

## WOODY PLANTS IN GRASSLANDS: POST-ENCROACHMENT STAND DYNAMICS

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**Abstract.** Woody plant abundance is widely recognized to have increased in savannas and grasslands worldwide. The lack of information on the rates, dynamics, and extent of increases in shrub abundance is a major source of uncertainty in assessing how this vegetation change has influenced biogeochemical cycles. Projecting future consequences of woody cover change on ecosystem function will require knowledge of where shrub cover in present-day stands lies relative to the realizable maximum for a given soil type within a bioclimatic region. We used time-series aerial photography (1936, 1966, and 1996) and field studies to quantify cover and biomass of velvet mesquite (*Prosopis velutina* Woot.) following its proliferation in a semidesert grassland of Arizona. Mapping of individual shrubs indicated an encroachment phase characterized by high rates of bare patch colonization. Upon entering a stabilization phase, shrub cover increases associated with recruitment and canopy expansion were largely offset by contractions in canopy area of other shrub patches. Instances of shrub disappearance coincided with a period of below-average rainfall (1936–1966). Overall, shrub cover (mean  $\pm$  SE) on sandy uplands with few and widely scattered shrubs in 1902 was dynamically stable over the 1936–1996 period averaging  $\sim 35\% \pm 5\%$ . Shrub cover on clayey uplands in 1936 was  $17\% \pm 2\%$  but subsequently increased twofold to levels comparable to those on sandy uplands by 1966 ( $36\% \pm 7\%$ ). Cover on both soils then decreased slightly between 1966 and 1996 to  $28\% \pm 3\%$ . Thus, soil properties influenced the rate at which landscapes reached a dynamic equilibrium, but not the apparent endpoint. Although sandy and clayey landscapes appear to have stabilized at comparable levels of cover, shrub biomass was 1.4 times greater on clayey soils. Declines in shrub cover between 1966 and 1996 were accompanied by a shift to smaller patch sizes on both sandy and clayey landscapes. Dynamics observed during the stabilization phase suggest that density-dependent regulation may be in play. If woody cover has transitioned from directional increases to a dynamic equilibrium, biomass projections will require monitoring and modeling patch dynamics and stand structure rather than simply changes in total cover.

**Key words:** aerial photography; dynamic equilibrium; edaphic constraints; encroachment phase; *Prosopis velutina*; Santa Rita Experimental Range; shifting mosaic; shrub encroachment; stabilization phase; woody biomass.

### INTRODUCTION

Grasslands and savannas occupy  $\sim 40\%$  of the land surface (Bailey 1996) and contribute 30–35% of the terrestrial net primary productivity (Field et al. 1998). As such, they play an important role in global carbon, water, and nitrogen cycles. Changes in land cover and land use are predominant drivers of global change (Vitousek 1992, 1994, Pielke et al. 2002). One of the most striking land cover changes in grasslands and savannas over the past 150 years has been the proliferation of trees and shrubs at the expense of perennial grasses. Although this shift in plant life-form

composition has been widely reported (reviewed by Archer 1994 and Van Auken 2000), relatively little is known of the rates and dynamics of woody plant cover change and the consequences for ecosystem biogeochemistry. What is known is controversial and few robust generalizations have emerged (House et al. 2003, Wessman et al. 2004).

Woody plant encroachment has a potentially important, but poorly documented impact on the terrestrial carbon cycle (Houghton et al. 1999, Pacala et al. 2001, Houghton 2003a). Quantifying the magnitude of carbon sequestration accompanying changes in woody plant abundance in drylands is an important factor in landscape- and regional-scale assessments of above-ground carbon pools with strong links to soil organic carbon. Carbon uptake and biomass accumulation may be maximal in developing stands and plateau in mature stands (Hurt et al. 2002). Knowledge of stand age

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structure is thus critical for forecasting ecosystem carbon sequestration potential. Given that woody plant encroachment in grasslands and savannas has been ongoing since the mid to late 1800s (Archer et al. 1988, Archer 1995), it stands to reason that some, and perhaps many, landscapes may be at or approaching maximum levels of cover, density or basal area; and hence maximum stand-level biomass. Determining the extent to which ecosystems may be approaching aboveground carbon sink saturation has important implications for land management and carbon trading markets (e.g., Burrows et al. 2002). What is the maximum shrub cover/density/biomass that might occur within a given bioclimatic region? The answer likely depends on soils and topography.

Soil properties (i.e., texture, depth, and fertility) and topography interact to influence patterns of woody plant abundance and distribution (Johnson and Tothill 1985, McAuliffe 1994). Combined, these factors determine how surface water, a critical resource in drylands, is distributed and utilized (Noy-Meir 1973, Tongway et al. 2001, Wilcox et al. 2003). Soil texture regulates the infiltration and percolation of rainfall, resulting in differential access to subsurface water based on life-form rooting patterns (e.g., deeply rooted shrubs vs. shallow rooted grasses [Jackson et al. 1996]). Generally, coarse-textured soils are thought to favor shrubs and finer-textured soils to favor grasses (Walker 1987, Scholes and Archer 1997). Topography-mediated patterns of runoff/run on can override or reinforce texture constraints on woody plant distribution, such that woodlands can develop on fine-textured soils that might otherwise be expected to support grassland and open savanna (e.g., Wu and Archer 2005). Patterns of change in woody plant cover and carbon stocks observed using remotely sensed imagery have been related to soil types (Archer 1995, Hudak and Wessman 1998, Asner et al. 2003); and recent studies have illustrated how soil properties may influence grassland/shrubland ecotone dynamics (Bestelmeyer et al. 2006) and aboveground primary production subsequent to shrub encroachment (Hughes et al. 2006). However the influence of soil properties on woody plant stand structure, dynamics, and stand development are not well known. Within a bioclimatic region, contrasting topo-edaphic landscape elements would be expected to differ in their susceptibility to woody plant encroachment and in their woody plant "carrying capacity." Shrub encroachment within a bioclimatic region may also depend on the seasonality of annual rainfall, with summer rainfall favoring grasses and winter rainfall favoring shrubs (Scholes and Walker 1993, Scholes and Archer 1997). Along these lines, it has been suggested that years of relatively high winter rainfall in the late 1970s triggered large increases in shrub densities in the southwestern United States (Brown et al. 1997).

Shrubs in the genus *Prosopis* have proliferated over much of the southwestern United States and in arid and

semiarid regions of Africa (e.g., MacDonald 1989), India (Sharma and Dakshini 1991), South America (Cabral et al. 2003), and Australia (e.g., van Klinken and Campbell 2001). Changes in velvet mesquite (*Prosopis velutina* Woot.) cover in desert grasslands on the Santa Rita Experimental Range (SRER) in southeastern Arizona have been particularly well chronicled (e.g., Fig. 1; McClaran 2003). Small (<1 m tall) *P. velutina* plants were first observed in 1902 (Griffiths 1904), and Wooten (1916) qualitatively noted an increase in their stature and abundance by 1915. Glendening (1952), working on the SRER on plots established in 1932 and re-inventoried in 1948–1949, found that cover increased on areas with <30% canopy cover and decreased on areas with >30% canopy cover. Based on these observations, he proposed woody cover would stabilize at approximately 30%. How accurate is this prediction? How well does it hold up over larger spatial scales and contrasting soil types?

Our objective was to quantify landscape-scale changes in stand structure, cover, and patch dynamics of *P. velutina* on contrasting interfluvial (hereafter "uplands") soils in desert grasslands of southeastern Arizona. A time-series of aerial photography (1936, 1966, and 1996) was used to (1) quantify rates and dynamics of cover change on two distinct geomorphic surfaces; (2) relate patterns of woody cover change to rainfall seasonality and test the hypothesis that shrub cover increases will follow years of relatively high winter precipitation (e.g., Brown et al. 1997); (3) test the hypothesis that the rate and extent of *P. velutina* encroachment would be highest on coarse-textured soils and lowest on fine-textured soils; and (4) evaluate Glendening's (1952) prediction that *P. velutina* cover would stabilize at 30%. Furthermore, we sought to use allometric equations relating *P. velutina* canopy cover to biomass in conjunction with canopy cover estimates derived from aerial photographs to quantify changes in aboveground carbon mass accompanying woody plant encroachment. To assess the accuracy of using aerial photography to estimate shrub biomass on landscapes, we used field data to quantify how much woody plant biomass we might be missing; and how long it takes *P. velutina* plants to reach sizes discernable on aerial photography.

## METHODS

### *Study site*

The study was conducted on the 21 514-ha Santa Rita Experimental Range (SRER) 45 km south of Tucson, Arizona, USA (31°49'58" N, 110°52'24" W; Fig. 2) along the western edge of the semidesert grassland region of the Sonoran Desert (Brown 1994). Annual precipitation is bimodal with a pronounced peak in late summer (July–September monsoon) and a lesser peak in winter; mean annual precipitation is positively associated with elevation, ranging from 296 mm at lower elevations (866 m) to 498 mm at upper elevations (1372 m). Physiognomy ranges from *Larrea tridentata* desert scrub

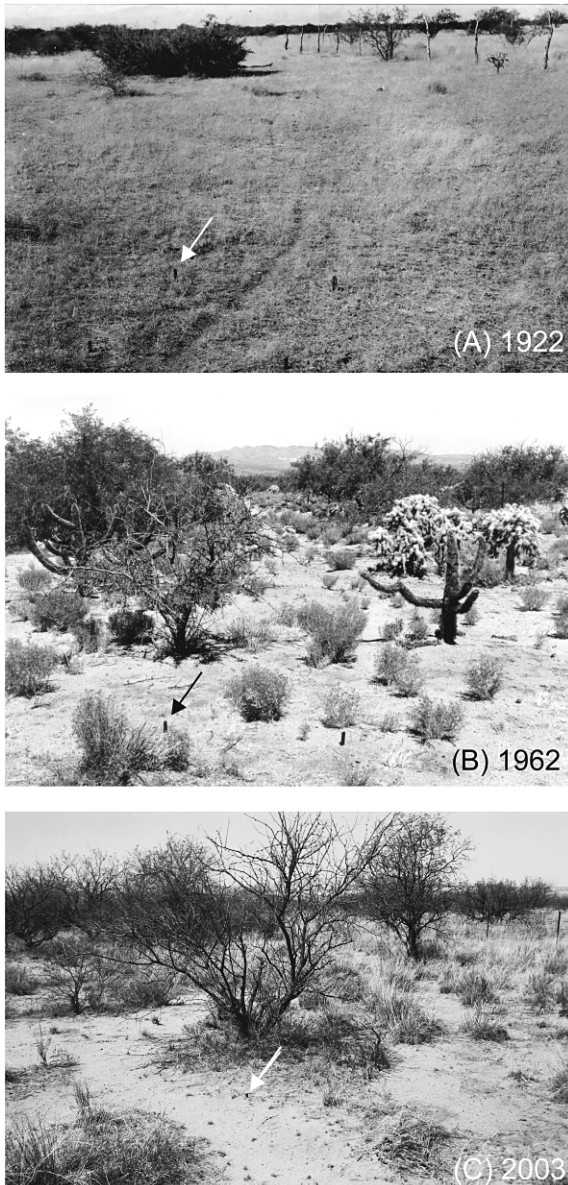


FIG. 1. Repeat ground photography (1922, 1962, and 2003) of vegetation change on a clayey soil site in a semidesert grassland in Arizona, USA (Photo Station 111, Santa Rita Experimental Range digital photo archive (<http://ag.arizona.edu/SRER/photos.html>)) at 1100 m elevation (400 m from our study site). Arrows denote fixed-location rebar. (A) Shrub cover was low in 1922; (B) by 1962, velvet mesquite (*Prosopis velutina* Woot.), cholla (*Opuntia* spp.), and burroweed (*Isocoma tenuisecta* Greene) abundance had increased markedly; and (C) mesquite abundance remained high through 2003, while cholla and burroweed abundance declined.

at the lowest elevations to *Quercus* spp. woodlands at the highest. *Prosopis velutina* is the dominant shrub at 990–1200 m elevation; other shrub species in this zone include *Celtis pallida* Torr., *Acacia greggii* Gray, and the subshrub *Isocoma tenuisecta* Greene (McClaren 2003) (*I.*

*tenuisecta* is not likely detected with image processing protocols employed).

To quantify the extent to which soils influence the rate and extent of shrub cover change and to minimize potential confounding effects of livestock grazing, fire, and precipitation, we confined our analyses to landscapes with similar land use history, topography, and elevation. Sites meeting these criteria were identified on replicated, nearly level landscapes in the *P. velutina* vegetation zone at ~1100 m elevation within Pasture 2S, a 557-ha management unit encompassing an area with no known history of fire or brush management. Changes in shrub cover were assessed using aerial photography from 1936, 1966, and 1996.

#### Precipitation, grazing, and upland soils

Mean annual precipitation (1922–2002; derived from four gauges between 1100 and 1200 m elevation and within 4 km radius of our study area) was 370 mm with an average summer (June–September) precipitation of 213 mm (CV = 0.3) and an average winter precipitation (October–May) of 158 mm (CV = 0.4) (McClaren 2003). In the 14 years prior to 1936, 43% of winters and 43% of summers experienced below-average rainfall (Fig.

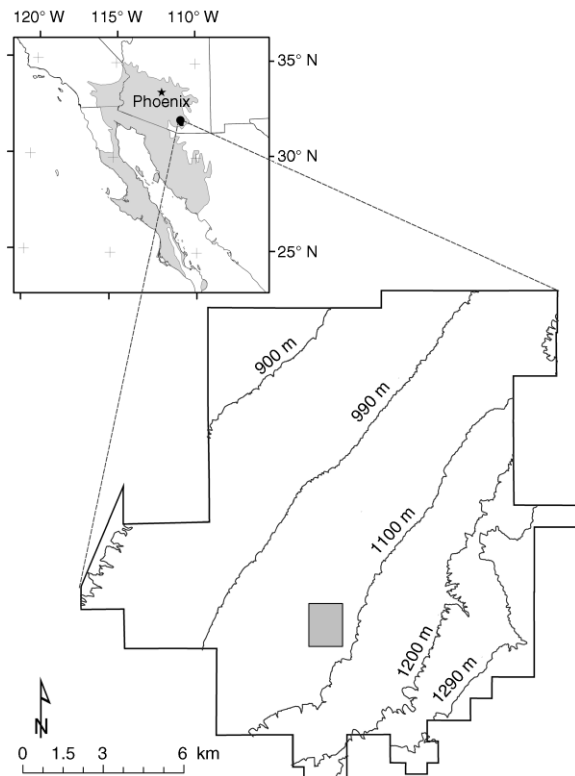


FIG. 2. Location of the Santa Rita Experimental Range (SRER) within the Sonoran Desert (depicted with gray in the inset map) spanning the southwest United States and northwest Mexico (after Brown et al. 1998). Elevation is represented with 90-m contour lines, and the extent of our study area is shown in gray.

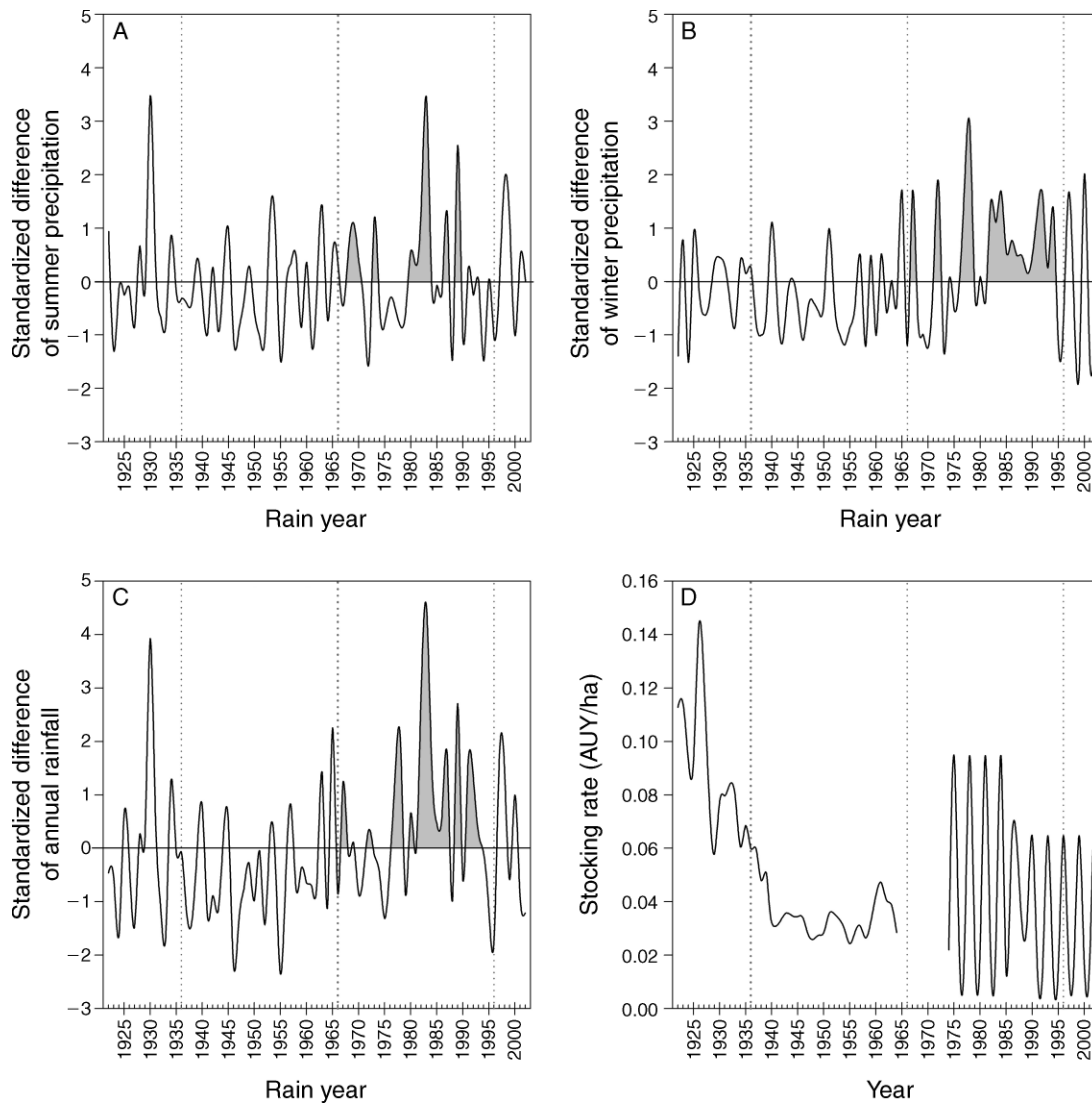


FIG. 3. Seasonal precipitation and cattle stocking rates on Pasture 2S of the Santa Rita Experimental Range from 1922 to 2003. Precipitation is represented as the standardized difference (seasonal average minus the long-term seasonal average divided by the standard deviation) for four rain gauges (Box, Eriopoda, Road, and Rodent) between 1100 and 1200 m elevation. Panels show (A) summer (June to September) precipitation; (B) winter (October to May) precipitation; (C) annual rainfall, which comprises winter and the following summer (October to September). (D) Cattle stocking rates are animal unit years (AUY) per hectare, where AUY is the number of cattle present over a calendar year. Data from 1965 to 1972 are not available; however, it is reasonable to assume that stocking rates were  $\sim 0.03$  AUY/ha prior to initiation of rotation experiment in 1972. Aerial photo dates are represented as vertical dotted lines. Periods of above-average rainfall from 1966 to 1996 are highlighted in gray.

3A, B). The period 1936 to 1966 was characterized by drier-than-average winters (70% of years), with 23% of years receiving below-average precipitation for the entire rain year (October–September) (Fig. 3C). In contrast, 1966–1996 was a relatively high rainfall period marked by extremely wet summers in 1984 and 1990; and few years of below-average annual rainfall (Fig. 3C). Winter rainfall from 1966 to 1996 was generally above average (57% of years), with the 13 consecutive winters preceding the 1996 image date exhibiting above-average winter rainfall.

Prior to establishment of the SRER in 1903, the area was subjected to heavy, year-long, unregulated cattle grazing. Shortly after establishment of the SRER, cattle were removed and reintroduced in 1916. Since that time, stocking rates and seasonal livestock use have varied (e.g., Pasture 2S; Fig. 3D). Year-long grazing was practiced from 1916 until 1972 with steadily decreasing stocking rates from a maximum of 0.174 animal unit years per ha in 1918. A rotational grazing system (Martin and Severson 1988) was implemented in 1972 and maintained through the 1996 image date.

Shrub cover was quantified on eight landscapes within a 200-ha portion of Pasture 2S. Soils on the SRER were mapped on the basis of age, texture, and depth as a third-order soil survey (Breckenfeld and Robinette 1997). Sampling was confined to areas classified as either the Holocene-age Combate-Diaspar complex or the late Pleistocene-age Sasabe-Baboquivari complex based on criteria described in Batchily et al. (2003); soil inclusions composed 10–15% of each soil complex (Breckenfeld and Robinette 1997). The Combate-Diaspar soils were Entisols (coarse-loamy, mixed, superactive, nonacid, thermic Ustic Torrifluvents). Soil profile development was minimal; the dominant subsurface texture for Combate soils was coarse sandy loam. Maximum clay content (mean  $\pm$  SE) was 16.8%  $\pm$  1.1% at a depth of 33  $\pm$  8.5 cm (mean  $\pm$  SE; from trenches characterized by Batchily et al. [2003]). The Sasabe-Baboquivari soils were Aridisols (fine, mixed, superactive, thermic Ustic Paleargids) with accumulations of clay at an average depth of 23.4  $\pm$  5.1 cm and an average maximum clay content of 24.9%  $\pm$  1.8% (Batchily et al. 2003). The dominant subsurface texture for Sasabe soils was sandy clay loam. For expediency, we will subsequently refer to these soil complexes by the contrasting subsurface textures: “sandy” for the Combate-Diaspar complex and “clayey” for the Sasabe-Baboquivari complex.

Arroyos and ephemeral drainages dissect the extensive alluvial fan terrace where the study was conducted, generating topo-edaphic heterogeneity. To standardize for this heterogeneity, we confined sampling to the nearly level uplands separating arroyos and drainages. Uplands were mapped within a geographic information system (GIS; ArcGIS v.9.0, Environmental Science Research Institute, Redlands, California, USA) by digitizing drainage channels on aerial photography and applying a 30-m buffer. Drainages and their buffer zones were excluded from cover change analysis. The resulting eight soil map polygons were buffered 70 m to minimize the likelihood of sampling in edaphic ecotones. Partitioning within the 200-ha area in this manner resulted in three “sandy” and five “clayey” landscapes that ranged from 1.0 to 7.2 ha in size.

#### *Aerial photography*

Aerial photo dates included February 1936 (scale 1:31 640, black/white), August 1966 (1:15 640, black/white), and June 1996 (1:40 000, color-infrared [CIR]). June 1996 photos were acquired as digital ortho-quarter quadrangles (DOQQ) from the U.S. Geological Survey. Film negatives for 1936 and 1966 imagery were scanned at 1200 dpi, geometrically corrected to the 1996 ortho-rectified base image with a root mean-square error of  $<1$  pixel (or 1 m), and resampled to a common spatial resolution (1 m) using ERDAS Imagine, Version 8.7 (Leica Geosystems, Atlanta, Georgia, USA). The sample unit in our analysis was a shrub patch, defined as a woody plant canopy that could represent an

individual plant or a cluster of plants with touching or overlapping canopies.

Automated image classification protocols were used to delineate shrub patches in geo-coded, ortho-rectified images. To remedy issues related to differences in photo scale, we resampled all images to a common spatial resolution (1 m). Shrub patches in the 1936 and 1966 images were delineated using a supervised classification applied to the panchromatic band and a texture layer (Asner et al. 2003). Red, green, and near-infrared image bands were used in the supervised classification of the 1996 CIR image. Texture served as a contrast index within a designated focal window passed across the image (Nellis and Briggs 1989, Anys et al. 1994). For this application, the texture layer distinguished dark shrub canopies from the surrounding bright soil or herbaceous vegetation. Texture was calculated as the variance within a  $3 \times 3$  pixel (0.6-m pixel size, 3.25 m<sup>2</sup>) window prior to resampling 1936 and 1966 images. Effort was made to maintain consistency with bands used to classify images, but incorporating the texture layer with the 1996 image bands overestimated the size of woody plant canopies. Therefore, we used the color and near-infrared bands, which outperformed other band combinations, to classify 1996 woody plant cover.

Supervised classification algorithms require derivation of signatures to represent all land cover classes contained in the image. Due to the differences in information content between panchromatic and CIR photography, we were able to extract grass cover, bare ground, and shrub canopy classes from the 1996 image while only reliably distinguishing shrub canopy from non-shrub classes in the 1936 and 1966 black and white photographs. Shadow can induce errors in vegetation cover estimates from panchromatic aerial photography (Whiteman and Brown 1998). We were unable to explicitly account for shadow effects with limited metadata for historic imagery. We recognize that shadow effects may have exaggerated perceived shrub patch canopy area; however, this potential error was minimized due to the flat terrain (circumventing topographic effects) and by using photo subsets from the center of the image (thus avoiding vignetting along edges). To alleviate the salt-and-pepper appearance of the output classified images, which commonly results from supervised classification algorithms applied on a pixel-by-pixel basis, a majority filter was applied to eliminate all patches comprising fewer than four pixels (Lillesand and Kiefer 2000). Therefore the smallest discernible shrub patch in the classified aerial photography was 4 m<sup>2</sup> in size.

Classification accuracies were assessed using a random sample of points stratified by image class. Random points on photographic images were assigned manually to the reference class “shrub” or “non-shrub” for 1936 and 1966 images ( $n = 100$  points) and “grass,” “shrub,” or “bare ground” for the 1996 image ( $n = 150$  points). Classification accuracies represent the level of agreement

between manual and automated image class assignments and are presented as error matrices along with Cohen's kappa ( $\hat{K}$ ) statistic, an estimate of accuracy that incorporates agreement that may occur by chance (Cohen 1960, Congalton and Green 1999). Values of kappa range from 0 to 1.0; values  $> 0.75$  indicate strong agreement beyond chance; values  $< 0.40$  reflect poor agreement.

To estimate the time required for woody plants to attain canopy sizes distinguishable on aerial photography, we made use of field canopy measurements made in 1932 and 1948 and stored in the SRER data archives (summarized in Glendening 1952). These data included canopy diameter measurements for all *P. velutina* trees in plots 200 m from our study site on clayey soils (see Plate 1). From this database, we extracted canopy dimensions for *P. velutina* plants present in 1948 but absent in 1932. Thus, the maximum age of selected trees would be 16 years. We plotted the size class distribution of these trees and used the 95th percentile as a break point to identify trees most likely to have established soon after the 1932 census. Canopy growth rates of these trees ( $\text{m}^2/\text{yr}$ ;  $n = 8$  trees) were estimated by dividing canopy area in 1948 by 16 years.

#### *Shrub cover*

Shrub percent cover on each landscape was determined by dividing the number of cells (i.e., pixels in classified photography) mapped as "shrub" by total number of cells in each landscape. Diagnostic procedures were applied to shrub cover data prior to analysis and studentized residuals ( $R$  student) were used to detect outliers. Repeated-measures analysis of variance (ANOVA) was used to assess whether changes in shrub cover on the sandy and clayey soils differed from each other 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, Cary, North Carolina, USA). Mauchly's criterion for sphericity was not violated; therefore univariate results for repeated-measures ANOVA are reported.

#### *Patch dynamics, structure, and biomass*

Shrub patch dynamics were analyzed with a two-tier approach utilizing patch size distributions generated from the automated classification in conjunction with manually delineated shrub patches randomly selected within each landscape. Shrub patch size derived from aerial photos was determined using cell (i.e., pixel) counts to represent patch area. Individual patches were defined by cell adjacency using an eight-neighbor rule. Statistical differences in patch size distributions by date and by soil type were assessed using Kolmogorov-Smirnoff two-sample tests (Daniel 1978). The test we report is  $KS_a$ , the asymptotic Komogorov-Smirnoff statistic, which reflects an adjustment for sample size ( $KS_a = KS \times n^{0.5}$ ). Patches intersecting predefined study

site boundaries were withheld from computations of size distributions.

To capture finer-scale patch dynamics (e.g., fragmentation of large patches, appearance of new patches, and coalescence of neighboring patches), we monitored a subset of individual shrub and non-shrub patches through time. In each landscape, we randomly selected 5–14 shrub patches spanning the range of sizes present on the 1936 aerial photography (to minimize potential bias, the number of patches selected was weighted by landscape area). Canopies of selected shrub patches were hand-digitized and changes in individual patch area were categorized as (1) no change (change in patch area  $< 15\%$ ), (2) growth by canopy expansion, (3) growth by coalescence with neighboring patches, (4) loss by canopy dieback (decrease in area without fragmentation into separate patches), (5) loss by fragmentation (decrease in area accompanied by creation of multiple small patches from a single larger patch), or (6) patch disappearance.

We also identified 11 to 17 circular 50- $\text{m}^2$  patches not occupied by shrubs (hereafter "non-shrub patches") on each landscape on the 1936 photo to monitor shrub recruitment and development in the 1966 and 1996 imagery. When shrubs subsequently occupied non-shrub patches, the occurrence was categorized as (1) establishment, (2) encroachment by a neighboring shrub patch, or (3) both. The probability of non-shrub patches being colonized by shrub patches was calculated and  $\chi^2$  analysis was used to test whether shrub colonization rates were affected by date or soil type.

Patch structure on contrasting soils was evaluated by measuring canopy dimensions of all shrub patches in 30  $\times$  30 m field plots ( $n = 5$  plots on sandy soils;  $n = 3$  plots on clayey soils) in 2004. Based on a preliminary study, patch canopy area was computed as a circle whose diameter was the average of the longest axis and its perpendicular bisector. On aerial photos, plants with contiguous or overlapping canopies appear as a single patch; thus, we also measured all shrubs whose canopies touched or overlapped as a single patch and recorded the number of individuals comprising the patch. Natural breaks in the size-class distributions were used to delineate patch size classes. We tested for differences in patch size, patch density, and number of individuals per patch between soils using ANOVA.

Total aboveground *P. velutina* biomass was nondestructively estimated using a regression equation developed for plants at our site:  $\ln TB = 1.6 \times \ln CA - 0.58$  ( $R^2 = 0.97$ ,  $F_{1,29} = 807.5$ ,  $df = 30$ ; S. Archer, unpublished data), where TB is total biomass (dry leaves + wood [kg]) and CA is field-measured canopy area ( $\text{m}^2$ ). *P. velutina* biomass density was then estimated from measurements of the canopies of all plants (or patches, in cases where plant canopies intersected) in eight 30  $\times$  30 m plots. These field-based biomass assessments were then used to quantify biomass missed with remotely sensed data and determine the relative contribution of various patch size classes to whole-plot aboveground woody biomass.

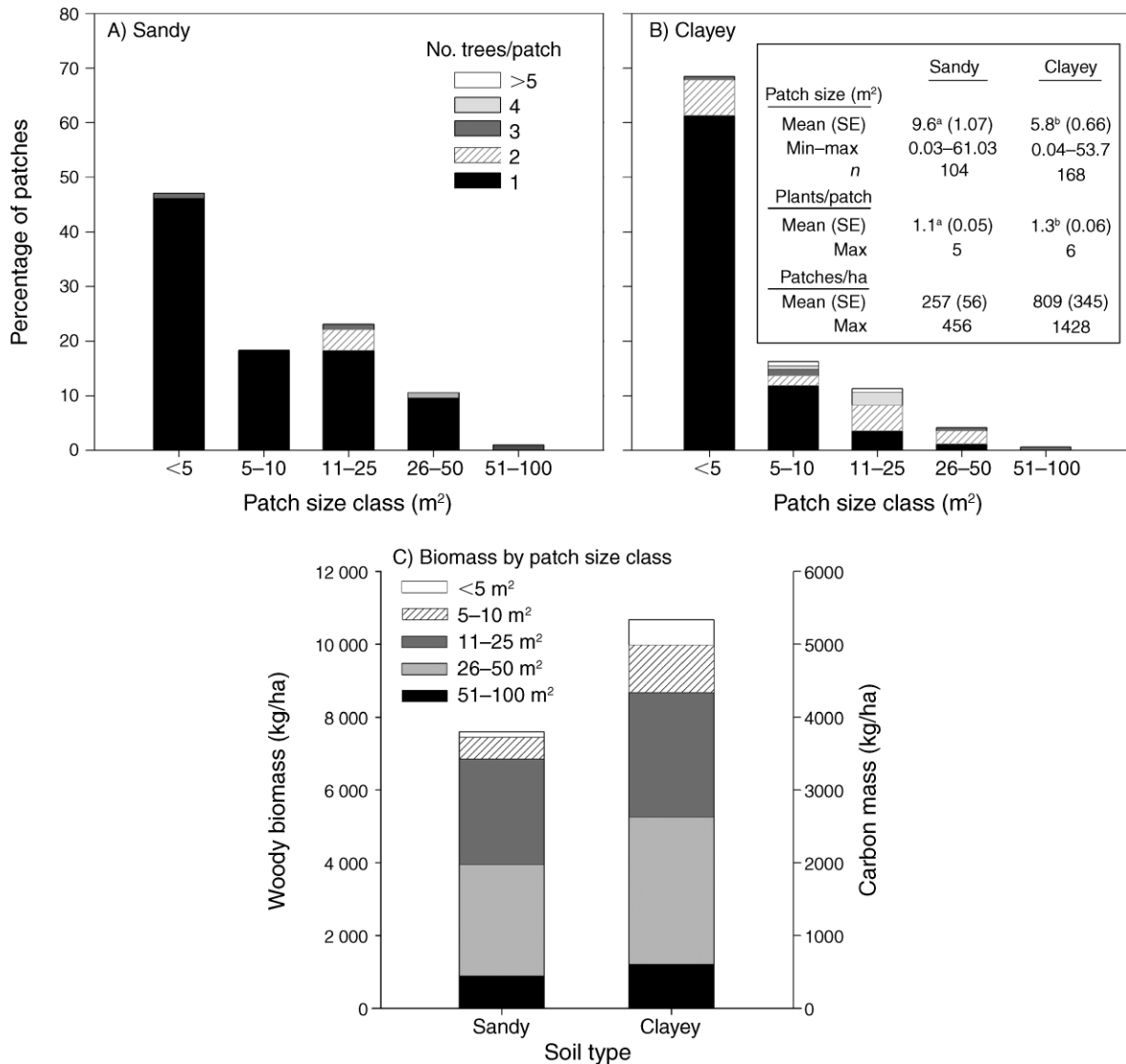


FIG. 4. *Prosopis velutina* Woot. (velvet mesquite) stand structure and aboveground woody biomass/carbon mass within eight 30 × 30 m plots on the Santa Rita Experimental Range (SRER) in southeastern Arizona. (A) Percentage of patches with various numbers of plants/patch on sandy ( $n = 104$  patches,  $n = 5$  plots) and (B) clayey ( $n = 168$  patches,  $n = 3$  plots) soils. All patches >51 m<sup>2</sup> had three or more trees per patch. The inset in (B) includes summary statistics for patch metrics; different superscript letters denote significant differences between groups ( $\alpha = 0.05$ ) based on Tukey's studentized range test. (C) Contribution of mesquite patches (by size class) to total aboveground woody plant and carbon mass in plots on sandy ( $n = 5$  plots) and clayey ( $n = 3$  plots) soils. Conversion to carbon mass was performed using the weighted average of carbon content in branches, twigs, leaves, and dead mesquite components.

Carbon mass was estimated by multiplying *P. velutina* biomass by 0.47 (a site-specific conversion that takes into account the relative contribution of leaf, twig, branch and trunk tissues to total aboveground mass; S. Archer, unpublished data).

## RESULTS

### Field assessments

Shrub cover in field plots was 99% *P. velutina*. Field measurements in 2004 revealed differences in the number of plants/patch ( $F_{1,270} = 6.04$ ,  $P = 0.015$ ), patch

size ( $F = 10.62$ ,  $df = 1$ ,  $P = 0.001$ ), and patch size-class distributions ( $KS_a = 1.654$ ,  $P = 0.008$ ) on sandy and clayey surfaces (Fig. 4A, B). *P. velutina* patches on sandy sites were less numerous, but larger than those on clayey sites with fewer plants/patch; and patch sizes were more strongly skewed toward smaller classes on clayey soils compared to sandy soils. On sandy soils, 45% of patches were below the detection limit on aerial photos (<4 m<sup>2</sup>), compared to 64% on clayey soils. Patches <5 m<sup>2</sup> canopy area constituted 1.9% and 6.5% of the aboveground *P. velutina* biomass/carbon mass on sandy

TABLE 1. Error matrix based on a random sample of points stratified by image class for 1936 ( $n = 100$  points), 1966 ( $n = 100$ ), and 1996 ( $n = 150$ ) classified aerial photographs.

Classified data by photo year	Reference data				Accuracies (%)		
	Shrub canopy	Non-shrub	Grass cover	Bare ground	Producer's	User's	Overall
1936							
Shrub canopy	34	5			87.2	85.0	
Non-shrub	5	55			90.2	91.7	
Reference total	39	61					89.0
1966							
Shrub canopy	32	6			84.2	80.0	
Non-shrub	8	54			87.1	90.0	
Reference total	40	60					86.0
1996							
Shrub canopy	47				94.0	100.0	
Grass cover	3		53	7	100.0	84.1	
Bare ground				40	85.1	100.0	
Reference total	50		53	47			93.3

Note: User's accuracy represents the probability that a pixel classified on the map actually represents that category on the ground, while producer's accuracy represents the probability of a reference pixel (known) being correctly classified.

and clayey sites, respectively (Fig. 4C). Carbon mass associated with *P. velutina* in plots on clayey sites was 1.4 times greater than that on sandy sites (Fig. 4C). The largest contribution to overall carbon mass on both soils was from patches in intermediate size classes (11–25 m<sup>2</sup> and 26–50 m<sup>2</sup>).

Empirical evidence for rates of *P. velutina* canopy growth was generated from 1932 and 1948 field measurements. Canopy size (mean  $\pm$  SE) of the eight largest plants measured in 1948 and deemed to have established circa 1932 was  $3.95 \pm 0.22$  m<sup>2</sup> (range = 3.18–4.67 m<sup>2</sup>), representing an average 16-yr growth rate of  $0.25 \pm 0.01$  m<sup>2</sup>/yr (range = 0.20–0.29 m<sup>2</sup>/yr).

#### Image classification accuracy

Automated image classifications yielded satisfactory measures of shrub canopy cover as determined by Cohen's kappa statistics (0.75, 0.68, and 1.00 for 1936, 1966, and 1996 images, respectively) and image classification accuracies derived from the error matrices (Table 1). Image quality was consistent across the study site within each image. Small differences in the ability to distinguish shrubs from the surrounding bare ground or grassy matrix between image dates were evident from the kappa statistics. Shrub canopy boundaries were somewhat less distinct in the 1966 image when resampled to common spatial resolution (1 m). Producer's accuracies for the shrub canopy class representing the probability of correctly classifying canopies from surrounding bare ground or grass were high (>84%) for all image dates.

#### Changes in shrub cover and patch size distributions

An inherent limitation of aerial photography is the inability to confidently distinguish individuals. The high degree of shrub aggregation on our study sites necessitated delineation of patches rather than individuals and hence precluded the use of individual plant-based

algorithms for estimating biomass. Automated image classification, which allowed broad spatial coverage, was not able to reliably distinguish between single- and multi-plant patches or to determine the number and size of individual canopies in multi-plant patches on the aerial photos available to us (Fig. 5). Thus, we could not use the imagery to quantify the size-class distributions of individual *P. velutina* plants. Furthermore, because our cover-biomass algorithms were based on individual plant measurements, we could not use them to estimate *P. velutina* aboveground biomass from aerial photos.

Mean (CV) shrub cover on 1936 aerial photos was 37% (0.2%) on sandy soils and 22% (0.6%) on clayey soils. One clayey landscape was an extreme statistical outlier ( $R$  Student = 3.93). Shrub cover on this precocious clayey landscape was exceptionally high in 1936 (44%) in comparison to all other landscapes on clayey soils (<20%). Removal of the outlier clayey landscape from the repeated-measures ANOVA revealed a strong soil type  $\times$  date interaction ( $F_{2,10} = 5.22$ ,  $P = 0.020$ ) that was otherwise masked ( $F_{2,12} = 9.62$ ,  $df = 2$ ,  $P = 0.003$ ; Fig. 6). Field surveys and a review of SRER records failed to reveal any differences in spatial context, land use, disturbance history, soils, or topography that might have caused this site to have such high shrub cover in 1936. Summaries that follow exclude the discordant clayey landscape.

Patch density on the two soil types was comparable on the 1936 aerial photos (Fig. 6B), but mean shrub cover was considerably higher on sandy soils (37%) than clayey soils (17%) (Fig. 6A). This cover-density dichotomy was the result of larger shrub patches on the sandy surfaces (Table 2). By 1966, cover was comparable on sandy and clayey landscapes (34% and 36%, respectively), owing to slight declines on sandy soils and a twofold increase on clayey soils. Shrub cover on both sandy and clayey surfaces then decreased between 1966 and 1996 (to 27% and 28%, respectively).



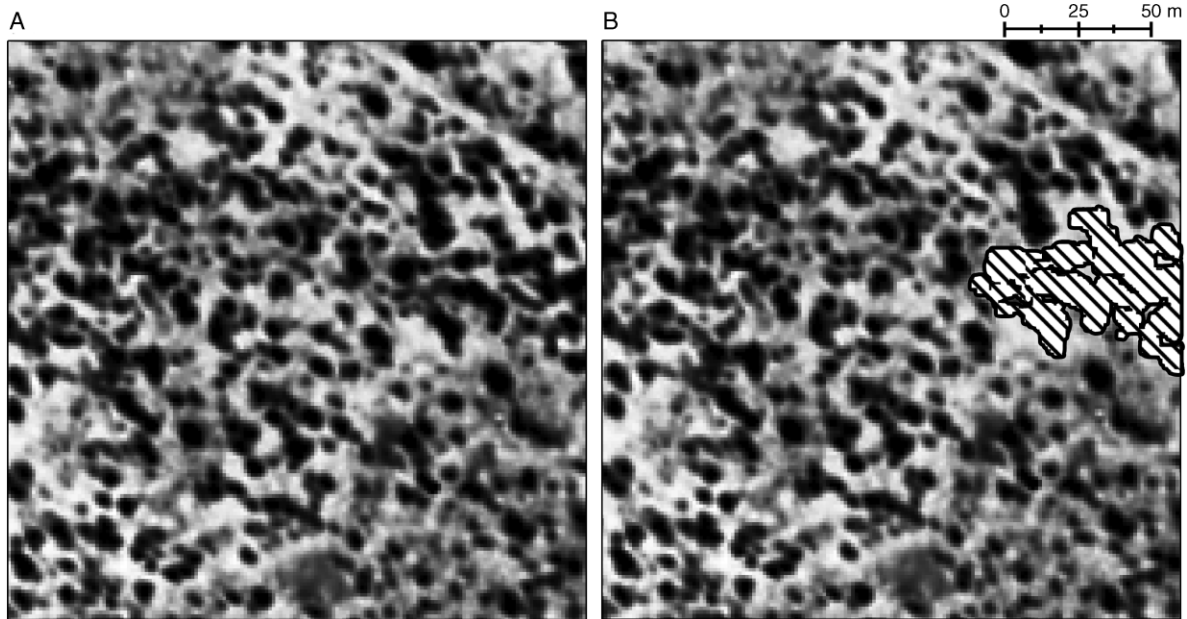


FIG. 5. Aerial photograph acquired February 1936 covering a 4.4-ha region of our study site on SRER in southeastern Arizona, highlighting shrub patch structure depicted in remotely sensed imagery. Panel (A) includes numerous *P. velutina* shrubs of various sizes; however, the algorithm in the automated supervised classification depicted multiple shrubs as a single large (2074-m<sup>2</sup>) entity (panel B, highlighted in cross-hatching). The inability to reliably distinguish canopies of individual plants precluded us from using time-series aerial photos to quantify changes in *P. velutina* size class distributions and biomass.

The 113% increase in shrub cover on clayey landscapes between 1936 and 1966 was accompanied by an increase in patch density (from 38 to 48 patches/ha; Fig. 6B). In contrast, cover remained stable on sandy surfaces at 35%, while patch density decreased from 39 to 33 patches/ha. Patch size distributions on the two soil surfaces in 1936 ( $KS_a = 2.937$ ,  $P < 0.0001$ ) and 1966 ( $KS_a = 2.465$ ,  $P < 0.0001$ ) were significantly different. Sandy landscapes were characterized by fewer, but larger patches than clayey landscapes (Fig. 6B, Table 2). Increases in patch density between 1966 and 1996 (from 33 to 53 and from 48 to 69 patches/ha for sandy and clayey sites, respectively) were accompanied by decreases in cover (Fig. 6A, B). By 1996, patch size distributions were similar on both soils ( $KS_a = 1.329$ ,  $P = 0.059$ ). Temporal comparisons of patch size distributions revealed a statistically significant shift to a greater proportion of small patches between 1966 and 1996 on both soils (sandy  $KS_a = 2.686$ ,  $P < 0.0001$ ; clayey  $KS_a = 1.804$ ,  $P = 0.0030$ ) with a twofold increase in the number of patches in the smallest size classes on both soils (see Plate 1).

#### Patch dynamics

Half (50%) of the individual shrub patches tracked on sandy soils ( $n = 28$  patches) declined in canopy area between 1936 and 1966, whereas 71% of the shrub patches on clayey soils ( $n = 35$  patches) maintained or increased their canopy area (Fig. 7A). From 1966 to 1996, a period of landscape-scale declines in total shrub

cover (Fig. 6A), the majority of individual shrub patches on both soil types (72% and 68%) declined in area (Fig. 7B). Four shrub patches disappeared between 1936 and 1966 (three on sandy and one on clayey soils); no losses were observed in the 1966 to 1996 period.

The proportion of 50-m<sup>2</sup> shrub-free patches in 1936 that contained shrubs in 1966 was significantly higher on clayey surfaces than sandy surfaces (55% vs. 23%;  $\chi^2 = 11.1$ ,  $df = 1$ ,  $P = 0.001$ ) (Fig. 8A). Cumulative counts in 1996 revealed that clayey surfaces maintained a significantly higher proportion of colonized patches ( $\chi^2 = 4.4$ ,  $df = 1$ ,  $P = 0.035$ ). On sandy sites, recruitment of shrubs into shrub-free areas was similar in both 1936–1966 (23% of shrub-free patches) and 1966–1996 (24% of shrub-free patches). In contrast, recruitment on clayey sites decreased dramatically from 54% of shrub-free patches between 1936 and 1966 to 20% between 1966 and 1996. When woody plant colonization was evaluated by period and soil type (i.e., new recruits in each time period), there was no statistically significant difference on the two soils from 1966 to 1996 ( $\chi^2 = 0.002$ ,  $df = 1$ ,  $P = 0.967$ ) (Fig. 8B). Shrub occupation of previously non-shrub patches was primarily via recruitment rather than expansion of nearby shrub canopies.

#### DISCUSSION

Woody plant abundance has increased in savannas and grasslands worldwide with potentially important (Pacala et al. 2001, Houghton 2003b), but as yet poorly quantified implications for the carbon, nitrogen, and

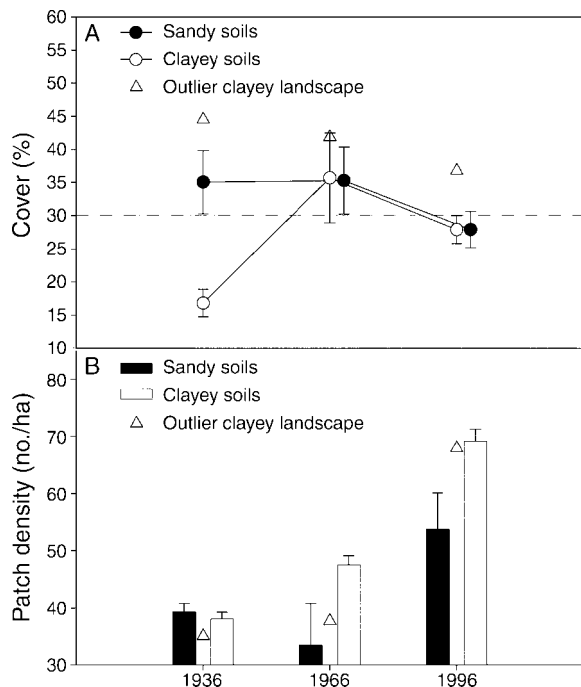


FIG. 6. Changes in (A) percent cover and (B) patch density for velvet mesquite patches on three sandy and four clayey soil landscapes at ~1100 m elevation on the SRER in southeastern Arizona; data are means with SE. One clayey landscape was a statistical outlier (see *Results* for details) and is displayed separately in both panels (open triangles). Test statistics do not include the outlier. The dotted line in (A) denotes the maximum mesquite canopy cover proposed by Glendening (1952). Alignment of the x-axis for sandy soils in 1966 and 1996 data points were offset slightly in panel (A) to display standard errors more clearly.

water cycles (Archer et al. 2001, Huxman et al. 2005). Changes in fractional woody plant cover correspond to changes in aboveground carbon (C) pools; changes in aboveground C pools are often accompanied by lagged changes in belowground C pools (Hibbard et al. 2003). Although woody cover appears to have peaked and stabilized on the desert grassland site in this study (see also McClaran and Angell 2006), soil organic carbon accumulation rates are still on a positive trajectory (Wheeler et al. 2007). Forecasting future changes in above- and belowground C pools will require resolution of uncertainties involving interactions among climate, soils, atmospheric CO<sub>2</sub> enrichment and disturbance. This study capitalized on the long-term, large-scale synoptic perspectives provided with historical aerial photography to quantify changes in woody plant cover over 60 years, while minimizing the potentially confounding effects of climate, topography, land use (livestock grazing and fire history), elevation, and shrub species.

*Aerial photography and woody plant biomass*

Remote sensing operations afford comprehensive and repeatable assessments of land cover change at broad

TABLE 2. Descriptive attributes for shrub patch size distributions from 1936, 1966, and 1996 derived from automated classification of woody plant cover on aerial photography for sandy and clayey soil surfaces.

Patch attributes	Soil type					
	Sandy			Clayey		
	1936	1966	1996	1936	1966	1996
Mean size (m <sup>2</sup> )	80.2	70.9	39.7	48.5	52.2	33.5
n (no. patches)	435	423	656	723	851	1327
CV†	1.9	1.6	1.4	2.3	2.4	1.4
Median†	37	33	17	23	20	18
Skewness†	5.5	4.2	3.6	10.5	12.3	3.9

† These statistics represent attributes of patch size distributions.

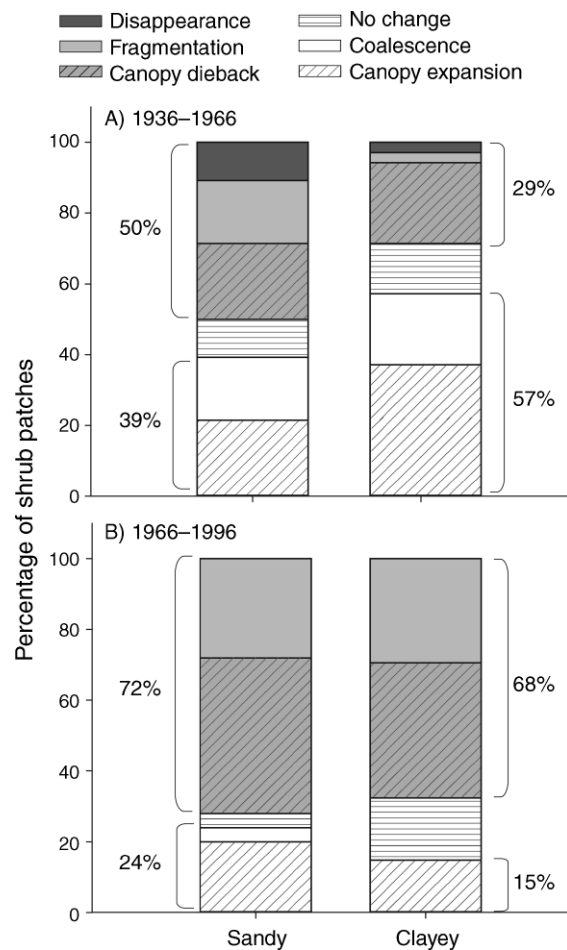


FIG. 7. Fate of individual mesquite canopy patches tracked on sandy (coarse sandy loam; n = 28 patches) and clayey (sandy clay loam; n = 35 patches) soils from (A) 1936 to 1966 and (B) 1966 to 1996. Patches were hand-digitized on aerial photography and classified as exhibiting (1) no change in size, (2) decrease in size via fragmentation or canopy dieback, (3) increase in size via coalescence or canopy expansion, or (4) disappearance.

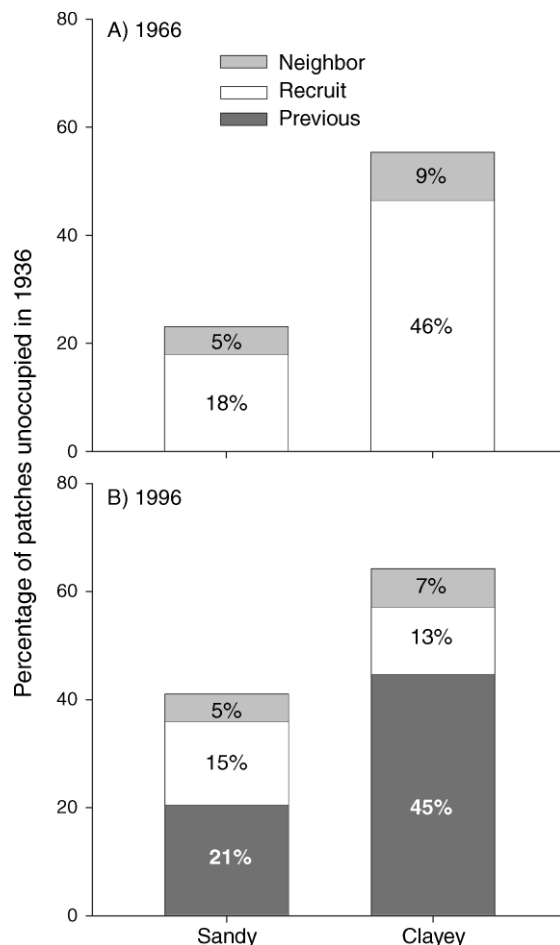


FIG. 8. Percentage of 50-m<sup>2</sup> patches not occupied by woody patches in 1936 that were later colonized in either (A) 1966 or (B) 1996 on sandy ( $n = 39$  patches) and clayey ( $n = 56$  patches) soils. Occupied patches were scored by whether developing woody patch cover resulted from the appearance of new individuals (“recruits”) or expansion of existing canopies (“neighbor”) in the vicinity of the 50-m<sup>2</sup> target area. Panel (B) represents cumulative occupation; the percentages of patches occupied in 1966 that remained occupied are denoted as “previous.”

spatial scales and yield a suite of tools for mapping and monitoring changes in vegetation cover (Asner et al. 2003, Okin and Roberts 2004, Okin 2007). As such, remote sensing plays an increasingly prominent role in estimating terrestrial plant biomass (reviewed by Lu 2006). Quantifying land cover classification accuracy and uncertainty associated with estimates of plant biomass is paramount (Foody 2002). One important, yet outstanding challenge associated with estimating biomass from remotely sensed imagery is to appropriately link field data to remotely sensed estimates of aboveground biomass (Lu 2006). Aerial photography provides opportunities to quantify woody patch dynamics and stand structure as a link to coarse resolution satellite imagery for improving accuracy of terrestrial

biomass and carbon storage estimates. However, in our case, the inability to distinguish individual shrub canopies on aerial photos was a major limitation for quantifying plant population structure and biomass. We undertook this study intending to estimate shrub aboveground carbon mass at landscape scales using plant canopy-area–biomass relationships developed in field studies. Unfortunately, the occurrence of multiple-plant shrub patches, aerial photo detection limits, and use of automated classification algorithms prevented delineation of individual shrub canopies. In this system, *P. velutina* biomass increases exponentially with canopy area (data not shown). Applying the nonlinear canopy area–biomass relationships derived for individual plants may therefore substantially overestimate biomass in cases where conglomerates of individual shrubs were treated as a single plant with a large canopy area. Indeed, many of the classified patches had canopy areas far beyond those of the largest *P. velutina* plants on the landscape (Table 3), and hence well beyond the range of data used to construct canopy area–biomass regressions. Manual classification may alleviate these problems with enhanced perception of individual plant canopies. However, there would be important trade-offs: observer-to-observer subjectivity, bias, and criteria for defining “a shrub” (e.g., Fensham and Fairfax 2007); and manual classifications could not be feasibly applied over large areas. In lieu of higher quality, higher resolution photographic imagery, one could develop canopy area–biomass algorithms at the scale of the patches that can be readily distinguished on the aerial photography.

Overestimates of aboveground biomass would be partially offset by failing to account for shrubs whose canopy areas are below detection limits on aerial photography. For the scale/quality of aerial photos available for this Sonoran Desert mesquite shrubland, we estimated that 6% of the shrub aboveground biomass on the landscape was associated with patches smaller than the minimum mapping unit (4 m<sup>2</sup>). The extent of underestimation would increase with increases in pixel size (i.e., spatial resolution) and with declines in image quality (Table 4). Although small shrubs comprised a relatively small fraction of the aboveground woody biomass, they represent a dynamic portion of the plant population with high growth potential and, presumably, the highest sensitivity to environmental stresses such as

TABLE 3. Maximum patch size and biomass for woody plant cover derived from 1936, 1966, and 1996 aerial photography using a supervised classification algorithm.

Image year	Maximum patch size (m <sup>2</sup> )	Biomass (kg)
1936	2074	109 648
1966	2636	160 769
1996	530	12 426

Notes: Patches less than four pixels (4 m<sup>2</sup>) in size were dissolved. Aboveground biomass was derived using an allometric relationship relating canopy area to biomass.

drought and fire. As such, detection limits of aerial photography constrain its utility in large-scale monitoring of woody plant population dynamics and in providing growth and age structure parameters for biogeochemical models.

#### *Seasonal precipitation and woody cover change*

Shifts from summer to winter rainfall have been widely hypothesized as a mechanism driving woody plant increases in drylands (Hastings and Turner 1965, Archer 1994). Brown et al. (1997) used time-series aerial photography to document changes in woody plant density in Chihuahuan Desert communities and argued that the threefold increases observed since the 1970s were the result of increased winter rainfall. Winter precipitation at our SRER site was also above average for the 1970s and 1980s, and we too observed a twofold increase in the number small (4–5 m<sup>2</sup>) patches on both soils over this time frame (inset histograms, Fig. 9). Interestingly, this increase in patch density corresponded to a net decline in total woody cover. Field surveys in 2004 also revealed the existence of numerous small (<1 m<sup>2</sup> canopy area) shrubs on both soils indicative of relatively recent recruitment of new plants. Based on our crude growth-rate estimates, such plants would have established in the late 1980s to early 1990s, an additional period of elevated winter precipitation.

Although there appears to be a loose correlation between increases in woody plant abundance on aerial photos and periods of increased winter precipitation, a cause–effect assertion is perhaps too simplistic for several reasons. First, when using time-series photography to relate approximate establishment dates to climatic factors, the time lag between when a plant actually establishes and when it reaches a size that can be detected on a photo must be taken into account: approximately 16 years, in our case. Thus, a 4-m<sup>2</sup> shrub on the 1996 image may have established in about 1980. Hence the climatic conditions in and around this time would be most germane for plants of this size. It should be noted that this growth estimate is very crude and reflects canopy expansion over a relatively dry period on landscapes with low initial shrub cover. For larger (older) plants, estimates of recruitment dates are much more elusive; and would be subject to many more caveats. Second, little is known about factors regulating recruitment of dryland shrubs. Episodic recruitment in response to specific climatic triggering events has been widely reported (e.g., Watson et al. 1997); and “snapshots” widely spaced in time are not likely to capture these. Thus there is the real risk of spurious correlations when relating decadal patterns of change to patterns of annual and seasonal climate. Third, the increase in patch densities observed in our study also coincided with above-average summer rainfall and hence above-average annual rainfall. It could well be that the combination of elevated summer and winter rainfall was key to promoting recruitment. Fourth, although recruitment

TABLE 4. Percentage of aboveground woody biomass that would not be captured with aerial photography using different size thresholds.

Detection limit (m <sup>2</sup> )	Biomass missed (%)	
	Sandy	Clayey
4	1.3	4.7
5	1.9	6.5
10	9.8	18.7
25	48.1	50.8
50	88.2	88.6

*Note:* Calculations of missed biomass were based on a field census of all *P. velutina* patches in eight 30 × 30 m plots on sandy ( $n = 104$  patches) and clayey ( $n = 168$  patches) soils on the Santa Rita Experimental Range in southeastern Arizona, USA.

of new shrubs was observed during the 1966–1996 period, rates of recruitment were comparable (sandy sites) to 4.3 times higher (clayey sites), between 1936 and 1966, a period of erratic and relatively non-remarkable fluctuation in winter precipitation; and a period of relatively dry summers. Fifth, although shrub patch density increased during the relatively high-rainfall 1966–1996 period, total cover actually declined. This decline in shrub cover encapsulated fragmentation of some preexisting patches, contributing to elevated density estimates. These reductions in shrub cover during a relatively wet period may reflect that *P. velutina* stands have reached a stage where density-dependent interactions may be regulating how the community responds to precipitation. A better understanding of the relationship between shrub recruitment and climate is needed if we are to confidently forecast vegetation response to future environmental conditions.

#### *Edaphic influences*

Topoedaphic heterogeneity influences the rates and dynamics of plant response to climate and disturbance. We hypothesized that the rate and extent of woody plant proliferation on coarse-textured desert grasslands soils would be greater than those occurring on finer-textured soils. Historic ground photography (ca. 1902) and earliest accounts of vegetation composition indicate *P. velutina* was largely absent from mid-to-low-elevation uplands on the SRER at the turn of the century (Griffiths 1904, 1910). However, by the date of the first available aerial photography in 1936, shrub cover on sandy upland landscapes had reached ~35%, a peak value relative to the 1966 and 1996 photo dates. Thus, it appears that the physiognomic conversion of desert grassland to shrubland occurred during the 34 years preceding the 1936 aerial photography. With the exception of one landscape, woody cover changes on clayey soils (e.g., Fig. 1) lagged well behind those on sandy soils, such that the grassland-to-shrubland transformation took about twice as long (~60 years) to occur. This is consistent with the general hypothesis that sandy soils should be more prone to woody plant encroachment than clayey soils. However, the fact that

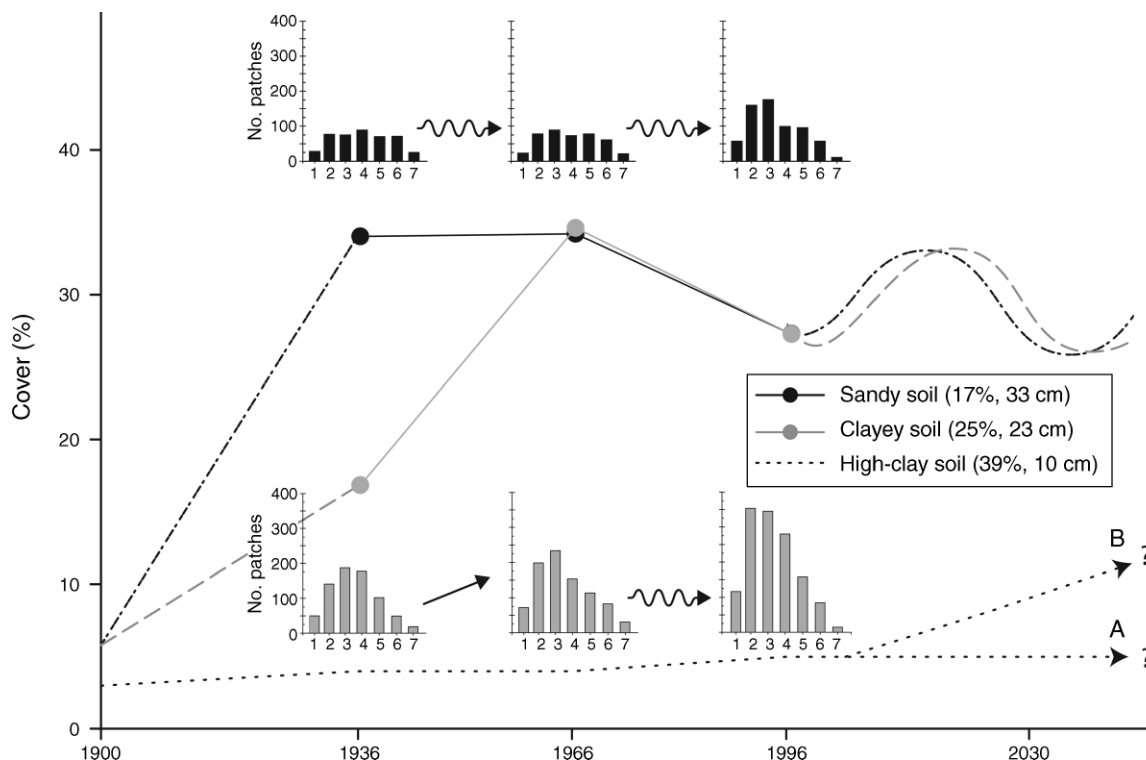


FIG. 9. Conceptual diagram depicting changes in woody plant cover (lines) and patch size structure (inset histograms) in two distinct phases: (1) an encroachment phase (denoted by straight arrow) with directional increases in woody plant cover and (2) a stabilization phase (denoted by wiggly arrow) characterized by patch dynamics and fluctuations in stand structure around a dynamic equilibrium. Woody plant cover was estimated by classifying aerial photographs (1936, 1966, and 1996) on two soils: sandy (black circles) and clayey (gray circles); peak clay content and depth to peak clay content are given in the key in parentheses (see *Methods* for more details). Shrub patch size distributions were delineated using natural breaks; x-axes on inset histograms correspond to the following size classes for patches: 1,  $\leq 5$  m<sup>2</sup>; 2, 6–10 m<sup>2</sup>; 3, 11–25 m<sup>2</sup>; 4, 26–50 m<sup>2</sup>; 5, 51–100 m<sup>2</sup>; 6, 101–250 m<sup>2</sup>; and 7,  $>250$  m<sup>2</sup>. Pre-1936 dashed lines are qualitative reconstructions based on historical accounts of Wooten (1916). Stand structure (inset histograms; sandy = black and clayey = gray) was significantly different on the two soils in 1936 ( $KS_a = 2.937$ ,  $P < 0.0001$ ) and 1966 ( $KS_a = 2.465$ ,  $P < 0.0001$ ). In the stabilization phase (1966–1996), woody stand structure on both soils was similar and exhibited statistically significant shifts in size distributions between years (sandy  $KS_a = 2.686$ ,  $P < 0.0001$ ; clayey  $KS_a = 1.804$ ,  $P = 0.0030$ ). Hypothesized trajectories are presented for early-Pleistocene (high clay content) upland landscapes (dotted lines) on which mesquite cover has remained low (McAuliffe 1995, McClaran 2003). Two future scenarios for woody cover on high-clay soil surfaces are indicated: (A) no future increases in mesquite cover due to an edaphic barrier to shrub establishment and (B) increasing shrub cover over time associated with lag in encroachment process.

shrub communities developing on the two soil types have converged around a comparable mean cover was a surprise. Our data suggest that these desert grassland landscapes undergoing shrub proliferation transitioned from a period of directional change to one of dynamic fluctuation beginning in the 1930s (sandy sites) and 1960s (clayey sites). If this interpretation is correct, and barring climate change, future projections of woody cover and biomass will be determined more by patch dynamics than by net changes in fractional cover. Although total woody cover has reached a comparable level on these contrasting soils, it is not yet clear how differences in stand structure (inset histograms, Fig. 9) might dictate their future dynamics and response to climate fluctuation, climate change or disturbance.

At what point might the clay content of upland soils constitute a barrier to woody plant encroachment? Shrub cover appears to have stabilized at  $\sim 35\%$  on

Holocene- and late-Pleistocene-age surfaces with clay contents ranging from 16.8% to 24.9%, respectively. However, other landscapes on the SRER characterized by soils of middle- (300 000 to 400 000 yr BP) to early- (400 000 to 2 000 000 yr BP) Pleistocene age (Batchily et al. 2003) with clay contents of 39% (from Fravolini et al. 2005) have resisted the shrub encroachment observed on other landscapes. These sites are characterized by grasslands with very little *P. velutina* cover ( $<5\%$ ; McAuliffe 1995, McClaran 2003). Thus, a threshold clay content conferring resistance to shrub encroachment may lie somewhere between  $\sim 25\%$  and 39% in this bioclimatic region.

What might the future hold for shrub encroachment on the early-Pleistocene surfaces currently dominated by grasslands? One possibility is that these older soils with their higher clay content will be resistant to shrub encroachment and the existing grassland physiognomy



PLATE 1. Mesquite (*Prosopis velutina*) shrubland in southeastern Arizona (USA) in July 2005, prior to the onset of the monsoon rains. The photograph captures a long-term study plot adjacent to one of our clayey soil study sites. Fence posts are approximately 1.2 m tall and illustrate the small stature of mesquite plants in the foreground. Conglomerate patches of overlapping canopies are evident in the background. Photo credit: D. Browning.

will be maintained indefinitely (Fig. 9, Scenario A). Alternatively, shrub encroachment on the early-Pleistocene surfaces may lag behind that observed on late-Pleistocene surfaces similar to the lag observed on late-Pleistocene soils relative to Holocene soils (Fig. 9, Scenario B). The “lag” scenario further begs the question: “At what level will woody cover on early-Pleistocene sites stabilize?” Recent and future changes in atmospheric CO<sub>2</sub> concentrations may favor shrubs over grasses (Morgan et al. 2007) and recent invasions of exotic grasses (McClaran and Anable 1992) may fundamentally alter fire regimes, thus complicating the extrapolation of past trends into the future. Resolution of these competing scenarios (Fig. 9A, B) in the context of projected climate change will be required if we are to project the future mix of herbaceous and woody vegetation in the region.

Although sandy and clayey landscapes appear to have stabilized at comparable levels of woody cover, they differ substantially in aboveground shrub biomass. Substantial differences in aboveground biomass in conjunction with the fact that development of shrub cover on clayey soils lagged well behind that on sandy soils, suggests edaphic influences change from the seedling to the post-establishment phase of the shrub life cycle. Our data suggest that conditions conducive to shrub seedling establishment and early persistence occur more frequently on sandy soils than on clayey soils; but that once established, the higher nutrient status and water-holding capacity of clay soils ultimately enhances woody plant productivity and biomass accumulation (Scholes 1990). Differences in aboveground woody

biomass reflected in size class structure on clayey and sandy soils may become more pronounced over time as small plants grow into larger size classes unless density-dependent regulation stabilizes woody biomass.

#### *Woody cover dynamic equilibrium*

The combined approach using patch and landscape perspectives to evaluate changes in woody plant cover over 60 years revealed patch-level fluctuations within the context of broad-scale stability. Based on field measurements of plant growth rates at the SRER site, Glendening (1952) predicted a maximum shrub cover of approximately 30%. Our time-series aerial photographic analyses generally support this prediction and further indicate that it appears to be robustly applicable on soils whose clay content and depth to peak clay content ranged from 16.8% to 24.9% and 33 to 23 cm, respectively. Furthermore, dynamic stabilization of shrub cover at ~30–35% in this Southwestern desert grassland is consistent with predictions of maximum cover that might be expected from an annual rainfall perspective. In a continental analysis of 854 sites, Sankaran et al. (2005) found that maximum woody cover in areas of Africa receiving less than 650 mm/yr mean annual precipitation (MAP) was controlled by and increases linearly with MAP. Their data predict that our site with a MAP of 370 mm would have a maximum shrub cover of ~37%. The concurrence of proposed regulatory mechanisms for African drylands and this North American system is promising and provides a framework for exploring how forecasted climate scenar-

ios might influence future woody plant dynamics across large spatial scales.

Landscape-scale shrub cover dynamics reflect the net outcome of plant recruitment, plant canopy expansion and reduction, and mortality. Our data from a patch-perspective suggest each of these factors co-occur and wax and wane at decadal time-scales consistent with the shifting mosaic model of ecosystem development first identified for forests (Bormann and Likens 1979) and subsequently proposed for savannas (Scholes and Archer 1997). At our desert grassland site, cover increases associated with shrub recruitment and canopy expansion outpaced cover declines associated with canopy reductions and mortality during the "encroachment phase," which continued until landscapes entered a "stabilization phase" wherein recruitment and canopy expansion appear to decrease and were roughly offset by reductions in canopy area. Regulation of shrub cover in this stabilization phase may depend on the intensity of shrub–shrub interactions and density-dependent regulation. The vast majority of species interactions research in savannas and grasslands invaded by woody plants has emphasized the effects of woody plants on herbaceous plants (House et al. 2003). The little that is known about intra- or interspecific interactions among woody plants and density-dependent regulation in shrublands and savannas has been largely inferred indirectly from pattern analyses (e.g., Duncan 1991, Martens et al. 1997, Scholes and Archer 1997). Removal experiments in shrublands have shown that the occurrence and intensity of shrub–shrub competition will vary with resource availability and rooting patterns (Manning and Barbour 1988, McPherson and Wright 1989, Scholes 1990). Experimental tests of shrub–shrub and tree–tree interactions in grasslands invaded by woody plants would be instructive next steps. Transitions from directional increases in woody cover in grassland and savanna systems to fluctuations around a dynamic equilibrium will necessitate re-evaluation of land management strategies and incorporation of patch dynamics into projections of change. Edaphic influences on changes in woody cover and biomass may be contingent on the stage of stand development and the nature of density-dependent interactions among shrubs. Once landscapes reach their woody cover "carrying capacity," predictions of future woody biomass and the rate and magnitude of plant and soil carbon storage will depend on quantifying shifts in population size structure rather than simple changes in net cover.

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