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Shrubland resilience varies across soil types: implications for operationalizing resilience in ecological restoration

Carissa L. Wonkka
Texas A&M University, cwonkka2@unl.edu

Dirac L. Twidwell
University of Nebraska-Lincoln, dirac.twidwell@unl.edu

Jacob B. West
Texas A&M University

William E. Rogers
Texas A&M University

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Shrubland resilience varies across soil types: implications for operationalizing resilience in ecological restoration

Carissa L. Wonkka,[1,3] Dirac Twidwell,[2] Jason B. West,[1] and William E. Rogers[1]

[1]*Department of Ecosystem Science and Management, Texas A&M University, College Station, Texas 77843 USA*
[2]*Department of Agronomy and Horticulture, University of Nebraska-Lincoln, Lincoln, Nebraska 68583 USA*

Abstract. In ecosystems with alternative stable states, restoration success can be thought of as overcoming the resilience of an undesirable state to promote an alternative state that yields greater ecosystem services. Since greater resilience of undesirable states translates into reduced restoration potential, quantifying differences in resilience can enhance restoration planning. In the context of shrub-encroached rangeland restoration, shrubland resilience is the capacity of a woody vegetated state to absorb management interventions designed to produce a more desirable grass-dominated state, and remain within its current regime. Therefore, differences in the resilience of a state can be quantified in a relative sense by measuring whether a state switches to an alternate state following perturbation or remains in its current stability domain. Here we designed an experimental manipulation to assess the contribution of soils to differences in the relative resilience of a shrub-invaded state. In this large-scale experiment, we repeated perturbations across a gradient of soil textures to inform restoration practitioners of differences in the relative resilience of shrubland occurring on different soil types to common rangeland restoration practices. On each soil type, we compared the relative ability of the shrubland state to withstand chemical and mechanical brush control treatments, commonly employed in this study region, to untreated controls. While the shrubland community composition did not differ prior to the study, its capacity to absorb and recover from brush removal treatments depended on soil type. Shrubland resilience to chemical and mechanical brush removal was highest on coarse soils. On these soils, brush removal temporarily restored grassland dominance, but woody plants quickly regained pretreatment levels of dominance. However, shrublands on fine soils did not recover following treatments, continuing to be grass-dominated for the duration of the study. This study highlights a simple approach for prioritizing restoration actions by mapping the locations of different soil attributes that support shrub-dominated states with differing levels of resilience to brush control. This experimental approach provides a basis for operationalizing resilience in restoration and prioritizing management actions across a range of environmental conditions, which is critical given the economic constraints associated with broad-scale mechanical and chemical interventions for rangeland restoration.

Key words: adaptive capacity; alternative state; brush removal; ecosystem management; fire; rangeland management; resilience; restoration ecology; woody encroachment

Introduction

In ecosystems with multiple stable states, restoration from a degraded state to an alternative, more desirable state requires overcoming its resilience, defined as the capacity to absorb disturbance and remain within the current domain of attraction (Holling 1973). Yet, operationalizing the resilience concept in restoration ecology has proven difficult (Nyström et al. 2008). This is because effective restoration requires practitioners to know the amount of disturbance or management intervention necessary to trigger a shift to an alternate ecosystem state (Standish et al. 2014). Therefore, the utility of the resilience concept has been limited in practice by the inability of scientists to quantify thresholds associated with management actions and ecosystem transformability (Twidwell et al. 2013*b*). Furthermore, basic quantification of ecological thresholds has proven to be a major challenge. Thresholds are not static and can shift as a function of the interplay among

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[3]Present address: Department of Agronomy and Horticulture, University of Nebraska-Lincoln, Lincoln, Nebraska 68583 USA. E-mail: cwonkka2@unl.edu

complex ecological relationships operating across various spatial and temporal scales, many of which are not readily apparent to the observer (Peters et al. 2004, Bestelmeyer et al. 2006). For these reasons, resilience continues to be viewed as a vague concept that has been difficult to apply and has had limited utility in the development of restoration strategies (Bennett et al. 2005, Groffman et al. 2006, Suding and Hobbs 2009).

An alternative to quantifying ecological thresholds is to ascertain when a threshold has been crossed by characterizing differences in the relative resilience of an ecological state to interventions conducted across identifiable and measurable ecosystem properties (Scheffer and van Nes 2007, Lindenmayer et al. 2008, Slocum and Mendelssohn 2008). Such an approach is an extension of the qualification of resilience described by Carpenter et al. (2001) that includes the resilience "of what" and "to what." A key to moving forward with operationalizing resilience in ecological restoration is to understand how the resilience of an undesirable or degraded state (i.e., "of what") to a specific type of restoration action (i.e., "to what") changes as parameters in the environment change over space and time (Beisner et al. 2003). Coupled with determinations of the location and extent of identifiable ecosystem parameters across the landscape, differences in the relative resilience of an ecological state can be mapped across an environmental gradient. Practitioners can then operationalize the resilience concept to implement restoration interventions strategically across large landscapes, with the knowledge that management interventions are more likely to be successful by focusing in areas where conditions are contributing to relatively lower ecological resilience (Wallington et al. 2005). For example, globally, rangelands have transitioned into alternative woody-dominated states as a result of anthropogenic changes in historic disturbance regimes, changes in land use and tenure, and factors associated with global environmental change such as nitrification, increased atmospheric carbon, changing patterns of precipitation, and increased temperatures (Archer et al. 1995, Buitenwerf et al. 2012, Taylor et al. 2012). In rangelands with alternative grassland and woody vegetation states, knowledge of the topoedaphic conditions that contribute to differences in the resilience of this new woody-dominated state (i.e., relative differences in the ability for invaded woody states to absorb disturbance and retain shrubland dominance across a topoedaphic gradient) would provide a basis for prioritizing interventions aimed at restoring grass dominance across large landscapes. Prioritizing intervention efforts is greatly needed in woody-invaded rangelands. Due to their extremely cost-prohibitive nature, mechanical and chemical treatments are currently applied on small areas relative to the scale of woody invasions (Taylor et al. 2012, Twidwell et al. 2013*a*). By prioritizing management in areas where it is more likely to overcome the resilience of the degraded state, a greater proportion of the landscape can be effectively restored using these interventions.

The objective of this study was to investigate differences in the resilience of a degraded shrubland state to restoration interventions as a function of different underlying soil conditions. To test this objective, we exposed a single brush-encroached semiarid rangeland state, which occurred across three soil types ranging in texture from coarse to fine, to commonly employed mechanical and chemical brush control methods. Brush control methods are used in this area with the intent of exceeding the ability of the shrubland state to absorb disturbance and transforming it to a grassland state with a distinct set of organizing structures and functions. Brush control with mechanical and chemical treatments can therefore provide a means of identifying relative differences in the resilience of this semiarid shrubland across soil conditions. We then used fire as a follow-up to mechanical and chemical treatments to assess whether shrubland closer to a tipping point, following initial perturbation with chemical and mechanical brush control, can be moved into a new basin of attraction, i.e., alternative stable state, with less intervention effort. Following Carpenter et al. (2001), our study accounts for the "of what" and "to what" conditions for qualifying resilience. The "of what" is a single *Prosopis–Acacia* shrubland state, the "to what" is one of three common rangeland restoration techniques, and we assess how underlying environmental conditions change the resilience "of what" and "to what" via replication across three soil types. For simplicity and to avoid tedious qualification of the resilience of this *Prosopis–Acacia* shrubland state to restoration interventions across soils, we hereafter simply refer to this state as having higher/lower resilience to a given treatment on a given soil type.

We used an approach consistent with studies in aquatic systems that have operationalized resilience similarly in order to investigate how changes in environmental conditions contribute to relative differences in resilience (e.g., Angeler et al. 2014), Following their approach, we infer differences in the resilience of an undesirable shrubland state to be a function of whether the shrubland rapidly returns to its pre-disturbance structure following treatment or remains in the new grass-dominated basin of attraction. Transitions between alternative states are associated with structural and compositional shifts that alter ecosystem function (Walker and Steffen 1993, Carpenter et al. 2001, Anderies et al. 2002). In our paper we account for both structural and compositional shifts. We focus on structural state variables, such as woody-plant cover and herbaceous cover, to measure the relative resilience of rangelands to perturbation. Alternative state shifts in rangelands are often tied to shifts in dominance of functional groups (i.e., a shift from shrub dominance to herbaceous dominance; Walker

et al. 1997, Carpenter et al. 2001). A rapid return to pre-disturbance structural configurations following brush control is evidence that the resilience of the pre-disturbance state has not been overcome and that self-perpetuating processes of the alternative, desired state have not been established (Allen et al. 2005). Alternatively, a long-term shift away from pre-perturbation conditions suggests that the resilience of the prior state has been overcome and the system has shifted into a new basin of attraction (Folke et al. 2004, Allen et al. 2005, Slocum and Mendelssohn 2008). In addition, we used compositional shifts resulting from brush control treatments to explore components of resilience related to adaptive capacity. Adaptive capacity is the ability of a system to cope with changing internal conditions and external drivers (Elmqvist et al. 2003, Carpenter and Brock 2008, Engle 2011). Under a resilience framework, adaptive capacity is considered to correspond to the degree of response diversity, or variation in species response to perturbation or environmental fluctuation, inherent in the species configuration that comprises the system (Elmqvist et al. 2003, Folke et al. 2004, Laliberté et al. 2010). We therefore characterize adaptive capacity by measuring compositional shifts and changes in the relative abundances of species that contribute to community structural responses to external drivers (in this case, restoration interventions). This approach, which combines an assessment of adaptive capacity with an experimental determination of relative resilience across soil textures, demonstrates the potential for scientific studies to inform restoration practitioners of the relative resilience of ecosystem states across different underlying environmental conditions, without necessitating that threshold dynamics be quantified for the resilience concept to be usefully applied.

Methods

Study area

This research was conducted at the Chaparrosa Ranch (28.9°N, 100.0°W), in Zavala County in southwest Texas, USA. The site is subtropical with hot summers and mild winters. Average annual rainfall is 560 mm, bimodally distributed with peaks in spring and fall (Jacoby et al. 1982). The system is comprised of two alternative stable states, a *Prosopis–Acacia* shrubland-dominated state and a grassland-dominated state interspersed with small shrub islands. The dominant species present in the shrubland state include mesquite (*Prosopis glandulosa* Torr), blackbrush acacia (*Acacia rigidula* Benth), guayacan (*Guaiacum angustifolium* Englem.), twisted acacia (*Acacia schaffneri* (S. Watson) F.J. Herm.), and whitebrush (*Aloysia gratissima* (Gillies and Hook.) Troncoso). All of the dominant shrub species have the capacity to vegetatively resprout in response to disturbance. The grassland state is comprised primarily of warm-season perennial tufted bunchgrasses. The dominant species are curly mesquite (*Hilaria belangeri* (Steud.) Nash), hairy grama (*Bouteloua hirsuta* Lag.), three-awn (*Aristida purpurea* Nutt.), and tanglehead (*Heteropogon contortus* (L.) P. Beauv. ex Roem. and Schult.). Plots 40 m × 25 m in size were established in *Prosopis–Acacia* shrublands on three different soil types in three different pastures located within a 15 km radius. The three pastures included in the study experienced differing land use histories representative of different historical land uses in the region. Historical land uses in the pastures include brush management with herbicide application in one pasture that was also periodically grazed, high-intensity low-duration grazing in another, and no reported brush management with periodic moderate grazing in the third (Mattox 2013). All three pastures were subject to periodic moderate grazing during the course of the study.

Experimental design

To test for differences in shrubland resilience to treatments across soils, we selected three soil types common in the study area that represented a range of soil textures from fine clays to coarse sands: Antosa-Bobillo sand association (ABC), Webb fine sandy loam soils (WEB), and Chacon clay loam soils (CKB; Soil Survey Staff, *available online*).[4] Three pastures were identified that included each of the three soil types. Brush control methods were randomly assigned to plots within each pasture–soil combination and completed in early spring 2011. This resulted in a randomized complete block design with three brush removal treatments (control, cut-herbicide, and mechanical) replicated twice in each pasture–soil combination (Fig. 1). In control treatments no brush removal occurred. In cut-herbicide treatments, we cut all woody brush at the base of the plant and sprayed a 15% Remedy (Dow AgroSciences, Indianapolis, Indiana, USA) herbicide/diesel mixture on the stumps of the cut trees and shrubs. We used roller-chopping with a pasture aerator (Lawson Manufacturing, now RanchWorx, Palm Harbor, Florida, USA) in mechanically treated plots. Roller-chopping uses a cylindrical, water-filled drum equipped with blades towed behind a tractor to cut and crush woody vegetation at the soil surface (Fulbright et al. 1991, Blanco et al. 2005). We chose roller-chopping rather than other mechanical methods for this study because, together with the cut-herbicide and control treatments, it provided a gradient of soil disturbance with high disturbance from roller-chopping, low soil disturbance from the cut-herbicide treatment, and no soil disturbance in control plots. Both the roller-chopping and cut-herbicide methods are commonly used for woody-brush control and removal in the study region (Welch 2000).

[4]http://websoilsurvey.nrcs.usda.gov/

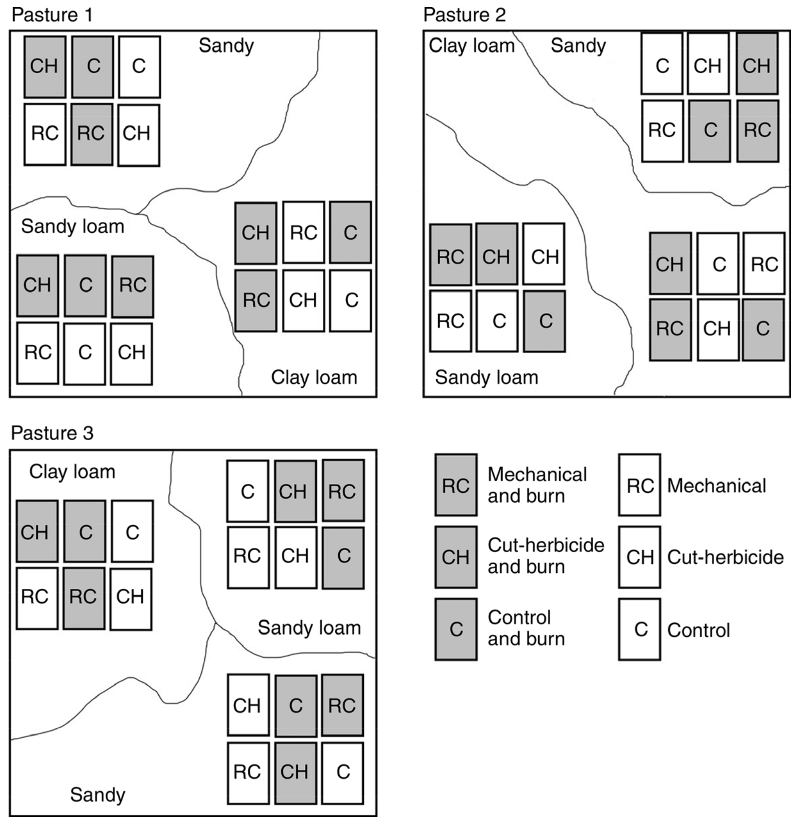

FIG. 1. Conceptual diagram of the experimental design carried out at the Chaparrosa Ranch in southwest Texas, USA. Treatments included: mechanical (removing brush by roller-chopping), cut-herbicide (all woody brush cut at the base of the plant and sprayed with herbicide), and untreated control, all replicated twice on each soil–pasture block. One of each of the replicates of each treatment on each soil–pasture block was treated with a follow-up prescribed burn.

Two years following mechanical and chemical applications in February of 2013, prescribed fires were conducted to attempt to move the system, if needed, into a new basin of attraction after being pushed closer to the tipping point separating shrubland and grassland states. Given past studies investigating the effectiveness of chemical and mechanical interventions for woody-plant encroachment in the study region, the a priori expectation was that mechanical and chemical treatments might be insufficient, by themselves, to surpass the resilience of the degraded shrubland state and move into an alternative grassland state, and fire could provide the additional input needed to meet this restoration goal (Scifres et al. 1979, McGinty and Ueckert 2001, Mitchell et al. 2004). Within each pasture–soil block, a prescribed fire treatment was randomly assigned to one of each brush removal treatment plots (control, cut-herbicide, and mechanical). The treatments in 2013, replicated and balanced across site and soil groups, were therefore: (1) control (no brush removal and unburned); (2) burned (no brush removal); (3) cut-herbicide (unburned); (4) cut-herbicide and burned; (5) mechanical brush removal (unburned); and (6) mechanical brush removal and burned. Each plot was separated from the others by vegetated buffers.

We collected data on woody-plant cover by species and height class (<0.5 m, 0.5–1.5 m, >1.5 m), number of stems and individuals of each woody-plant species, total herbaceous cover, total litter cover, and percent bare ground once each year during peak perennial grass production from 2010 (pretreatment) until 2013. The percentage of each quarter plot covered by woody plants, woody plants in each height class, woody plants of a given species in a given height class, herbaceous plants, litter, and bare ground was visually estimated to the nearest 5% for each of the four quarters of the plot and then averaged across quarters to determine total plot cover of each class. Shrub cover was assumed to comprise all of the area within the outline of the shrub canopy. Five 1-m^2 subplots were established within each plot to measure fuels using a fixed-area method (Mueller-DomBois and Ellenberg 1974) to determine fuel structure and fine-fuel loading prior to burning. Within each subplot we visually estimated percent cover and measured the depth of cured grass fuel. In addition, we visually estimated cover and depth

of fine and coarse woody debris for each fuel class (Fosberg and Schroeder 1971). We collected fuel data every six weeks during the period between application of brush removal treatments in fall 2010 and setting the fires in February 2013. We clipped, dried, and weighed all fuels in 20 1-m^2 quadrats outside of the experimental plots in order to calibrate visual biomass estimates for each subplot with harvested biomass measurements. Fire temperatures at each subplot were recorded during the prescribed burn using ceramic tile pyrometers painted with 10 temperature-indicating lacquers (OMEGALAQ liquid temperature lacquers; Omega, Stamford, Connecticut, USA) that melted from 79°C to 640°C. The percentage of scorch was visually estimated immediately following the burns for each subplot.

Data analysis

Repeated measures analysis of variance (ANOVA) was used to test whether shrubland states moved into an alternative basin of attraction after implementing brush control treatments or, alternatively, quickly recovered following treatment and therefore remained in the same state. ANOVA tested for differences in total woody-plant cover, woody-plant cover for each of the three height classes, percent herbaceous cover, and percent bare ground among soil types in a randomized complete block design. Soil type (ABC, WEB, and CKB) and pasture were the blocking variables with pasture modeled as a random effect because the pastures represent a random sample of all potential land use histories. Brush removal treatment (control, cut-herbicide, and mechanical) was a fixed effect applied at the plot level. We compared all response variables among soils and treatments by estimating least square means with a Tukey's adjustment for post hoc multiple comparisons for each year of the study (Maxwell 1980, Toothaker 1993).

In order to prevent a state change as a function of adaptive capacity, significant compositional shifts would be necessary as subdominant species compensated for reductions in the abundance of a previous functional dominant. We first used nonmetric multidimensional scaling (NMDS) with Bray-Curtis distances to explore the trajectory of change in woody-plant community composition over time among soils and brush removal treatments. We used site scores for the first two axes of the NMDS for each plot as dependent variables in repeated measures multivariate ANOVA to determine if the treatments resulted in significantly different woody-plant communities. Soils and the interaction of brush removal treatments by soil types were included as terms in the analysis to explore treatment differences across soil types. We then calculated changes in the relative abundance of the most dominant species from 2010 to 2013 to identify the species contributing to differences in adaptive capacity across soils and treatments. We used ANOVA to determine differences in the mean change in the relative abundance of each species across treatment and soil combinations. In the event of an alternative state change, it would be expected that the relative abundance of one or multiple dominant species would be significantly lower in brush removal treatments at the end of the study, compared to the control, and that this would occur concomitantly with relatively insufficient increases in other shrub species. This is interpreted as insufficient adaptive capacity to prevent an alternative state change. In contrast, significant increases in relative abundance would be expected for some species at the end of the study to compensate for decreases in functional dominants if sufficient adaptive capacity were present to mitigate for the effects of restoration actions and prevent the emergence of a more desired alternative state. We tested for changes in relative abundance of the most dominant woody-plant species with ANOVA for a randomized complete block design using the change in relative abundance from pretreatment to final sampling period as the dependent variable.

Tukey's post hoc analysis on pretreatment (2010) data was used to assess whether shrubland woody-plant cover differed across soil types prior to initiating treatments. We used NMDS for year 2010, prior to treatments to determine if shrubland community composition differed across soil types at the start of the experiment.

To test whether communities close to a tipping point following initial perturbation could be moved into a new basin of attraction, we conducted repeated measures ANOVA for years 2012 and 2013 with a model similar to that used for comparing woody cover among soils and treatments, but additionally including fire (burned, unburned) and its interaction with brush-clearing treatments as fixed dependent variables. We set $\alpha = 0.05$ to determine significance in all analyses. We evaluated the difference in the percentage of scorch, temperature, and fuel loading among treatments on different soils with ANOVA for complete randomized block design with treatment as a fixed effect and soil and pasture as blocking variables. Visual cover estimates and height measurements of live herbaceous and 1-h, 10-h, and 100-h dead fuels from the 20 calibration quadrats were regressed against plot biomass determined through oven drying and weighing all clipped materials. The fitted regression was used to estimate fuel loading for all subplots. All analyses were performed using the R statistical computing package (R Development Core Team 2010).

To inform practitioners of differences in shrubland resilience to chemical and mechanical treatment that can be used to prioritize restoration actions across the biogeographic distribution of this *Prosopis–Acacia* shrubland, we used spatial data from the Soil Survey Geographic database (SSURGO) to map differences

Table 1. Repeated measures analysis of variance results of tests for differences among woody-plant cover in response to different brush removal treatments on different soil types in the three years following treatment application at the Chaparrosa Ranch in Zavala County, Texas, USA.

Cover and variable	SS	MS	Num df	Den df	*F*	*P*
Percent woody cover						
Treatment	3536.60	1768.30	2	15.68	22.24	<0.001
Soil	2065.40	1032.68	2	17.22	10.67	<0.001
Pasture	972.30	486.13	2	17.28	7.11	0.01
Year	3545.70	1772.87	2	49.19	21.91	<0.001
Treatment × soil	826.00	206.50	4	17.38	2.55	0.08
Treatment × year	3554.60	888.66	4	49.26	12.12	<0.001
Percent woody cover (<0.5 m)						
Treatment	19.62	9.81	2	67.88	2.18	0.12
Soil	170.80	85.40	2	77.16	19.90	<0.001
Pasture	6.32	3.16	2	77.65	0.78	0.46
Year	363.89	181.95	2	68.34	45.21	<0.001
Treatment × soil	14.04	3.51	4	76.70	0.87	0.48
Treatment × year	252.02	63.00	4	56.45	18.47	<0.001
Percent woody cover (0.5–1.5 m)						
Treatment	1878.14	939.07	2	15.65	23.47	<0.001
Soil	1310.02	655.01	2	17.41	16.45	<0.001
Pasture	376.04	188.02	2	17.48	6.01	0.01
Year	1283.00	641.50	2	47.32	15.79	<0.001
Treatment × soil	875.81	218.95	4	17.51	5.39	0.01
Treatment × year	1472.08	368.02	4	117.23	11.41	<0.001
Percent woody cover (>1.5 m)						
Treatment	714.32	357.16	2	16.15	23.09	<0.001
Soil	95.37	47.68	2	17.43	2.04	0.16
Pasture	164.64	82.32	2	17.47	5.47	0.01
Year	78.79	289.40	2	49.61	18.43	<0.001
Treatment × soil	64.18	16.04	4	17.64	1.02	0.42
Treatment × year	756.49	189.12	4	30.01	12.23	<0.001

Note: Treatments include chemical and mechanical brush removal, applied in 2011.

in the resilience of the shrubland state as a function of the distributions of ABC, WEB, and CKB soils across the Southern Texas Plains ecoregion. Maps were created at a 1-km^2 resolution. Based on our data, categorical classifications were assigned to these shrubland–soil associations to denote areas of higher and lower relative resilience.

Results

Differences in resilience across soil types

Total woody cover differed among brush removal treatments, across soils, and across years 2010–2013 (Table 1). Total woody-plant cover did not differ among treatments prior to treatment (Tukey's HSD: control vs. cut-herbicide, $P = 0.093$; control vs. mechanical, $P = 0.267$; cut-herbicide vs. mechanical, $P = 0.439$). It did, however, differ among soils prior to treatment in 2010. Prior to mechanical and chemical treatment, total woody cover was higher on clay CKB soils than sandy ABC soils or sandy loam WEB soils, which did not differ from each other. (Tukey's HSD: CKB vs. ABC, $P < 0.001$; WEB vs. ABC, $P = 0.872$; WEB vs. CKB, $P = 0.002$). Total woody cover decreased in the first year following brush control treatment on all soils. However, it began to recover to pretreatment levels in the second year following treatment on coarser sandy ABC and WEB soils, indicating that the community did not enter a new basin of attraction (Fig. 2). By 2013, woody-brush cover on cut-herbicide plots had returned to within 10% of controls on ABC and WEB soils. Similarly, woody cover in mechanically treated plots was within 10% of controls for ABC soils and completely recovered on WEB soils. In contrast, total woody-brush cover on both mechanical and cut-herbicide plots on the fine-textured clay CKB soils remained lower than cover on control plots by ~35% for the duration of the study (Fig. 2).

There was a significant treatment × year interaction for all three woody-brush height classes (Table 1). In the large height class, cut-herbicide and mechanical treatments dropped to 0% cover following treatment and remained low for the duration of the study. There was a slight increase in cover of the large height class in 2013 on mechanical plots as some shrubs had already

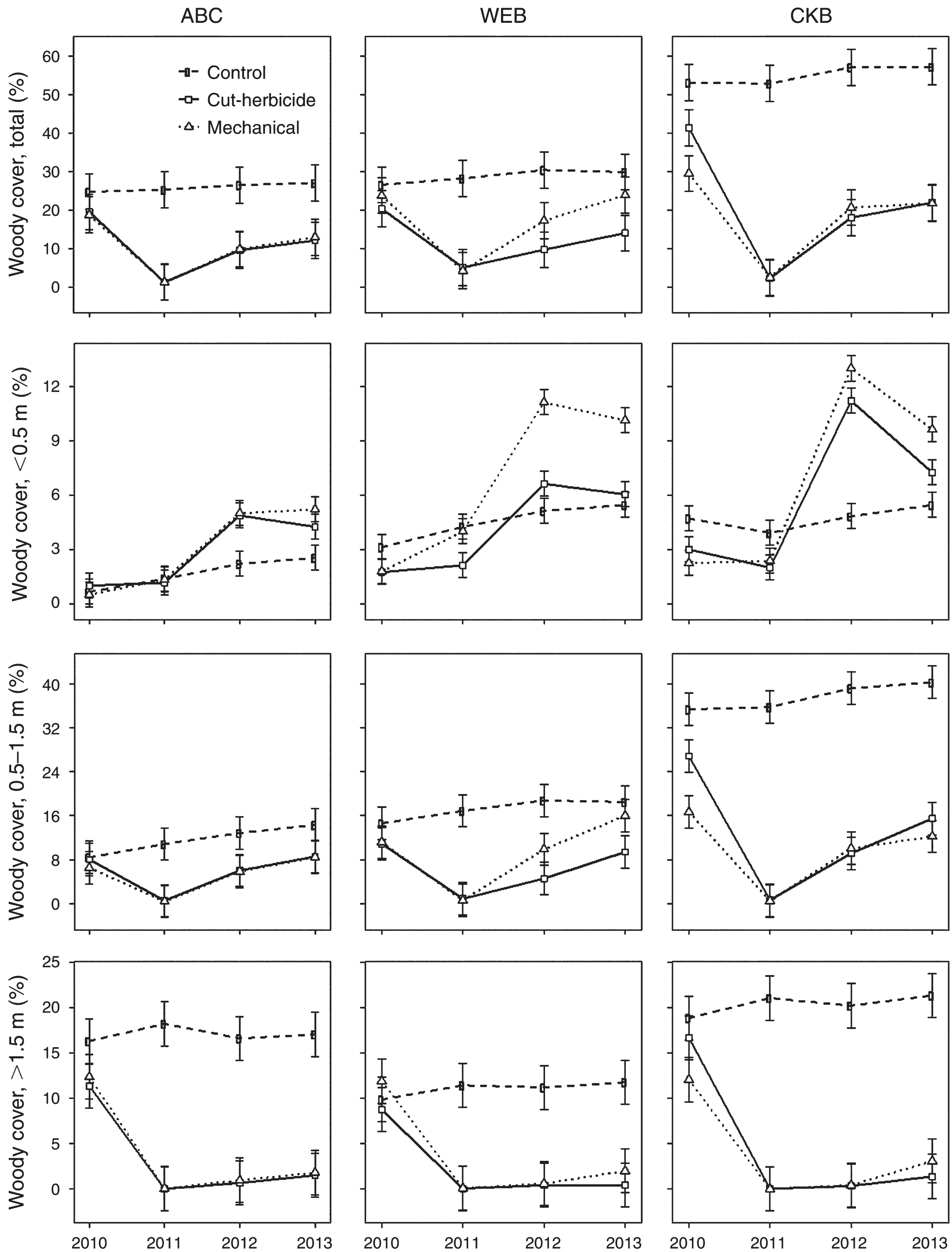

FIG. 2. Changes (mean ± SE) in total woody-brush cover and woody-brush cover in each of three height classes (<0.5 m, 0.5–1.5 m, and >1.5 m) in response to different methods of brush removal (untreated control, cut-herbicide, and mechanical) from 2010 to 2013 on three different soil types: sandy (ABC), sandy loam (WEB), and clay loam (CKB). Year 2010 represents pretreatment conditions.

TABLE 2. Repeated measures analysis of variance results of tests for differences among herbaceous plant cover and bare ground in response to different brush removal treatments on different soil types in the three years following treatment application at the Chaparrosa Ranch in Zavala County, Texas, USA.

Cover and variable	SS	MS	Num df	Den df	*F*	*P*
Percent bare ground						
Treatment	824.90	412.40	2	65.67	2.31	0.111
Soil	3681.90	1840.90	2	73.61	9.71	<0.001
Pasture	647.90	323.90	2	74.01	2.38	0.101
Year	14 740.80	7370.40	2	65.97	41.25	<0.001
Treatment × soil	952.50	238.10	2	73.56	1.33	0.273
Treatment × year	14 081.00	3520.30	4	33.02	20.99	<0.001
Percent herbaceous cover						
Treatment	1074.50	537.24	2	15.04	3.38	0.061
Soil	1206.60	603.31	2	11.52	4.27	0.042
Pasture	1350.70	675.37	2	13.53	4.56	0.033
Year	5373.70	2686.87	2	50.01	16.73	<0.001
Treatment × soil	1142.30	285.57	4	5.77	1.78	0.264
Treatment × year	6198.10	1549.5	4	29.50	12.73	<0.001

Note: Treatments include chemical and mechanical brush removal, applied in 2011.

attained this class on all soils, but cover still remained substantially below that of controls three years following clearing on all soil types (Fig. 2). There was no significant difference in medium woody cover for either cut-herbicide or mechanically treated plots on ABC soils in the final year of sampling (Tukey's HSD for 2013: cut-herbicide vs. control, P = 0.22; mechanical vs. control, P = 0.18) or for the mechanical treatment on WEB soils (Tukey's HSD for 2013: mechanical vs. control, P = 0.26). There was a significant, but very small (<5%) difference between control and cut-herbicide plots on WEB soils in the final year of sampling (Tukey's HSD for 2013: cut-herbicide vs. control, P = 0.043). On CKB soils, however, medium woody cover remained ~25% lower in cut-herbicide and mechanically treated plots in the final year of the study (Fig. 2). Although not significantly different among treatments, small woody cover showed a consistent trend across soils, with an initial increase two years following treatment, and then a decline toward pretreatment levels for both brush removal treatments as the initial regrowth following treatment reached the medium height class (Fig. 2).

There was a significant year × treatment interaction for both herbaceous cover and bare ground (Table 2). Herbaceous cover was higher and percent bare ground lower in mechanically and chemically treated plots on all soil types in 2012 and 2013, after an initial drop in herbaceous vegetation and increase in bare ground in the sampling period directly following treatment. This trend of high herbaceous cover and low percent bare ground was particularly pronounced on CKB soils. On CKB soils, multiple comparisons showed significant differences in 2012 and 2013 among treated plots and control plots in herbaceous cover (Tukey's HSD: control vs. cut-herbicide, P = 0.018; control vs. mechanical, P = 0.017) and percent bare ground (Tukey's HSD: control vs. cut-herbicide, P = 0.018; control vs. mechanical, P = 0.043) (Fig. 3). Multiple comparisons revealed no differences among treatments on other soil types, suggesting grass dominance had only been restored following brush reduction on CKB soils (Fig. 3).

Perturbation with fire

We followed mechanical and chemical brush removal treatments with fire to determine if plots that remained in a shrub-dominated state following initial brush removal treatments could be pushed into the grass-dominated basin of attraction with fire. Fire did not cause a reduction in shrub cover or increase in herbaceous cover in mechanically treated, chemically treated, or control plots. Burned plots did not differ from unburned plots in total percent woody cover, percent woody cover of any height class, herbaceous cover, or percent bare ground (Tables 3 and 4). Additionally, multiple comparisons revealed no differences between burned or unburned plots on any soil for any treatment other than CKB control plots, which had significantly higher woody cover in the burned plots initially (Fig. 4). It is important to recognize that, although fuel loads differed among treatments ($F_{2,43}$ = 3.25, P = 0.049) with cut-herbicide highest and mechanically treated lowest, fuel accumulations were lower than the recommended 2240 to 3360 kg/ha needed for effective prescribed burning in the study region (Lyons et al. 1998) for all treatments on all soil types (Table 5). Therefore, the fire temperatures were low, on average, for all treatments and the resulting low-intensity

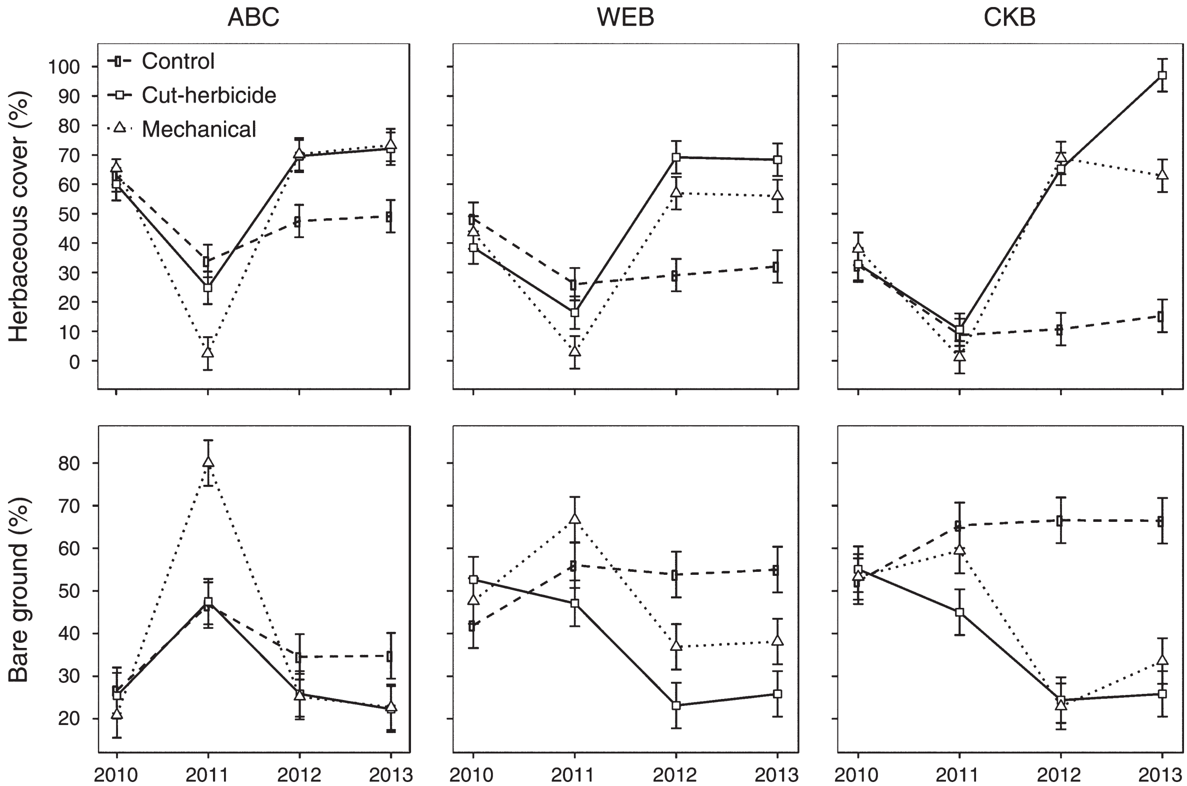

FIG. 3. Changes (mean ± SE) in herbaceous cover and bare ground in response to different methods of brush removal (untreated control, cut-herbicide, and mechanical) from 2010 to 2013 on three different soil types: sandy (ABC), sandy loam (WEB), and clay loam (CKB). Year 2010 represents pretreatment conditions.

burns did not carry across the discontinuous fuel bed. As a result, the percentage of the plot scorched was low and extremely variable for all treatments on all soil types (Table 5).

Adaptive capacity

NMDS of the shrub community showed significant shifts in the compositional trajectory of shrublands following restoration interventions on ABC and WEB soils, but not on the CKB soils that underwent a state transition from shrub to grass dominance. Composition did not differ among soils prior to treatment (standard errors on two NMDS axes overlap for all soil types in 2010). On CKB soils, a regime shift from high shrub–low grass cover to a grassland-dominated state with high grass–low shrub cover (Fig. 2) corresponded to changes in structure, not shrub composition. Composition was similar on control plots and treated plots for the duration of the study (Fig. 5). In contrast, NMDS results suggest a shift in compositional trajectory at the end of the study for cut-herbicide treatment on ABC soils and both cut-herbicide and mechanically treated plots on WEB soils (Fig. 5; standard errors on the two NMDS axes did not overlap at the beginning and end of the study for these respective treatments).

Changes in the relative abundance of individual species reveal differences in the adaptive capacity of *Prosopis–Acacia* shrublands to brush removal across soil types. On ABC soils, whitebrush (*Aloysia gratissima*) increased significantly more in relative abundance in brush removal treatments compared to the control ($F_{4,43}$ = 5.39, P = 0.012) and compensated for significant reductions in one of the most dominant species, honey mesquite (*Prosopis glandulosa*; $F_{4,43}$ = 5.46, P = 0.008). In contrast, restoration interventions did not lead to significant decreases in relative abundance of mesquite on WEB soils ($F_{4,43}$ = 0.6, P = 0.567). Only a significant increase in the relative abundance of spiny hackberry (*Celtis ehrenbergiana*) was observed ($F_{4,43}$ = 5.47, P = 0.008). On CKB soils, relative abundance of mesquite was significantly lower in brush removal treatments, and no species increased sufficiently in response to this reduction (Table 6).

Mapping relative resilience related to soil texture

Using the locations of the three soils included in the study, we mapped resilience of the shrubland state to chemical and mechanical treatments across the Southern Texas Plains EPA ecoregion (Fig. 6) in order to provide a basis for prioritizing management

Table 3. Analysis of variance results of tests for differences among woody-plant cover in response to different brush removal treatments and prescribed fire on different soil types in the three years following treatment application at the Chaparrosa Ranch in Zavala County, Texas, USA.

Cover and variable	SS	MS	Num df	Den df	*F*	*P*
Percent woody cover						
Treatment	1095.2	547.6	2.0	15.9	20.5	<0.001
Fire	2.9	2.9	1.0	71.2	0.1	0.743
Soil	467.2	233.6	2.0	17.0	10.2	0.001
Year	158.3	158.3	1.0	71.2	5.9	0.018
Treatment × soil	315.5	78.9	4.0	17.2	2.9	0.051
Treatment × fire	70.5	35.2	2.0	71.2	1.3	0.277
Fire × soil	140.6	70.3	2.0	71.2	2.6	0.080
Percent woody cover (<0.5 m)						
Treatment	106.1	53.0	2.0	17.3	11.8	<0.001
Soil	184.0	92.0	2.0	19.7	17.6	<0.001
Fire	0.0	0.0	1.0	72.3	0.0	0.972
Year	21.6	21.6	1.0	72.3	5.0	0.028
Treatment × soil	32.4	8.1	4.0	19.8	1.9	0.153
Treatment × fire	23.7	11.8	2.0	72.3	2.8	0.070
Soil × fire	12.7	6.4	2.0	72.3	1.5	0.235
Percent woody cover (0.5–1.5 m)						
Treatment × soil	594.7	297.4	2.0	15.8	18.0	<0.001
Soil	239.6	119.8	2.0	17.1	10.5	0.001
Fire	0.7	0.7	1.0	71.2	0.0	0.837
Year	239.3	239.3	1.0	71.2	14.4	<0.001
Treatment × soil × soil	365.3	91.3	4.0	17.3	5.5	0.005
Treatment × soil × fire	54.5	27.3	2.0	71.2	1.6	0.202
Soil × fire	19.1	9.5	2.0	71.2	0.6	0.567
Percent woody cover (>1.5 m)						
Treatment	487.3	243.7	2.0	15.7	39.3	<0.001
Soil	16.3	8.1	2.0	17.0	1.4	0.270
Fire	5.9	5.9	1.0	71.1	1.0	0.332
Year	26.8	26.8	1.0	71.1	4.3	0.041
Treatment × soil	30.6	7.6	4.0	17.3	1.2	0.332
Treatment × fire	14.5	7.2	2.0	71.1	1.2	0.316
Soil × fire	27.5	13.7	2.0	71.1	2.2	0.116

Note: Treatments include chemical and mechanical brush removal, applied in 2011, and prescribed fires conducted in the late dormant season of 2013.

intervention. Brush removal treatments are more likely to be effective on finer clay soils, given that they showed low resilience to chemical and mechanical brush removal. These soils occur on 35322 ha (1.5% of the land area in the ecoregion). High resilience of the shrubland state to mechanical and chemical treatments on the coarse soils included in the study resulted in a return to shrub dominance within three years of treatment. These coarse soils occur on 131386 ha (3% of the land area) within the Southern Texas Plains ecoregion.

Discussion

The results of this study demonstrate that the resilience of *Prosopis–Acacia* dominated rangelands to chemical and mechanical brush removal varies across a range of soil types. Shrubland community composition did not differ among soil types prior to mechanical or chemical treatment, yet showed contrasting abilities to recover, suggesting that soil texture mediates shrubland resilience to brush removal. Shrubland states located on fine-textured clay soils were the least resilient of the shrubland soil type associations studied here. On both coarser sandy and sandy-loam soils, woody plants quickly regained pretreatment levels of dominance and the reestablishment of grassland dominance was short lived. This rapid return to a pre-disturbance configuration without an intervening perturbation is evidence that the resilience of the pre-disturbance state has not been overcome and the self-perpetuating processes and structures of the desired grass-dominated state have not been reinstated on these soils (Allen et al. 2005). However, grass-dominance persisted and woody-plant abundance remained low on clay soils for the duration of the study. Given the lower resilience of shrublands on

Table 4. Analysis of variance results of tests for differences among herbaceous plant cover and bare ground in response to different brush removal treatments and prescribed fire on different soil types in the three years following treatment application at the Chaparrosa Ranch in Zavala County, Texas, USA.

Cover and variable	SS	MS	Num df	Den df	*F*	*P*
Percent bare ground						
Treatment	1538.7	769.3	2.0	15.8	17.5	<0.001
Soil	221.0	110.5	2.0	17.0	4.0	0.037
Fire	7.7	7.7	1.0	71.1	0.2	0.679
Year	42.5	42.5	1.0	71.1	1.0	0.331
Treatment × soil	518.5	129.6	4.0	17.3	2.9	0.052
Treatment × fire	424.1	212.0	2.0	71.1	4.8	0.011
Soil × fire	210.9	105.5	2.0	71.1	2.4	0.100
Percent herbaceous cover						
Treatment	11 424.2	5712.1	2.0	15.0	19.8	<0.001
Soil	733.3	366.6	2.0	17.3	1.5	0.258
Fire	206.3	206.3	1.0	44.1	0.7	0.403
Year	440.9	440.9	1.0	22.0	1.5	0.230
Treatment × soil	2299.2	574.8	4.0	17.2	2.0	0.142
Treatment × fire	25.6	12.8	2.0	44.1	0.0	0.957
Soil × fire	1260.1	630.1	2.0	44.1	2.2	0.126

Note: Treatments include chemical and mechanical brush removal, applied in 2011, and prescribed fires conducted in the late dormant season of 2013.

clay soils to chemical and mechanical treatments, brush removal intervention is more likely to be successful on fine-textured than on coarse-textured soils. This approach therefore provides a means for managers to prioritize interventions based on the relative resilience of shrublands across the landscape.

A potential mechanism for the rapid return of woody-plant dominance on sandy and sand-loam soils relative to fine-textured clays is related to the role of soil water dynamics in strengthening positive feedbacks underpinning shrubland resilience. The positive feedback between woody-plant productivity and redistribution of soil water is considered an important driver of resilience in woody-plant-dominated savannas (Anderies et al. 2002, Nippert et al. 2013). Woody plants redirect water resources to lower soil layers, funneling precipitation into deeper soils along stem and root systems (Walker et al. 1981). This adds to the soil moisture available to these plants in zones where their roots are distributed. Adult woody plants with deep roots have also been shown to redistribute water to clones with shallower roots (Ratajczak et al. 2011), increasing shrubland productivity by providing new clones with deeper soil water and releasing them from competitive exclusion by grasses (Nippert et al. 2013). In addition, lower grass biomass resulting from shading out by shrub canopies reduces total uptake by grasses in the upper layers of soil, allowing for more percolation of precipitation to deeper soils, where it is readily available to woody plants (Bond 2008, Ratajczak et al. 2014). Abiotic conditions that strengthen this positive feedback could increase the resilience of the woody-dominated state to perturbation aimed at shifting the system toward grass dominance. Given these dynamics, soil water-holding capacity and infiltration patterns, which are largely related to soil texture (Larcher 2003), could be important determinants of post-treatment grass–tree dynamics. Fine-textured soils have greater water-holding capacity because of larger surface areas relative to mass and, as a result, smaller pore spaces between soil particles (Tuller and Or 2004). Coarse-textured soils will therefore allow for more movement of water through the soil profile. More infiltration to deeper soils strengthens the feedbacks between soil–water and shrub productivity, potentially increasing the resilience of the shrubland state to chemical and mechanical brush treatments on coarse relative to fine soils. Anderies et al. (2002) models the resilience of managed rangelands, relating the sizes of the basins for grass-dominated and shrub-dominated states to several parameters. Among those parameters is the competitive effect of woody shrubs on grasses through the limitation of water. Given the link between soil texture and movement of precipitation through the system, coarse soils have the potential to increase the competitive effect of shrubs on grasses, resulting in larger basins of attraction for shrubland states on coarse- relative to fine-soil textures. Shrublands with larger basins of attraction would more readily absorb shocks such as chemical and mechanical brush control treatments. In this study, brush removal overcame the resilience of the woody-dominated state on finer textured clay soils with greater water-holding capacity, but was ineffective at overcoming the resilience of the woody-dominated state on coarser texture soils with lower water retention capacity and higher infiltration rates. Our explanation of these patterns is reinforced

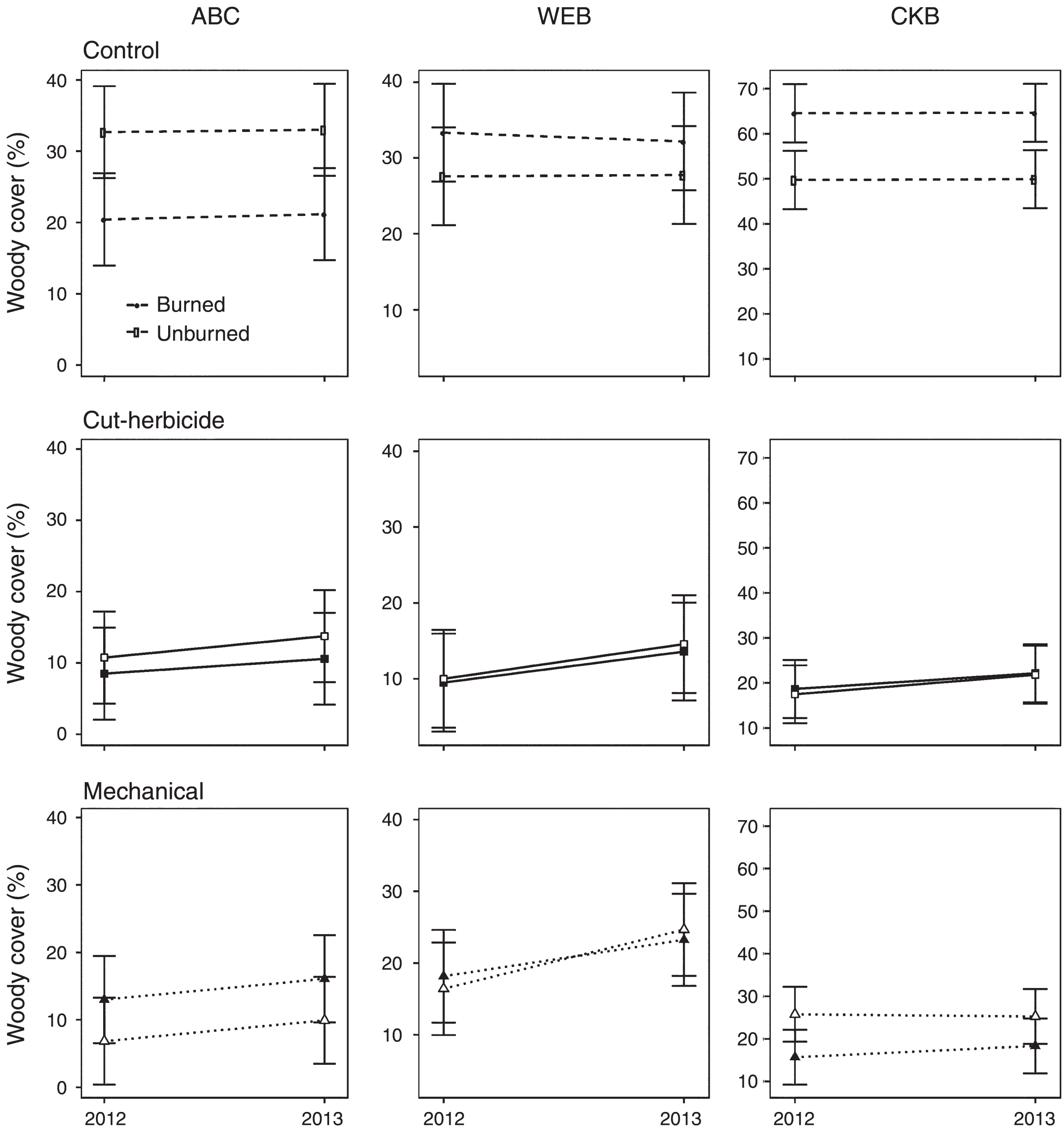

FIG. 4. Changes (mean ± SE) in total woody-brush cover in response to prescribed burning in plots previously exposed to different methods of brush removal (untreated control, cut-herbicide, and mechanical) on three different soil types: sandy (ABC), sandy loam (WEB), and clay loam (CKB). Year 2012 represents pre-burn conditions.

by observations in other systems. For instance, in South African savanna, acacia growth increased where grass was removed on fine-textured soils, but similar grass removal had no effect on acacia growth on coarser textured soils, suggesting that grasses limited the recharge of deeper soils on fine-textured soils, but not on coarse-textured soils (Knoop and Walker 1985).

Abiotic conditions that promote grass dominance could weaken the feedbacks driving woody-plant resilience to treatment as well. In addition to large water-holding capacity that may favor grass dominance, clay soils in the study area had higher pretreatment densities of mature woody plants. Studies have found that savanna trees enhance physiochemical soil properties (Tiedemann and Klemmedson 1973). Several studies found higher pools of nitrogen available for mineralization, increased soil organic carbon, and increased abundance of microbes under trees than in open areas in savanna systems (Belsky et al. 1989, Weltzin and Coughenour 1990, Scholes and Archer 1997). This

TABLE 5. Mean and standard error for fuel load, scorch, and temperature among brush removal treatments (untreated control, hand-cutting followed by herbicide, and roller-chopping) on different soil types (ABC is sandy, WEB is sandy loam, CKB is clay).

Soil type and treatment	Fuel load (kg/ha)		Scorch (%)		Temperature (°C)	
	Mean	SE	Mean	SE	Mean	SE
ABC						
Control	1356.57	278.57	<1	0.33	13	7.09
Cut-herbicide	1189.52	197.96	15	12.58	114	64.66
Mechanical	785.51	75.62	9	4.70	69	34.96
WEB						
Control	1688.23	402.96	5	2.33	89	41.52
Cut-herbicide	1438.28	267.14	47	12.03	210	90.13
Mechanical	1154.65	176.72	15	7.67	93	22.86
CKB						
Control	878.44	148.34	1	1.33	65	7.47
Cut-herbicide	1940.30	719.05	23	20.55	80	55.31
Mechanical	676.50	58.99	7	2.03	60	9.99

Note: Fuel was measured immediately prior to conducting prescribed burns, scorch immediately following burns, and temperatures were recorded during the fire.

enhancement can lead to greater grass response to brush removal in areas with previous high densities of woody plants, such as the clay soils in this study, relative to areas with lower initial densities (Scholes and Archer 1997).

In addition to mechanical and chemical treatments, fire treatments were implemented to assess whether communities closer to a tipping point, following initial perturbation, could be moved into a new basin of attraction with less intervention effort. In our study, two years of below-average rainfall following brush removal (Long et al. 2013, Grigg 2014) led to discontinuous fuels and low biomass levels, contributing to small amounts of area burned within plots and low fire temperatures (as indicated by our pyrometers) and intensities across all treatments and soil types. As a result, fire did not cause a shift from a shrub-dominated to a grass-dominated state on any soil type. This result is expected given that low-intensity fires, such as those utilized here, do not exceed woody-plant mortality thresholds (Twidwell et al. 2013*b*). Many of the woody plants in our study plots are resprouting plants. Resprouting is a common life history strategy in highly disturbed ecosystems such as grasslands that experience frequent fires (Bond and Midgley 2003). Resprouting provides a mechanism for woody-plant tolerance to low-intensity fires, especially during the dormant season when woody plants are not actively photosynthesizing (Scasta et al. 2014). Woody plants are able to withstand low-intensity fires through non-structural carbohydrate storage in stems, roots, and lignotubers, as well as belowground meristematic tissues insulated from high temperatures by the soil (Clarke et al. 2010, 2013). Additional studies incorporating a broad range of fire intensities across a soil texture gradient could help elucidate levels of intervention necessary to move shrubland associations on different soil textures into grass-dominated basins of attraction following chemical and mechanical perturbation.

The presence of subdominant species that contribute to ecosystem function in similar manners as dominant species, but that respond differently to environmental changes or disturbance, provide higher adaptive capacity (Elmqvist et al. 2003, Leary and Petchey 2009). In our study, spiny hackberry and whitebrush increased in relative abundance in mechanically treated plots on coarser soils. These originally less dominant species show propensity for contributing to the adaptive capacity of this shrubland by compensating for the loss of functionally equivalent, but more dominant species. Compensation by less dominant, but functionally equivalent species following loss of dominants in a system is tied to the idea of response diversity. Response diversity is defined as variability in species responses to perturbation and has emerged as an important metric for measuring the adaptive capacity of an ecosystem (Elmqvist et al. 2003). In our study, response diversity was increased by spiny hackberry and whitebrush, which have been found to respond more favorably to mechanical disturbance than other species in this region (Scifres et al. 1979, Koerth et al. 1989). These species both have large root crowns that increase the amount of meristematic tissue and belowground carbon storage available for resprouting following mechanical disturbance such as roller-chopping that leaves root crowns intact, damaging only aboveground tissues (Flinn et al. 1992). Opportunities to contribute to adaptive capacity were realized on sandy ABC soils, which exhibited greater resilience to brush removal and did not undergo a regime shift toward grass dominance. On this association, whitebrush increased sufficiently to replace structural changes occurring as a result of reductions in mesquite. This compositional change provides

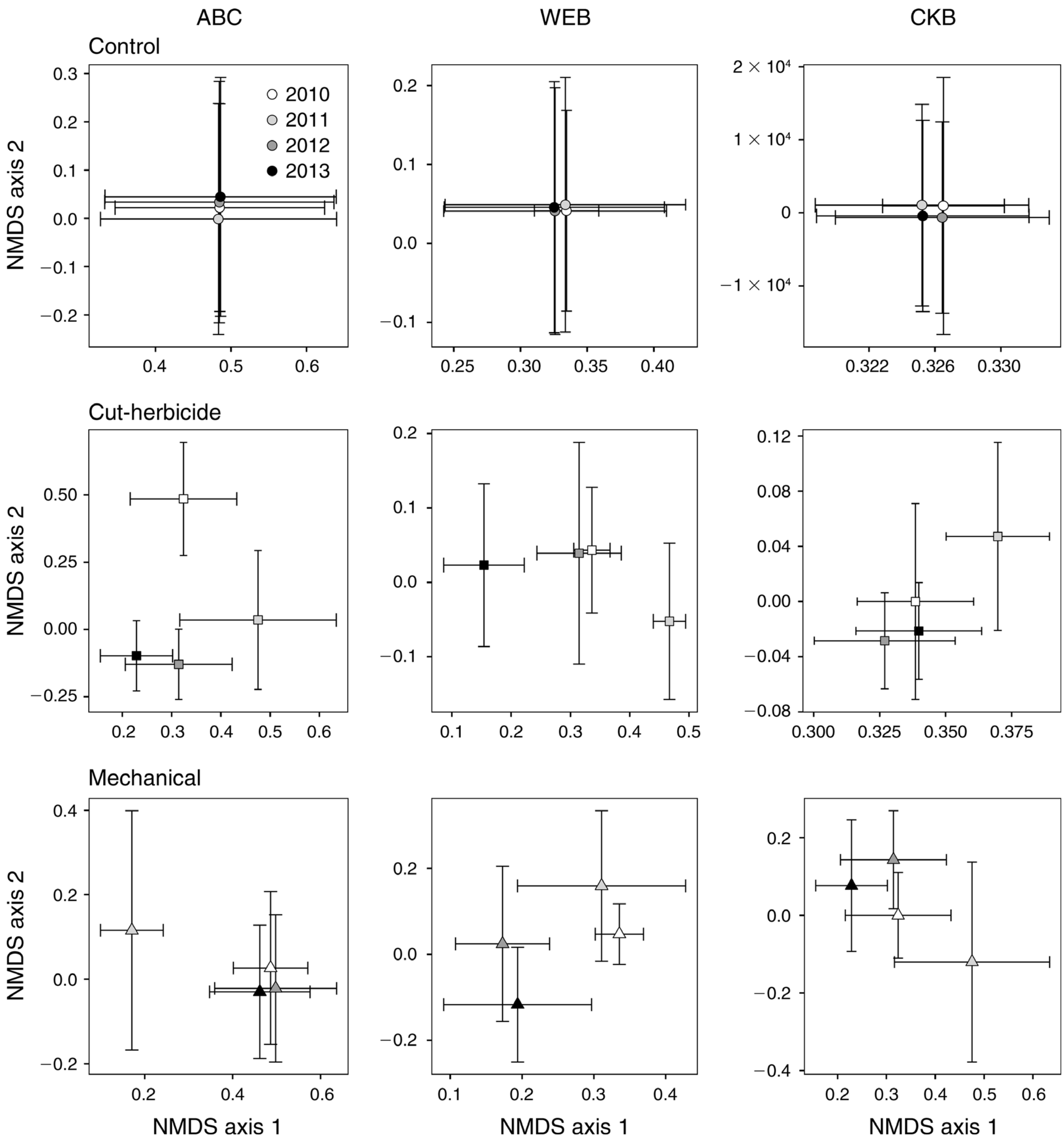

FIG. 5. Nonmetric multidimensional scaling of woody brush communities for years 2010 (pretreatment) through 2013 for each soil × brush removal treatment combination. The mean and standard error on nonmetric multidimensional scaling (NMDS) axis 1 and NMDS axis 2 for each year of the study are displayed in order to assess divergence in community compositional trajectories over time following treatment. Treatments and years are coded as follows: Shapes represent brush removal treatments of control (circles), cut-herbicide (squares), and mechanical (triangles); Colors represent years: 2010 (white), 2011 (light gray), 2012 (dark gray), and 2013 (black).

evidence for an asynchronous shift in ecosystem components as species with similar functional roles respond differently to perturbation. Spiny hackberry showed a similar propensity for contributing to adaptive capacity on sandy-loam WEB soils, but restoration interventions did not produce a lasting impact on these soils. None of the functional dominants (mesquite and acacia species) were significantly reduced for any brush removal treatment on sandy-loam soils. Other studies have also documented no change or increase in the relative abundance of dominant mesquite and acacia following the destruction of meristematic tissues with brush removal (Fulbright and Beasom 1987, Fulbright 1996). Thus, adaptive capacity

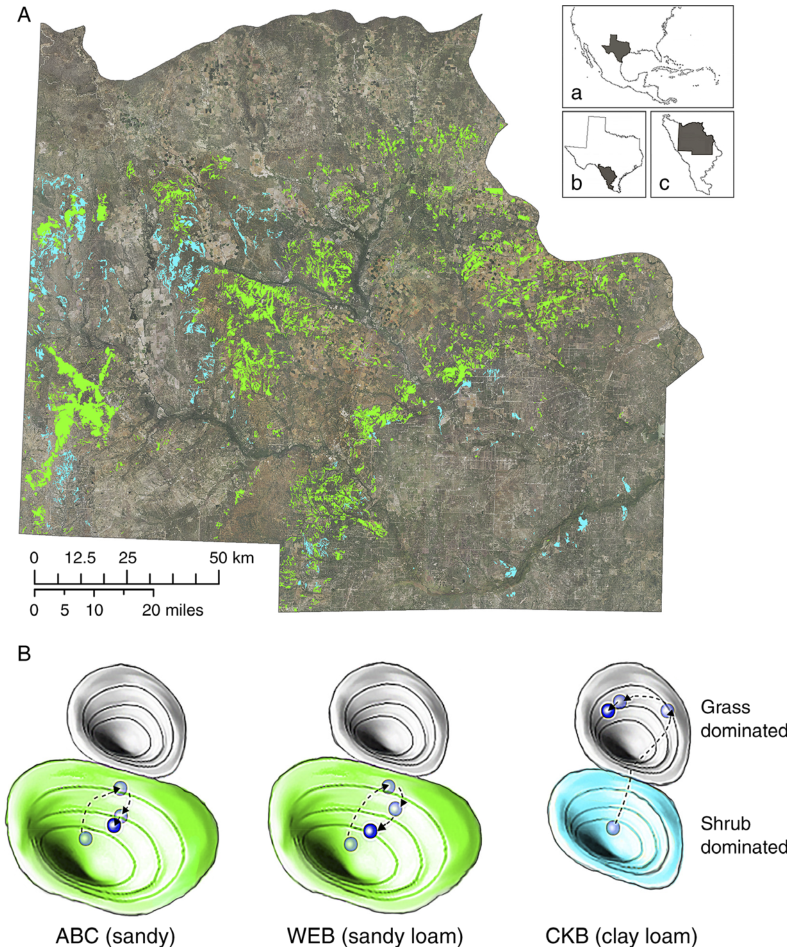

Fig. 6. Map and conceptual model of relative resilience across soil types in the Southern Texas Plains ecoregion. Panel (A) depicts resilience across the landscape, with blue indicating areas of lower resilience and green indicating areas of higher resilience. Insets show the location of the Southern Texas Plains ecoregion within (a) North America and (b) Texas, and (c) the portion of the ecoregion represented in our map. Resilience was mapped for counties containing soils included in the study. Panel (B) depicts the relative resilience of the shrubland associations on the three soils included in the study (coarse to fine depicted left to right). Each pair of basins represents alternative grass-dominated (upper basin) and shrub-dominated (lower basin) states. Resilience was not overcome in shrub-dominated states colored green. Blue basins indicate a regime shift from shrub-dominated to grass-dominated states. The ball for each set of basins depicts the trajectory (dashed arrows) of the state during the four years of the study based on shrub and herbaceous cover data. Figure adapted from Walker et al. (2004).

may be present in this association, but its contribution to resilience and transformability was not observed in this study due to the lack of a decline of any dominant species. These findings are consistent with the literature; ecosystems with higher response diversity have greater adaptive capacity (Scheffer et al. 2012). Lower response diversity might therefore explain the lower resilience on CKB soils, where reductions in mesquite dominance were not compensated for by concomitant increases in other species.

Conclusion

Operationalizing resilience in restoration interventions has proven extraordinarily difficult since the concept was introduced four decades ago (see Holling 1973). Difficulties in applying the concept are often a function of the complexities of interactions in ecological systems and their influence on underlying mechanisms driving transitions among alternative states. Complex systems often exhibit nonlinear dynamics (Peters et al. 2004), and the resilience of alternate configurations depends on the interactions among the species present in the system and their abiotic environment, increasing the complexity of system responses to disturbance (Carpenter et al. 2001, Anderies et al. 2002, Allen et al. 2005). In this study, we show a simple approach that can provide a basis for prioritizing restoration actions by identifying differences in the relative resilience of a woody-dominated

Table 6. Mean change and standard error in relative abundance (contribution of each species to total woody cover) between 2010 and 2013 of the eight most dominant species for each of the brush removal treatments applied in 2011 (untreated control, hand-cutting followed by herbicide, and roller-chopping) on different soil types (ABC is sandy, WEB is sandy loam, CKB is clay).

Soil type and species	Scientific name	Control		Cut-herbicide		Mechanical	
		Mean	SE	Mean	SE	Mean	SE
ABC							
Mesquite	*Prosopis glandulosa*	**−0.014**	**0.014**	**−0.095**	**0.054**	**−0.031**	**0.024**
Blackbrush	*Acacia rigidula*	−0.005	0.010	0.010	0.014	0.004	0.018
Whitebrush	*Aloysia gratissima*	**0.022**	**0.011**	**0.067**	**0.037**	**0.003**	**0.024**
Twisted acacia	*Acacia schaffneri*	0.002	0.009	0.015	0.008	−0.002	0.023
Hackberry	*Celtis ehrenbergiana*	0.017	0.023	0.028	0.027	0.044	0.019
Guyacon	*Guaiacum angustifolium*	0.010	0.011	−0.013	0.023	0.017	0.009
Persimmon	*Diospyros texana*	−0.002	0.018	−0.067	0.036	−0.031	0.022
Brasil	*Condalia hookeri*	−0.062	0.022	−0.073	0.020	−0.034	0.020
WEB							
Mesquite	*Prosopis glandulosa*	−0.015	0.013	−0.022	0.016	−0.019	0.038
Blackbrush	*Acacia rigidula*	0.001	0.008	0.035	0.038	−0.014	0.014
Whitebrush	*Aloysia gratissima*	0.018	0.004	0.041	0.012	0.024	0.019
Twisted acacia	*Acacia schaffneri*	0.004	0.008	−0.016	0.030	0.012	0.019
Hackberry	*Celtis ehrenbergiana*	**0.006**	**0.008**	**0.004**	**0.014**	**0.047**	**0.031**
Guyacon	*Guaiacum angustifolium*	0.018	0.012	−0.027	0.012	−0.017	0.006
Persimmon	*Diospyros texana*	0.008	0.005	−0.023	0.012	−0.015	0.009
Brasil	*Condalia hookeri*	−0.016	0.009	−0.015	0.018	−0.021	0.003
CKB							
Mesquite	*Prosopis glandulosa*	**−0.028**	**0.021**	**−0.162**	**0.055**	**0.009**	**0.021**
Blackbrush	*Acacia rigidula*	0.013	0.006	−0.032	0.019	−0.033	0.031
Whitebrush	*Aloysia gratissima*	0.032	0.013	−0.014	0.060	0.030	0.039
Twisted acacia	*Acacia schaffneri*	0.021	0.017	0.042	0.026	0.000	0.013
Hackberry	*Celtis ehrenbergiana*	−0.003	0.004	0.005	0.013	0.015	0.010
Guyacon	*Guaiacum angustifolium*	0.000	0.020	−0.016	0.023	−0.064	0.019
Persimmon	*Diospyros texana*	−0.008	0.020	−0.005	0.005	−0.003	0.009
Brasil	*Condalia hookeri*	−0.008	0.002	−0.004	0.012	−0.021	0.009

Note: Species shown in boldface type differed significantly in relative abundance among treatments within a soil type.

state to common brush control techniques across an environmental gradient. In our study region, our results show mechanical and chemical brush controls are most likely to meet long-term restoration goals on fine-textured clay soils, where shrubland resilience to these treatments is lowest. Similar experimental approaches can provide a foundation for operationalizing resilience in restoration and prioritizing management actions, especially if experiments link underlying environmental characteristics to parameters in existing models when seeking to determine the relative resilience of specific states to restoration interventions. Restoration prioritization is critical given the limitations associated with broad-scale application of mechanical and chemical brush control (Twidwell et al. 2013*a*). For example, U.S. federal agencies spend tens of millions of dollars ($US) on mechanical and chemical brush removal treatments in an effort to restore grass dominance in this study region and the surrounding ecoregions; yet, the costs of these treatments limit their use to a small amount of the land area within their management jurisdiction (Twidwell et al. 2013*a*). Given the extremely cost-prohibitive nature of mechanical and chemical brush control, determining the relative resilience of a shrubland across a gradient of soil textures can provide a means for achieving the most effective use of funds for increasing the effectiveness and duration of brush removal.

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