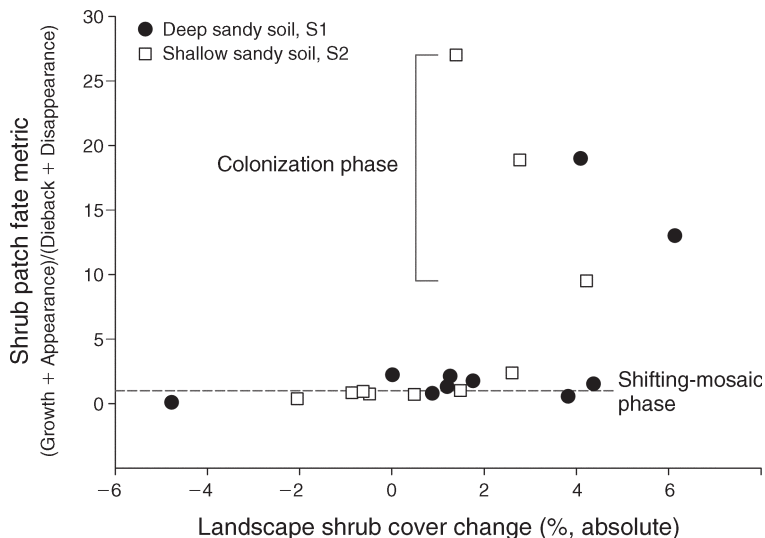
Fig. 9. Integrative view of colonization and shifting-mosaic phases of shrub proliferation over 71 years on deep (S1) and shallow (S2) sandy soils (see *Methods: Soils* for soil descriptions). The relationship between patch demographics (*y*-axis) and net changes in cover (*x*-axis) reveal the early periods marked by high colonization, and later stages wherein patches demonstrate roughly equal proportions of growth and dieback (dashed horizontal line). Vegetation dynamics were generated from time-series aerial photography over a 150-ha landscape in the northern Chihuahuan Desert (New Mexico, USA).

phases emerge (Fig. 9). Between 1960 and 1967 a transition occurred in that net changes in cover (decreases, increases, or stasis) were characterized by roughly equal proportions of patch growth and dieback. The transition to a shifting-mosaic phase of shrub proliferation in the mid-1960s following an early period characterized by shrub colonization has also been demonstrated at a Sonoran desert grassland site (Browning et al. 2008). In our present study the synchronized transition to the shifting-mosaic phase of shrub proliferation on both soils coincided with periods of above-average rainfall that followed the 1950s drought; however trajectories for shrub cover on deep and shallow sandy soils diverged. In the following section we explore the role of soil depth and mechanisms regarding available soil moisture in divergent patterns in shrub cover and patch dynamics.

Soil properties and water availability

Contrasting soil properties of the deep sandy and shallow sandy soils likely interacted with the rainfall patterns to yield differences in the timing and distribution of plant-available water. Soil depth and texture are important determinants of the distribution of moisture in the soil profile, thereby influencing divergent plant community dynamics. The prominent distinguishing properties of the dominant soils in this study most relevant to soil-water dynamics were the depth to petrocalcic horizon and the amount of subsurface (deeper than 5 cm) clay. Presence of a petrocalcic horizon and higher clay content in the top meter of the shallow soil impart a higher near-surface water-holding capacity for the shallow than for the deep sandy soil

(Duniway et al. 2007). Higher water-holding capacity of the shallow soil allows for a larger fraction of infiltrated rainwater to be retained closer to the soil surface (<1 m) than in the deep soil. Thus, the shallow soil is capable of retaining more water within the reach of shallow-rooted grasses and forbs whereas in the deep sandy soil, excess water would drain from this shallow rooting zone and be exclusively accessible to species with prominent deep-rooting systems, such as mesquite (Gibbens and Lenz 2001, Duniway et al. 2010).

Differences in soil depth and plant-available water-holding capacity are known to influence grass and shrub dynamics during periods of below-average rainfall (Herbel et al. 1972, Eggemeyer and Schwinning 2009). Grasses on the deep soil disappeared over the course of the 1950s drought (by 1960, see Fig. 5) while grass cover on the shallow soil persisted. Our findings at a finer temporal resolution corroborate observations by Herbel et al. (1972) on similar deep and shallow sandy soils who observed nearly total grass loss by 1954 on deep sandy soils and retention of some grasses on shallow sandy soils. In a different long-term assessment of the grass resilience to the 1950s drought, Yao et al. (2006) identified soil texture as the primary soil property related to the retention of grass cover. Although the loss of grass was substantial on both soils over this period (1950 to 1956), losses incurred on the shallow sandy soil were considerably lower. Reductions in grass cover due to the 1950s drought can be viewed as setting the stage for shrub establishment by creating available space and reducing competition for soil moisture. The strong positive correlation between shrub colonization
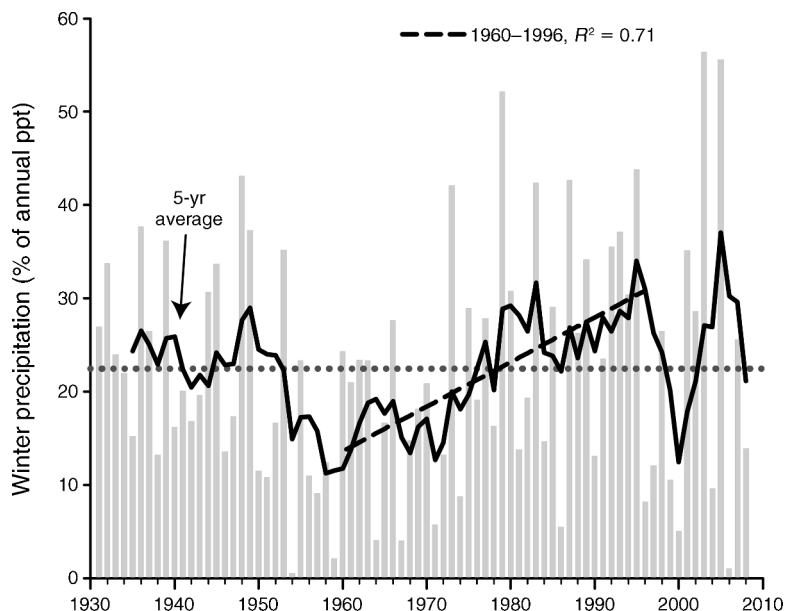
Fig. 10. Percentage of precipitation (ppt) for a rain year (1 November–31 October) that fell in winter months (1 November–28 February; gray bars). A five-year running average of winter contribution to annual precipitation is illustrated with a heavy black line, and the long-term average (1930–2008) winter contribution (22%) is shown as a dotted line. The fitted linear regression (dashed line) illustrates the strong linear trend from 1960 to 1996, spanning the shifting-mosaic stage of shrub proliferation.

on shallow sandy soils and the percentage of years with below-average precipitation supports this proposition.

Different patch-based growth responses to precipitation on the deep and shallow sandy soils can be attributed to the influence of soil properties on depth of wetting and competition by grasses. Mesquite patches on the deep soil had a more consistent, positive response to the frequency of wet years across both the entire study period (patch growth and coalescence) and post-colonization period (coalescence), suggesting soil-water dynamics resulted in more efficient utilization of precipitation by mesquite patches growing on the deep sandy soil. This difference in water-use efficiency by mesquite could be due to lack of a root-limiting layer on the deep sandy soil allowing mesquite to capitalize on available soil moisture at depths greater than 1 m and/or increased competition for near-surface soil water from grasses on the shallow sandy soil.

The majority of annual rainfall at this site (~62%) occurs between July and October. Conversely, we determined that on average, an additional 22% of annual rainfall occurs during the winter months of November through February. During the middle of the study period, from 1954 to 1972, the percentage of winter annual precipitation was far below average (running 5-yr average; Fig. 10) followed by a period of increased winter precipitation for the remainder of the study period. Specifically, the percentage of annual rainfall during the winter months exhibited a clear linear trend of increasing winter precipitation from 1960 to 1996 ($R^2 = 0.71$; Fig. 10). Interactions between soil properties, seasonal distribution of rainfall, and plant phenology govern the effective use of rainfall by plants, thereby influencing vegetation dynamics.

Seasonal distribution of precipitation is important not only from the perspective of plant phenology (i.e., timing), but also due to the intensity of rainfall events. Smaller rain events that occur during the hot spring and summer growing seasons tend not to penetrate deep into the soil profile due to high evapotranspirational demands (Wainwright 2006, Duniway et al. 2010). Additionally, summer precipitation occurs as intense, convective thunderstorms that generate substantial runoff—a problem likely more important on the gently sloping deep sandy soil than the flatter shallow sandy soil. In contrast, precipitation during the cool winter months in the form of lower intensity frontal systems (producing less runoff) occurs when most plants are senescent and evapotranspirational demands are low, allowing for deeper penetration of wetting fronts (Duniway et al. 2010). Coarser subsurface texture and lack of a petrocalcic horizon in the deep sandy soil would allow these winter wetting fronts to penetrate much deeper (>1 m). The combined increase in annual precipitation and contribution of winter precipitation that began ca. 1960 likely contributed to the strong correlation between patch growth on the deep sandy soil with the frequency of years that were not dry in the post-colonization phase (Table 5) and greater increases in shrub cover.

Implications for management.—Soils with sandy surface textures are common in water-limited ecosystems (see Fig. 2). Our results provide convincing evidence that ecological potential of sandy soils, encapsulating potential net primary production, plant community compo-

sition, and response to climate and management (e.g., Bestelmeyer et al. 2009), varies greatly with the subsurface soil properties governing water and root distribution. These differences in ecological potential seem to be most apparent in response to drought. While plants on all soil types would likely suffer deleterious effects of extreme drought, evidence suggests that sandy soils with higher subsurface water-holding capacity have a greater resilience to drought so that the threshold conditions that trigger an ecological state change (i.e., transition from a shrub-invaded grassland to a shrub-land state) would occur sooner on deep sandy soils. It follows that soils with low subsurface water-holding capacity would be more susceptible to the deleterious effects of drought and prompt preemptive consideration for management.

Observed differences in shrub demographics (at Level −1 [see Fig. 1 for description of level]) provided the initial conditions upon which soil properties (i.e., depth and subsurface texture) (Focal level) and rainfall (Level +1) mediated grass and shrub responses to disturbance, notably the 1950s drought. We propose the interaction between soil properties and precipitation prompted the divergence in shrub cover on the two soils with similar grazing histories that resulted in different ecological states: a shrubland supporting higher shrub cover on the deep sandy soils (Appendix A) and a shrub-invaded grassland on the shallow sandy soil (Appendix B).

Management implications of our long-term multi-scale assessment of shrub and grass dynamics suggest that efforts to remediate grasslands occurring on sandy soils should be focused on sites that have some near-surface water-holding capacity rather than sites charac-terized by deep coarse-textured soils that pose challenges to grass recovery and survival under conditions of highly variable and/or below-average precipitation.

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Supplemental Material

Appendix A

Photograph of a field sampling site selected to show mapped soil class S1 (*Ecological Archives* A022-050-A1).

Appendix B

Photograph of a field sampling site selected to show mapped soil class S2 (*Ecological Archives* A022-050-A2).