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On the brink of change: plant responses to climate on the Colorado Plateau

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Abstract. The intensification of aridity due to anthropogenic climate change in the southwestern U.S. is likely to have a large impact on the growth and survival of plant species that may already be vulnerable to water stress. To make accurate predictions of plant responses to climate change, it is essential to determine the long-term dynamics of plant species associated with past climate conditions. Here we show how the plant species and functional types across a wide range of environmental conditions in Colorado Plateau national parks have changed with climate variability over the last twenty years. During this time, regional mean annual temperature increased by 0.18°C per year from 1989–1995, 0.06°C per year from 1995–2003, declined by 0.14°C from 2003–2008, and there was high interannual variability in precipitation. Non-metric multidimensional scaling of plant species at long-term monitoring sites indicated five distinct plant communities. In many of the communities, canopy cover of perennial plants was sensitive to mean annual temperature occurring in the previous year, whereas canopy cover of annual plants responded to cool season precipitation. In the perennial grasslands, there was an overall decline of C_3 perennial grasses, no change of C_4 perennial grasses, and an increase of shrubs with increasing temperature. In the shrublands, shrubs generally showed no change or slightly increased with increasing temperature. However, certain shrub species declined where soil and physical characteristics of a site limited water availability. In the higher elevation woodlands, *Juniperus osteosperma* and shrub canopy cover increased with increasing temperature, while *Pinus edulis* at the highest elevation sites was unresponsive to interannual temperature variability. These results from well-protected national parks highlight the importance of temperature to plant responses in a water-limited region and suggest that projected increases in aridity are likely to promote grass loss and shrub expansion on the Colorado Plateau.

Key words: arid; climate change; national parks; plant canopy cover; plant community composition; precipitation; southwestern United States; temperature.

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Introduction

Warming in dryland ecosystems of the southwestern U.S. is predicted to be among the most rapid in the U.S. due to human-enhanced climate change (Karl et al. 2009). Mean annual temperatures are projected to increase 4–8°C under high emissions scenarios by the year 2100 (Christensen et al. 2007, Karl et al. 2009), and the magnitude and frequency of days with extreme

temperatures is expected to increase dramatically (Diffenbaugh et al. 2005). Although annual precipitation is more difficult to predict, most climate models predict a 5–10% reduction in the southwestern U.S. by the year 2100 (Christensen et al. 2007). Lower precipitation and higher temperatures will result in a large decrease in both surface and subsurface soil moisture (Pulwarty et al. 2005).

Soils, including their pedogenesis, morphological, physical, and chemical characteristics, contribute to the hydrologic properties of a site and thus water availability to plants. The depth of the soil profile above a water- and root-restrictive layer (e.g., bedrock, caliche, claypan) defines the volume of soil in which water can be held and from which roots can extract retained water (Cable 1969). However, fractures in the restrictive layer can allow water penetration to greater depths and provide plant roots with access to deep soil moisture (Noy-Meir 1973). Soil texture also influences plant water availability. Low percolation rates in fine-textured soil results in water remaining in surface zones where it is exposed to high evaporative rates. Clay particles can adsorb water too tightly for plants to access, thus creating low plant water availability.

Decreased soil moisture in already arid regions is likely to have a large impact on the abundance and distribution of dryland plant species, as it may further stress many plants already at their physiological limits (Archer and Predick 2008). Morphological and physiological adaptations can increase tolerance to low soil moisture, including rooting depth, photosynthetic pathway, and leaf and stomatal characteristics (Ehleringer et al. 1999). Perennial plant species with roots below the zone of high evaporation at the soil surface are more likely to survive periods of drought and high temperature than shallow-rooted species (Walter 1971). Plants with a water-saving photosynthetic pathway (C_4, CAM), drought deciduousness, or high cavitation resistance are also more likely to tolerate low water availability. Annual plants avoid water stress by completing their life cycles when temperature and moisture regimes are favorable for growth. Key demographic processes, such as reproduction, recruitment, and mortality, as mediated by biotic and physical interactions can also affect plant response to water stress (Peet and Christensen 1980).

Differential survival rates of plant species in the face of climate change may lead to novel plant community assemblages. Shrub expansion into perennial grasslands is well documented, but the drivers of this change are controversial (Archer et al. 1995). Climate, livestock, and fire suppression are commonly invoked to explain these regional vegetation shifts. Sites that are relatively well protected from human land use, such as national parks, can provide valuable insight into how climate change has affected plant community composition.

To address how climate change may affect plant species in a dryland setting, we utilized annual monitoring data for the last twenty years (1989–2008) from five spatially separated areas of three national parks on the Colorado Plateau. The Colorado Plateau is a high elevation region at the boundary of two climate zones, making it particularly susceptible to extreme fluctuations in climate (Schwinning et al. 2008). The occurrence of plant species with a wide range of traits (e.g., annuals and perennials; shallow- and deep-rooted; C_3, C_4, and CAM photosynthetic pathways) makes the Colorado Plateau a model location to understand how different plant functional types are likely to respond to climate change.

Methods

Vegetation and environmental measurements

In 1989, permanent vegetation plots were established representing a minimum of three replicate sites spaced 1–85 km apart for each major plant community found in five national park areas (Arches, Natural Bridges, and the three districts of Canyonlands; Fig. 1). These park areas have been excluded from livestock grazing since the mid 1960s–1970s, but they were grazed before this time. At each plot, 100 permanently marked 0.5 m × 0.5 m quadrats were evenly spaced 2 m apart along two 100 m transects (Schelz et al. 2002). Canopy cover class (1 = 0–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, 6 = 95+%) was annually recorded for each species in the quadrats between April to early June (when most plants reach peak biomass). Each plot was generally visited within the same 10–14 day period every year. Repeat photographs were

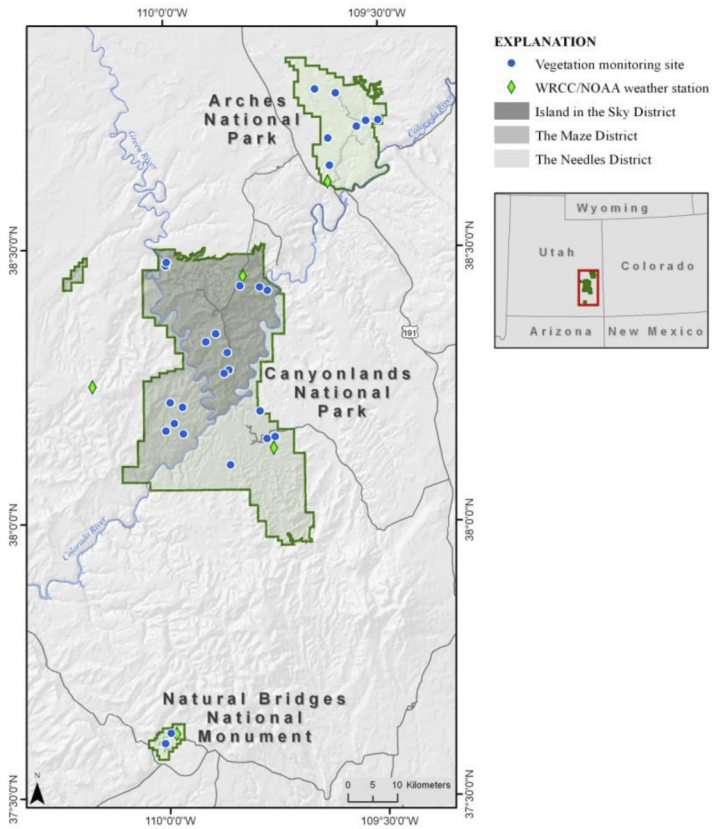

Fig. 1. Map of the vegetation monitoring sites and Western Regional Climate Center (WRCC)/National Oceanic and Atmospheric Administration (NOAA) weather stations within the five national park areas on the Colorado Plateau in southeastern Utah.

also taken to provide supplemental qualitative information. Total monthly precipitation and mean monthly temperature for each site were obtained from the nearest weather station in the Western Regional Climate Center Network (⟨http://www.wrcc.dri.edu⟩). A monthly aridity index was calculated by taking the quotient of monthly precipitation and monthly potential evapotranspiration (PET). PET was calculated using an equation modified for the U.S. intermountain west (Jensen and Haise 1963):

$$\mathrm{PET} = \frac{R_s}{2450}(0.025T_{mean} + 0.08) \qquad (1)$$

where R_s is monthly solar radiation (kJ m^{-2} day^{-1}) and T_{mean} is the monthly mean of daily air temperature (°C). For each site, elevations were determined from a Digital Elevation Model, soil series were determined from soil survey maps, and soil texture was analyzed using the hydrometer method from samples (N = 20 per plot) at 0–10 cm depth. Depth to impermeable layer was determined by driving a rod with a diameter of 0.8 cm into the soil (N = 15 per plot).

Statistical analyses

Mean canopy cover of each species was the response variable and was calculated by assigning cover class midpoint values to each quadrat and taking the mean of all quadrats. Only plots that were measured in all or most years of the study were included in the analysis (N = 29). Non-metric multidimensional scaling and cluster analysis was performed to designate plant communities using plant species with high relative cover (>30%) in plots in R (R Development Core Team 2008) with the vegan package (Oksanen et al. 2008). All years were included in the scaling to account for shifts in plant community composition through time. Certain species

were aggregated into plant functional types based on expected similarities in their response to environmental conditions. Species richness was calculated by summing the total number of species at each plot.

Multiple regression was performed on dominant plant species (1–3 per community) and functional type (5–8 per community) canopy cover. Due to the high number of explanatory variables in the regression models, we used a two-step approach: first regressing cover with annual means of climate variables (precipitation, temperature, aridity index) one and two years prior to vegetation sampling, and then regressing cover with monthly means of climate variables one year prior to vegetation sampling. Time (year) was also used in the regression models to account for interannual changes in cover not explained by climate variables. We performed regressions by plant community and by site within a plant community, as there was high variability in plant species and functional type canopy cover among sites. Cover data were arcsine square root transformed when assumptions of normality and homogeneity of variance were not met and are presented as the back-transformed values. Only dominant plant species and functional types that were significantly related to annual and monthly climate variables are presented.

Regression diagnostics using the car package in R (Fox 2009) revealed that multicollinearity among climate variables and between climate variables and time was evident in the models (variance inflation factor > 10). We accounted for multicollinearity in the multiple regression models by using a hierarchical partitioning approach (Chevan and Sutherland 1991, Mac Nally 2000) with the hier.part package in R (Walsh and Mac Nally 2007). Hierarchical partitioning is an analytical method of regression that quantifies the relative importance of each explanatory variable to the total explained variance of the regression model, both independently and together with the other explanatory variables, calculated for all possible candidate models. We report the independent effect of each variable to explained variability in the full model and determined the statistical significances of independent effects based on the upper 99% confidence level of Z-scores generated by a randomization routine (Mac Nally 2000). This strict confidence level was used to account for multiple comparisons.

Results

During the past twenty years, regional mean annual temperature in the study area significantly increased by 0.18°C per year from 1989–1995, 0.06°C per year from 1995–2003, and declined by 0.14°C from 2003–2008, representing an overall increase of 0.05°C per year over the past twenty years (Fig. 2a). There was high interannual variability in precipitation, which ranged from 129 mm in 1989 to 327 mm in 2006 (Fig. 2b). Nonmetric multidimensional scaling of the monitoring sites resulted in five distinct plant communities, determined by the dominant plant species or functional type: (1) perennial grasslands domi-

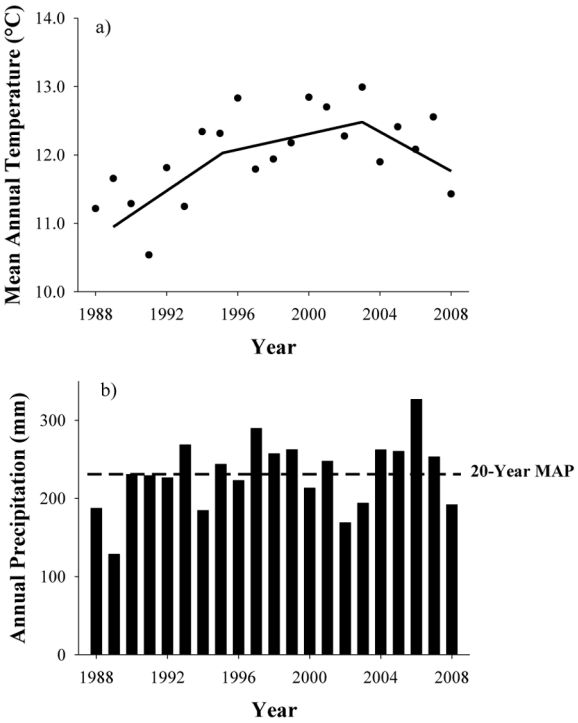

Fig. 2. (a) Regional mean annual temperature (°C) and (b) annual precipitation (mm) from 1988–2008 for all WRCC/NOAA weather stations (N = 5) in the five national park areas. Regional trend in mean annual temperature shown by fitted piecewise regression ($P < 0.0001$) and 20-year mean annual precipitation (MAP) shown with annual precipitation.

nated by C_3 (*Stipa hymenoides* and *S. comata*) and C_4 perennial grasses (*Hilaria jamesii*, *Bouteloua gracilis*, and *Sporobolus* spp.) (Welsh et al. 2003), shrublands dominated by (2) *Coleogyne ramosissima*, (3) *Artemisia tridentata/Sarcobatus vermiculatus*, (4) *Atriplex* species (*A. confertifolia, A. gardneri, and A. corrugata*), and (5) a woodland dominated by *Pinus edulis/Juniperus osteosperma* (Appendix: Fig. A1).

The mean annual temperature in the previous year (12 months preceding vegetation measurements; pMAT) was the best predictor of canopy cover of perennial plants (Table 1). The months of the previous year in which canopy cover was most strongly correlated to temperature depended on the plant species or functional type. Mean annual temperature with a two-year lag significantly explained the variance of shrub cover in perennial grasslands and *Sarcobatus vermiculatus* cover. There was a minimal effect of precipitation at a monthly, seasonal, or annual scale on canopy cover of perennial plants, even when precipitation lag times up to 2 years prior to vegetation sampling were included in the analyses. The aridity index was not a better predictor than temperature alone, but it did significantly explain the variance of *Artemisia tridentata* cover. In most plant communities, the cover-temperature relationship was independent of time. However, cover was significantly related to time and temperature for *Coleogyne ramosissima*, *Juniperus osteosperma*, and multiple understory shrub species in the pinyon-juniper woodlands. Therefore, an environmental factor that covaried with temperature through time may have also explained changes in cover of these plant species. Previous October–March precipitation was the best predictor for annual plants.

Perennial grasslands

The perennial grassland sites were on very deep, rapidly permeable, well-drained soils formed from aeolian deposits and alluvium. The C_3 perennial grasses decreased by 3.2 to 16.3% canopy cover at six of the eight sites sampled over a 5°C increase in pMAT ($r = -0.44$ to -0.69, $P < 0.05$; Fig. 3a). The sites with the highest initial C_3 perennial grass canopy cover had the greatest rates of decline. Cover did not significantly change with increasing temperature at sites with very high sand content (>85%, Table 2; White Crack and Salt Valley). Canopy cover of C_3 perennial grasses was most sensitive to increases in summer (July–September) temperatures ($r = -0.47$, $P < 0.0001$). Repeat photography showed grass canopy cover loss resulted from reduced cover of living plants and death of individuals.

Ephedra viridis was the most common shrub in the perennial grasslands. At two of the sites where the initial canopy cover was >2% (White Crack and Gray's Pasture), cover increased by 2.3 and 2.8% canopy cover, respectively, over a 4°C increase in pMAT ($r = 0.47$ and 0.50, $P < 0.05$; Fig. 3b) in years when late spring-summer (May–July) temperatures were high ($r = 0.42$, $P < 0.001$). Repeat photography showed that increases in *E. viridis* canopy cover were primarily due to vegetative spread from established individuals. Canopy cover of perennial forbs and cacti was generally low (3% and 1%, respectively) in perennial grasslands and did not change with increasing pMAT.

In contrast to perennial grasses, the canopy cover of annual species was not related to pMAT, but rather to the preceding cool season (October–March) precipitation (Fig. 3c). Sites with low initial C_3 perennial grass canopy cover (Musselman Canyon, Harvest Scene, and Jasper Canyon) showed the highest increases of 21.3 to 39.7% over a 156 mm increase in cool season precipitation ($r = 0.67$ to 0.82, $P < 0.05$). Sites with high declines (Gray's Pasture, North Flat) or no change in C_3 perennial grass canopy cover (White Crack, Salt Valley) with increasing pMAT had a relatively low annual species canopy cover increase of 6.0 to 12.9% over a 156 mm gradient in cool season precipitation ($r = 0.45$ to 0.64, $P < 0.05$). Since annuals composed most of the species richness and exotic species canopy cover, cool season precipitation was also positively related to both measures (species richness: $r = 0.50$, $P < 0.0001$; exotic species canopy cover: $r = 0.33$, $P < 0.0001$).

Shrublands

Dominant shrubs in shrublands had a mixed relationship with increasing pMAT. As expected, these relationships depended on site factors and plant species traits within shrubland communities.

Coleogyne ramosissima-dominated communities.—

Table 1. The independent effects (percent of R^2) of climate variables and time (year) to explain plant species and functional type canopy cover as determined by hierarchical partitioning. Only the plant species and functional types that were explained by climate variability are shown. Bold values designate significant independent effects based on the upper 99% confidence level of Z-scores generated by a randomization routine (Mac Nally 2000).

	Perennial Grasslands			Shrublands				Woodlands	
Climate Variable	C3 Perennial Grasses	Shrubs	Annuals	*Coleogyne ramosissima*	*Artemisia tridentata*	*Sarcobatus vermiculatus*	*Atriplex* spp.	*Juniperus osteosperma*	Shrubs
Year	9.6	12.7	11.1	**33.9**	15.6	3.1	19.4	**41.9**	**33.2**
pMAP	8.9	4.7	7.5	9.4	7.2	2.4	2.8	6.2	5.1
p2MAP	7.0	0.6	2.0	7.4	6.2	0.2	2.2	1.6	5.8
pOMP	4.8	17.8	**57.7**	3.7	5.9	0.5	4.3	1.4	2.6
pMAT	**37.8**	**33.9**	1.4	**29.2**	**33.5**	**51.9**	**49.2**	**32.3**	**26.3**
p2MAT	15.9	**26.4**	11.8	7.0	7.2	**29.0**	18.2	5.2	15.6
ARID	16.0	3.9	8.6	9.5	**24.3**	12.9	3.9	11.6	11.3

Note: Climate variable abbreviations are: pMAP, mean annual precipitation in the previous year, p2MAP, mean annual precipitation with two year lag, pOMP, October-March precipitation of the previous year, pMAT, mean annual temperature in the previous year, p2MAT, mean annual temperature with two year lag, ARID, Aridity Index (pMAP/pPET, where pPET is potential evapotranspiration in the previous year).

Sites dominated by *C. ramosissima* occurred on a variety of soil types (Table 2). Cover of *C. ramosissima* at two (Devil's Garden and Chimney Rock) of the six sites increased by 6.0 and 6.5% canopy cover, respectively, over a 4°C increase in pMAT ($r = 0.46$ and 0.50, $P < 0.05$; Fig. 4a), whereas the rest (Willow Flat, Monument Basin, Panorama Point, and Lower Jump) showed no change. The responsive sites were at a higher elevation (1600–1660 m versus 1440–1550 m; Table 2) and had shallower soils (14–17 cm versus 24–67 cm) than the non-responsive sites.

Artemisia tridentata/Sarcobatus vermiculatus-co-dominated communities.—The canopy cover of the C_3 shrub *A. tridentata* and C_4 shrub *S. vermiculatus* declined by 3.7% ($r = -0.65$, $P < 0.05$; Fig. 4b) and 10.3% ($r = -0.62$, $P < 0.05$; Fig. 4c), respectively, over a 3°C increase in pMAT at the Courthouse Wash site. In contrast, there was little or no change at the other sites. Soils at all sites were derived from stream alluvium, but soils at the Courthouse Wash site had higher sand (82% versus 65–71%), lower silt (9% versus 20–22%), and were shallower (35 cm versus >40 cm) relative to the other sites.

Atriplex species (A. confertifolia, A. gardneri, and A. corrugata)-dominated communities.—Canopy cover of *Atriplex* species (C_4 shrubs) was initially low and declined by 2.0 to 10.5% at four of the six sites over a 5°C increase in pMAT ($r = -0.47$ to -0.71, $P < 0.05$; Fig. 4d). These sites had shallow (<30 cm) soils derived from residuum and slope alluvium from sandstone and shale high in clay and silt (>60%). Repeat photographs showed that declines resulted from reduced cover of living shrubs and individual mortality. Canopy cover of *Atriplex* spp. was most correlated with fall-spring (October–March) temperatures ($r = -0.38$, $P < 0.001$).

Understory plant species/functional types in all shrubland communities.—Canopy cover of C_3 perennial grasses was low in shrublands (most sites had an average of <1% across all years). Four out of the sixteen shrubland sites had >1% canopy cover and experienced a 1.0 to 2.6% decline over a 5°C increase in pMAT ($r = -0.47$ to -0.62, $P < 0.05$). The C_4 perennial grasses were more common in shrublands than C_3 perennial grasses, having up to 15% canopy cover. Seven out of the nine shrubland sites where initial C_4 perennial grass canopy cover was >2% experienced declines of 1.2 to 5.3% over a 5°C increase in pMAT ($r = -0.47$ to -0.63, $P < 0.05$). Perennial forb cover did not correlate with pMAT. Cacti canopy cover was low in shrublands (average <1% across all years) and showed little change with pMAT. Canopy cover of annual species was highest in *Artemisia tridentata/Sarcobatus vermiculatus*-codominated shrublands and, like perennial grasslands, increased in all shrubland communities with increases in prior year cool season precipitation. Species richness across all years in shrubland communities was significantly lower than perennial grasslands ($t = 10.86$, $P <$

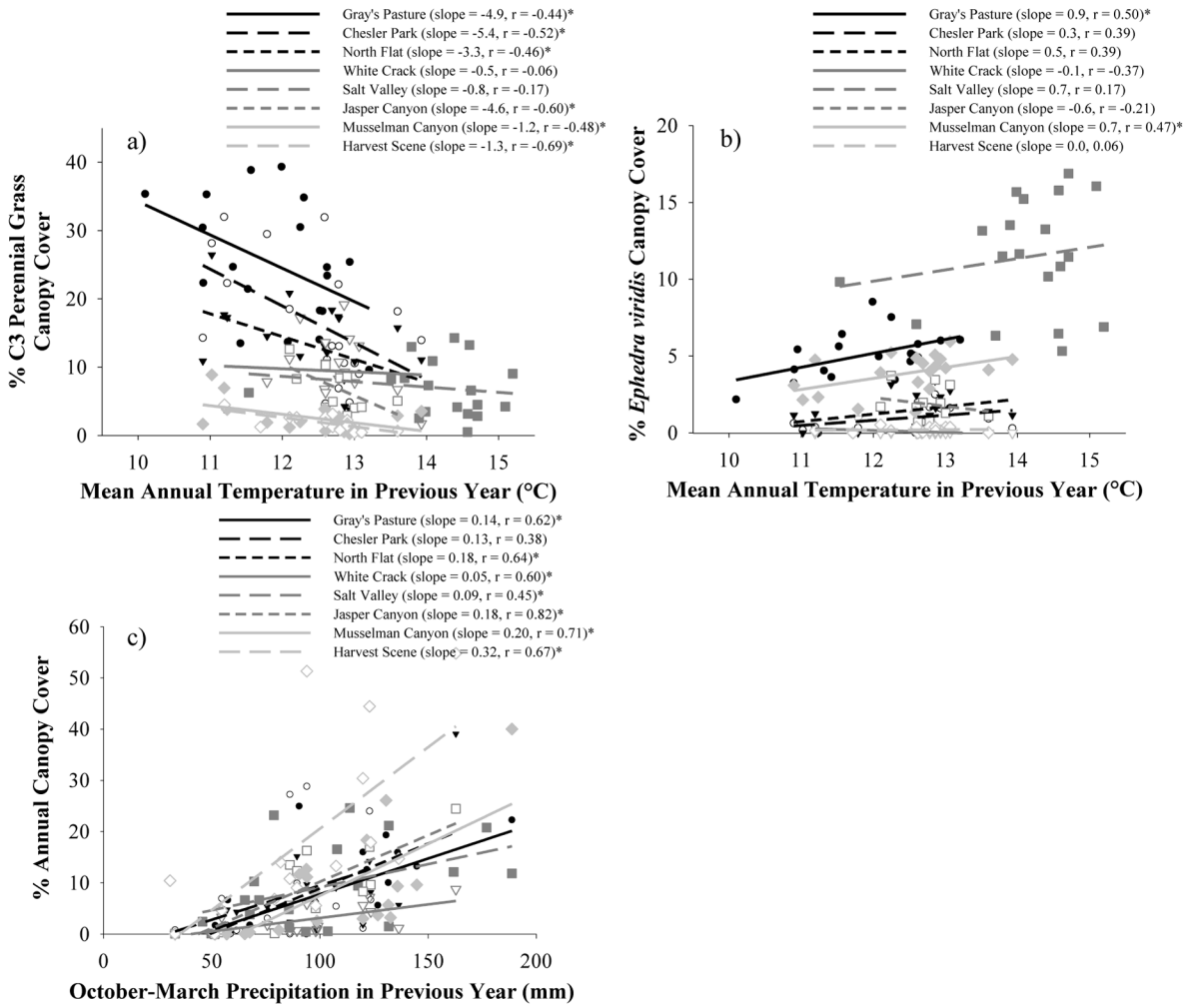

Fig. 3. Canopy cover of (a) C_3 perennial grasses and (b) *Ephedra viridis* for each perennial grassland site relative to mean annual temperature in the previous year (°C). (c) Annual species canopy cover for each perennial grassland site relative to previous October-March precipitation. Slope and correlation coefficient (r) shown for each perennial grassland site. An asterisk (*) indicates $P < 0.05$.

0.0001) and woodlands ($t = 6.44$, $P < 0.0001$) and was related to cool season precipitation ($r = 0.48$, $P < 0.0001$).

Woodlands

Communities dominated by *Pinus edulis* and *Juniperus osteosperma* in this study occurred on shallow (<30 cm) Rizno soils interspersed with rock outcrops (Table 2). Canopy cover of *P. edulis* did not change with increasing pMAT. At two sites (Grandview Point and Murphy Point) where initial *J. osteosperma* cover was >5% cover, the tree cover increased by 4.0 and 11.6%, respectively, over a 3°C increase in pMAT ($r = 0.57$ and 0.74, $P < 0.05$; Fig. 5a). Similar to sites dominated by *C. ramosissima*, the largest increase in *J. osteosperma* with increasing temperature occurred at sites with the shallowest soils. Canopy cover of shrubs also increased in woodlands by 6.7 to 8.2% over a 3°C increase in pMAT ($r = 0.55$ to 0.63, $P < 0.05$; Fig. 5b), with the greatest increase occurring when summer temperatures were high (May–July; $r = 0.40$, $P < 0.001$). Most shrubs that showed an increase in canopy cover were species typically found at lower elevation (*C. ramosissima* and *Ephedra viridis*). As with *J. osteosperma*, the

Table 2. Elevation, soil characteristics (soil series, texture, depth), and change (Δ) in distance and elevation from nearest weather station for each vegetation monitoring site by plant community.

Site	Elevation (m)	Soil Series	Sand (%)	Clay (%)	Silt (%)	Soil Depth (cm)	Δ Distance (km)	Δ Elevation (m)
Perennial Grasslands								
Gray's Pasture	1830	Begay	72	15	13	30	2.1	126.3
Chesler Park	1710	Begay	71	14	15	50	10.3	196.2
North Flat	1600	Mido	71	22	7	47	18.6	85.7
White Crack	1400	Begay	91	8	1	41	17.0	54.7
Salt Valley	1500	Mido	87	10	4	65	19.1	260.5
Jasper Canyon	1400	Mido	79	10	11	37	18.4	−391.1
Musselman Canyon	1360	Begay	74	13	13	20	5.1	−340.0
Harvest Scene	1430	Mido	70	20	10	44	15.7	−360.8
Coleogyne ramosissima Shrublands								
Chimney Rock	1660	Rizno	77	14	9	17	17.9	−129.1
Devil's Garden	1600	Crosscan family	72	17	12	14	18.2	354.5
Willow Flat	1440	Mido, calcareous	85	9	7	49	9.0	199.5
Monument Basin	1550	Bluechief	61	19	20	24	17.0	36.1
Panorama Point	1490	Pocum family	81	13	7	26	12.7	246.5
Lower Jump	1470	Arches	85	10	4	67	6.6	−44.5
Artemisia tridentata/Sarcobatus vermiculatus Shrublands								
Courthouse Wash	1270	Patterfield	82	10	9	35	3.4	23.5
Upheaval Bottom	1200	Thoroughfare	65	13	22	...	14.5	−498.8
Cave Spring	1510	Mido	67	12	21	42	1.6	−1.1
Salt Pocket	1500	Mido, sodic surface	71	9	20	74	0.8	−12.3
Atriplex spp. Shrublands								
Cache Valley	1330	Persayo	31	43	27	25	14.6	83.5
Lower Cache Valley	1330	Hanksville	36	41	23	36	16.1	86.5
Amoeba Butte	1400	Tsaya family or Moenkopie	39	31	30	15	6.8	−300.5
Taylor Canyon	1220	Tsaya family or Moenkopie	32	27	41	10	14.5	−479.7
Murphy Hogback	1490	Tsaya family or Moenkopie	29	31	40	15	14.7	−209.9
Taylor Canyon 2	1220	Tsaya family or Moenkopie	42	39	19	13	14.5	−481.5
Pinus edulis/Juniperus osterosperma Woodlands								
Murphy Point	1880	Rizno/rock outcrop	68	22	10	10	12.4	172.8
Grandview Point	1910	Rizno/rock outcrop	74	18	8	6	15.6	205.4
Lizard Rock	1690	Rizno	79	12	9	16	17.0	−105.3
Mesa Top	1890	Rizno	62	17	21	27	3.1	−90.2
Rim Rock	1930	Rizno	69	15	16	25	1.1	−53.2

Note: An ellipsis indicates no data.

sites that showed the largest increase in shrub canopy cover with increasing pMAT (Murphy Point, Grandview Point, and Mesa Top) were those that had the highest initial cover (10–25% cover compared to 3–7%).

Discussion

When water is not limiting, Colorado Plateau plant species are able to tolerate maximum temperatures higher than those recorded during this study (Loik and Harte 1996). Thus, the changes in plant cover associated with increasing temperature we observed were most likely due to lower plant-available soil moisture. As expected, plant species in this region were differentially affected by increasing temperature based on their lifespan, rooting depth, water-use efficiency, and the soil and physical characteristics of a site that may have regulated water availability.

Perennial grasslands

In the perennial grasslands, we observed an overall decline in cover of C_3 perennial grasses, no change for C_4 perennial grasses, and a small increase in *Ephedra* with increases in temperature. Grasses have fibrous roots with flexible walls, limiting their ability to vertically transport water (Steudle 2000). Thus, they rely heavily on moisture in surface soils. On the Colorado

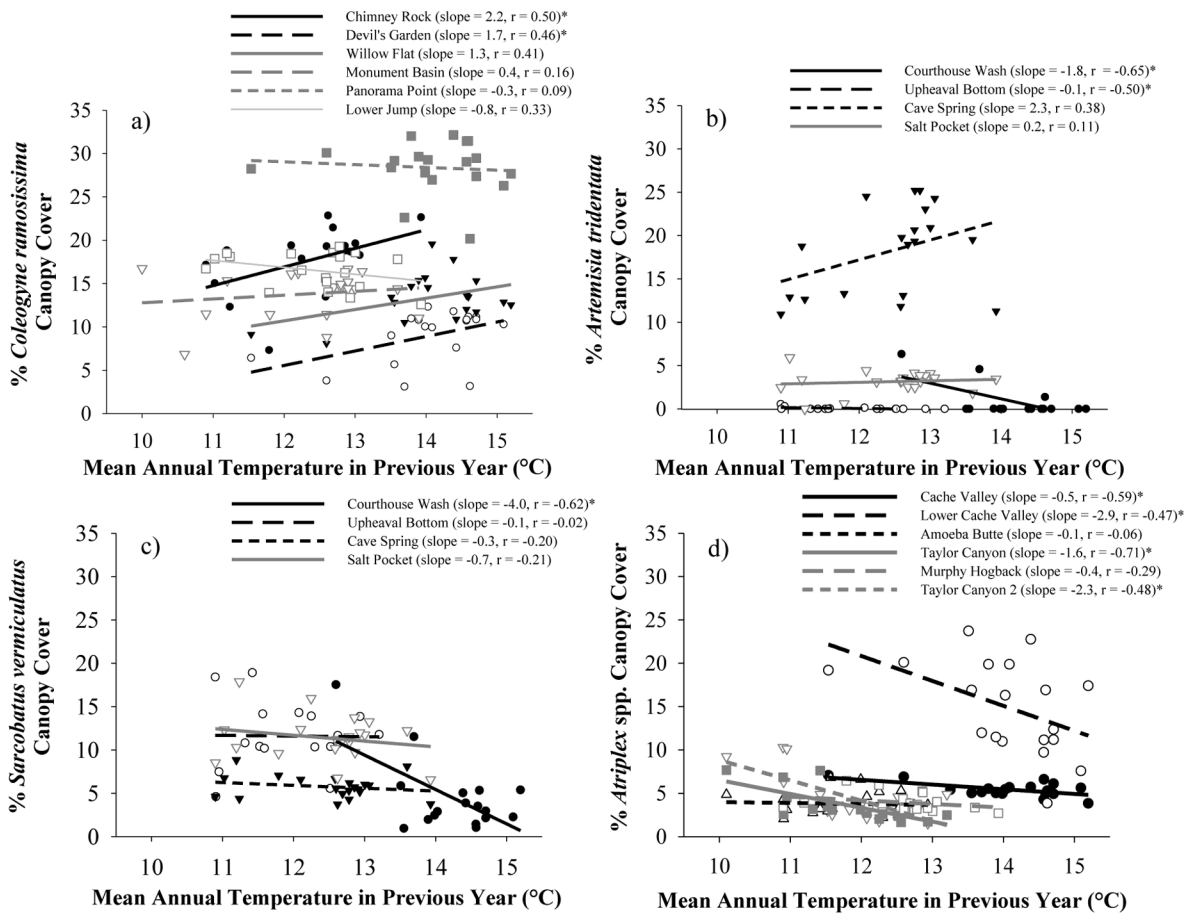

Fig. 4. Canopy cover of (a) *Coleogyne ramosissima*, (b) *Artemisia tridentata*, (c) *Sarcobatus vermiculatus*, and (d) *Atriplex* spp. (*A. confertifolia, A. gardneri, and A. corrugata*) for each shrubland site where it was dominant relative to mean annual temperature in the previous year (°C). Slope and correlation coefficient (r) shown for each shrubland site. An asterisk (*) indicates $P < 0.05$.

Plateau, grasses derive ~85% of their moisture from surface soils compared to ~54% for shrubs (Ehleringer 2001). Because evaporation rates are higher at the soil surface than at depth, we expected the shallow-rooted grasses to be more vulnerable to increasing temperatures than deeper-rooted shrubs. This pattern occurred, as grasses declined and the shrub *Ephedra viridis* increased with increased pMAT. Repeat photography at our study sites also showed the canopy cover of the shrubs *Ceratoides lanata* and *Coleogyne ramosissima* increased during the study period. Unfortunately, these two shrub species were not sufficiently represented within or across plots to quantify this increase. Photos revealed that the increase for *C. lanata* was due to both the growth of existing individuals and recruitment of new plants, whereas the increase of *C. ramosissima* was solely due to growth of existing individuals.

Sites with the highest initial C_3 perennial grass cover showed the greatest decline in cover with increasing pMAT. C_3 perennial grasses may have performed better at these sites because they were at relatively high elevation and were on deep soils with ~70% sand, conditions which create high soil water availability. The resultant high cover at these sites may have led to strong competition for water under dry conditions created by high temperatures. The grasses least vulnerable to increasing temperature occurred on deep soils with a very high sand content (87–

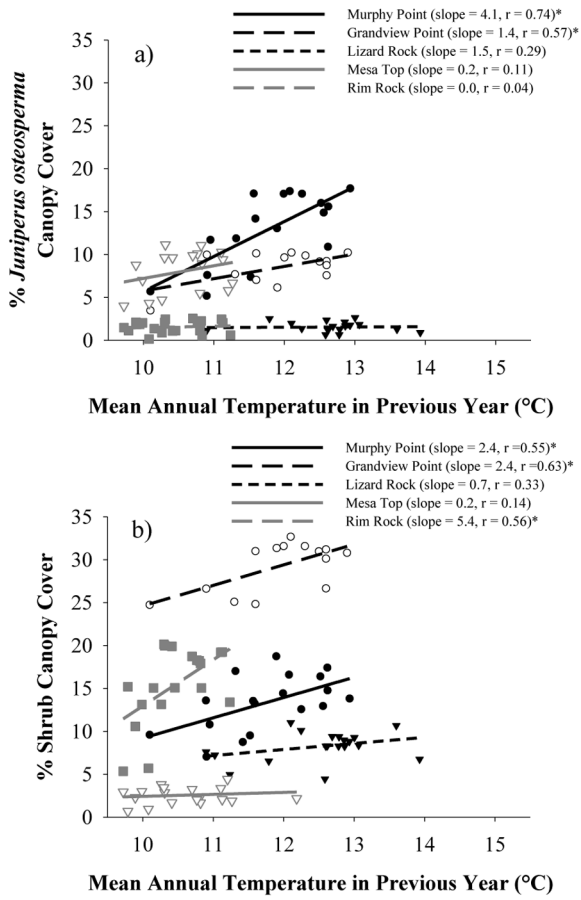

Fig. 5. Canopy cover of (a) *Juniperus osteosperma* and (b) shrub species for each pinyon-juniper woodland site relative to mean annual temperature in previous year (°C). Slope and correlation coefficient (r) shown for each woodland site. An asterisk (*) indicates $P < 0.05$.

91%), which would allow water to move below the high evaporative zone. The lack of apparent effect of pMAT on C_4 grasses relative to C_3 perennial grasses at the grassland sites may be due to their higher temperature optimum for photosynthesis (Ehleringer 1978) and lower stomatal conductance rate, decreasing the potential for water loss (Knapp 1993). Lower aboveground biomass of the C_4 relative to the C_3 perennial grasses likely decreased soil water depletion.

Small increases in *Ephedra viridis* cover may have been due to increased soil moisture availability as C_3 perennial grasses declined, but *Ephedra* has many drought adaptations, including extensive surface and subsurface roots that can extract water from 2 m depth (Yoder and Nowak 1999); an evergreen condition, allowing growth whenever water is available; photosynthetically active stems; small, scale-like leaves, reducing transpiration; and few vessel elements in the stem, which reduces cavitation during drought (Carlquist 1988). The growth of *Ephedra* may not have been affected by high temperature because it receives much of its water from winter precipitation (Yoder and Nowak 1999), when temperatures are low.

An increase in annual species canopy cover with higher cool season precipitation was similar across perennial grassland sites. Cover in a given year is dependent on whether conditions were favorable for seed production in the previous years, as well as whether precipitation was sufficient for both seed germination and plant establishment in the current year.

Shrublands

Our results show that *C. ramosissima* increased in canopy cover with increasing pMAT, *A. tridentata* and *S. vermiculatus* had a mixed response, and cover of *Atriplex* species declined. *Coleogyne ramosissima* is evergreen and well adapted to high temperatures (Summers et al. 2009). In addition, as it occurred on very shallow soils, we presume that it had roots following fractures in the bedrock, allowing it access to deep water derived from winter precipitation (Schwinning et al. 2005).

The decline of *Artemisia tridentata* and *Sarcobatus vermiculatus* canopy cover with increasing pMAT at Courthouse Wash, but not the three other sites, may be related to landscape position. The Courthouse Wash site is on an alluvial terrace >5 m above the wash, likely resulting in a water table beyond the reach of most shrub roots. In contrast, the other sites are located closer to the floodplain, and thus roots likely have access to supplemental water, which could account for the overall lack of decline with increasing temperature. *Sarcobatus vermiculatus* was expected to be less sensitive to temperature than *A. tridentata* because it is a phreatophyte well adapted to hot desert regions and because it can drop leaves in the summer (Branson et al. 1976). In contrast, *A. tridentata* has a low photosynthetic temperature optima and is at

the southern end of its distribution on the Colorado Plateau (Caldwell 1985). However, it does minimize water loss by exploiting water early in the growing season when temperature is low, shedding leaves in the summer, having high cavitation resistance, and reducing transpiration and hydraulic conductance when temperature is high (Kolb and Sperry 1999).

In contrast to other shrubs in this study, canopy cover of *Atriplex* species declined at most sites with increasing temperature. *Atriplex* communities commonly occurred on shale-derived soils with high clay and silt content (Table 2). Low water infiltration rates results in most water occurring at the soil surface where evaporation is high. *Atriplex* species have extensive root systems, but they are very shallow (Dobrowolski et al. 1990). Therefore, reduced canopy cover with pMAT was likely due to limited access to deep soil water. Similar to the C_3 perennial grasses in grasslands, *Atriplex* communities that have been able to support high cover in past wetter years may be unable to do so in hotter or drier years.

Woodlands

Plant species in pinyon-juniper woodlands increased or showed no cover change with pMAT. Given the drought sensitivity of *Pinus edulis* (Breshears et al. 2005), it was surprising we found no canopy cover changes across our sites, despite differences in elevation. Repeat photography indicated a few trees adjacent to the plots died during the study. All our sites were on very shallow soils, indicating the *P. edulis* in our plots was exploiting deep water in bedrock fractures. Less mortality of the species was also observed in this region relative to others during the large regional 2002 die-off, and access to deep water may have partially accounted for this (Breshears et al. 2005).

Juniperus osteosperma increased in canopy cover with pMAT at two of our five sites. Similar to *Coleogyne ramosissima* sites, the largest increases in *J. osteosperma* were on shallow soils. *Juniperus osteosperma* is highly adapted to drought, tolerating a wide range of leaf water potentials and having high cavitation resistances (McDowell et al. 2008). *Juniperus osteosperma* is also better able to utilize surface soil water in the summer than many plants (Williams and Ehleringer 2000). Shrubs typically found at lower elevation may have increased in cover with increases in pMAT due to increased water availability at higher elevation. In contrast to C_3 perennial grasses in grasslands and *Atriplex* shrubs, woodland shrub canopy cover increased with increasing temperature at sites that already had high initial cover by the expansion of existing individuals.

Plant responses to temperature versus precipitation

Most ecologists agree that water availability is the primary limiting factor in arid regions. However, the patterns of precipitation and their consequences receive far more research attention than high temperature that increases evapotranspiration rates and limits the effectiveness of water input. There are several possible reasons why temperature was better correlated to plant canopy cover than precipitation in this study. First, plots were up to 19 km away and/or 500 m higher or lower in elevation than the nearest weather station (Table 2). Given the high spatial variability of precipitation on the Colorado Plateau, there may have been discrepancies between precipitation at the weather station and the vegetation plots. Second, the timing and amount of individual precipitation events relative to the phenological stage of the plant has a large impact on how plants respond to the precipitation. Furthermore, most precipitation events in arid regions are <5 mm and cannot be utilized by plants (Lauenroth and Bradford 2009). Third, the air temperature at which precipitation occurs heavily influences how much and to what depth a given precipitation event affects soil moisture levels, the rate of evapotranspiration, and the time soils stay moist. Fourth, regional temperature and precipitation in March–October are negatively correlated ($r = -0.45$, $P < 0.0001$). As a consequence, years with high warm-season temperatures typically accompany low warm-season precipitation. Lastly, plant species and functional types were most sensitive to high temperatures in the late spring and summer, when water stress may be driven by temperature controls on evapotranspiration, rather than precipitation inputs.

Future outlook

The response of plant species and functional types to climate change in the relatively undisturbed national parks over the last twenty years

allows for accurate forecasting of the impacts of climate change on plant community composition for the Colorado Plateau. Increases in temperature on the Colorado Plateau over the last twenty years suggests a 5°C increase in MAT by the year 2100, which is within the projected model estimates for the southwestern U.S. of 4–8°C. Our results suggest perennial grasslands of the region exposed to this increase in temperature will likely have further declines and possible extirpation of C_3 perennial grasses. Such declines will have large ecosystem implications, including loss of livestock forage and habitat and food for wildlife. Perennial grasslands with very high sand content are likely to be buffered to some degree against these declines. If there are shrub species present capable of rapid growth and reproduction, such as *Ephedra* spp. or *Ceratoides lanata*, they may fill in some of the spaces left by the grass loss. If this does not occur, increased soil erosion by wind and water can be expected (Munson et al. 2011), reducing site fertility and negatively affecting water quality and quantity.

It is more difficult to determine critical temperatures for shrub species in shrublands, but our results emphasize the importance of shrub rooting depth, soil depth, soil texture, and other environmental characteristics that affect water availability. Shrubs with access to deep soil water will likely be the least affected by increasing temperature, but long-term persistence and reproduction will depend on infrequent recruitment events. Given its increase in canopy cover with warmer temperature, *Coloeogyne ramosissima* is likely to expand its range into currently warmer zones (Bowns and West 1976) and into grassland and woodland plant communities. However, past evidence has shown that the shrub requires enhanced winter precipitation to establish (Cole and Webb 1985) and thus such expansion would also rely on precipitation timing. All shrub species will likely have greater difficulty surviving on shallow, fine-textured soils unless they are able to access water through cracked bedrock.

Based on the current minimum elevation required for *Pinus edulis* growth, its occurrence is likely to decline at the lowest end of its elevational distribution and be replaced by *Juniperus osteosperma* as temperatures become warmer. Pinyon-juniper woodlands are likely to become more dominated by shrubs that can move up in elevation as temperature increases. Transitions of shrub distribution along an elevation gradient have occurred before in the southwestern U.S. in the last 1000 years in response to climate change (Cole and Webb 1985).

Although the current precipitation regime is dominated by small events, fewer, more intense events in the future could increase perennial vegetation cover on soils with high infiltration capacity (Heisler-White et al. 2008). This is because even if total annual precipitation decreases, more intense events can shift soil moisture deeper in the profile, thereby reducing the temporal variability of water variability compared to the surface layer (Fay et al. 2008). Similarly, the availability of deep soil water from winter precipitation may become more critical for plant survival on the Colorado Plateau as high summer temperatures mask the effectiveness of summer monsoonal precipitation.

The loss of grass and expansion of shrubs has been noted worldwide (Archer et al. 1995). Land use practices may have initiated this vegetation shift in our study sites before park establishment, as they are currently contributing to this change outside of the parks (Rosenstock 1996, Fernandez et al. 2008). Our results suggest that shrub expansion and grass loss have occurred over a broad spatial extent in parks, which have been ungrazed by livestock since the early 1970s and have had no wildfires or suppression. It is clear that climate has played a large role in facilitating this shift and will likely continue to affect future alterations of plant community composition on the Colorado Plateau.

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Appendix

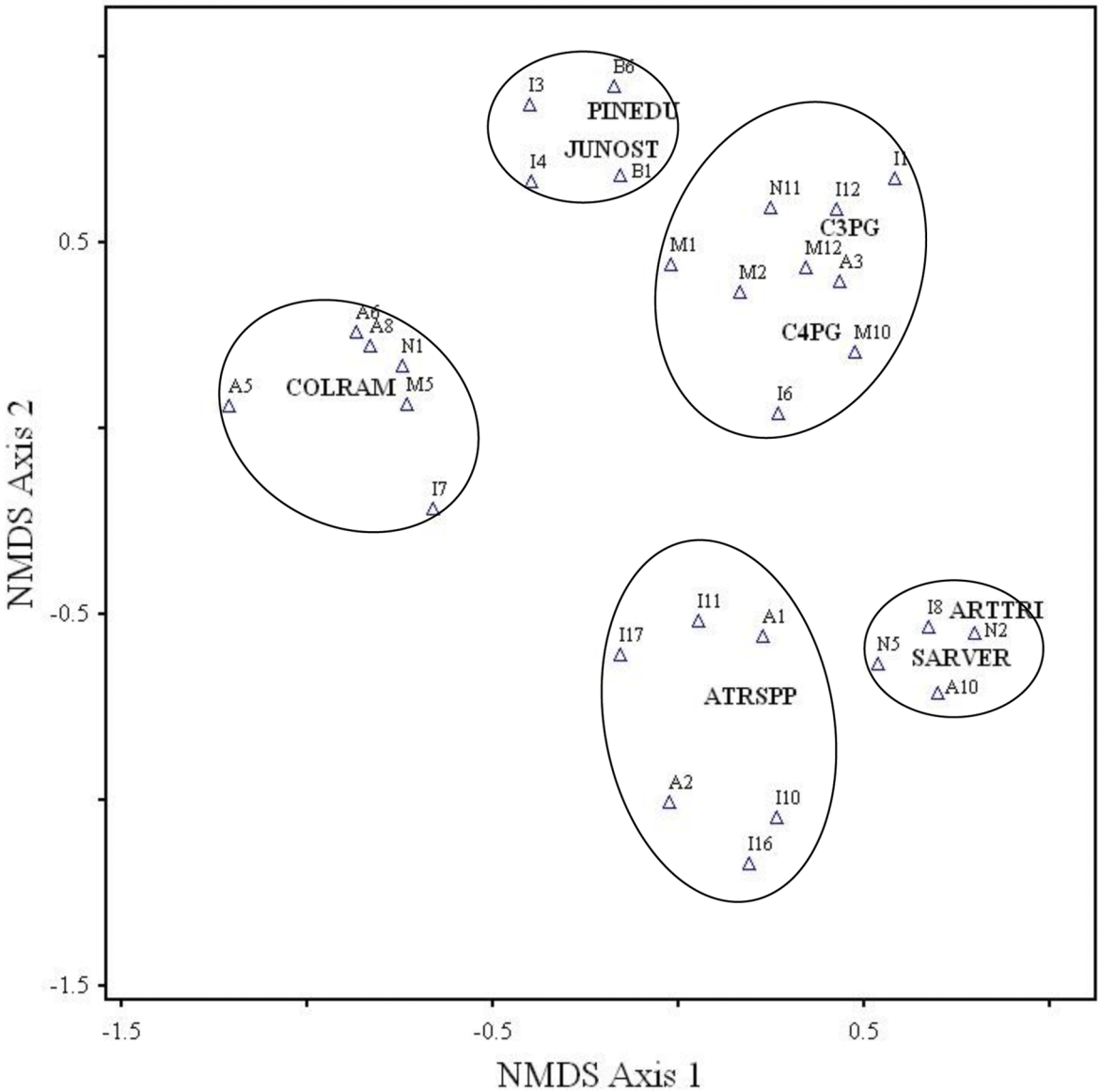

Fig. A1. Scatter plot of vegetation monitoring sites and dominant species/functional types (C3PG = C3 perennial grasses, C4PG = C4 perennial grasses, COLRAM = *Coleogyne ramosissima*, ATRSPP = *Atriplex* spp., ARTTRI = *Artemisia tridentata*, SARVER = *Sarcobatus vermiculatus*, PINEDU = *Pinus edulis*, JUNOST = *Juniperus osteosperma*) relative to the first and second nonmetric multidimensional scaling axes. Sites grouped by hierachical cluster, which designates plant community (Perennial grassland: I1 = Gray's Pasture, N11 = Chesler Park, M2 = North Flat, I12 = White Crack, A3 = Salt Valley, M12 = Jasper Canyon, I6 = Musselman Canyon, M10 = Harvest Scene; Coleogyne-dominated shrubland: A5 = Panorama Point, A6 = Devil's Garden, A8 = Willow Flat, I7 = Monument Basin, N1 = Lower Jump, M5 = Chimney Rock; *Artemisia*/*Sarcobatus* co-dominated shrubland: A10 = Courthouse Wash, I8 = Upheaval Bottom, N2 = Cave Spring, N5 = Salt Pocket; *Atriplex* spp.-dominated shrubland: A1 = Cache Valley, A2 = Lower Cache Valley, I11 = Amoeba Butte, I16 = Taylor Canyon, I17 = Murphy Hogback, I10 = Taylor Canyon 2; *Pinus*/*Juniperus* co-dominated woodland: I3 = Murphy Point, I4 = Grandview Point, M1 = Lizard Rock, B1 = Mesa Top, B6 = Rim Rock).