

## Plant responses, climate pivot points, and trade-offs in water-limited ecosystems

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**Abstract.** Plant species in dryland ecosystems are limited by water availability and may be vulnerable to increases in aridity. Methods are needed to monitor and assess the rate of change in plant abundance and composition in relation to climate, understand the potential for degradation in dryland ecosystems, and forecast future changes in plant species assemblages. I employ nearly a century of vegetation monitoring data from three North American deserts to demonstrate an approach to determine plant species responses to climate and critical points over a range of climatic conditions at which plant species shift from increases to decreases in abundance (climate pivot points). I assess these metrics from a site to regional scale and highlight how these indicators of plant performance can be modified by the physical and biotic environment. For example, shrubs were more responsive to drought and high temperatures on shallow soils with limited capacity to store water and fine-textured soils with slow percolation rates, whereas perennial grasses were more responsive to precipitation in sparse shrublands than in relatively dense grasslands and shrublands, where competition for water is likely more intense. The responses and associated climate pivot points of plant species aligned with their lifespan and structural characteristics, and the relationship between responses and climate pivot points provides evidence of the trade-off between the capacity of a plant species to increase in abundance when water is available and its drought resistance.

**Key words:** arid; Chihuahuan Desert; climate change; Colorado Plateau; cross-site; desertification; early warning sign; long-term monitoring; plant canopy cover; Sonoran Desert.

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### INTRODUCTION

Over one-third of terrestrial ecosystems are water limited because they have potential evapotranspiration losses that are twice as high as the precipitation inputs they receive (UNEP 1997). The timing and amount of water available to plants in these semiarid and arid ecosystems may be further restricted by local climatic factors that modify the transport of moisture in air masses, soil and landscape characteristics that influence the movement and distribution of water, and root

competition that can deplete soil moisture at a fine scale (Loik et al. 2004). Plant water use ultimately depends on the structural and physiological limitations of the species and the plasticity of the individual plant to extract water at different soil depths and periods of time. These limitations of water on plant performance from the regional to plant scale are likely to be exacerbated by global change predictions of an increasingly warm and dry climate across many semiarid and arid areas (Christensen et al. 2007).

Assessing the vulnerability of plant species to

increases in aridity in already water-limited ecosystems is important because these ecosystems are prone to abrupt and potentially irreversible land degradation or desertification, characterized by shrub encroachment, invasion by exotic species, and the loss of total perennial vegetation cover (UNCCD 1994). These changes in plant cover can reduce the productive capacity and diversity of a site, alter food and habitat for wildlife and domestic livestock, and lead to the loss of soil resources (Munson et al. 2011a). Warming and drying conditions can also intensify the impact to and recovery potential of vegetation affected by land-use practices (Archer et al. 1995).

Two important metrics can be used to understand changes in the performance of plant species and forecast future species assemblages with respect to water availability: (1) the magnitude of a plant species' response, which can be defined by the capacity of a plant species to increase in abundance when water is available (and decrease in abundance when water is not available), and (2) the critical amount of water availability that causes a plant species to shift from increases to decreases in abundance. Plant responses to climate are either measured in experimental and observational frameworks at the plot-level or assessed at large spatial scales using correlations between the current climate and observed species distributions (species distribution and bioclimate envelope models; Pearson and Dawson 2003). There are few comparisons of plant responses across sites or assessments of dynamic climate-vegetation relationships that incorporate non-climatic factors at large spatial scales (Guisan and Thuiller 2005). These approaches can improve our ability to forecast climate change impacts on plant species abundance and distribution (Munson et al. 2011b, 2012, *in press*).

The shift from increases to decreases in plant abundance over a range of climatic conditions can be defined as a climate pivot point. This point is an important indication of drought resistance, as plant species with a low precipitation pivot point or high temperature pivot point are able to maintain positive increases in abundance with low water input or high evaporative demand. Plant species that cross climate pivot points have reduced capacity for growth and survival, but these changes are generally revers-

ible as climatic conditions become more favorable. Extreme or sustained climatic conditions beyond a pivot point, which negatively affect the cover of a dominant species or collectively influence many plant species, may lead to the permanent alteration of a plant species' assemblage and affect ecosystem function. These transitions or thresholds are conceptually well-defined (Holling 1973, May 1977) and have become a framework to address vegetation response to climate change and land-use intensification (Scheffer et al. 2001, Kéfi et al. 2007), yet there are few data to define the environmental conditions which can lead to them. A climate pivot point provides an empirically derived indicator of decreased plant performance and can serve as an early warning sign of increased vulnerability of crossing a threshold into an altered ecosystem state.

Drought resistance, indicated by the climate pivot point, comes at an energetic and physiological cost, such that a species with high drought resistance is unlikely to have a large response when water is more abundant (Parsons 1968, Oriens and Solbrig 1977, Grime 1979). The main reason for this trade-off is that plant carbon gain is coupled with water loss through the opening of stomata, which creates strong selective pressure for plants to either increase their growth rates during periods of water availability (at the cost of low drought resistance) or increase their water use efficiency to withstand drought (at the cost of low growth rate; Mooney 1972). Past studies have assessed the response-resistance trade-off in crop cultivars (Hurd 1974) and within plant functional types (Pockman and Sperry 2000, Angert et al. 2009) at small spatial scales, but this important principle remains untested across plant functional types and at broad spatial scales. An assessment of how the lifespan and structural and physiological traits of a plant species influences its position on the response-resistance continuum can lead to an understanding of how plant species assemblages are shaped by water availability and may change with future climates.

My objectives are to (1) demonstrate an approach to assess plant species responses and climate pivot points in relationship to water availability and (2) test whether there is a trade-off between the ability of a plant species to

increase when water is available and its resistance to water shortages by examining the relationship between responses and climate pivot points. To meet these objectives, I pair long-term climate and vegetation monitoring data at sites across the Colorado Plateau, Sonoran and Chihuahuan Deserts. I highlight the responses and climate pivot points of two dominant shrub species that have increased in abundance over vast regions of North American warm deserts (Archer et al. 1995) and a dominant perennial bunchgrass species in cold deserts. Because environmental characteristics influence water availability, I show how landform and soil texture in the Sonoran Desert, and biotic factors on the Colorado Plateau, can influence the response and climate pivot point of these dominant plant species. In the Chihuahuan Desert, I use a suite of woody and herbaceous plant species to test the response-drought resistance trade-off.

## METHODS

### Sites

The two sites in the Sonoran Desert, the Desert Laboratory and the Santa Rita Experimental Range in southern Arizona (Fig. 1, Table 1), experience mixed summer-winter precipitation and few days with freezing temperatures. The Arizona Upland plant species assemblage at the Desert Laboratory is dominated by shrubs (*Larrea tridentata* [creosote bush] and *Ambrosia deltoidea* [triangle-leaf bursage]), leguminous trees (e.g., *Cercidium microphyllum* [foothill palo verde]), and cacti. The assemblage at the Santa Rita Experimental Range is dominated by  $C_4$  grasses and the shrub *Prosopis velutina* (velvet mesquite) (plant nomenclature follows USDA Plants Database: <http://plants.usda.gov>). Both Sonoran Desert sites vary considerably in landform and soil type. Soil on the hill slope and upper piedmont of Tumamoc Hill, a volcanic outcrop at the Desert Laboratory (Spencer et al. 2003), consists of coarse sandy loam colluvium. At lower elevations, alluvium with gravelly sandy loam and loamy sand textures deposited in mid-Pleistocene times has well-developed petrocalcic horizons (cemented calcium carbonate layers). Alluvium of similar textures deposited in Holocene times dissects these older Pleistocene deposits, but it is relatively undevel-

oped and has low accumulation of calcium carbonate (McAuliffe 1994). The mesquite savanna at the Santa Rita Experimental Range occurs on a gently sloping piedmont that contains a mosaic of different-aged surfaces with sandy loam, loamy, and clay loam soil textures (Breckenfield and Robinett 2003).

The two sites on the Colorado Plateau, Arches and Canyonlands National Parks in southeastern Utah, experience cold temperatures in winter, have a higher proportion of winter precipitation than the Sonoran Desert, and have distinct plant assemblages dominated by  $C_3$  and  $C_4$  perennial grasses (perennial grasslands), shrub species of the Great Basin such as *Artemisia tridentata* (big sagebrush) (sagebrush shrublands), and shrub species of warm deserts such as *Coleogyne ramosissima* (blackbrush) (blackbrush shrublands). Soils at plots at Arches and Canyonlands National Parks used in this study are sandy loams and loamy sands interspersed with exposed sandstone (Munson et al. 2011b), physical attributes common to the region.

Five sites in the Chihuahuan Desert were used: Big Bend National Park in Texas and the Seville National Wildlife Refuge, White Sands Missile Range, Holloman Air Force Base, and the Jornada Experimental Range in New Mexico. These sites experience the highest proportion of summer precipitation compared to the Sonoran Desert and Colorado Plateau, and they are dominated by  $C_4$  grasses (e.g., *Bouteloua eriopoda* [black grama]) and shrubs (e.g., *Larrea tridentata* and *Flourensia cernua* [tarbush]). All Chihuahuan Desert plots and transects in this study are on uplands consisting of rolling plains and alluvial fan piedmonts that have loamy sand to sandy clay loam soils. It was not possible to control for historical livestock grazing that occurred at all of the sites in this study, but sites have been protected from livestock since at least the 1970s or experience light to moderate grazing (Santa Rita and Jornada Experimental Ranges). There is military training in select areas at White Sands Missile Range and Holloman Air Force Base, but only undisturbed control or reference plots were used in this study.

### Data

I compiled long-term repeat measurements of vegetation and climate at sites across the Sonoran

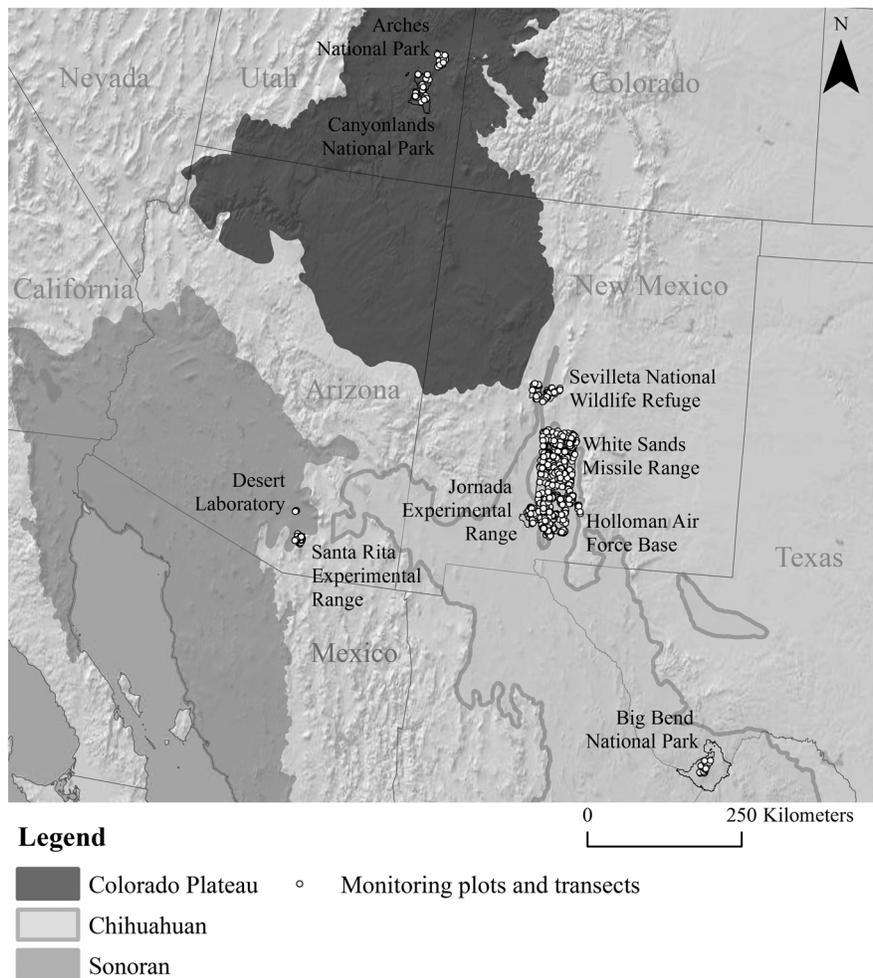


Fig. 1. Long-term vegetation monitoring plots and transects at sites in the Sonoran Desert, Colorado Plateau, and Chihuahuan Desert.

Desert (1928–2009), Colorado Plateau (1989–2008), and Chihuahuan Desert (1915–2010; Table 1). Vegetation measurements at sites consisted of plant species canopy cover estimated by (1) mapping or assigning cover values to represent the areal extent of plants or plant parts inside plots, or (2) recording the plant species that crossed a transect line or was intercepted by a point projected down to the canopy level from the transect line (line-intercept and line point-intercept). More detailed site descriptions and explanations of vegetation measurements can be found in Munson et al. (2011b, 2012, *in press*). The landform and soil characteristics of plots and transects at sites were determined from geologic

maps and soil surveys (Breckenfield and Robinett 2003, Spencer et al. 2003). Climate measurements consisted of mean monthly temperature and precipitation from long-term weather stations nearest to the vegetation plots and transects (<http://www.ncdc.noaa.gov>) and were supplemented with rain gauge data. I also used the Palmer Modified Drought Index, which is a calculation of the balance between moisture supply and demand that uses both temperature and precipitation variables. Monthly temperature, precipitation, and the drought index were aggregated into annual, summer (June–September), and winter (October–March) periods.

Table 1. Description of long-term vegetation monitoring sites in three North American deserts, including coordinates, area, elevation, climatic means, the method(s) of measurement, measurement units, and range and interval of years the measurement was conducted.

Site(s)	Coordinates (Lat, Long)	Area (km <sup>2</sup> )	Elevation (m)	Mean annual (summer/winter)		Method(s)	Measurement units	Years measured (interval)
				Precip (mm)	Temp (°C)			
Sonoran Desert								
DL	32°13' N, 111°00' W	4	245–960	300 (145/123)	21.2 (27.3/15.3)	mapped	7 (100 m <sup>2</sup> ) plots	1928–2001 (3–17 yr)
SRER	31°54' N, 110°53' W	215	914–1310	376 (214/146)	17.9 (25.2/12.6)	line-intercept	40 (30 m) transects	1956–2009 (1–7 yr)
Colorado Plateau								
ARCH	38°43' N, 109°35' W	1,677	975–2194	219 (81/107)	12.4 (23.5/12.4)	assigned cover	1600 (0.25 m <sup>2</sup> ) plots	1989–2008 (1–2 yr)
CANY	38°20' N, 109°52' W							
Chihuahuan Desert								
BIBE	29°16' N, 103°13' W	13,495	978–1698	252 (143/88)	16.0 (25.0/9.3)	mapped, assigned cover, line-intercept, line-point intercept	2036 (1–1000 m <sup>2</sup> ) plots; 392 (30–40 m) transects	1915–2010 (1–15 yr)
JRN	32°31' N, 106°48' W							
SEV	34°21' N, 106°53' W							
WSMR	33°10' N, 106°26' W							
HAFB	32°51' N, 106°06' W							

Notes: Site abbreviations are: DL, Desert Laboratory; SRER, Santa Rita Experimental Range; ARCH, Arches National Park; CANY, Canyonlands National Park; BIBE, Big Bend National Park; JRN, Jornada Basin Experimental Range; SEV, Sevilleta National Wildlife Refuge; WSMR, White Sands Missile Range; HAFB, Holloman Air Force Base.

### Analyses

As a primary objective of this study was to demonstrate an approach to assess climate-vegetation relationships, I chose a subset of species in each desert for analyses. I selected dominant species from the Sonoran Desert (*Larrea tridentata* and *Prosopis velutina*) and Colorado Plateau (*Achnatherum hymenoides*). In the Chihuahuan Desert, I included a greater number of plant species to determine variation in species responses and climate pivot points. The canopy cover of plant species was calculated by summing the area, intercept lengths, or points occupied by all vegetative units of dominant plant species divided by the total area of the plot, transect length, or points sampled. I used the mean canopy cover value of all plots or transects at a site for each year a study was conducted. To normalize plant species cover that was estimated using different methods at different sites, I calculated the change in cover of plant species

per unit time:

$$\text{Change in cover} = \frac{\ln(\text{cover}_{t2}/\text{cover}_{t1})}{t2 - t1} \times 10$$

where  $\text{cover}_{t2}$  is plant cover in year  $t2$  and  $\text{cover}_{t1}$  is plant cover in the previous sampling year,  $t1$ . The denominator scales the change in cover according to how much time elapsed between plant measurements, which also varied among studies and sites. The change in cover index is analogous to specific growth rate in microbiology and population ecology (e.g., Monod 1949), but typically has not been used for plant cover at large scales. A positive value of this index indicates that a plant species increased in cover over the interval between measurements, whereas a negative value indicates that it decreased in cover.

I related the change in cover of plant species to the means of climate variables over the plant measurement interval. It is possible that plant

species went through both increases and decreases in cover in response to climate events at a fine temporal scale, but this was not possible to assess based on the relatively long interval between plant measurements. To determine plant species responses and pivot points in relation to climate, I used an approach that accounts for spurious correlations and potential multicollinearity among climate variables (Murray and Conner 2009). First, I used zero-order correlations between the changes in plant cover and mean annual and seasonal temperature, precipitation, and the drought index. Change in cover values that were significant outliers in the multiple regressions were identified and removed using a Bonferroni Outlier Test (Companion to Applied Regression package in R; Fox 2009). I evaluated the relative importance of each significant climate variable to explain changes in cover of plant species with a hierarchical partitioning (HP) approach. HP is a form of multiple regression that ranks the independent contribution of each explanatory variable to the total explained variance of the regression model through incremental partitioning, thereby accounting for potential correlation between explanatory variables (Chevan and Sutherland 1991). Second, I performed simple linear regression between the change in cover of plant species and the most significant climate variables identified in the HP analyses. The slope between the change in cover and a climate variable indicated the magnitude of change in cover of a plant species with respect to climate, which I define as a plant “response” (Fig. 2). The point where the regression slope intersected the x-axis (the x-intercept) indicated a transition between gains and losses of cover, which I define as a “climate pivot point.” Third, I performed analysis of covariance with planned contrasts to test for differences in plant species responses to climate and their climate pivot points by landform and soil texture at the Sonoran Desert sites (plant species assemblage was similar across physical characteristics at a site), and plant assemblage at the Colorado Plateau sites (soil type and landform were similar across plant species assemblages at a site), which are non-climatic factors that can influence water availability. I also performed quantile regression to assess the relationship between plant responses and climate pivot points and analysis of

variance to test for differences in responses and climate pivot points among plant functional types (designated according to the lifespan, structural, and physiological traits of plant species). Because of the large spatial extent of studies on the Colorado Plateau and in the Chihuahuan Desert, I nested study site as a subfactor in the analyses, but found that it was not significant and therefore not retained in subsequent analyses. All statistical analyses were performed in R (R Development Core Team 2012).

## RESULTS

At the Desert Laboratory, the response of *Larrea tridentata*, a dominant shrub in the Sonoran and other warm deserts of the southwestern United States, was positive with respect to increasing winter precipitation on plots located on piedmont and old alluvial surfaces, but not on young alluvial surfaces (ANCOVA:  $F_{2,28} = 3.11$ ,  $P < 0.05$ ; Fig. 3a). The shrub had a similar response (piedmont:  $0.008 \pm 0.003$ ; old alluvial:  $0.010 \pm 0.004$ ) but a lower winter precipitation pivot point on the piedmont ( $114 \pm 11$  mm) compared to old alluvial ( $146 \pm 10$  mm) surfaces ( $F_{1,20} = 2.12$ ,  $P < 0.05$ ). There were increases in cover of *Prosopis velutina* (a shrub and tree genus that has spread across warm deserts of North America) on sandy loam soils at the Santa Rita Experimental Range, but it had no significant response to temperature; whereas the shrub had a moderate negative response on loam soils ( $-0.74 \pm 0.22$ ) and a large negative response on clay loam soils ( $-1.54 \pm 0.58$ ) with respect to increasing mean annual temperature ( $F_{2,56} = 3.81$ ,  $P < 0.05$ ; Fig. 3b). The temperature pivot point for the shrub increased from clay loam ( $16.8 \pm 0.5^\circ\text{C}$ ) to loam ( $17.4 \pm 0.3^\circ\text{C}$ ) to sandy loam ( $19.8 \pm 1.2^\circ\text{C}$ ) soils, but there was only a significant difference between clay loam and sandy loam ( $F_{1,37} = 2.28$ ,  $P < 0.05$ ). At the Arches and Canyonlands National Parks sites there was no response of *Achnatherum hymenoides* to increasing winter precipitation in blackbrush shrublands, but there was a moderate positive response in perennial grasslands ( $0.08 \pm 0.02$ ) and a large positive response ( $0.23 \pm 0.05$ ) in sagebrush shrublands ( $F_{2,51} = 10.28$ ,  $P < 0.001$ ; Fig. 3c). There was a tendency (not significant) for the winter precip-

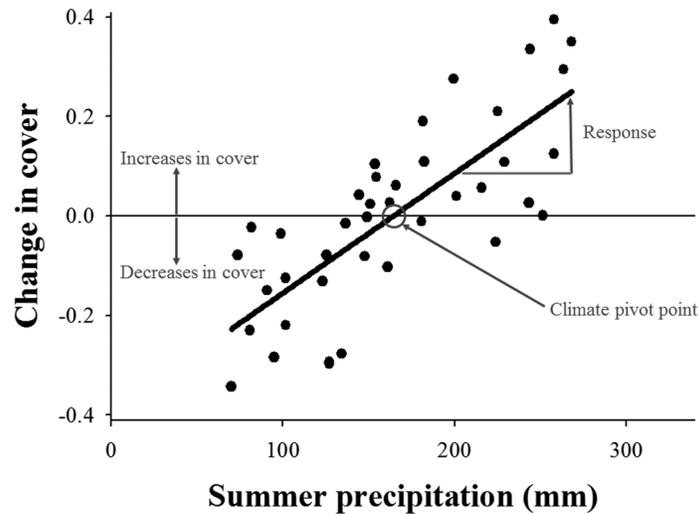


Fig. 2. Conceptual diagram of the change in cover index at long-term monitoring sites in relation to precipitation. The slope indicates the response of a plant species with respect to climate and the x-intercept indicates the climate pivot point, which is a transition between increases and decreases of cover.

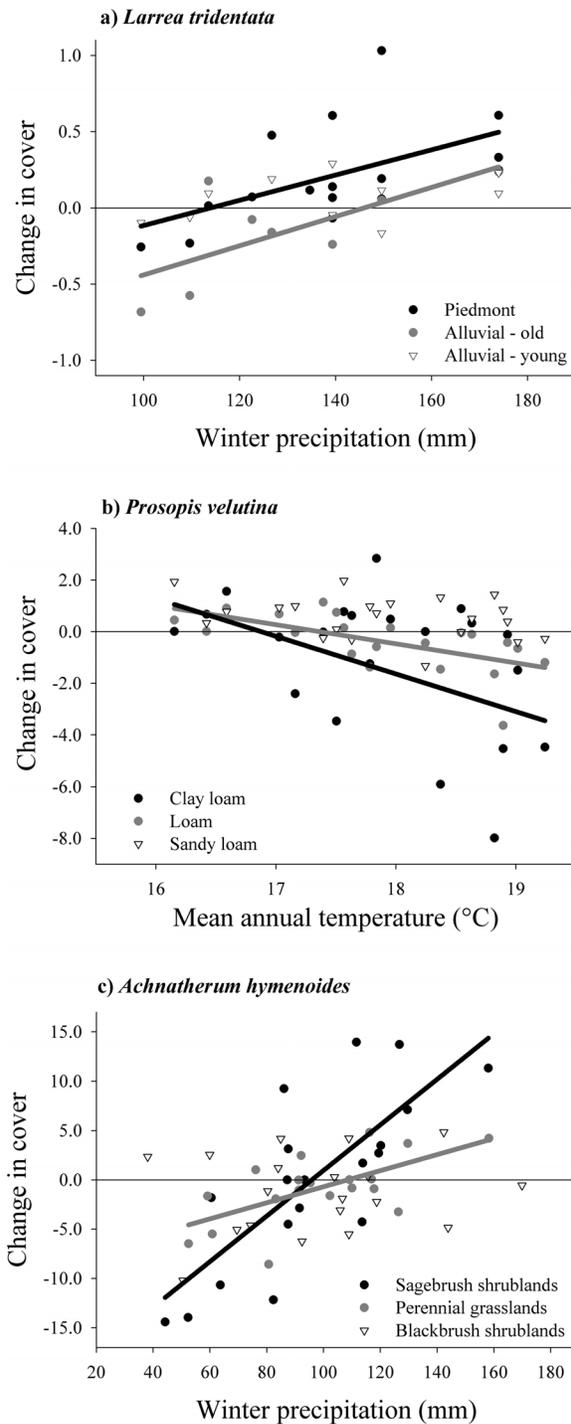
itation pivot point of *Achnatherum hymenoides* in sagebrush shrublands to be lower ( $96 \pm 6$  mm) than perennial grasslands ( $108 \pm 7$  mm;  $F_{1,34} = 1.45$ ,  $P = 0.17$ ). While most of the variability of *L. tridentata* and *A. hymenoides* was climatically explained by winter precipitation and *P. velutina* by mean annual temperatures, all dominant species were sensitive to multiple aspects of climate (Appendix: Fig. A1).

At the regional scale of the Chihuahuan Desert, the changes in cover of a large suite of plant species spanning different plant functional types were best explained by summer precipitation (Appendix: Fig. A1). The responses of these plant species to summer precipitation were positively related to their pivot points ( $r^2 = 0.40$ ,  $P < 0.0001$ ; Fig. 4). An upper bound on the maximum response of plant species increased as the summer precipitation pivot point increased. Plant species responses and pivot points with respect to summer precipitation separated by plant functional type. Annual forbs had the highest response, followed by annual grasses, then perennial forbs, perennial grasses, deciduous shrubs, and evergreen shrubs (Appendix: Fig. A2). Evergreen shrubs and perennial grasses had lower summer precipitation pivot points than the other plant functional types.

## DISCUSSION

Plant responses and climate pivot points provide important insights to contemporary shifts in species abundance and composition and can be used at multiple spatial scales to forecast future changes in plant species assemblages. For example, species with low precipitation pivot points are likely to be the first to decline with future droughts, and a threshold of decreased ecosystem productivity may result in the future if dominant species or a large number of species cross pivot points by losing cover with respect to climate. Calculated from canopy cover, a frequently used measurement of plant abundance, these plant metrics provide a much needed approach to monitor and assess the state and rate of change in dryland ecosystems (Vogt et al. 2011). Plant responses and climate pivot points expand on popular bioclimate-envelope predictions of changes in plant abundance and distribution because they do not assume that plant species are in equilibrium with the current climate (Pearson and Dawson 2003). The metrics are also calculated from plot-based vegetation measurements, which make it possible to incorporate non-climatic factors that influence climate-plant relationships.

Drought and high temperatures limit water



←

Fig. 3. The change in cover of *Larrea tridentata* in relationship to winter precipitation in plots at the Desert Laboratory on three different landforms (a) (piedmont:  $r^2 = 0.31$ ,  $P < 0.05$ , alluvial-old:  $r^2 = 0.48$ ,  $P < 0.05$ , alluvial-young:  $r^2 = 0.13$ ,  $P = 0.30$ ); the change in cover of *Prosopis velutina* in relationship to mean annual temperature on three soil textures in upland landscape positions at the Santa Rita Experimental Range site (b) (sandy loam:  $r^2 = 0.12$ ,  $P = 0.16$ , loam:  $r^2 = 0.39$ ,  $P < 0.01$ , clay loam:  $r^2 = 0.28$ ,  $P < 0.05$ ); and change in cover of *Achnatherum hymenoides* in relation to winter precipitation in three plant communities (c) (sagebrush:  $r^2 = 0.59$ ,  $P < 0.01$ , grassland:  $r^2 = 0.39$ ,  $P < 0.01$ , blackbrush:  $r^2 = 0.02$ ,  $P = 0.57$ ) at Canyonlands and Arches National Parks.

availability and have an impact on vegetation of dryland ecosystems (Munson 2011b, 2012, in press). My results from this synthesis expand on these findings by demonstrating that landform, soil, and biotic characteristics at a site can modify the availability and use of water among desert plants. At the Desert Laboratory in the Sonoran Desert, the response of *Larrea tridentata* and its pivot point in relation to winter precipitation was dependent on whether the shrub was growing on a piedmont or alluvial plain landform and the age of soil development. The lower winter precipitation pivot point of *L. tridentata* in piedmont compared to a Pleistocene-aged alluvial surface suggests that the shrub is more drought-stressed in the lower landform position, which has been confirmed with shrub water potential measurements (Halvorson and Patten 1974). The piedmont typically receives more precipitation than the alluvial plain (Humphrey 1933; this difference could not be demonstrated in my study because there was only one long-term weather station), and colluvial boulders and gravel in piedmont positions may reduce evaporative water loss for desert plants. *L. tridentata* was more susceptible to drought on Pleistocene-aged alluvial surfaces compared to more recent Holocene surfaces because the older surface contains shallow petrocalcic horizons, which may limit rooting depth and storage of soil water, or hold water at shallow depths where it is more susceptible to evaporation (McAuliffe 1994). Therefore, shallow and relatively imper-

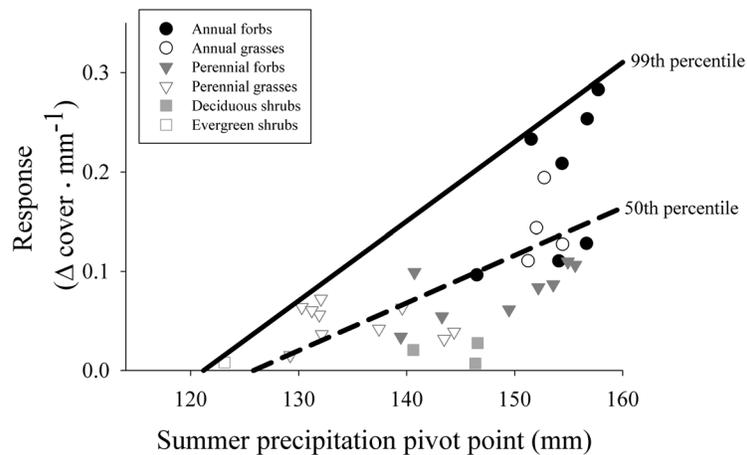


Fig. 4. The mean responses and pivot points of plant species (grouped by functional type) with respect to summer precipitation across sites in the Chihuahuan Desert. Solid and dashed lines represent the 99th ( $y = 0.008x - 0.988$ ) and 50th ( $y = 0.004x - 0.467$ ,  $r^2 = 0.40$ ,  $P < 0.0001$ ) percentiles, respectively.

meable layers in desert soil horizons may exacerbate the intensity of drought for deeply rooted shrubs and are more suitable for shallow rooted plant species, including perennial grasses and cacti, which can take advantage of precipitation with limited soil percolation.

The response of *Prosopis velutina* in upland landscape positions to increasing temperature at Santa Rita Experimental Range was not likely due to temperature inhibiting growth directly, since this shrub grows in warmer climates (Turner et al. 1995). Instead, temperature likely constrained plant water availability by creating a high atmospheric demand for water. Although the timing and amount of precipitation receives far more research attention, drought has become increasingly driven by temperature in the twenty-first century in the western United States (Gutzler and Robbins 2011) and its effect on desert plants should also be considered (Munson et al. 2011b). Soil texture influenced shrub response to temperature through its control on hydraulic properties: *P. velutina* was likely unresponsive to temperature on sandy loam soils because these soils have high hydraulic conductivity, which facilitates percolation into the rooting zone below surface layers that have high evaporative losses. The negative responses of *P. velutina* to temperature intensified as the soils became increasingly fine-textured because water was likely held closer to the surface and exposed

to evaporative losses. Experimental additions of summer precipitation confirm that *P. velutina* has greater and more prolonged water uptake and higher water potentials on coarse- relative to fine-textured soils at Santa Rita Experimental Range (Fravolini et al. 2005). Desert shrubs also have a greater vertical rooting distribution and hydraulic conductance on coarse- relative to fine-textured soils (Sperry et al. 2002). Increases in temperature pivot point with increasing sand content suggest that *P. velutina* and other deep-rooted species are less susceptible to drought when they are growing on soil textures with high permeability. Although the transects represented by this study at Santa Rita Experimental Range occur on upland settings, other studies have shown that the physiological performance of *P. velutina* (Barron-Gafford et al. 2012) and other desert shrubs (Munson et al. 2011b) are invariant to climate when they have access to a supply of deep groundwater in lowland positions.

Climate can have direct effects on vegetation, but the indirect effects mediated through plant competition and facilitation can be important, especially when there is a high degree of niche overlap (Adler et al. 2012). Across the Arches and Canyonlands National Parks sites on the Colorado Plateau, the plant assemblage in which *Achnatherum hymenoides* was growing had an influence on its response to winter precipitation. The cool-season perennial bunchgrass had a

moderate positive response and pivot point in grasslands where it was dominant, but this relationship changed in shrublands where it was subdominant. There was a lack of response to winter precipitation in blackbrush shrublands, which may be attributed to the very dense growth form of *Coleogyne ramosissima* and its dimorphic root system which allows the shrub to take up shallow soil moisture and overlap with the perennial bunchgrass (Ehleringer and Cook 1991). In contrast, the response of *Achnatherum hymenoides* was greater and the winter precipitation pivot point lower in sagebrush shrublands, which may be attributed to *Artemisia tridentata* growing more sparsely than *C. ramosissima* and having access to supplemental groundwater at most plots in this study (Munson et al. 2011b), a pattern of water use that may have led to decreased competition with perennial grasses at shallow depths. These results demonstrate how the potential for overlap in intra- and interspecific water use can be an important modifier of plant responses and their climate pivot points. Niche separation of water use partially explains the coexistence of species and maintenance of diversity in water-limited regions and is likely to increase in importance with the intensification of drought. A more explicit consideration of species interactions within the response-resistance framework can improve forecasts of future species assemblages (Gilman et al. 2010).

There was a substantial amount of variation in the change in cover in all three dominant desert plant species that was not explained by the interactive effects of climate over the measurement interval, soil, landform, and biotic factors. This unexplained variance is likely attributable to climatic events that affect the abundance of plant species at short temporal scales, differences between temperature and precipitation measured at the weather station and vegetation monitoring plots and transects, and additional environmental factors that were not accounted for in this study (e.g., nutrient availability and microtopography; Yao et al. 2006). The measurement of vegetation at a high temporal resolution, direct soil water monitoring, and characterization of other abiotic and biotic factors at the plot level can improve the accuracy of estimating plant responses and climate pivot points. Although for this study I chose sites that currently experience minimal land

use disturbance, it is possible that historical grazing and light current land use may have interacted with climate to affect vegetation cover.

The positive relationship between these two metrics with respect to summer precipitation across the Chihuahuan Desert region supports a central theory in plant ecology that there is an inherent trade-off between the capacity of a plant to respond when there are abundant resources and its ability to tolerate resource shortages (Parsons 1968, Grime 1979, Smith and Huston 1989). In arid and semiarid regions, there is strong selective pressure for a plant to either accelerate growth and maximize reproductive output before the onset of drought or to tolerate drought through structural adaptations and increased water-use efficiency (Mooney 1972, Orians and Solbrig 1977). Indeed, the stomatal conductance and transpiration rates of desert annual forbs and grasses have large responses to changes in water potential relative to perennial herbaceous and shrub species, as many annuals complete their life cycle before the onset of drought (Ehleringer and Mooney 1983). My results demonstrate that the trade-off between plant response and drought resistance is upheld for plant species across a warm desert, and that plant functional types defined by lifespan and structural and physiological traits in dryland ecosystems are good predictors of where a plant falls along the response-resistance spectrum and how species assemblages may change under future climates.

The upper bound on the maximum response of a plant species that increased with summer precipitation pivot point likely represents the physiological or energetic limits of a plant species to respond to water availability in relation to its efficiency of water use. These limits have been well documented through physiological measurements at the scale of individual plants. For example, increased efficiency and recovery performance of stem xylem among desert woody plant species comes at the cost of increased vulnerability to cavitation (Pockman and Sperry 2000). Stomatal closure to prevent this hydraulic failure reduces the photosynthetic capacity of a plant despite continued metabolic demand, which may ultimately result in carbon starvation (McDowell et al. 2008). Within a guild of desert annual plants, there is an inverse relationship between the relative growth rates and intrinsic

water-use efficiencies among species (Angert et al. 2009). Although I did not detect differences in plant responses or climate pivot points among plant photosynthetic pathway in this study, plants with CAM and  $C_4$  pathways have the potential to be more drought resistant than  $C_3$  plants due to their water-conservation strategies. Structural constraints, such as the amount of woody tissue or the degree of leaf drop are important, as many semi-woody perennial forbs and deciduous shrubs fall well below the upper response limit. It is likely that the lower a plant species falls below the upper response limit, the greater resource constraints limit its ability to respond or increase in water-use efficiency. In addition to plant physiological and structural restrictions, soil, landform, and biotic interactions may modify plant response and climate pivot point as previously shown, or other plant resources such as nutrient availability may impose limitations. Although a physiological basis for a response-resistance trade-off was not found by comparing the physiological traits among Chihuahuan Desert perennial grasses (Fernandez and Reynolds 2000), future studies can test the mechanisms for the trade-off found in this study across plant functional types and those that may exist in other water-limited systems. Connecting physiological mechanisms (e.g., hydraulic failure and carbon starvation) with plant responses and climate pivot points observed at large spatial scales can provide a robust prediction of plant assemblages that may occur in the future.

Plant responses in my study were based on the change in plant cover, and I could not always distinguish whether this was due to the growth of existing individuals or the establishment of new individuals. At sites where individual plants were mapped (Desert Laboratory and Big Bend National Park), results indicated that changes in plant cover were largely due to the former explanation. The change in cover metric is not meant to be a replacement for understanding the reproductive capacity, dispersal ability, and the capability of species to adapt to changes in climate. Such studies are necessary to completely understand the long-term viability of species. For example, it is not well understood how the genetic variation and phenotypic plasticity within a desert plant species may explain differences

in its response and climate pivot point among different soils, landforms, and biotic conditions in this study, and the degree to which these drivers will influence vegetation dynamics under future climates. It is unlikely that the responses and climate pivot points of long-lived desert plant species shifted over the monitoring period of our study, but this historical record could be compared with a future period or one in the paleo-record to mark significant departures. Experimental studies and modeling efforts can complement this synthesis to provide a mechanistic understanding of plant reductions in cover below climate pivot points.

As I demonstrate in this synthesis, plant responses and climate pivot points can be determined from readily available plot- and transect-based vegetation measurements at different spatial scales to provide an understanding of the performance of plant species over a range of climatic conditions and to forecast changes in plant species assemblages under future climates. Physical and biotic characteristics at a site modify the availability of water in semiarid and arid ecosystems to influence plant abundance, and they must be considered in assessments of climate-plant relationships. Plant responses and climate pivot points provide a standardized framework for comparison of a species across landform and soil types, plant communities, or to determine whether species have unique or shared responses to climate. The approach has broad utility, as it can be implemented at multiple spatial scales from the plot to regional level, used to compare treatment effects within an experiment, supplemented with other indices of plant abundance such as density and biomass, or modified to assess community-level patterns, including changes in plant diversity. In this study, plant responses and climate pivot points were determined across North American deserts, but these metrics can be applied to other water-limited regions and tested in more mesic ecosystems to provide a more complete understanding of how climate impacts vegetation change.

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SUPPLEMENTAL MATERIAL

APPENDIX

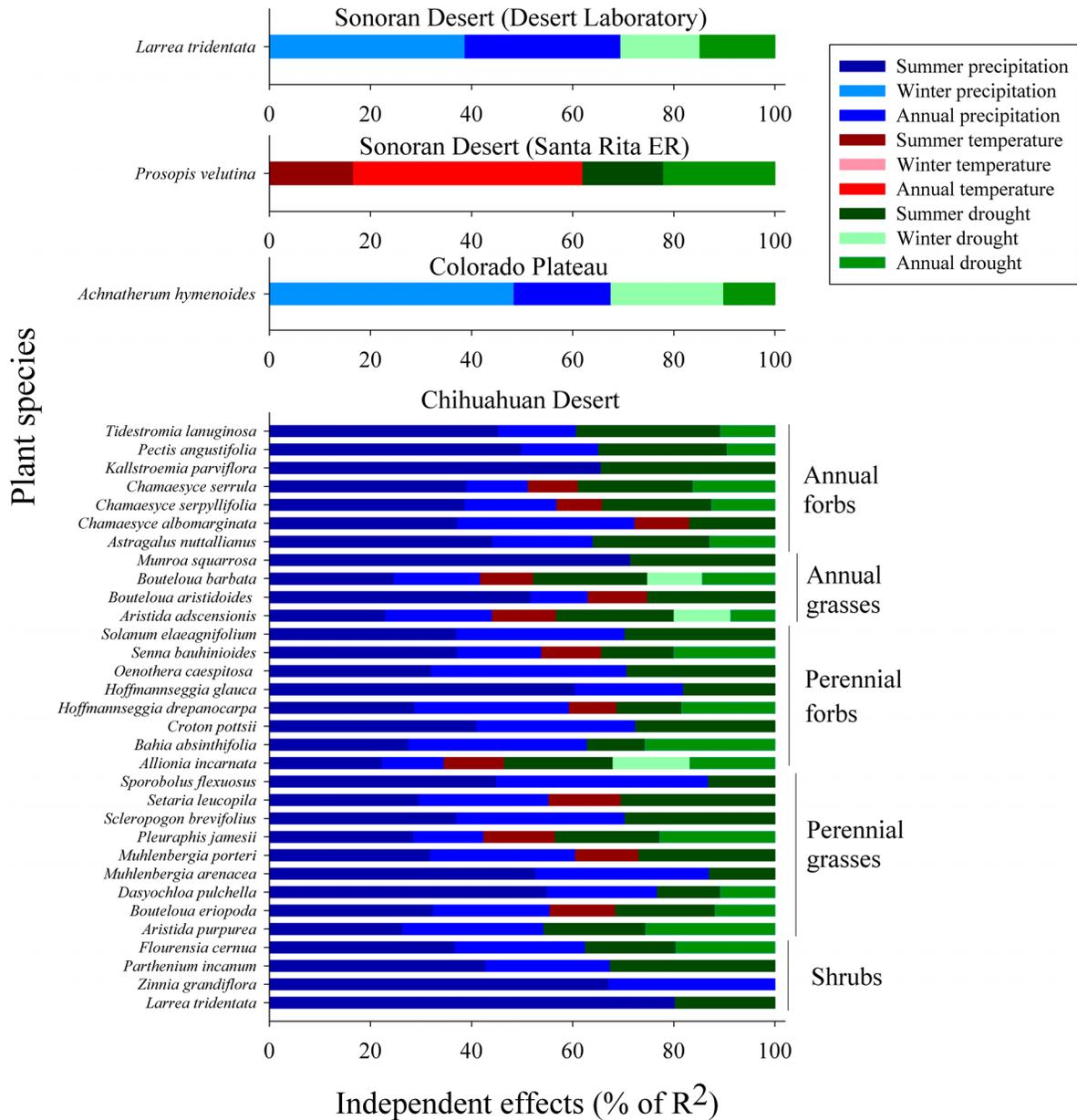


Fig. A1. The independent effects (% of  $R^2$ ) of mean annual and seasonal temperature, precipitation, and aridity to explain change in plant species canopy cover as determined by hierarchical partitioning in the Sonoran Desert, Colorado Plateau, and Chihuahuan Desert. Plant functional types are shown to the right of the independent effects of plant species in the Chihuahuan Desert.

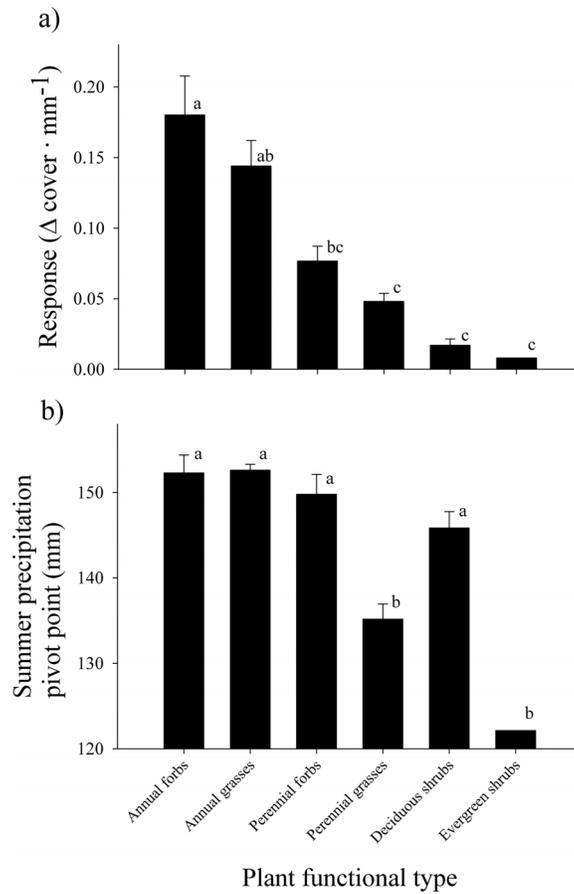


Fig. A2. Response (a; change in cover per mm of summer precipitation) and pivot point (b; mm of summer precipitation) means ( $\pm$  SE) of plant functional types in the Chihuahuan Desert that represent variation among species within a functional type. Different letters designate significant differences (Tukey's  $P < 0.05$ ).