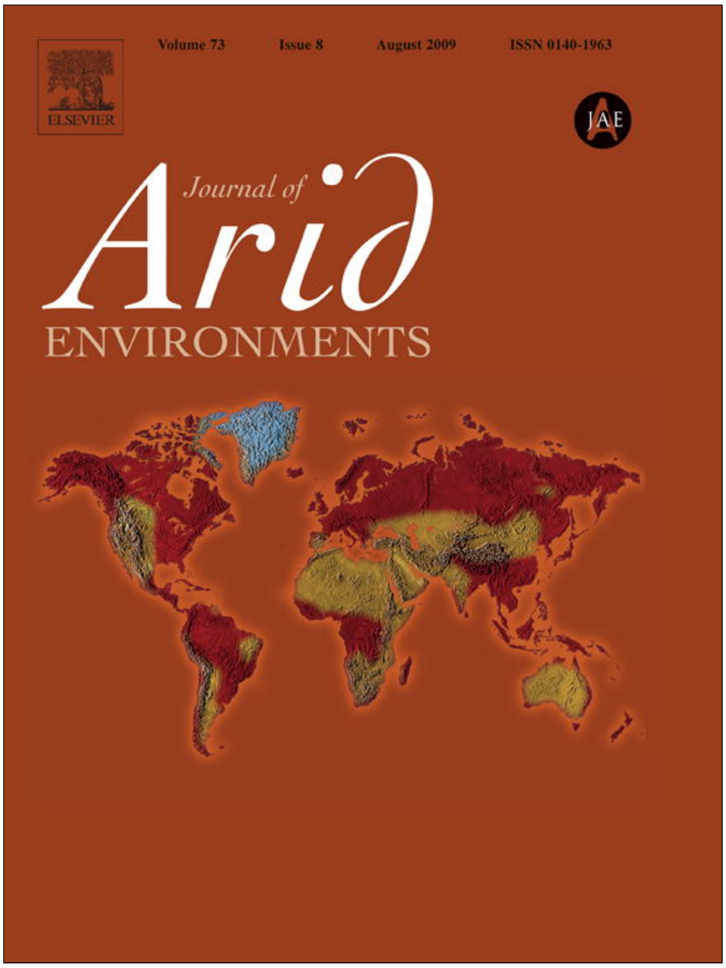
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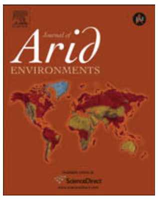

Review

Post-fire plant recovery in the Mojave and Sonoran Deserts of western North America

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ABSTRACT

Increasing wildfire activity is one of the most pressing management concerns in arid lands of the American West. To examine post-fire recovery of perennial vegetation in the Mojave and Sonoran Deserts, I analyzed data systematically synthesized from the literature. Post-fire sprouting by desert perennials is generally limited but varies among species. For example, only 3–37% of *Larrea tridentata* sprouted compared to 64–86% of *Yucca schidigera*. Four of five studies measuring recovery of perennial cover reported close relationships ($r^2 = 0.67–0.99$) between time since fire (TSF) and cover. In fact, three studies measuring the longest TSF ($\geq$37 years) found that cover had returned to within 10% cover of unburned areas within approximately 40 years. Conversely, post-fire species composition exhibited little convergence with unburned composition in five of six studies even 47 years after fire. *Sphaeralcea ambigua*, *Gutierrezia* spp., *Achnatherum speciosum*, *Encelia* spp., *Hymenoclea salsola*, and *Baileya multiradiata* had the highest burned:unburned abundance ratios, although overall post-fire community composition differed between the Mojave and Sonoran Deserts. Analyzing the literature as a whole suggested some generalities (e.g., that perennial cover reestablishes faster than composition), but more work is required for improving specific knowledge about plant recovery among fires, sites, species, and climates.

1. Introduction

Recovery and succession following disturbances are poorly understood in arid lands, probably partly due to the long time periods over which perennial vegetation changes compared to more mesic regions (McAuliffe, 1988). With desertification and increasing human use of arid lands, understanding recovery is important both for developing theory about community dynamics and for practical purposes including modeling carbon storage, designating future land uses, or planning revegetation treatments (Lovich and Bainbridge, 1999; Leger, 2008). As in mesic regions, plant recovery following disturbance in arid lands hinges on two basic factors: legacies (e.g., individual plants, seeds) that persist through the disturbance and their subsequent response to the post-disturbance environment; and propagules (seeds and mobile vegetative reproductive structures such as cactus joints) arriving from off-site and their response. In turn, contingency effects, such as disturbance severity (Webb et al., 1987), community invasibility by exotic species (Chambers et al., 2007), local species adaptations to changed conditions (Leger, 2008), and precipitation (Bakker et al., 2003), affect these basic factors. This complexity makes recovery rates and trajectories difficult to predict, suggesting that analyzing data from many different disturbances and studies could be useful for identifying potential patterns.

Plant community cover and species composition are major measures of recovery to either pre-disturbance or conditions on nearby areas not experiencing the disturbance. Legacies and off-site propagules can affect these measures. Sprouting by legacy perennials can both re-build cover while reestablishing pre-disturbance species. Sprouting vigor also hinges upon many contingency effects: disturbance severity affects biomass available to support sprouting and dictates post-disturbance conditions, timing influences carbohydrate levels for inducing sprouting, and climate affects opportunities for sprouting and sprout survival (Whelan, 1995). Sprouting frequency likely is species specific, with some species unable to sprout (Minnich, 1995). In addition to being influenced by individuals that sprout or escape the disturbance, community composition is affected by on-site propagules and dispersal from off-site. However, many long-lived perennial species do not form large, persistent soil seed banks (Kemp, 1989) or have abilities for long-distance seed dispersal (Bowers et al., 1997). These observations suggest that

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failing averting the disturbance or sprouting, there is potential for slow recovery of long-lived desert perennials. Furthermore, even in the absence of additional disturbance, new compositional trajectories or stable states could arise that do not result in returning to pre-disturbance or undisturbed conditions. This may be especially true for novel disturbances, to which native ecosystems have not evolved, or if external influences (e.g., climate, nitrogen deposition, exotic species abundance) have changed (e.g., Chambers et al., 2007).

The Mojave and Sonoran Deserts of western North America exemplify an arid region increasingly being exposed to a novel disturbance: fire. Although native vegetation contributes to fuel loads, exotic annual plants (e.g., *Bromus* and *Schismus* spp., *Pennisetum ciliare*) have augmented fuel load and continuity in these deserts (Brooks and Minnich, 2006). These exotic plants enable fire spread, in contrast to historical or exotic-free conditions where sparse and discontinuous fuels limit fire extent (Esque and Schwalbe, 2002). Fire is not thought to have been prevalent historically in these deserts, prior to pervasive exotic species invasion since the early to mid-1900s (e.g., Rogers and Vint, 1987; Brooks and Minnich, 2006). More than 677,000 ha burned in the Mojave Desert from 1980 to 2005, consuming 5% of the land area of this desert (Brooks and Matchett, 2006). In the Arizona Upland Subdivision of the Sonoran Desert (Brown, 1994), 100,000 ha burned in a single fire complex, the 2005 Cave Creek Fire (Allen, 2007). This fire was the second largest fire ever recorded in the state of Arizona in the United States. These examples illustrate that fire is now a major disturbance to which biota and human uses of these deserts have only recently been exposed.

No synthesis is available of post-fire plant recovery in these deserts, where increasing portions of the landscape are recovering from fires. Systematic reviews provide a reproducible method for synthesizing literature and evaluating evidence for addressing hypotheses or questions (Fazey et al., 2004). The systematic approach differs from traditional reviews by including all literature meeting pre-defined search criteria, which can help support numerical analyses for providing balanced appraisals of available data. These syntheses can identify patterns and trends that may not be apparent by considering original studies on a case-by-case basis. Shortages in original data also can be recognized since all available data meeting search criteria are included. Synthesized data can be analyzed using several different techniques, ranging from descriptive statistics to inferential statistics and meta-analysis (Stewart et al., 2005). Suitable techniques depend on the objectives of the analyses, nature of the data, and number of studies constituting the sample size. Although uncommon for analyzing data in systematic reviews, multivariate techniques such as ordination also could be used to analyze community data derived from the literature. In this approach, data from studies would be included in a species × study matrix resembling original community studies that consist of species × sampling unit matrices (McCune and Grace, 2002).

I used a systematic review approach and a combination of descriptive statistics, regression, community similarity analysis, and ordination techniques to evaluate five questions about post-fire perennial plant recovery in the Mojave and Sonoran Deserts:

(1) What are post-fire sprouting frequencies of desert species?
(2) How quickly does perennial plant cover reestablish following fire?
(3) Are species composition and time since fire (TSF) related?
(4) Which post-fire species exhibit the highest burned:unburned abundance?
(5) Does post-fire species composition differ between deserts?

2. Materials and methods

2.1. Study area

The approximately 124,000-km^2 Mojave Desert (Rundel and Gibson, 1996) is in the southwestern United States, and the 310,000-km^2 Sonoran Desert (Crosswhite and Crosswhite, 1982) is in both the southwestern United States and Mexico. The two deserts share a boundary at the southeastern part of the Mojave and the northwestern part of the Sonoran. Both are warm deserts, though the Sonoran has warmer winter temperatures and exhibits a more subtropical climate (Brown, 1994). The Mojave is predominately a winter rainfall desert, whereas precipitation is more evenly distributed throughout the year in the Sonoran Desert. An example weather station (Las Vegas, Nevada, USA, 662 m elevation) in the eastern Mojave Desert has reported averages of 11 cm/yr of precipitation, July daily maximum temperature of 40 °C, and January daily minimum temperature of 1 °C (1937–2007 records; WRCC, 2008). A weather station (Ajo, Arizona, USA, 1914–2007 records) at a comparable elevation (549 m) in the north-central Sonoran Desert has reported the following for the same measures: 21 cm/yr of precipitation, 39 °C July average maximum, and 5 °C January average minimum. Prominent, characteristic species that differ between the deserts include the tree *Yucca brevifolia* inhabiting the Mojave and the columnar cactus *Carnegiea gigantea* in the Sonoran Desert (Brown, 1994). Both deserts exhibit a shrubland physiognomy, with scattered cacti, forbs, and perennial grasses (Keeler-Wolf, 2007; Schoenherr and Burk, 2007). *Larrea tridentata* shrublands occupy vast areas in both deserts. Annuals comprise major portions of live biomass during moist periods and are often most prevalent below shrub canopies, although interspaces also are inhabited depending on the annual species, site factors, and precipitation (Beatley, 1974).

2.2. Literature search

I obtained literature in 2008 using a reproducible procedure consisting of: (1) searching the article databases of Agricola (covers the 1500s to the present), Biological Abstracts (1969–present), JSTOR (covers individual journals since their inception up to 2005–2006), and Google Scholar (http://scholar.google.com/; all years) using combinations of the key words succession, disturbance, fire, recovery, change, Mojave, and Sonoran in the article title and key words; (2) examining reference lists in located papers; (3) searching other reviews of Mojave and Sonoran Desert vegetation including Humphrey (1963), Brooks and Minnich (2006), Keeler-Wolf (2007), Schoenherr and Burk (2007), and desert species in the U.S. Forest Service Fire Effects Information System (http://www.fs.fed.us/database/feis/); and (4) running a cross-reference search in Google Scholar to examine papers that cited articles located by procedures 1–3. To qualify for inclusion in the analysis, studies had to meet the following criteria: monitor vegetation after wildfire or prescribed fire in the Mojave or Sonoran Desert, report quantitative data on post-fire sprouting or plant community composition, and include data on unburned areas for comparison with burned areas. Since most studies reported data on perennial rather than annual composition, the analysis included only studies of perennials based on the Natural Resources Conservation Service (NRCS, 2008) classification of longevity. Only published data were included, except for Abella et al. (2008) for which I had access to full community data.

2.3. Data analysis

For assessing sprouting frequency, I constructed a study × species matrix of sprouting percentages. I used simple linear regression to examine the relationship of TSF and perennial cover within studies.

Table 1
Summary of studies meeting inclusion criteria that examined post-fire perennial plant recovery in the Mojave and Sonoran Deserts of western North America.

Reference	Veg. type[a]	No. fires[b]	Fire size (ha)	Data type		Comm. measure	Time since fire[e]	
				Sprout	Comm.[d]		Years	Method
Mojave Desert								
Abella et al. (2008)	CR-BB	1	348	×	×	Cover	2	–
Brooks and Matchett (2003)	BB	3	–[c]		×	Cover	6–14	CR
Callison et al. (1985)	BB	7	–		×	Cover	1–37	CR
Lei (1999)	BB	4	8–4000		×	Density	1–17	CR
Medica et al. (1994)	MS	1	35		×	Cover, density	2–8	PP
Minnich (1995)	BB, JT	13	–	×	×	Cover, density	1–47	CR
Webb et al. (2003)	BB	3	–		×	Cover, density	4–41	PP
Sonoran Desert								
Abella et al. (in press)	UP-MS	1	2		×	Cover	2	–
Brown and Minnich (1986)	CR-MS	3	500–6000	×	×	Cover	3–5	–
Cave and Patten (1984)	UP-MS	2	1–84		×	Density	1-2	–
McLaughlin and Bowers (1982)	UP-MS	1	11,500	×	×	Cover, density	1–2	–
O'Leary and Minnich (1981)	CR-MS	1	3725		×	Frequency	5	–
Rogers and Steele (1980)	UP-MS	2	65–105	×		–	4	–
Wilson et al. (1995)	UP-MS	1	–		×	Density	1	–

[a] General vegetation types listed in the source publications: BB, blackbrush (*Coleogyne ramosissima*) shrubland; CR, creosote (*Larrea tridentata*) shrubland; JT, Joshua tree (*Yucca brevifolia*) woodland; MS, mixed shrub; and UP, Arizona Upland Subdivision of the Sonoran Desert (giant saguaro [*Carnegiea gigantea*]-small tree-mixed shrub).
[b] Number of fires examined for which unburned data were available for comparison.
[c] Size not provided in source publication.
[d] Community data representing the species present and their abundance.
[e] Time after fire in which measurements were made, and methods for studies that reported recovery through time: CR, chronosequence; PP, permanent plots.

I averaged cover within studies that reported data from multiple fires of the same TSF, and I did not include cover of *Agropyron* spp. in Callison et al.'s (1985) study since these species were seeded. To analyze literature reporting community data, I extracted the data from the original publication, updated species nomenclature to NRCS (2008), and computed a relative measure of abundance for each species in each study. Relative abundance was computed as the proportion a given species contributed to the total abundance of all species in a sampling unit (plot, transect, or site) within a study (McCune and Grace, 2002). This measure was expressed as a percentage summing to 100% on a sampling unit basis when all species were included. I used this relative measure to standardize abundance because studies reported plant cover, density, or frequency, and this standardization also permitted the isolation of community composition from total community abundance. To explore changes in post-fire species composition through time, I computed a Sørensen similarity index (McCune and Grace, 2002) of burned:unburned species composition (based on relative abundance) and regressed TSF with this index within studies. I also computed a similarity matrix comparing burned sampling units for each TSF within studies to analyze trajectories in burned composition. I analyzed patterns in individual species by calculating a ratio of burned:unburned relative abundance based on mean relative abundance in all community studies. Species abundances were averaged across fires within a study if that study examined multiple fires.

To examine variation in community composition between the Mojave and Sonoran Deserts, I averaged composition on a study basis separately for burned and unburned areas. I used non-metric multidimensional scaling (NMS; autopilot thorough setting) in the software PC-ORD (McCune and Mefford, 1999) to ordinate burned and unburned species composition. To isolate the relative difference between burned and unburned composition, I further ordinated burned composition using unburned composition as a covariate using the NMS successional vector subroutine.

3. Results

3.1. Literature

Fourteen studies met inclusion criteria for analysis, seven in both the Mojave and Sonoran Deserts (Table 1). Five of the studies reported sprouting data and 13 studies reported community data. Six studies measured recovery through time using either chronosequence or permanent plot approaches. Three studies made measurements $\geq$37 years after fire, with 47 years being the longest TSF. All of the studies examined wildfires except for Cave and Patten (1984), who included one site burned by prescribed fire.

Table 2
Percent of plants sprouting after fire in the Mojave and Sonoran Deserts in western North America.

Species	Reference[a]				
	1	2	3	4	5
Acacia constricta					68
Acacia greggii					75
Ambrosia deltoidea			1		1
Ambrosia dumosa		8			
Brickellia coulteri					0
Calliandra eriophylla					68
Canotia holacantha					0
Carnegiea gigantea			0		0
Cylindropuntia acanthocarpa		8	0		3
Cylindropuntia bigelovii		6			2
Cylindropuntia leptocaulis					0
Echinocereus engelmannii					0
Echinocereus fasciculatus			3		
Encelia farinosa		5			0
Ephedra nevadensis			9		
Ephedra spp.					2
Ferocactus cylindraceus					5
Fouquieria splendens					0
Hyptis emoryi		40			
Justicia californica		57			
Krameria grayi					18
Larrea tridentata	5	3	37	18	7
Lycium spp.					21
Mammillaria grahamii					0
Mammillaria spp.			2		
Olneya tesota					0
Parkinsonia microphylla			25		13
Prosopis juliflora			32		5
Simmondsia chinensis					15
Yucca brevifolia				17	
Yucca schidigera	64			86	

[a] 1, Abella et al. (2008); 2, Brown and Minnich (1986); 3, McLaughlin and Bowers (1982); 4, Minnich (1995); and 5, Rogers and Steele (1980).

3.2. Sprouting

Post-fire sprouting was measured for 31 species in one or more studies (Table 2). Sprouting frequency varied sharply among species within studies. Rogers and Steele (1980), for instance, reported that only 1% of *Ambrosia deltoidea* sprouted compared to 75% of *Acacia greggii*. On the other hand, there was less variation in sprouting of a given species among studies for species measured in more than one study. For example, two studies both recorded 1% sprouting for *A. deltoidea* and 0% for *C. gigantea*, and all studies recorded $<$10% sprouting for *Cylindropuntia acanthocarpa*, *Cylindropuntia bigelovii*, and *Encelia farinosa*. Sprouting of *L. tridentata*, measured in all five studies, ranged from 3 to 37% with three of the studies reporting $\leq$7%. *Yucca schidigera* exhibited the highest sprouting, ranging from 64 to 86%, among the nine species measured in two or more studies.

3.3. Cover

Four of the five studies measuring reestablishment of perennial cover reported close relationships ($r^2 = 0.67$–0.99) between TSF and cover (Fig. 1). In the three studies measuring the longest TSF ($\geq$37 years), cover had returned to within 10% cover of unburned areas within approximately 40 years. Moreover, two studies reported recovery to the same (Callison et al., 1985) or higher (Minnich, 1995) cover than unburned areas within 40 years.

3.4. Species composition

In contrast to cover, burned species composition showed weak trends for resembling unburned composition with increasing TSF among six studies (Fig. 2). Half of the studies, in fact, reported negative relationships of TSF and burned:unburned similarity. A permanent plot study, Medica et al. (1994), found the strongest positive relationship with similarity increasing by 17% from 2 to 8 years after fire.

The relative abundance of some species was higher on burned than unburned areas (Table 3). Other species, such as *Ephedra nevadensis*, were versatile with similar relative abundance in both burned and unburned habitat even if their absolute abundance declined on burns. Eight species or genera, consisting of *A. deltoidea*, *Hymenoclea salsola*, *E. nevadensis*, *Gutierrezia*, *Encelia*, *Chamaesyce polycarpa*, *S. ambigua*, and *Achnatherum speciosum*, comprised 50% of the total relative abundance on burns averaged across studies. In contrast, *Coleogyne ramosissima* and *Grayia spinosa* were among the major post-fire decreasers, with *Coleogyne* exhibiting a 15-fold decline and *Grayia* not recorded after fire.

3.5. Between-desert variation

Both burned and unburned species composition differed between the Mojave and Sonoran Deserts (Fig. 3a, b). Unburned composition, however, was greater than two-fold more similar between deserts (15 ± 22% [Sørensen similarity mean ± standard deviation]) than burned composition (7 ± 10%). Unburned

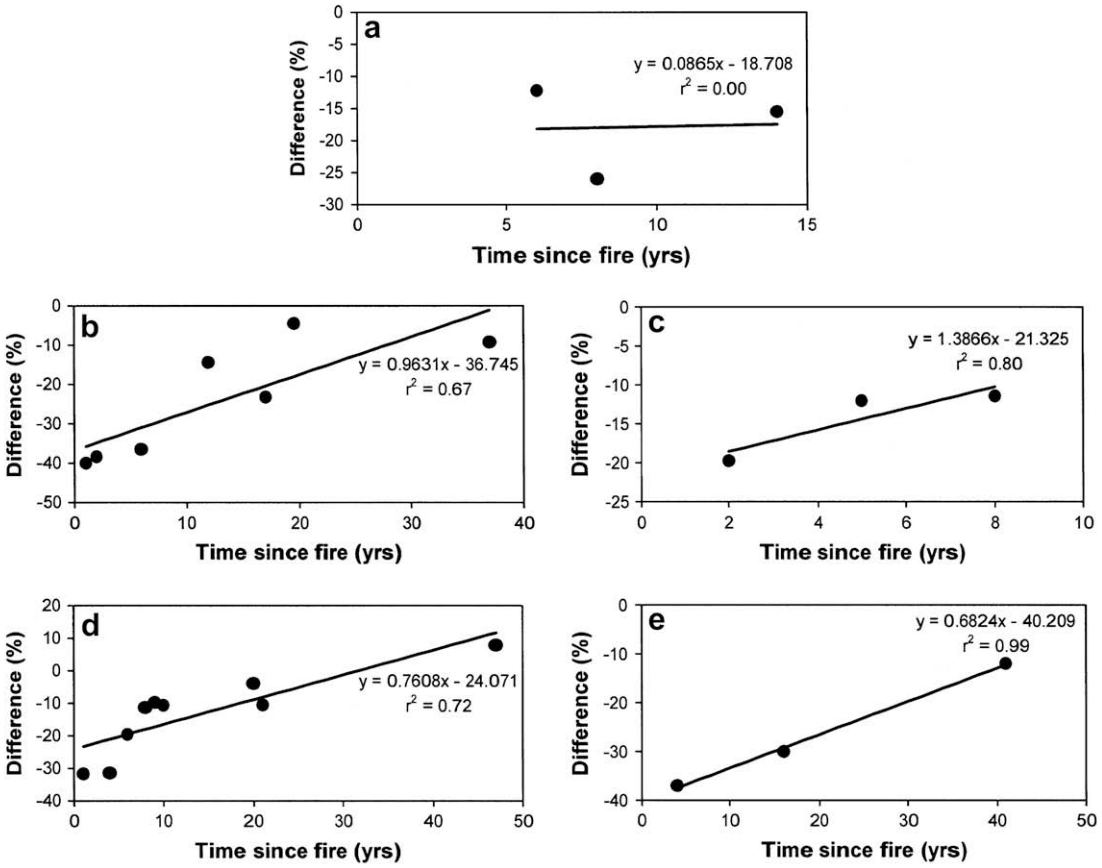

Fig. 1. Relationship of time since fire and total perennial plant cover for five studies using either chronosequence (a, b, and d) or permanent plot (c and e) approaches in the Mojave Desert of western North America. *Y*-axes are burned minus unburned cover to provide a measure of recovery standardized for unburned cover where values of zero represent equal burned and unburned cover. (a) Brooks and Matchett (2003). (b) Callison et al. (1985). (c) Medica et al. (1994). (d) Minnich (1995). (e) Webb et al. (2003).

composition also was more similar than burned composition among studies within deserts. The similarity of species composition among studies averaged 39 ± 23% (unburned) and 16 ± 14% (burned) in the Mojave and 17 ± 24% (unburned) and 7 ± 6% (burned) in the Sonoran Desert. When burned composition was standardized using unburned composition as a covariate to provide a measure of the relative difference between burned and unburned areas, burned composition remained different between deserts (Fig. 3c). Thus, both raw burned composition and the relative change between burned and unburned composition differed between deserts. Variation in individual species between deserts on burned areas portrayed in the ordinations was less clear than for overall species composition, although some species (e.g., *Yucca baccata*, *Prunus fasciculata*) did show affinities for one desert.

4. Discussion

4.1. Analysis limitations

Several factors could have affected results. One challenge in analyzing plant community data derived from the literature is that the abundance of all species is not necessarily reported due to journal space limitations or other reasons. For example, Minnich (1995) reported the most abundant species and included an "other" species category. Thus, there were species that could not be included in this analysis of that study. However, the "other" species in Minnich's (1995) study constituted an average of only 6% of relative community cover. Similarly, McLaughlin and Bowers (1982) included an "other" category that comprised only a "trace" of cover, and Brooks and Matchett (2003) reported the 15 most abundant species. The other 10 community studies indicated reporting data for all perennial species. This analysis also did not include annuals, which only half the studies measured. Annuals constitute major portions of species richness and biomass in moist years, underscoring a need for future research that determines long-term fire effects on annual communities (Esque and Schwalbe, 2002).

Studies reported different measures of abundance including cover only (4 studies), density only (3 studies), frequency only (1 study), and cover and density or frequency (5 studies). Thus, I was able to use cover as the measure to derive relative abundance in 9 of 13 studies (69%). Cover, density, and frequency emphasize different components of prominence in a community, although the relativization procedure I employed placed abundance on the same scale summing to 100% on a study basis.

The analysis of TSF effects on cover and composition were restricted to the Mojave Desert, which contained the only studies reporting chronosequence or permanent plot data for more than a few years after fire (Table 1). Although it meant that comparisons of Mojave and Sonoran Desert composition were derived from studies of different TSF, I chose to average TSF composition of the Mojave studies to take advantage of as much of the available data as possible. Correlation coefficients (r^2) of TSF and composition also were either ≤ 0.3 (4 of 6 studies) or Sørensen similarity differed by $<20\%$ from the shortest to longest TSF (remaining two studies; Fig. 2). This suggested that averaging composition across TSF was justified because there were no strong, directional, compositional shifts with TSF.

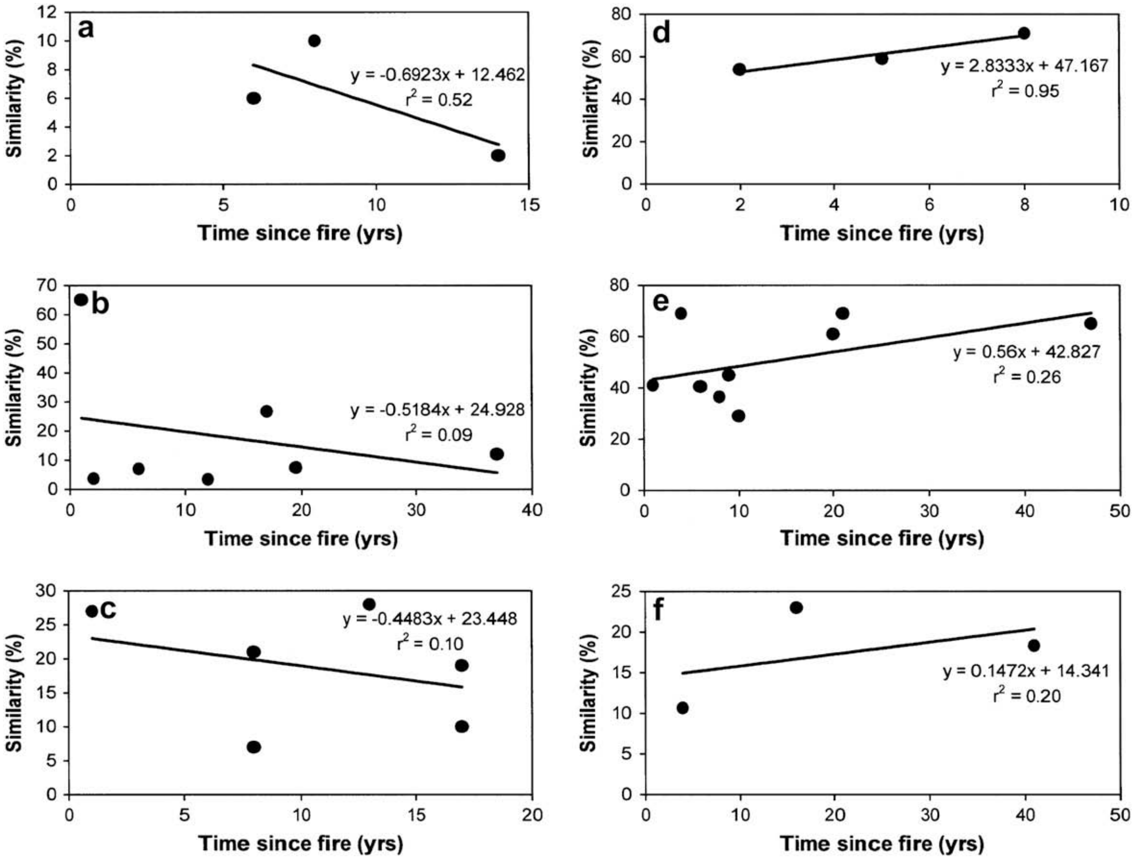

Fig. 2. Relationship of time since fire and the Sørensen similarity of burned and unburned perennial species composition for six studies in the Mojave Desert of western North America. Sørensen similarities range from 0 to 100%, with 100% representing identical species compositions. (a) Brooks and Matchett (2003). (b) Callison et al. (1985). (c) Lei (1999). (d) Medica et al. (1994). (e) Minnich (1995). (f) Webb et al. (2003).

As Whelan (1995) noted, individual fires differ in physical characteristics such as flame length or rate of spread, with these characteristics hinging upon topography, fuel, and fire weather. Little information about fire characteristics was given about fires within or among studies. Obtaining information on fire characteristics can be difficult, especially for large fires where fire behavior varies spatially, because these studies were retrospective and evaluated fires that had occurred as early as the 1940s (Minnich, 1995). Potential differences in fire characteristics do not preclude the categorical burned–unburned comparisons that were the focus of this study, although fire characteristics in combination with post-fire climate could be important sources of variation in fire responses within and among studies.

4.2. *Sprouting*

Although only five studies measured post-fire sprouting, some trends appeared evident from available data. In comparing species, Cactaceae had notably low sprouting percentages, with none of the nine measured species exhibiting sprouting >8% (Table 2). There was also some evidence that species with low-growing, compact crowns have low sprouting percentages. For instance, two *Ambrosia* species and *E. farinosa* never exceeded 8% sprouting. This limited sprouting could be related to flames consuming the entire aboveground biomass (Brown and Minnich, 1986) and the fact that these species are prodigious seed producers (Tesky, 1993), thereby not evolving strong sprouting capability. However, taller plants did not necessarily exhibit consistently high sprouting. The tree *Yucca brevifolia*, for example, sprouted five-fold less frequently than the medium-tall shrub *Y. schidigera* in Minnich's (1995) study. Although *Y. schidigera* had the highest average sprouting for species measured in two or more studies, it could be informative to assess survival of the sprouts longer than the <5 years used in most studies (c.f. Minnich, 1995). Narog and Wilson (2003) highlighted that fire-related mortality of *C. gigantea* continued 10 years post-fire in the upper Sonoran Desert, and delayed mortality of plants in general is not uncommon after fire (Whelan, 1995). In addition to canopy morphology and plant traits, fuel loads below perennial canopies could be informative for explaining both avoidance of fire and sprouting capability, but these relationships have been little studied (Patten and Cave, 1984; Brooks and Minnich, 2006).

Although I found that sprouting overall was limited among the 31 species examined in Mojave and Sonoran Desert studies, it is unclear how general this finding may be for other arid lands. For example, 16 months after a summer burn in the Chihuahuan Desert in western Texas, Worthington and Corral (1987) classified only a few species (e.g., *Gutierrezia* spp.) as non-sprouters. Sixteen species were classified as sprouters, with 11 of these species exhibiting 100% sprouting. This high sprouting could be related to fire intensity, as these authors judged the fire to be a "cool" burn and it was a small fire of only 30 ha. Based on observations at 10 fires in shrublands of the northern Chihuahuan Desert in New Mexico, Kittams (1972) observed that 12 of 14 major shrub/tree species had sprouting abilities. Little information on sprouting was found from other deserts. This is an important research need because regeneration events by seed for many long-lived desert perennials are infrequent (Callison et al., 1985; Guo, 2004), so sprouting could be critical to maintain post-fire populations of these species. For species capable of sprouting, post-fire sprouting depends on many factors including the timing of the burn and the degree of plant damage (in turn hinging upon fire characteristics, fuel, and traits of the target species; Rogers and Steele, 1980; Minnich, 1995; Brooks and Minnich, 2006). Further research is warranted to determine sprouting potential after different types and timings of fires for desert perennial communities, and whether treatments are feasible to induce sprouting or promote survival of sprouts when assisting revegetation is a management goal.

4.3. *Cover, composition, and time since fire*

Although perennial cover had reestablished to near levels of unburned areas within approximately 40 years after fire, different species contributed to the cover on burned compared to unburned areas. Fire largely replaced communities of long-lived dominants such as *C. ramosissima* or *C. gigantea* with species (e.g., *Encelia* spp.) considered to be shorter lived (Vasek, 1983). Even 40 years after fire, there was little indication in five of six studies that burned species composition was converging with unburned composition. In fact, some studies suggested a trend for composition to further diverge with increasing TSF (Fig. 2). There are many examples of persistent disturbance effects on composition following other types of disturbance in these deserts. Guo (2004), for instance, found that composition changed little following 50 years of protection from grazing and human disturbance in the Sonoran Desert. In the western Mojave Desert, Webb et al. (1987) concluded that centuries were required for long-lived *C. ramosissima* to recolonize debris flows and cleared pipeline areas. Climate change, nitrogen deposition, and resurgence of exotic grasses creating potential for

Table 3
Relative abundance of the 30 most abundant perennial species in burned and unburned species composition in the Mojave and Sonoran Deserts of western North America. Species are arranged in order of decreasing burned:unburned relative abundance.

Species	Burned	Unburned	Ratio[b]
	Mean (no. studies)[a]		
Sphaeralcea ambigua	5.2 (6)	0.2 (2)	21.0
Gutierrezia microcephala	1.2 (1)	0.1 (1)	16.3
Achnatherum speciosum	4.4 (4)	0.6 (5)	7.7
Gutierrezia sarothrae	5.3 (3)	0.8 (3)	6.6
Senna covesii	1.2 (1)	0.2 (1)	5.6
Encelia virginensis	3.9 (4)	0.7 (4)	5.6
Thamnosma montana	2.2 (4)	0.4 (4)	5.0
Hymenoclea salsola	7.1 (5)	2.2 (5)	3.2
Chamaesyce polycarpa	5.3 (1)	1.7 (1)	3.1
Baileya multiradiata	3.1 (3)	1.0 (2)	3.1
Prunus fasciculata	1.0 (4)	0.4 (4)	2.7
Calliandra eriophylla	0.9 (1)	0.4 (1)	2.0
Astragalus nuttallianus	1.8 (2)	1.2 (2)	1.5
Parkinsonia microphylla	4.6 (3)	3.2 (3)	1.4
Ephedra nevadensis	6.6 (7)	4.6 (7)	1.4
Pleuraphis rigida	2.6 (1)	2.2 (2)	1.2
Encelia farinosa	2.2 (4)	1.8 (4)	1.2
Cylindropuntia echinocarpa	1.4 (4)	1.4 (5)	1.0
Lycium andersonii	2.6 (5)	2.7 (6)	1.0
Yucca baccata	0.5 (3)	0.9 (3)	0.6
Menodora spinescens	0.4 (2)	0.8 (3)	0.5
Cylindropuntia acanthocarpa	0.6 (5)	1.1 (6)	0.5
Yucca schidigera	0.6 (3)	1.1 (3)	0.5
Ambrosia deltoidea	8.2 (4)	16.9 (4)	0.5
Larrea tridentata	3.0 (5)	7.9 (6)	0.4
Ambrosia dumosa	1.0 (4)	3.0 (3)	0.3
Yucca brevifolia	0.4 (3)	1.5 (3)	0.3
Ericameria cooperi	0.2 (3)	1.8 (3)	0.1
Coleogyne ramosissima	1.8 (6)	27.5 (7)	0.1
Grayia spinosa	0.0 (0)	2.1 (3)	0.0

[a] Mean relative abundance (in percent, averaged for 13 studies, where absences equal zero) and the number of studies (of 13) in which a species was recorded. Relative abundance (derived from cover, density, or frequency depending on the source publication) was calculated on an individual study basis as the relative proportion of the total abundance for all species a given species contributed. Values summed to 100% for each individual study. The 30 species in the table comprise 79% of the total relative abundance for burned composition and 90% for unburned composition.

[b] Ratio of burned:unburned relative abundance.

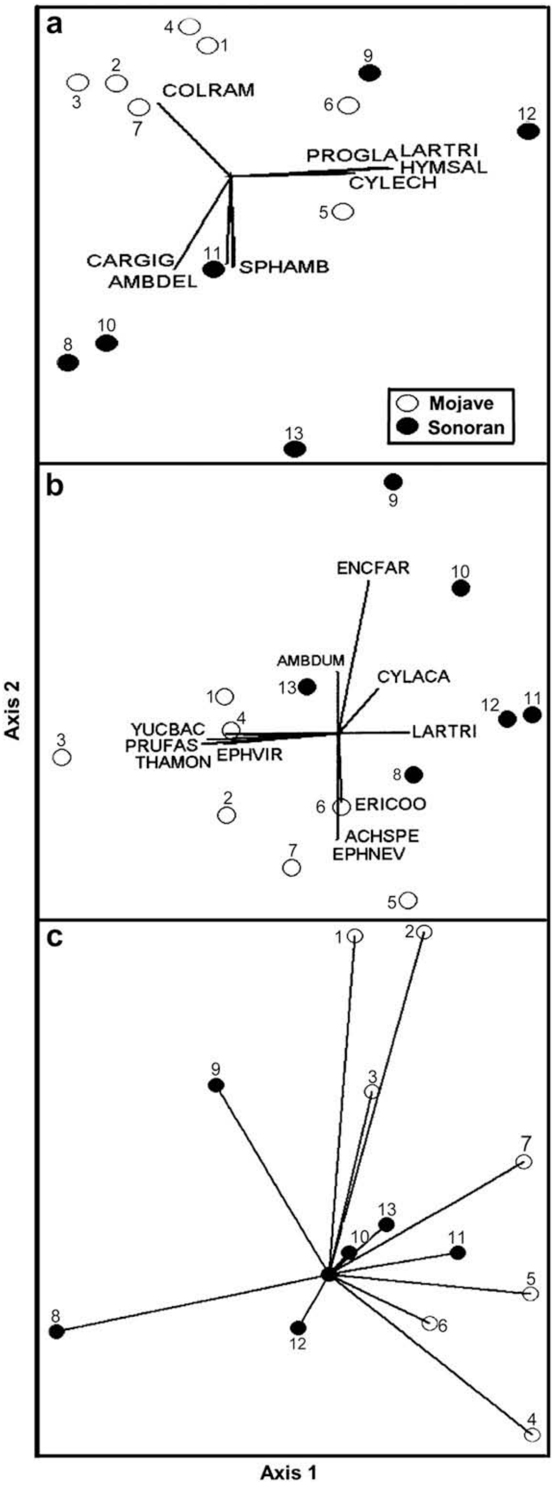

Fig. 3. Non-metric multidimensional scaling ordination of (a) unburned, (b) burned, and (c) standardized burned perennial species composition for 13 studies measuring post-fire plant recovery in the Mojave and Sonoran Deserts of western North America. The total numbers of species in ordinations were 104 (a), 114 (b), and 127 (c). In (a) and (b), species are vectors where vector lengths and directions are proportional to correlations with ordination axes (r^2 cutoff = 0.40 for (a) and 0.25 for (b)). In (c) burned composition was standardized with unburned composition as a covariate where vector lengths depict the relative deviance of burned from unburned composition. Species abbreviations for (a) and (b): ACHSPE, *Achnatherum speciosum*; AMBDEL, *Ambrosia deltoidea*; AMBDUM, *Ambrosia dumosa*; CARGIG, *Carnegiea gigantea*; COLRAM, *Coleogyne ramosissima*; CYLACA, *Cylindropuntia acanthocarpa*; CYLECH, *Cylindropuntia echinocarpa*; ENCFAR, *Encelia farinosa*; EPHNEV, *Ephedra nevadensis*; EPHVIR, *Ephedra viridis*; ERICOO, *Ericameria cooperi*; HYMSAL, *Hymenoclea salsola*; LARTRI, *Larrea tridentata*; PROGLA, *Prosopis glandulosa*; PRUFAS, *Prunus fasciculata*; SPHAMB, *Sphaeralcea ambigua*; and THAMON, *Thamnosma montana*.

re-burning, complicate projections of recovery of species composition on desert burns (e.g., Bakker et al., 2003; Knapp et al., 2008).

4.4. Individual species

Just as in mesic regions, these deserts contain species that benefit from disturbance. Dominant post-fire species (Table 3) also are major colonizers of other types of disturbances. For instance, Carpenter et al. (1986) found that three (*S. ambigua*, *Gutierrezia microcephala*, and *H. salsola*) of the 10 most abundant post-fire species I recorded were 2–3 times more abundant on agricultural fields abandoned for 50–70 years than in undisturbed habitat in the eastern Mojave Desert. *A. speciosum* and *Thamnosma montana*, with the third and seventh highest burned:unburned abundance, exhibited 2–4 times more cover on streets of a townsite abandoned 51 years earlier (Webb and Wilshire, 1980). The post-fire dominants *Encelia* and *H. salsola* also were both more abundant on abandoned roads or cleared pipeline corridors in several studies in these deserts (e.g., Prose et al., 1987; Bolling and Walker, 2000).

Some species exhibited versatility by being dominants in both burned and unburned habitat (e.g., *Ambrosia* spp., *E. nevadensis*), at least in terms of their relative importance within communities even if their raw abundance declined after fire. This post-fire pattern also followed patterns observed following other types of disturbance. Vasek (1983), for example, found that *Ambrosia* occurred in undisturbed vegetation but also exhibited a 23% mean relative cover (the second most important species) in an eight-year-old road construction pit in the eastern Mojave Desert.

A demographic approach tracking the fates of individual plants or propagules could be useful for understanding precisely how post-fire dominants become established (e.g., Chambers, 2000; Buhk and Hensen, 2006). On a burn in Sandy Valley in the eastern Mojave Desert, Lei (1999) reported that *Gutierrezia sarothrae* averaged 3.2 and *Encelia virginensis* 2.3 plants/100 m^2, comprising 89% of the total perennial density eight years after fire. However, these species totaled only a combined 0.18 seeds/m^2 600 m inside the burn at the soil surface and only 0.08 seeds/m^2 in the 0–3 cm soil seed bank (Lei, 2001). Seed density of these species also was sparse in a paired unburned area (0.41 seeds/m^2 surface, 0.26 seeds/m^2 seed bank). Price and Reichman's (1987) study of seed banks in unburned habitat in the Sonoran Desert supported these results, where seeds of only eight perennial species (of 26 taxa identified to species) were detected and these at low abundance. These data are consistent with the generalization that many perennial species do not form large, persistent soil seed banks (Kemp, 1989). These observations suggest a post-fire colonization pattern by dispersal of seed from unburned areas, or by the rare surviving plants within burns, rather than by a persistent seed bank. However, in Lei's (1999, 2001) studies, surface + soil densities of 26 seeds/100 m^2 on the burn are more than sufficient to produce the observed 5.5 plants/100 m^2 of *Gutierrezia* and *Encelia* if there is anything less than a 5:1 seed:plant ratio. The precise mechanisms for how post-fire dominants become established remain elusive.

Several factors could limit post-fire reestablishment of long-lived, late-successional dominants such as *C. ramosissima*, *L. tridentata*, or *C. gigantea*. The shorter lived post-burn colonizers may have more frequent and copious seed production events and abilities for longer distance dispersal than the long-lived dominants (Bowers et al., 1997). Thus, large burns and burns where remnant seed producers are eliminated may be the slowest to become recolonized (Lei, 2001). Furthermore, nurse plants benefit many long-lived species, such as *C. gigantea*, by providing safe sites for regeneration (Padilla and Pugnaire, 2006). These nurse plants may be destroyed by fire, and it is unclear whether the early post-fire colonizers can serve in this role. Many other factors, including competition from exotic plants, herbivory, or climate change, also could limit the reestablishment of late-successional species (Lovich and Bainbridge, 1999).

4.5. Desert comparisons

Fire did not result in convergence of species composition between deserts, suggesting that there are not shared overall post-fire compositions (Fig. 3). These differences probably follow available species pools, where *Y. baccata*, for instance, was an important Mojave post-fire species whose range does not extend to the Sonoran Desert. However, there were some post-fire shared genera and species with similar traits common as post-fire colonizers in both deserts. For instance, *Sphaeralcea* was an important post-fire genus in both deserts, and *Ambrosia* was a versatile genus in both deserts attaining relatively high abundance in burned and unburned habitat. The species traits that dominant post-fire colonizers generally exhibited in both deserts were relatively short life spans (often <40 years; Bowers et al., 1997), ready establishment from seed that has potential for long-distance dispersal, and ability to colonize areas without fertile island structure (e.g., Tesky, 1993; Marshall, 1994).

5. Conclusion

Results of this systematic review suggest several observations and hypotheses about post-fire plant recovery. First, perennial cover reestablishes more rapidly than species composition. Cover of burned areas will resemble cover of unburned areas within approximately 40 years after fire. Similar to other types of severe disturbance in these deserts, there was generally little evidence of convergence of species composition with unburned areas even 47 years after fire (the longest TSF studied). It is possible that reestablishment of communities consisting of long-lived dominants such as *C. ramosissima* requires centuries to millennia (Lovich and Bainbridge, 1999), assuming that exotic species invasions, further fire, and climate change do not interfere with community development. Second, post-fire dominants (e.g., *S. ambigua*) are major colonizers following a wide variety of disturbance types. Third, a better understanding of contingency effects likely could enhance our understanding of post-fire responses. For instance, fire characteristics, post-fire weather, grazing, exotic species, and soil type could affect post-fire community development, but these influences have been little studied. Fourth, given that post-fire communities are persistent and occupy increasingly large portions of the landscape, research on the functioning of these communities in comparison to unburned communities is warranted. It is unclear, for example, if or for how long carbon storage differs between burned and unburned communities. In terms of ecotourism economic functions, unfortunately it appears that recovery time of charismatic species like *Y. brevifolia* and *C. gigantea* is long. Fifth, our understanding of recovery and succession following disturbance in arid lands lags behind that of mesic regions (McAuliffe, 1988). The systematic review approach highlighted a need for further original studies of wildfires and experiments manipulating contingency effects to provide mechanistic explanations for recovery processes. Further research also could promote understanding of functional shifts in fire-dominated landscapes, assist resource managers in choosing whether to actively promote revegetation of burns, and how revegetation might be successfully accomplished.

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References

Abella, S.R., Engel, E.C., Lund, C.L., Spencer, J.E., 2008. Early post-fire recovery on a Mojave Desert burn: dominance by native perennials and reduced *Bromus rubens*. Report Submitted to Bureau of Land Management. Las Vegas Field Office, Las Vegas, Nevada, USA.

Abella, S.R., Gunn, J.L., Daniels, M.L., Springer, J.D., Nyoka, S.E. Using a diverse seed mix to establish native plants on a Sonoran Desert burn. Native Plants Journal, in press.

Allen, C.D., 2007. Interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. Ecosystems 10, 797–808.

Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X., Ambrose, L.G., Waddington, J., 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications 13, 137–153.

Beatley, J.C., 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55, 856–863.

Bolling, J.D., Walker, L.R., 2000. Plant and soil recovery along a series of abandoned desert roads. Journal of Arid Environments 46, 1–24.

Bowers, J.E., Webb, R.H., Pierson, E.A., 1997. Succession of desert plants on debris flow terraces, Grand Canyon, Arizona, U.S.A. Journal of Arid Environments 36, 67–86.

Brooks, M.L., Matchett, J.R., 2003. Plant community patterns in unburned and burned blackbrush (*Coleogyne ramosissima* Torr.) shrublands in the Mojave Desert. Western North American Naturalist 63, 283–298.

Brooks, M.L., Matchett, J.R., 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. Journal of Arid Environments 67, 148–164.

Brooks, M.L., Minnich, R.A., 2006. Southeastern deserts bioregion. In: Sugihara, N.G., van Wagtendonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E. (Eds.), Fire in California's Ecosystems. University of California Press, Berkeley, California, USA, pp. 391–414.

Brown, D.E. (Ed.), 1994. Biotic Communities: Southwestern United States and Northwestern Mexico. University of Utah Press, Salt Lake City, Utah, USA.

Brown, D.E., Minnich, R.A., 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. American Midland Naturalist 116, 411–422.

Buhk, C., Hensen, I., 2006. "Fire seeders" during early post-fire succession and their quantitative importance in south-eastern Spain. Journal of Arid Environments 66, 193–209.

Callison, J., Brotherson, J.D., Bowns, J.E., 1985. The effects of fire on the blackbrush (*Coleogyne ramosissima*) community of southwestern Utah. Journal of Range Management 38, 535–538.

Carpenter, D.E., Barbour, M.G., Bahre, C.J., 1986. Old field succession in Mojave Desert scrub. Madroño 33, 111–122.

Cave, G.H., Patten, D.T., 1984. Short-term vegetation responses to fire in the upper Sonoran Desert. Journal of Range Management 37, 491–496.

Chambers, J.C., 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. Ecological Applications 10, 1400–1413.

Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whitaker, A., 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77, 117–145.

Crosswhite, F.S., Crosswhite, C.D., 1982. The Sonoran Desert. In: Bender, G.L. (Ed.), Reference Handbook on the Deserts of North America. Greenwood Press, Westport, Connecticut, USA, pp. 163–319.

Esque, T.C., Schwalbe, C.R., 2002. Alien annual grasses and their relationships to fire and biotic change in Sonoran desertscrub. In: Tellman, B. (Ed.), Invasive Exotic Species in the Sonoran Region. University of Arizona Press and the Arizona-Sonora Desert Museum, Tucson, Arizona, USA, pp. 165–194.

Fazey, J., Salisbury, J.G., Lindenmayer, D.B., Maindonald, J., Douglas, R., 2004. Can methods applied in medicine be used to summarize and disseminate conservation research? Environmental Conservation 31, 190–198.

Guo, Q., 2004. Slow recovery in desert perennial vegetation following prolonged human disturbance. Journal of Vegetation Science 15, 757–762.

Humphrey, R.R., 1963. The role of fire in the desert and semidesert grassland areas of Arizona. Tall Timbers Fire Ecology Conference Proceedings 2, 45–62.

Keeler-Wolf, T., 2007. Mojave Desert scrub vegetation. In: Barbour, M.G., Keeler-Wolf, T., Schoenherr, A.A. (Eds.), Terrestrial Vegetation of California. University of California Press, Berkeley, California, USA, pp. 609–656.

Kemp, P.R., 1989. Seed banks and vegetation processes in deserts. In: Leck, M.A., Parker, V.T., Simpson, R.L. (Eds.), Ecology of Soil Seed Banks. Academic Press, New York, pp. 257–281.

Kittams, W.H., 1972. Effects of fire on vegetation of the Chihuahuan Desert region. Tall Timbers Fire Ecology Conference Proceedings 12, 427–444.

Knapp, A.K., Beier, C., Briske, D.D., Classen, A.T., Luo, Y., Reichstein, M., Smith, M.D., Smith, S.D., Bell, J.E., Fay, P.A., Heisler, J.L., Leavitt, S.W., Sherry, R., Smith, B., Weng, E., 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. BioScience 58, 811–821.

Leger, E.A., 2008. The adaptive value of remnant native plants in invaded communities: an example from the Great Basin. Ecological Applications 18, 1226–1235.

Lei, S.A., 1999. Postfire woody vegetation recovery and soil properties in blackbrush (*Coleogyne ramosissima*) shrubland ecotones. Journal of the Arizona-Nevada Academy of Science 32, 105–115.

Lei, S.A., 2001. Postfire seed bank and soil conditions in a blackbrush (*Coleogyne ramosissima* Torr.) shrubland. Bulletin of the Southern California Academy of Sciences 100, 100–108.

Lovich, J.E., Bainbridge, D., 1999. Anthropogenic degradation of the southern California desert ecosystem and prospects for natural recovery and restoration. Environmental Management 24, 309–326.

Marshall, K.A., 1994. *Ambrosia deltoidea*. Fire Effects Information System [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Available from: http://www.fs.fed.us/database/feis/.

McAuliffe, J.R., 1988. Markovian dynamics of simple and complex desert plant communities. American Naturalist 131, 459–490.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B., Mefford, M.J., 1999. PC-ORD: Multivariate Analysis of Ecological Data. Version 4. User's Guide. MjM Software Design, Gleneden Beach, Oregon, USA.

McLaughlin, S.P., Bowers, J.E., 1982. Effects of wildfire on a Sonoran Desert plant community. Ecology 63, 246–248.

Medica, P.A., Saethre, M.B., Hunter, R.B., 1994. Recovery of a desert community after fire in the northern Mojave. In: Fletcher, A. (Ed.), The Desert Tortoise Council Proceedings of 1994 Symposium. Desert Tortoise Council, Inc., San Bernadino, California, USA, pp. 68–92.

Minnich, R.A., 1995. Wildland fire and early postfire succession in Joshua tree woodland and blackbrush scrub of the Mojave Desert of California. San Bernardino County Museum Association Quarterly 42, 99–106.

Narog, M.G., Wilson, R.C., 2003. Delayed mortality: saguaro cacti are still dying 10 years after wildfire!, P2.9. In: Second International Wildland Fire Ecology and Fire Management Congress and Fifth Symposium On Fire And Forest Meteorology. American Meteorological Society, Boston, Massachusetts, USA.

Natural Resources Conservation Service, 2008. The PLANTS Database. National Plant Data Center, Baton Rouge, LA. http://plants.usda.gov Available from:

O'Leary, J.F., Minnich, R.A., 1981. Postfire recovery of the creosote bush scrub vegetation in the western Colorado desert. Madroño 28, 61–66.

Padilla, F.M., Pugnaire, F.I., 2006. The role of nurse plants in the restoration of degraded environments. Frontiers in Ecology and the Environment 4, 196–202.

Patten, D.T., Cave, G.H., 1984. Fire temperatures and physical characteristics of a controlled burn in the upper Sonoran Desert. Journal of Range Management 37, 277–280.

Price, M.V., Reichman, O.J., 1987. Distribution of seeds in Sonoran Desert soils: implications for heteromyid rodent foraging. Ecology 68, 1797–1811.

Prose, D.V., Metzger, S.K., Wilshire, H.G., 1987. Effects of substrate disturbance on secondary plant succession: Mojave Desert, California. Journal of Applied Ecology 24, 305–313.

Rogers, G.F., Steele, J., 1980. Sonoran Desert fire ecology. In: Stokes, M.A., Dieterich, J.H. (Eds.), Proceedings of the Fire History Workshop, General Technical Report RM-81. U.S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA, pp. 15–19.

Rogers, G.F., Vint, M.K., 1987. Winter precipitation and fire in the Sonoran Desert. Journal of Arid Environments 13, 47–52.

Rundel, P.W., Gibson, A.C., 1996. Ecological Communities and Processes in A Mojave Desert Ecosystem: Rock Valley, Nevada. Cambridge University Press, New York.

Schoenherr, A.A., Burk, J.H., 2007. Colorado Desert vegetation. In: Barbour, M.G., Keeler-Wolf, T., Schoenherr, A.A. (Eds.), Terrestrial Vegetation of California. University of California Press, Berkeley, California, USA, pp. 657–682.

Stewart, G.B., Coles, C.F., Pullin, A.S., 2005. Applying evidence-based practice in conservation management: lessons from the first systematic review and dissemination projects. Biological Conservation 12, 270–278.

Tesky, J.L., 1993. *Encelia farinosa*. Fire Effects Information System [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. http://www.fs.fed.us/database/feis/ Available from:

Vasek, F.C., 1983. Plant succession in the Mojave Desert. Crossosoma 9, 1–23.

Webb, R.H., Wilshire, H.G., 1980. Recovery of soils and vegetation in a Mojave Desert ghost town, Nevada. Journal of Arid Environments 3, 291–303.

Webb, R.H., Steiger, J.W., Turner, R.M., 1987. Dynamics of Mojave Desert assemblages in the Panamint Mountains, California. Ecology 68, 478–490.

Webb, R.H., Murov, M.B., Esque, T.C., Boyer, D.E., DeFalco, L.A., Haines, D.F., Oldershaw, D., Scoles, S.J., Thomas, K.A., Blainey, J.B., Medica, P.A., 2003. Perennial vegetation data from permanent plots on the Nevada Test Site, Nye County, Nevada. U.S. Geological Survey Open-File Report 03-336. U.S. Geological Survey, Tucson, Arizona, USA.

Whelan, R.J., 1995. The Ecology of Fire. Cambridge University Press, New York.

Wilson, R.C., Narog, M.G., Koonce, A.L., Corcoran, B.M., 1995. Postfire regeneration in Arizona's giant saguaro shrub community. In: DeBano, L.F., Gottfried, G.J., Hamre, R.H., Edminster, C.B., Ffolliott, P.F., Ortega-Rubio, A. (Eds.), Proceedings of Conference on Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA, pp. 424–431. General Technical Report RM-GTR-264.

Worthington, R.D., Corral, R.D., 1987. Some effects of fire on shrubs and succulents in a Chihuahuan Desert community in the Franklin Mountains, El Paso County, Texas, no. 3. In: Powell, A.M. (Ed.), Contributed Papers of the Second Symposium on Resources of the Chihuahuan Desert Region United States and Mexico. Chihuahuan Desert Research Institute, Alpine, Texas, USA.

WRCC [Western Regional Climate Center], 2008. Western U.S. Historical Climate Summaries. Western Regional Climate Center, Reno, Nevada, USA. Available from: http://www.wrcc.dri.edu/.