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ECOSYSTEMS

Agricultural Legacies in the Great Basin Alter Vegetation Cover, Composition, and Response to Precipitation

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ABSTRACT

The land-use history of an ecosystem influences current structure and possibly response to modern disturbances and stresses. In semiarid systems the nature of land-use legacies is poorly understood, confounding efforts to establish sustainable management approaches. We compare previously cultivated and non-cultivated lands in Owens Valley, California, where cultivation once extended to 34% of the valley floor but was largely discontinued by 1940, to measure the influence of past disturbance on modern vegetation. We combined historic maps of cultivated and non-cultivated land with an extensive vegetation survey, historic aerial photographs, and satellite measurements of vegetation response to precipitation variability to examine the importance of land-use history in determining the sensitivity of vegetation to annual variations in precipitation. Remote sensing analysis showed that total plant cover on previously cultivated lands was lower and fluctuations in cover were marginally more dependent on precipitation compared with plant cover on non-cultivated lands. We then compared modern plant assemblages within cultivated and non-cultivated land to determine if compositional differences could explain the current patterns of vegetation cover. We found lower species richness on previously cultivated parcels, and higher frequency and cover of perennial grasses on non-cultivated lands. Therefore, we showed differences in land-cover patterns, isolated a mechanism that could account for the differences (species differences), and developed a method for remotely analyzing land regions that have experienced historic anthropogenic disturbance.

Key words: land-use legacy; Great Basin; Owens Valley; precipitation variability; historic cultivation; remote sensing; linear spectral mixture analysis.

INTRODUCTION

Land-use history is recognized as an important contributor to the structure of modern ecosystems (Foster and others 2003). Yet, we know little of how land-use history will impact the response of ecosystems to current and future climate changes (Dale 1997; Foster and others 2002). Further, management of vegetation for multiple purposes (for example, cattle grazing, wildlife habitat, water resources, and so on) is problematic unless the

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controls on vegetation cover are very well understood. These issues are of particular importance in arid and semi-arid regions, where land is exposed to a variety of land use pressures and precipitation is characteristically low and variable. Therefore, to the extent that legacies of past land-use exist in arid and semi-arid systems, they may be key to understanding patterns of vegetation cover and vegetation response to precipitation. Land-use history is an often-overlooked component of ecosystem research and land management, despite the fact that many arid and semi-arid landscapes are currently in some stage of succession following agricultural abandonment (Knapp 1992a; Stylinski and Allen 1999).

Evidence from many sites worldwide indicates that legacies of past disturbance are apparent for centuries following disturbance and can dramatically influence ecosystem processes (Foster and others 2003). In arid and semi-arid lands, the dominant human land-uses (both past and present) are grazing, cultivated agriculture, urbanization, mineral exploration, and water management, all of which can result in extensive changes in land-cover (Vitousek and others 1997). These changes can include the loss of biodiversity and riparian habitat (Patten 1998; Fairbanks and others 2002), establishment of exotic plants (Young and others 1972; D'Antonio and Vitousek 1992), and reduced grazing productivity (Young and Longland 1996). In areas where cultivated agriculture is abandoned, lack of further land development may lead to reestablishment of plant cover resembling nearby non-disturbed lands. However, legacies of past land-use in these environments may include reduced species diversity, shifts in the dominant life form, and/or increased dominance of non-native species (Webb and others 1988; Knapp 1992a; Stylinski and Allen 1999) for a long period following the shift in use (Carpenter and others 1986; Lovich and Bainbridge 1999).

Plant communities affected by or resulting from past land uses may be compromised with regard to productivity or resistance to future environmental stress. Cultivation removes perennial plant biomass, and alters soil density (Knapp 1992b), soil microbial processes (Evans and Belnap 1999), and seed banks (Bekker and others 1997; Bossuyt and Hermy 2001). In addition exotic species have a greater presence in the vicinity of human-caused disturbance (Vitousek and others 1996), which increases rates of invasion in many environments (Weaver and others 2001). When established, invading species can alter successional pathways (Prose and others 1987) and, in some cases, alter the disturbance regime and the stability of the resulting ecosystem (D'Antonio and Vitousek 1992; Mack and D'Antonio 1998). The presence of invasive plants and/or overall low species diversity have been shown to affect plant community drought resistance (Hooper and Vitousek 1997; Tilman 1997), which may influence the vegetation response to precipitation decades after agricultural abandonment.

This paper extends on a more general analysis of plant cover response to water availability (both groundwater and precipitation) in the Owens Valley, California (Elmore and others 2003), by examining the role of cultivation in the early 1900's Owens Valley on late twentieth century vegetation cover and composition. In our previous work, we noted that lands dominated by exotic annuals, including some lands that were previously cultivated, exhibited an amplified response to precipitation (Elmore and others 2003). However, in that work we made no attempt to study past land-use patterns (for example, through the use of historic maps or air photography) or to identify plant assemblages that could be associated with previously cultivated land. In this current effort, we use historic maps of cultivated land (approximately 1905–1931) and annually acquired remotely sensed measurements of the fractional vegetation cover (1992–1998; data developed and used in Elmore and others 2000, 2003) to generally compare the vegetation cover through time within a more comprehensive data set of previously cultivated and non-cultivated lands. Using a recent vegetation map, we further attempt to identify the legacy of past land-use on modern vegetation composition that may account for any observed differences in vegetation cover. It is a general goal of this paper to identify methods by which remote sensing could be used to identify and analyze regions with a common history of cultivation.

Site Description

Owens Valley is located in eastern California, between the Sierra Nevada and the White-Inyo Mountains (centered on 37.2 N, 118.2 W; Figure 1). Precipitation is low (50-year median, 14 cm, Bishop, CA, USA), however spring runoff into Owens Valley from the Sierra Nevada is substantial. A portion of this runoff contributes to a shallow (< 5 m depth) groundwater aquifer across the valley floor (Hollett and others 1991). Beneath the alluvial fans, on the side slopes of the Sierra Nevada or White/Inyo Mountains, groundwater is deeper (> 5.5 m) and the soils are well drained. Our study

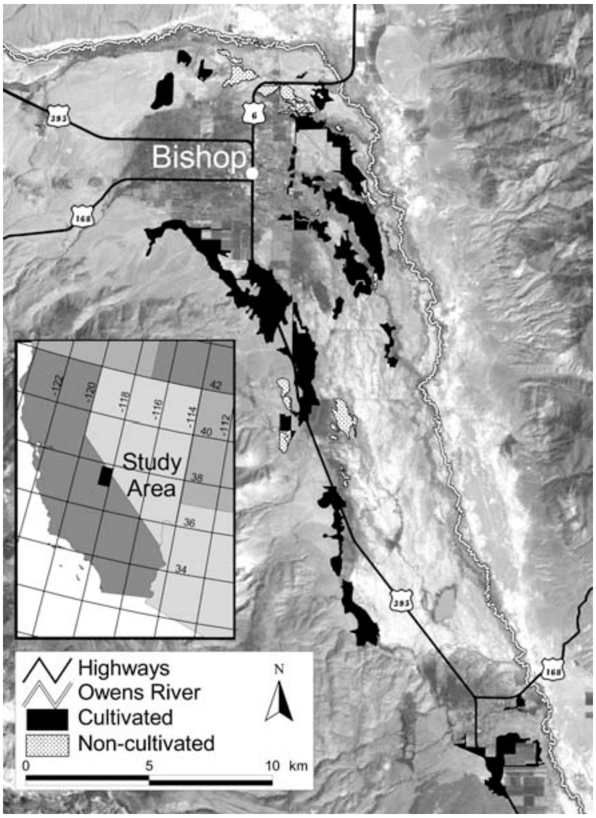

Figure 1. The study area: northern Owens Valley, California, showing parcels included in this study. Cultivated areas were extensive in 1926 (beyond that shown here) and were largely abandoned by 1944. Previously cultivated areas selected for this study are in *black* and *shaded areas* are non-cultivated lands. Background image is Landsat TM Band 2 acquired in September 1992.

area encompasses the towns of Bishop and Big Pine in the northern Owens Valley, and includes currently undeveloped lands on both the valley floor with shallow groundwater and alluvial fan with deep groundwater.

Vegetation of the valley floor is generally characterized as alkali meadow and vegetation of the alluvial fans is generally classified as Great Basin xeric scrub. Alkali meadow is primarily dominated by two native, perennial grass species, *Distichlis spicata* and *Sporobolus airoides* (nomenclature follows Hickman 1993). Grass cover may be high, and varying amounts of shrubs, particularly *Atriplex lentiformis* ssp. *torreyi, Sarcobatus vermiculatus* (Hickman 1993), and *Chrysothamnus nauseosus* may co-occur (Inyo 1990). At least two sub-species of *C. nauseosus* exist in Owens Valley. *C. nauseosus.* ssp. *consimilis* is common within phreatophytic communities, whereas *C. nauseosus* ssp. *hololeucus* is characterized as growing in well-drained soils (Hickman 1993). On the alluvial fans, where groundwater is more than 5 m deep, the shrub *Artemisia tridentata* dominates. Owens Valley vegetation also includes the non-native annuals *Bassia hyssopifolia* and *Salsola tragus.*

Land-use History

Between 1,000 and 2,000 Paiute occupied Owens Valley in the early nineteenth century, and these indigenous people used lands from the valley floor to the mountain crests (Sauder 1994). Within our study area, there were 2 major year-round population centers at the time of European contact, one on Bishop Creek, west of modern Bishop, and the second along Baker Creek, near Big Pine (Lawton and others 1979). At these locations the Paiute used irrigation (creeks were dammed with boulders to spread the creek-water) to enhance the growth of native grasses and forbs (Steward 1933). Because the Paiute never plowed the soil, their irrigation practices, which can be characterized as mimicking spring floods, had minimal impact on ecosystem structure (Steward 1930).

Settlement of Owens Valley by people of European origin began in 1860 with small self-sufficient farms that raised cattle and converted alkali meadow to grain fields (Sauder 1994). By 1874, most of the prime bottomland sites were being utilized by European farmers. Thus, new arrivals were forced to cultivate the surrounding alluvial fan sagebrush lands, which were unexpectedly fertile. By 1900, there were 424 homesteads in the valley, covering 57,000 ha, and at the peak of agriculture activity in 1925, 58,000 ha ($\sim$34% of the valley) was under cultivation (Sauder 1994). In 1913, a 400-km aqueduct between the Owens River and the City of Los Angeles (LA) was completed, and from 1905 to 1935, most of the land and water rights in the valley were acquired or purchased by LA. The shift in ownership of 1,000 km^2 caused an abrupt and almost total abandonment of cultivated land in the valley (Mustard and others 2005).

The comparison of previously cultivated land with non-cultivated land is possible because land-use patterns in the 1920's were well documented by LA. Farmers used both poorly drained meadows and well drained sagebrush lands during the same period for similar agricultural activities. Land on the Owens River flood plain and regions with highly alkaline soils may be two areas that farmers avoided for cultivated agriculture (Sauder 1994). Finally, the process of abandonment was driven by the rapid and wide-scale land purchase by LA. Neither land productivity nor location within the valley influenced LA's interest in purchasing land, therefore a variety of land types were abandoned at roughly the same time (Sauder 1994), unlike most other regions of the United States.

METHODS

Vegetation Composition

Data on vegetation composition and cover in the mid-1980's (1985–1987) were collected by the Los Angeles Department of Water and Power (LADWP) in a valley-wide survey of 2100 parcels of less than 1–320 ha. Parcels were delineated to depict units of relatively homogeneous vegetation, and parcel boundaries were generally visible on 1981 aerial photography (Inyo 1990). Vegetative composition of each parcel was measured along an average of five transects, each 33 m in length. The number of transects increased with parcel size. The line-point transect method (Heady and others 1959; Bonham 1989) was utilized to identify plant species, and their relative cover, within each parcel (data available at Inyo County Water Department and the Los Angeles Department of Water and Power). We used this data set in previous work (Elmore and others 2003) to summarize the distribution of plant communities and their response to groundwater and precipitation. However, in this current work we include species cover information from the original transects conducted in the mid-1980's rather than summary statistics.

At the time of the survey, parcels that contained less than 5% vegetation cover were not measured and designated ''barren lands''. Most of these barren lands are indeed abandoned cultivated lands, some dating to the 1920s. In previous work, using only these barren lands as examples of abandoned agricultural land, we suggested that an amplified vegetation response to precipitation may be a legacy of past land cultivation (Elmore and others 2003). Here we extend this work by examining a more comprehensive database of previously cultivated lands derived from historic maps and air photos (described in the next section), and by making a specific attempt to identify plant species associations with cultivated and non-cultivated land. However, species associations could not be identified for lands labeled ''barren'' because the vegetation survey conducted in the mid-1980's does not provide species level information for these lands. Therefore, cultivated lands that have not seen significant native species reestablishment since abandonment were not used in this work. This fact also means that there is no overlap with the lands studied by Elmore and others (2003).

Identifying Non-cultivated and Cultivated Parcels

A detailed land-use map, created by Charles H. Lee (approx. 1926), was used as a base map of the maximum extent of cultivated land. Additional maps produced by Shuey in the 1960s depicting land cover as he remembered it in 1905, 1913, and 1918 and Ritch (approx. 1931) were used to confirm which areas were cultivated and, in some areas, to increase the maximum area of cultivation. Because the maps of Shuey, Lee and Ritch span a quarter of century during which time the valley was undergoing a dramatic land-use transition, we are confident that they capture the extent of maximum cultivation. Cultivated land in 1944 was identified using digitized aerial photographs. Lands cultivated in the historic maps, but not cultivated in the 1944 air photography were designated ''cultivated lands'', and those that had no record of cultivation were designated ''non-cultivated lands''. The extent of the historic maps (cultivated and non-cultivated land) included 575 surveyed parcels.

Parcels were selected in which the center of the parcel was identified as cultivated or non-cultivated. In most cases, parcel boundaries were the same as the boundaries of cultivated land in the historic maps. Because our unit of measurement for vegetation composition was the parcel, it was not appropriate to subdivide parcels into cultivated and non-cultivated sections. Mixed parcels, those that had a history of partial cultivation, were removed from the analysis when the maps of Shuey and Ritch confirmed that less than 50% of the parcel was cultivated. Parcels that were 50–100% cultivated in any of the historic maps were retained in the analysis as cultivated parcels. Non-cultivated parcels rarely contained even a small fraction (for example, < 5%) of cultivated land.

To address the possibility that land-use patterns and geomorphological patterns within the valley were correlated we applied several criteria to select the parcels that would be used in the analysis. The first was to divide the study area into three regions: parcels east of the Owens River, parcels west of the Owens River, and parcels within 100 m of the Owens River. The east–west division attempted to address differences between soils derived from the Sierra Nevada (west side) and those derived from the White-Inyo Mountains (east side), which experienced different hydrology and may have historically supported different plant communities or, equally likely, may have been used by farmers in slightly different ways. However, because the number of parcels on the east side of the Owens River was small (91), and lacked sufficient surveyed cultivated parcels, they were removed from the analysis. Furthermore, only 6 of 126 parcels within 100 m of the river were cultivated, so all 126 were removed from the analysis.

The west-side parcels (358) were further stratified between cultivated and non-cultivated history based on soil type and current land-use practices. Soils were determined from Natural Resources Conservation Service (NRCS) Soil Survey Geographic (SSURGO) data and were incorporated into our GIS database for comparison with the vegetation parcels. We restricted the analysis to parcels with aridisols and entisols (the most common soils in the valley), thus avoiding the rare mollisol. Further, we identified a large region of poorly drained alkaline soils found in the southern half of the study region by the presence of an argillic horizon in the NRCS soils data. Elevated surface reflectance from Landsat TM in the visible wavelengths supported the idea that soils in this region were characteristically more alkaline than the surrounding landscape (the region between Rt. 395 and the Owens River south of Bishop; Figure 1). We analyzed these parcels as a separate non-cultivated group of parcels (40 parcels; data not shown), in parallel with the other non-cultivated parcels. Finally, we removed all parcels mapped as having received irrigation water since abandonment. In this water-limited landscape, irrigation increases total plant cover independent of the precipitation patterns we were interested in studying. These selection criteria resulted in 40 cultivated and 22 non-cultivated parcels that were not biased in terms of geomorphic setting, henceforth described as the cultivated and non-cultivated lands (Figure 1).

Measuring Vegetation Cover

We assessed total vegetation cover and vegetation response to precipitation variability in cultivated and non-cultivated parcels using Landsat Thematic Mapper (TM) data sets acquired annually from 1992 through 1998, 10 years following the vegetation survey. Annual precipitation (measured by water year) over this period was highly variable, alternating between low precipitation (< 15 cm/y) and high precipitation (> 30 cm/y). Variability of this magnitude is not uncommon for the region (Graumlich 1993), and this period represents the best example of high variability within the 20-y of the Landsat TM record (Figure 2).

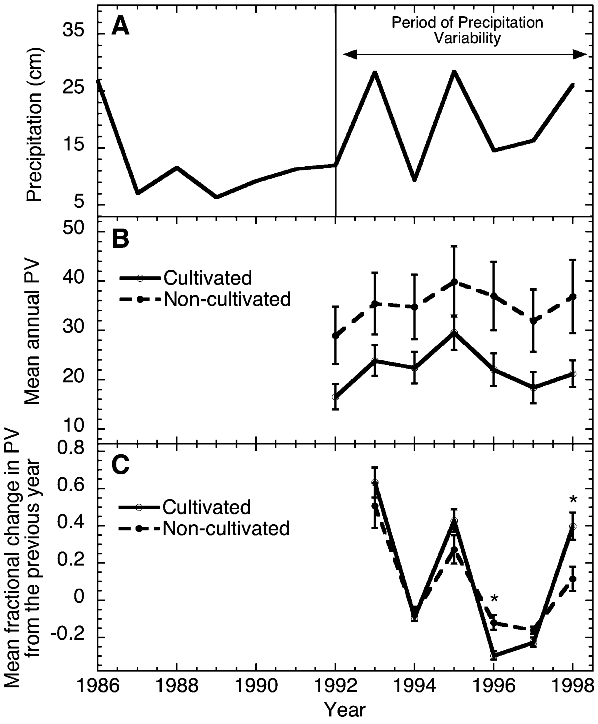

Figure 2. **A** Precipitation in Owens Valley is characteristically variable (represented here with data from the rain gauge at the Bishop airport), and the period from 1992 through 1998 showed the highest precipitation variability, annually. Data are water-year precipitation (precipitation between October (previous year) and September, of each year). **B** Annual vegetation cover, and **C** annual change in vegetation cover relative to the previous year for cultivated and non-cultivated lands. In **B** data from individual years is significantly different between land types with the exception of 1995 ($P < 0.05$). In **C**, years marked with a *asterisk* are significantly different ($P < 0.05$). All *error bars* are one standard error from the mean.

Seven Landsat TM data sets acquired during each September of 1992–1998 were carried forward from previous work in the Owens Valley (Elmore and others 2000, 2003). Important aspects of the processing are summarized here. We did not perform an independent atmospheric removal on each data set, but aligned the data spectrally using temporally invariant surface features. This procedure assured that changes among data sets were representative of physical changes in the surface properties and were not due to changes in the sensor or spatially-uniform differences in atmospheric conditions between acquisition dates. The data were then coregistered to within one pixel (30 m × 30 m) using automated ground-control-point selection software (Elmore and others 2000).

Each data set was analyzed for fraction of photosynthetic vegetation (PV) cover using Spectral Mixture Analysis (SMA) (Adams and others 1986; Mustard and Pieters 1987). This technique calculates the relative abundances of materials thought to be important surface components of the study area. In SMA, these spectrally and physically distinct materials are termed endmembers. For this analysis, we chose four endmember spectra: (1) PV, chosen from a well-watered meadow close to the Owens River; (2) a light colored, fine grained soil; (3) a dark, organic rich soil; and (4) shade, to account for albedo and illumination effects. It is assumed that pixel radiometric response is the linear combination of these endmember spectra, each scaled by their respective fractional cover. The resulting fraction of the PV endmember is an estimate of green plant cover for each pixel (Smith and others 1990a, b). We have successfully used the technique for several applications in the Owens Valley (Elmore and others 2000, 2003).

Seven parameters of vegetation cover and response to precipitation variability were calculated from the annual measurements of PV and its variability. Five indicators were derived from the annual mean PV: (1) the 7-y mean PV; (2) the coefficient of variation in PV; (3) the mean annual change in PV for each pair of consecutive years from 1992 through 1998 (that is, current year PV minus previous year PV divided by previous year PV); (4) the average of PV for wet years (1993, 1995, 1998); and (5) the average of PV for dry years (1992, 1994, 1996, 1997). Secondly, we calculated (6) the correlation (R), and (7) slope of the regression between PV and water-year precipitation.

Statistical Analysis

Plant species associations with the two land categories (cultivated and non-cultivated) were identified using a chi-squared (χ^2) test applied to the mid 1980s vegetation map data. Our null hypothesis (H_{null}) was that each species was equally present between land types. Therefore, the expected presence/absence of each species (where H_{null} = true) was scaled based on the total number of parcels with that species. We measured species presence by counting the number of parcels in which each of 85 total species was found. Using the χ^2 test with the Yates correction for continuity we determined if the measured species distributions were different from evenly distributed. Finally, the mean species cover (fractional) and the total number of species were calculated for each parcel, and compared between land types.

RESULTS

Photosynthetic Vegetation Variability

Of the seven different measures derived from the remote sensing time series of PV, five were significantly different between cultivated and non-cultivated lands ($P < 0.05$; Table 1). The most significant difference was that mean PV was greater for non-cultivated lands in all years ($P = 0.033$) as well as dry and wet years separately ($P < 0.05$; Figure 2B). The coefficient of variation ($P = 0.011$) and the correlation coefficient of the regression between PV and precipitation ($P = 0.049$) were greater for cultivated lands. A difference in annual vegetation cover change was seen in 2 years (1996 and 1998; $P < 0.05$) (Figure 2C), but average annual response across all years was not significantly different between land types ($P = 0.170$). The small difference in variability in plant cover between land types was due to sensitivity to precipitation, as demonstrated by higher plant cover correlation with precipitation within cultivated lands compared with non-cultivated lands ($P = 0.049$). However, the slope of this correlation was not significantly different ($P = 0.360$; Table 1).

Plant Species Composition Differences

Non-cultivated lands supported more species per parcel than cultivated lands (6.5 species/parcel as compared to 4.7 species/parcel for cultivated land; $P < 0.001$). Cultivated parcels averaged 65 ha in size and non-cultivated parcels averaged 17 ha. Therefore, cultivated parcels supported on average 0.072 species/ha and non-cultivated parcels supported 0.38 species/ha.

Species more often present on non-cultivated land included seven native species and no non-native species (Table 2). Of particular note was the native bunch grass, *Sporobolus airoides*, which is one of the more common species in the valley and one of two native grasses that dominate alkali meadow. The second native grass, *Distichlis spicata*, was non-differentiated in terms of presence, but exhibited higher plant cover when found on non-cultivated parcels. Therefore, non-cultivated lands were characterized by the native meadow grasses (*S. airoides* and *D. spicata*) combined with an assemblage of other native species that were often not present on cultivated lands.

The native shrub *Atriplex canescens* was the only species more often present on previously cultivated lands. The native shrub *Chrysothamnus nauseosus*, which was present on 20 of 22 non-cultivated parcels and 39 of 40 cultivated parcels, exhibited

Table 1. Statistics for Non-cultivated and Cultivated Parcels Generated from the Remote Sensing Time Series of Photosynthetic Vegetation Cover

		Non-cultivated (n =22)	Cultivated (n = 40)	P-value
1	Mean PV (7-y)	34.98	21.68	0.033
2	Coefficient of variation (standard deviation divided by the mean)	0.13	0.24	0.011
3	Mean annual change in PV relative to previous year	0.09	0.14	0.170
4	Wet year PV (mean plant cover from 1993, 1995, and 1998)	37.39	24.63	0.048
5	Dry year PV (mean plant cover from 1992, 1994, 1996, and 1997)	33.17	19.46	0.025
6	Correlation with precipitation (correlation coefficient in plant cover vs. precipitation regression)	0.28	0.43	0.049
7	Slope with precipitation (slope parameter in PV vs. precipitation regression)	0.33	0.36	0.360

higher plant cover on cultivated parcels than on non-cultivated parcels. If the statistical threshold is lowered ($P < 0.10$) then several additional species were found to be more common on cultivated lands relative to non-cultivated, for example, the shrub *Artemisia tridentata* and the non-native annual *Salsola tragus*, which were each found on 65% of cultivated parcels. It may be appropriate to consider *Salsola tragus* ($P = 0.07$) as significantly more often present on cultivated parcels due to the fact that it is an annual and its abundance changes considerably from year to year.

DISCUSSION

In Owens Valley the vegetation of previously cultivated lands (60–80 years following abandonment) differs from vegetation on nearby non-cultivated land with regard to total plant cover, species composition, and vegetation response to precipitation during some years. Vegetation cover is an important indicator of ecosystem processes [for example, forage quantity and quality as well as nesting locations (Kennedy and others 2000), wind and fluvial erosion (Belnap and Gillette 1998; Okin and others 2001), and energy transfer between the land surface and the atmosphere (Bremer and others 2001)]. The long-term persistence of a land-use legacy, following only 20–40 years of agricultural disturbance, represents significant ecosystem reorganization. The dissimilarities in total PV and PV correlation with precipitation between previously cultivated and non-cultivated lands are interesting results, and if shown to be a consistent feature of Owens Valley vegetation, could have important consequences for predicting ecosystem responses to future climate changes.

The most significant difference between vegetation on cultivated and non-cultivated lands was total pant cover. Cultivated lands have apparently not regained plant cover to a level that is consistent with native lands in the region. This may reflect plant community factors such as a shift from grass to shrub species (discussed below), or it may be more symptomatic of soil quality differences between lands. Although we did not address these issues, there are several edaphic factors that may retard the regeneration of vegetation on previously cultivated lands, including elevated erosion rates due to lower plant cover (Okin and Gillette 2001), textural differences that impact water absorption and seed germination (Belnap 1995), and the absence of nitrogen fixing cryptogrammic crusts on the soil surface (Evans and Belnap 1999).

We focus our discussion on an association between vegetation cover and species-level differences in plant community composition. Generalizations are difficult, but some of our results may provide the necessary link: we found cultivated lands to exhibit (1) dominance by the shrub *Chrysothamnus nauseosus* ($P < 0.05$; Table 2), (2) increased frequency of the exotic annual *Salsola tragus* ($P = 0.07$), and (3) decreased cover and frequency of the perennial native grasses *Distichlis spicata* and *Sporobolus airoides*, respectively ($P < 0.05$; Table 2). Finally, (4) cultivated lands had fewer plant species (0.072 species ha^{-1} as compared to 0.36 species ha^{-1} for non-cultivated land; $P < 0.001$). We hypothesize that each of these differences may have had an effect on total vegetation

Table 2. All Species Measured in More than Four Parcels, Showing Number of Parcels with Each Species and the Average Species Cover in Inhabited Parcels.

		Number of parcels in which species was identified[c]		Presence absence	More often present	Mean species cover when present (%)		Greater cover when present
Species name[a]	Sp. info code[b]	Non-cultivated	Cultivated	*P*-value[d]	$P < 0.05$	Non-cultivated	Cultivated	$P < 0.05$[e]
Chrysothamous nanseosus	NP	20	39	0.9057		3	6	Cultivated
Artemista tridentata	NP	11	26	0.5757		<1	6	
Selsola tragus	EA	6	26	0.0729		<1	1	
Distichlis Spicala	NP	13	18	0.5734		14	4	Non-cultivated
Atriplex Canescans	NP	3	23	0.0189	Cultivated	2	2	
Sporobolous atroides	NP	13	8	0.0213	Non-cultivated	4	8	
Achnaltherum hymenoides	NP	5	16	0.3734		<1	<1	
Atriplex leviformis torreyl	NP	7	14	0.9824		5	4	
Sarcobatus vermiculatus	NP	12	9	0.0848		3	1	
Ephedra nevadensis	NP	8	11	0.7162		3	1	
Salcix sp.	NP	5	13	0.6521		24	15	
Atriplex confertifolia	NP	7	10	0.8126		2	<1	
Populus fermontii fremontii	NP	2	15	0.0734		<1	2	
Bassia hyssopifolia	EA	5	11	0.9261		<1	2	
Bramus madritensis rubens	EA	4	11	0.6571		<1	<1	
Juncus ballicus	NP	9	5	0.0485	Non-cultivated	2	2	
Bramus tectorum	EA	4	9	0.9478		<1	2	
Leymus triticoides	NP	7	6	0.2740		4	3	
Glycyrrhiza lepidota	NP	5	7	0.8039		2	2	
Grayia spinosa	NP	7	5	0.1762		<1	<1	
Elymu elymoides	NP	5	7	0.8839		1	<1	
Stephanomeria sp.	NPA	2	10	0.2888		<1	<1	
Terradymia axillasis	NP	6	6	0.4537		2	<1	
Chrysothamous taratifolius	NP	4	7	0.7994		3	<1	
Ericameria coopei	NP	5	5	0.5294		3	1	
Hymenociea safsola	NP	4	6	0.9745		<1	<1	
Psorothamnus polydenius	NP	4	6	0.9745		1	2	
Achmathamnus speciosum	NP	5	5	0.5294		3	1	
Eriogonum fasciculatum	NP	4	5	0.8309		4	<1	
Meliotus alba	EA	5	4	0.3627		10	17	
Rosss woodsii	NP	3	6	0.8309		4	3	
Pyrocoma racemosa	NP	6	2	0.0492	Non cultivated	<1	<1	
Robinia pseudoccacia	EP	0	8	0.0840		N/A	<1	
Carex sp.	NP	5	2	0.1112		4	<1	
Leymus cinereus	NP	5	1	0.0431	Non-cultivated	<1	<1	
Coleogyne ramosissima	NP	4	2	0.2421		3	<1	
Vulpia microstachys	NA	1	5	0.5915		<1	<1	
Mancheranthera carnosa	NP	4	1	0.1067		<1	<1	
Atriplex polycarpa	NP	1	4	0.7977		6	12	
Helianthus annus	NA	4	1	0.1067		<1	<1	
Psorothamnus urborescens	NP	3	2	0.4975		1	<1	
Astragalus levifiginosus	NP	4	0	0.0297	Non-cultivated	<1	N/A	
Atriplex parryl	NP	4	0	0.0297	Non-cultivated	<1	N/A	
Lotus corriculatus	EP	4	0	0.0297	Non-cultivated	1	N/A	
Arabis sparsiflor var. arcuala	NP	2	2	0.9328		<1	<1	

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[a] *Nomencleture follows Hickman 1993.*

[b] *N, native; E, exotic; A, annual; P, perennial.*

[c] *Out of 22 non-cultivated and 40 cultivated.*

[d] *P-value derived from a chi-squared test with the Yares correction for continuity.*

[e] *Actual P-value not shown.*

cover, and to a lesser extent, vegetation dependence on precipitation.

The native perennial shrub *C. nauseosus*, although nearly ubiquitous on both non-cultivated and cultivated parcels, exhibited higher cover on cultivated lands. Conversely, the grasses *S. airoides* and *D. spicata* were found to have lower cover on cultivated lands. Therefore, the general pattern was to have greater shrub cover and lower grass cover. This structural difference may be partly responsible for decreasing the total plant cover. Higher woody vegetation cover has been associated with several ecosystem level changes, including increased spatial and temporal heterogeneity of water and nutrient resources leading to lower plant cover (Schlesinger and others 1990; Asner and others 2004). Further, due to variation in the capability of *C. nauseosus* to utilize groundwater resources rather than precipitation (Flanagon and others 1992; Donovan and Ehleringer 1994), it may be worth considering that this dominant shrub is more often the more precipitation dependent sub species (*C. n.* ssp. *hololeucus*) within cultivated lands. Therefore, a switch between meadow grasses and the shrub *C. nauseosus* might be associated with both lower PV cover and increased dependence on precipitation.

For the valley floor parcels, the mosaic of shrub and grass canopies present in uncultivated parcels appears to have been replaced in cultivated parcels by shrub canopies surrounded by low perennial native grass cover and higher cover of the exotic annual *Salsola tragus* (Table 2). In the Owens Valley, the perennial native grasses *D. spicata* and *S. airoides* are found in many regions of high plant cover, sometimes as dominant species (that is, meadows) and in other locations these grasses inhabitat zones between shrub canopies. Therefore, it is consistent with this understanding that non-cultivated lands, which exhibited consistently higher plant cover, would contain a more frequent occurrence and higher cover of grasses. Conversely, *S. tragus*, a frequent component of the modern post-agricultural succession, has been highlighted in other studies of land-use legacies as an early colonizer that persists for decades following disturbance (Knapp 1992a), often replacing native perennial meadow grasses that do not readily reoccupy abandoned lands (Richter and others 2002). *S. tragus* grows well during wet years during which its extensive root system exploits available soil moisture, in dry years its seeds persist in the soil (Allen and Knight 1984). These autecological characteristics increase the precipitation sensitivity of vegetation within landscapes it occupies, particularly as compared to non-cultivated lands dominated by perennial meadow grasses(Oesterheld and others 2001; Elmore and others 2003). We saw some evidence for an increased dependence on precipitation in the previously cultivated lands studied here (Table 1, Figure 2). Other work has highlighted the role of *S. tragus* and other exotic annuals in increasing the precipitation dependence of vegetation (Elmore and others 2003).

Another difference found between vegetation on previously cultivated and non-cultivated lands was plant species diversity (indicated here by the number of plant species per unit area), which has been shown to relate to productivity and plant community resistance and resilience to environmental stress (Johnson and others 1996; Tilman and others 1996). This line of thought suggests that lands with fewer plant species might be expected to exhibit lower vegetation cover, and perhaps greater sensitivity to precipitation variability (Loreau and others 2001). Long-term patterns of winter precipitation derived from the dendrochronological record in the Sierra Nevada highlight consistently low precipitation and the presence of 5- to 10-year droughts and annual variability in precipitation over much of the past 1,000 years (Graumlich 1993). Diverse species assemblages, including the representation of multiple functional groups (for example, variation in groundwater dependence, nitrogen fixing capacity, drought deciduousness, and annual-perennial status), may be influenced by the predominant climate pattern to confer traits such as higher rain use efficiency (Schlesinger and others 1990) and generally higher plant cover than would be expected given the low annual precipitation (Schulze and others 1996). Regardless of the mechanism, the functionality that enables high plant cover in this arid environment may be disrupted by a short period of cultivation.

Remote sensing time series of vegetation cover might be used to identify regions with a history of disturbance. Bradley and Mustard (2005) identified regions of amplified response to precipitation and attributed this response to cheat grass invasion within Great Basin scrubland vegetation. It is an intriguing idea to apply such an approach to identify previously cultivated lands in arid and semi-arid environments. A plausible methodology would be to classify an image based on its total plant cover and correlation with precipitation, and then associate regions with high variability with a land-use history of cultivation. In previous work (Elmore and others 2003), we found that the most extreme cases (for example, lands dominated by *S. tragus* with little or no native plant regeneration) could be identified in this way. However, the variability in total cover and response to precipitation within the majority of previously cultivated lands analyzed here was found to be large and overlapping with that of non-cultivated lands. Therefore, previously cultivated and non-cultivated lands could not be uniquely separated from non-cultivated lands using PV time series alone.

A limited number of studies have demonstrated the long-term influence of agricultural disturbance on plant communities in semi-arid regions (Carpenter and others 1986; Knapp 1992a; Stylinski and Allen 1999). Within the time-span of these studies (typically less than 100 y), plant communities on disturbed lands did not fully resemble communities on adjacent non-disturbed lands. Our results describe a successional sere that is consistent with these documented patterns and useful in explaining the disparity in spatial and temporal patterns of vegetation growing on previously cultivated lands. Regardless of the underlying mechanisms, characteristics of native plant communities have not been regained by plant communities inhabiting previously cultivated land to the level of non-cultivated land even after 60–80 y. Understanding the controls on vegetation cover and change through time in these environments requires a sound knowledge of land-use history.

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