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Sensitivity of dryland plant allometry to climate

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Abstract

1. Patterns of plant biomass partitioning are fundamental to estimates of primary productivity and ecosystem process rates. Allometric relationships between above-ground plant biomass and non-destructive measures of plant size, such as cover, volume or stem density are widely used in plant ecology. Such size-biomass allometry is often assumed to be invariant for a given plant species, plant functional group or ecosystem type.

2. Allometric adjustment may be an important component of the short- or long-term response of plants to abiotic conditions. We used 18 years of size-biomass data describing of 85 plant species to investigate the sensitivity of allometry to precipitation, temperature or drought across two seasons and four ecosystems in central New Mexico, USA.

3. Size-biomass allometry varied with climate in 65%–70% of plant species. Closely related plant species had similar sensitivities of allometry to natural spatiotemporal variation in precipitation, temperature or drought. Annuals were less sensitive than perennials, and forbs were less sensitive than grasses or shrubs. However, the differences associated with plant life history or functional group were not independent of plant evolutionary history, as supported by the application of phylogenetically independent contrasts.

4. Our results demonstrate that many plant species adjust patterns in the partitioning of above-ground biomass under different climates and highlight the importance of long-term data for understanding functional differences among plant species.

KEYWORDS
arid, Chihuahuan Desert, climate change, drought, ecosystem, long-term ecological research, net primary production, phylogenetic

1 | INTRODUCTION

Allometry, which describes the relationships among an organism's physical or physiological attributes and its size, provides important functional information about how plants partition resources, including patterns that are fundamental to process-based ecosystem models (Diaz et al., 2004; Jiang & Wang, 2017; Korner, 1995; Luo, Field, & Mooney, 1994; Montane et al., 2017). Plant species differ in the allometric relationships among tissue types (Poorter et al., 2015; Price & Weitz, 2012; Wright et al., 2004) and may also diverge in the degree to which allometry is influenced by environmental variables, such as climate. Adjustments of allometry in response to climate can

occur through phenotypic plasticity and through the process of natural selection shifting the population to a new trait distribution (e.g. Conn, Pedmale, Chory, Stevens, & Navlakha, 2017; Franks, Weber, & Aitken, 2014; Niklas & Enquist, 2002; Vizcaino-Palomar, Ibanez, Gonzalez-Martinez, Zavala, & Alia, 2016). For example, plants supplemented with water can plastically increase traits, such as specific leaf area, or decrease traits, such as starch-storage tissue in roots (von Arx, Archer, & Hughes, 2012). Plant allometry may evolve with changes in climatic niches across plant lineages (Vasseur et al., 2018), although in some cases, even strong selection cannot disrupt fundamental allometries (Trejo, Rosell, & Olson, 2018).

Allometric relationships between above-ground plant biomass and non-destructive measures of plant size, such as cover, volume or stem density are widely used to estimate plant biomass (Byrne, Lauenroth, Adler, & Byrne, 2011; Eisfelder et al., 2017; Niklas & Enquist, 2001; Sala & Austin, 2000; Singh, Laurenroth, & Steinhorst, 1975), which is an important metric of ecosystem productivity and carbon storage (Callahan, 1984). These size-biomass allometries have been used to approximate productivity in ecosystems as diverse as forests (Chave et al., 2014; Roxburgh, Paul, Clifford, England, & Raison, 2015), coastal marshes (Lu et al., 2016), alpine meadows (Redjadj et al., 2012), boreal shrublands (He et al., 2018) and arid grasslands (Mowll et al., 2015). Non-destructive estimates of biomass are particularly important in long-term studies where measurements are repeated on the same individuals or plots (e.g. Elmendorf et al., 2012; Muldavin, Moore, Collins, Wetherill, & Lightfoot, 2008; Rudgers et al., 2014; Xia, Moore, Collins, & Muldavin, 2010) because destructive harvests would reduce data quantity or quality.

Despite the widespread use of size-biomass allometry in plant ecology (Catchpole & Wheeler, 1992), this approach can fail to provide accurate estimates of biomass. Allometry is often assumed to be invariant for a given plant species, plant functional group or ecosystem type. Studies commonly apply allometric equations from single time points, locations or treatments to generalize plant biomass estimates – and diversity indices based on these estimates – across broad spatial or temporal scales. While invariant allometric scaling relationships have been detected (McBranch et al., 2019; Niklas & Enquist, 2001), partitioning to leaves/stems/roots can vary with the environment (Poorter et al., 2012; Reich et al., 2014; Schenk & Jackson, 2002). For example, substantial variability in volume-biomass allometry has been detected across sites or biomes in several studies on trees (e.g. DeLucia, Maherali, & Carey, 2000; Forrester et al., 2017; Fortin, Couwenberghe, Perez, & Piedallu, 2018). Thus, assuming invariant size-biomass allometry could over- or underestimate plant biomass relative to true values.

In ecosystems with large year-to-year variability in climate, such as drylands, allometry may respond strongly to temperature, rainfall or soil moisture (Anfodillo, Petit, Sterck, Lechthaler, & Olson, 2016). For instance, a recent study revealed that dry years reduced the steepness of the relationship between community biomass and non-destructive proxies, such as the normalized difference vegetation index (NDVI) (Onodi et al., 2017). Meta-analysis of 164 studies suggested that sensitivity of *within-plant organ* allometry is common: drought

experiments altered plant biomass partitioning ratios, favouring root over shoot biomass and altering ratios of reproductive to vegetative biomass (Eziz et al., 2017). Similarly, treatments such as competition (Yu & Gao, 2011) or nitrogen addition (Dziedek et al., 2017) can alter patterns of biomass partitioning (but see Bernacchi, Coleman, Bazzaz, & McConnaughay, 2000; Peng & Yang, 2016). While experimental approaches are useful for detecting whether or not allometry is invariant, they do not capture the continuous variation in allometry that characterizes natural systems under variable climate regimes.

Adjustments of allometry may be important components of the short- or long-term responses of plants to climate change (Bjorkman et al., 2018; Nicotra et al., 2010; Reich et al., 2014). Comparative studies on the sensitivity of allometry to climate can refine projections of future plant biomass and associated ecosystem processes. For example, if the allometric relationship between plant biomass and a non-destructive proxy takes a shallower slope when climate is hotter or drier, then using an invariant allometric equation will overestimate plant biomass in a more arid future. Unresolved questions include the following: is the sensitivity of size-biomass allometry to climate predictable from plant relatedness or by plant functional group or life history? And how much do plant species diverge in allometric sensitivity to different aspects of climate, such as temperature versus precipitation?

Here, we used 18 years of plant species-specific biomass data from the Sevilleta Long-Term Ecological Research Program to investigate the degree to which plant allometry was sensitive to spatiotemporal variation in precipitation, temperature or drought. Our dataset spanned 85 plant species, 24 plant families, three functional groups (forb, grass, shrub), two seasons (spring, fall) and four dryland ecosystems in central New Mexico, USA. Investigating size-biomass allometry in drylands helps to fill a gap in datasets that are currently richer for mesic terrestrial ecosystems (e.g. Poorter et al., 2012). Our approach improves upon recent work (Onodi et al., 2017) by comparing sensitivities among plant species and functional groups as well as examining the relative importance of alternative climate variables.

We used allometric equations relating harvested above-ground plant biomass to non-destructive measurements of plant species cover and volume to address the following questions across four dryland ecosystems: (1) *Is it common for allometry to be sensitive to climate?* For 85 plant species, we compared the goodness of fit of statistical models in which allometry was invariant with climate against models in which allometry varied with temperature, precipitation or drought. (2) *Is the sensitivity of allometry to climate predictable from plant phylogenetic relatedness, functional group identity, life history strategy, or photosynthetic pathway?* We predicted that herbaceous plants would have higher potential to adjust allometry than woody species and that closely related species would resemble one another more than distantly related species (see also Poorter et al., 2012). We expected that annuals would have greater opportunity than perennials to accrue fitness benefits from sensitivity to climate during a single year. In addition, annual plants may respond faster to climate than perennials through evolutionary changes in allometry (e.g. Vasseur et al., 2018), as rates of molecular evolution

are faster in short-lived herbaceous plants than in long-lived woody species (Smith & Donoghue, 2008). Alternatively, in perennials, the process of natural selection is expected to favour trait combinations that increase long-term survival over diverse climate years, and these traits may include high plasticity in allometry. We predicted that plants with drought-adapted photosynthetic pathways (C_4/CAM) would have allometries that were less sensitive to climate than C_3 plant species, although a global analysis did not find such differences for biomass partitioning among plant organs within individual plants (Poorter et al., 2012). For only the plant species in which allometry was sensitive to climate, we asked (3) *To which climate variables is allometry most sensitive: temperature, precipitation, or drought?* We anticipated that a majority of species would be sensitive to drought indices that combine the stressors of heat and low rainfall (e.g. Rudgers et al., 2018). Finally, we applied allometries to non-destructive cover and volume estimates in four ecosystems to evaluate (4) *How much does climate-sensitive allometry influence estimates of aboveground primary production?*

2 | MATERIALS AND METHODS

2.1 | Study site

The Sevilleta National Wildlife Refuge (SNWR), New Mexico, spans transition zones from Chihuahuan Desert vegetation to the southwest, Great Plains grassland to the northeast, Colorado Plateau vegetation to the northwest, and piñon-juniper dominated woodlands at high elevations. At low elevations, woodlands transition to juniper savannas, then to grasslands. We collected size-biomass data in four ecosystem types: Plains grassland (34.3348, −106.631, elevation 1,671 m), Chihuahuan Desert grassland (34.3331, −106.737, elevation 1,615 m), desert shrubland (34.3331, −106.737, elevation 1,651 m) and piñon-juniper woodland understorey (34.368, −106.535, elevation 1,976 m), thereby enabling the detection of sensitivity of allometry to variation in climate across space.

2.2 | Plant allometry data

For each plant species, we selected ~10–30 individuals that spanned the natural range of variation in plant cover in each season and year of study. We estimated plant cover and height with a non-destructive method within 1 m × 1 m quadrats divided into 100 grid squares (10 cm × 10 cm) (Muldavin et al., 2008). Every year for 18 years, volume (visual % cover multiplied by average height to the nearest cm) was recorded on individual plants at peak biomass (September/October) and in spring (April/May) to capture seasonal differences in size and include species that grew during only one season. Spring and fall biomass can be decoupled because heavy winter rains, which feed spring annuals, can occur independently of summer monsoons. So, it is important to consider the two seasons separately, regardless of plant life history. Above-ground biomass was collected for each individual, returned the laboratory, sorted into live or dead components, dried for 4 days at 60°C, and then weighed to the nearest 0.01 g.

Additional details are provided in the data package and R script, available via the Environmental Data Initiative (see Data Accessibility).

For each plant species, we recorded functional group, life-history strategy and photosynthetic pathway (C_3, C_4, CAM) from the USDA Plants Database and linked resources (USDA & NRCS, 2018). We recognized three functional groups: grasses (22 species), forbs (herbaceous non-grasses; 53 species) and shrubs (10 species). We analysed two life-history groups: annual (23 species) or perennial (62 species). The few biennials were binned with annuals, and species with flexible life histories (annual to perennial) were lumped with perennials. Only 3 of the 85 species were CAM, so CAM and C_4 were combined (36 species) to reflect similarity in water conservation relative to C_3 (49 species).

2.3 | Climate data

Climate variables were recorded at four long-term meteorological stations located in the Great Plains grassland (34.3348, −106.631), the ecotone between Great Plains and Chihuahuan Desert grassland (34.3592, −106.691), the ecotone between Chihuahuan Desert grassland and shrubland (34.3331, −106.737), and in the piñon-juniper woodland (34.368, −106.535). Distances from each site to the nearest weather station ranged from 50 m to 450 m. We used meteorological data during 1999–2017 for air temperature, relative humidity and precipitation. Hourly climate data were summarized to daily values. Then, missing data for any given day (e.g. temporary equipment failure) were gap-filled using daily data from the geographically nearest LTER met station.

For each plant species, we evaluated the relative importance of three climate variables: temperature, precipitation and drought. For each climate variable, we used data over the prior 6 months of the growing season for spring (ending 31 May) or fall (ending 30 October). Growing degree days (GDD) had a base temperature of 0°C to obtain a 6-month average of daily GDD values for spring or fall. Precipitation was summed over 6 months. Because precipitation alone does not override the strong effect of temperature on water availability in drylands (Williams et al., 2013), we calculated the *SPEI* (Standardized Precipitation Evapotranspiration Index) to incorporate potential evapotranspiration using the Thornthwaite method (Vicente-Serrano, Begueria, & Lopez-Moreno, 2010). The Standardized Precipitation Evapotranspiration Index was integrated over 6 months using methods in Vicente-Serrano et al. (2010) on the daily, gap-filled climate data across all sites. Negative *SPEI* values indicate more arid conditions. Each climate variable was scaled to mean = 0 and standard deviation = 1.

2.4 | Climate sensitivity of allometry for each plant species

For each species and season, we regressed above-ground biomass on plant cover or volume with the intercept forced through the origin (*lm* <STATS>, R Core Team, 2018) following our prior methods in Muldavin et al. (2008). Then, we used model selection procedures (*AICc* <MuMIn> Bartoń, 2018) to evaluate the relative importance of

TABLE 1 Candidate models for evaluating the sensitivity of allometry to climate

Model	Specification
Invariant	Biomass ~ Size
Growing degree days	Biomass ~ Size + Growing Degree Days + Size × Growing Degree Days
Precipitation	Biomass ~ Size + Precipitation + Size × Precipitation
Drought	Biomass ~ Size + SPEI + Size × SPEI

Note: For each combination of plant species and season (spring or fall), we built four models in which Size = Plant Cover (visually estimated %) and four models in which Size = Plant Volume (% cover × height).

four candidate models described in Table 1 (Anderson, 2008). Plant species were included if allometry data were available for at least three spatiotemporal instances of climate (years × geographic sites; mean = 6, max = 35 for common species; Table S1).

2.5 | Effect size

The interaction term (*I*) in each climate-variant model (e.g. Size × Precipitation, Table 1) estimated the magnitude of sensitivity of allometry to climate. For example, a positive estimate of (*I*) for Plant cover × Precipitation indicated that plants grew denser per unit cover with more precipitation (Figure 1). Conversely, a negative (*I*) indicated that plants grew sparser with more precipitation. We combined model selection results across plant species × season combinations (*N* = 121, Supporting Information). We used vote counting, phylogenetic comparative techniques (phylogenetically independent contrasts, *PICs*, Garland, Harvey, & Ives, 1992; phylogenetic logistic regression, Ives & Garland, 2014), and meta-analysis to address the following questions.

1. *Is it common for allometry to be sensitive to climate?*

We scored each plant species as 'climate-sensitive' if the Invariant model (Table 1) was worse (Δ*AICc* > 2) than the best climate-variant model *and* if the (*I*) for Size × Climate was significantly different from zero (*p* < .05). If the climate-insensitive model essentially tied the best climate-sensitive model (Δ*AICc* ≤ 2), we conservatively scored it as 'climate-insensitive', regardless of the *p*-value. We tallied cases in which allometry was sensitive to a climate variable. We also built generalized linear models (*glmer*, Pinheiro, Bates, DebRoy, & Sarkar, 2016) with a binomial distribution of insensitive to climate (=0) or sensitive to climate (=1) to test whether sensitivity differed by season; models for species observed in both seasons included plant species identity as a random intercept.

2. *Is the sensitivity of allometry to climate predictable from plant phylogenetic relatedness, functional group identity, life history strategy, or photosynthetic pathway?*

Phylogenetic signal: To assess the degree to which closely related species shared similar sensitivities to climate, we pruned the time-calibrated
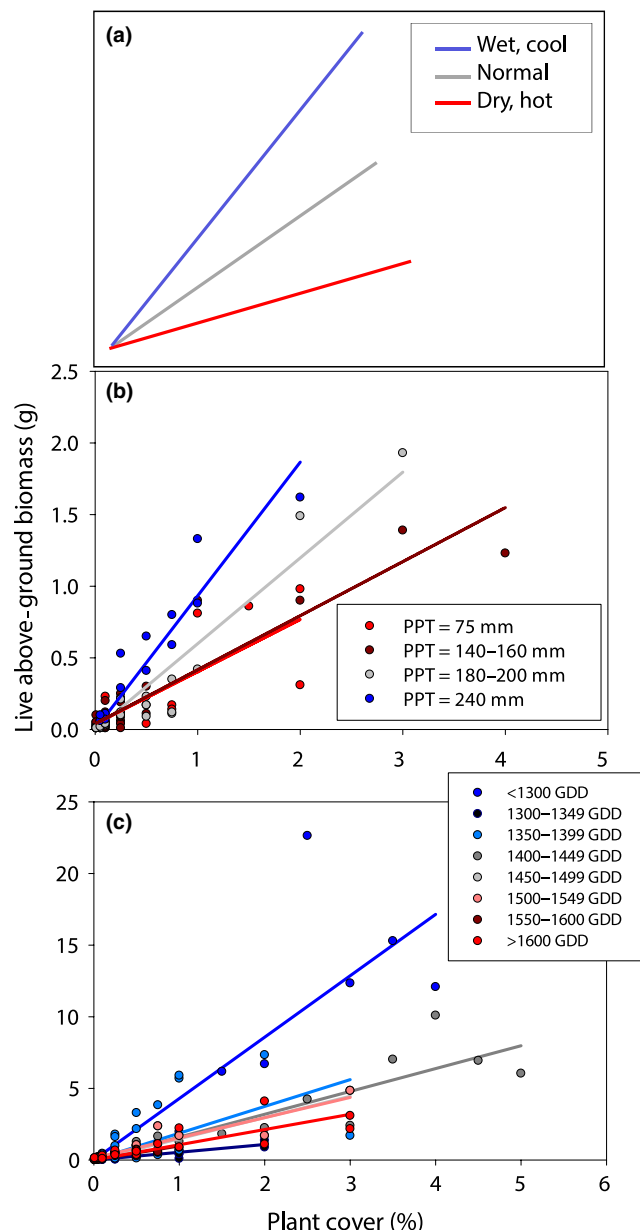
FIGURE 1 Size-biomass allometry that is sensitive to climate. (a) Hypothetical example in which plants become denser (steeper slope) in wet, cool years (blue line) relative to normal (average) climate years (grey line) and dry, hot years (red line). (b) Size-biomass allometry for the C_4 annual forb, *Chamaesyce serrula* (Euphorbiaceae), in fall; plants became denser with greater precipitation (PPT). (c) Size-biomass allometry for the C_4 perennial grass, *Muhlenbergia arenicola* (Poaceae); in spring, plants became less dense under hotter conditions based on growing degree days (GDD)

31,383-species Qian and Jin (2016) plant phylogeny to include focal taxa (details in Supporting Information). For the occurrence of sensitivity to climate (invariant vs. sensitive), we calculated phylogenetic signal as Ives' *s2* (Ives & Garland, 2014; *binaryPGLMM* <APE> Paradis & Schliep, 2018). For the magnitude of sensitivity, (*I*) (Table 1), we calculated phylogenetic signal as Pagel's λ (Pagel, 1999; *phylosig* <PHYTOOLS> Revell, 2012). We used only cover-biomass models so that (*I*) was directly comparable across plant species (Supporting Information).

2.6 | Phylogenetic logistic regression and phylogenetically independent contrasts

To account for non-independence of species due to shared evolutionary history (Garland et al., 1992), we used phylogenetic comparative techniques. To ask whether the occurrence of sensitivity (invariant vs. sensitive) was predicted by functional group identity, life history or photosynthetic pathway, we used phylogenetic logistic regression (Ives & Garland, 2014; *binaryPGLMM* <APE> Paradis & Schliep, 2018). For analyses on continuous sensitivity (*I*), we obtained PICs using package <APE> (Paradis & Schliep, 2018) with general linear models (described above). In the *PIC*s, functional group was coded as binary, where 0 = herbaceous (grasses and forbs) or 1 = woody (shrubs) because grasses form a single clade. Analyses used original branch lengths in millions of years, but alternative analyses assuming all = 1 or Grafen branch lengths produced qualitatively similar results (*results not shown*).

2.7 | Functional group identity, life-history strategy, or photosynthetic pathway

We used generalized linear models with a binomial response (invariant vs. sensitive) and the fixed effects of season and one of the following predictors: functional group, life-history strategy or photosynthetic pathway. We evaluated the importance of the predictors with a log-likelihood ratio test that compared model fit against a null model. Models included plant species identity as a random effect to account for plant species observed in both seasons (nested within life history, functional group or photosynthetic pathway). Models were also constructed separately for each season without a random effect of plant species, which returned similar results.

3. *To which climate variables was allometry most sensitive: temperature, precipitation, or drought?*

For the plant species × season combinations in which a climate-sensitive model (Table 1) was the best fit (*N* = 93 of 121), we conducted meta-analysis (Koricheva et al., 2013) separately for spring versus fall observations (*rma.mv* <METAFOR> Viechtbauer, 2010). The response was the effect size (*I*) from the best climate-specific cover model, weighted by the sample size, giving larger weights to species sampled more intensively. Models included the fixed effects of climate predictor (GDD, precipitation, drought) and either plant functional group, life-history strategy or photosynthetic pathway, plus the interaction. We assessed the magnitude of sensitivity using likelihood ratio *chi-squared* tests against null models that either did not include the predictor or did not include the interaction term.

4. *How much does climate-sensitive allometry influence estimates of aboveground primary production?*

We applied size-biomass allometries to non-destructive cover and volume estimates for plant species occurring in 1 m × 1 m quadrats in each of the four ecosystems (*N* = 22–100 quadrats per ecosystem). We then compared the estimate of total plant above-ground biomass (summed over all species present in the quadrat) between the best fit model for each species, which accounted for species that were climate-sensitive, or a climate-invariant model for each species, which fit a single size-biomass regression through harvest data from all years × sites of collection. Our climate-invariant prediction method is less conservative than the typical approach of using allometric relationships from a single time point, because it does use data from all years of collection, which inherently captures a broader range of possible allometries. Because ecosystems had different time series, we tested for significant differences between predicted biomass from climate-sensitive versus climate-insensitive methods using a general linear mixed-effects model for each ecosystem type that included the factors of year (as categorical), allometry method (sensitive vs. insensitive) as well as their interaction along with the random, repeated factor of quadrat identity (LMER, LM4 package, R Core Team, 2018).

3 | RESULTS

1. *Is it common for allometry to be sensitive to climate?*

Of the size-biomass allometries for 121 plant species × season combinations, 70% varied with climate (65% minimum, after correcting for a 5% false detection rate). Plant size-biomass allometries were similarly likely to be sensitive to climate in the fall season (79% of 76 cases, 74% corrected; 3.8 species were expected by chance alone) as in the spring (71% of 45 cases, 66% corrected) (log-likelihood ratio X^2 = 1.1, *p* = .29). This similarity held when we included only 36 plant species sampled in both spring and fall (X^2 = 1.8, *p* = .18). In fall, 30 of these 36 species had climate-sensitive allometries; the null expectation was 1.8 species significant by chance alone. In spring, 26 of 36 species were climate-sensitive.

Generally, plant cover was better than or equivalent to plant volume as a predictor of live biomass in our set of 85 dryland plant species. Cover was as good as or better than volume for 76% of total cases and

TABLE 2 Phylogenetic signal in sensitivity of cover-biomass plant allometry to three climate variables

		Magnitude of sensitivity		
Climate variable	Season	Pagel's λ	*P*	*N*
Drought	Fall	0.868	.007	76
Precipitation	Fall	0.954	<.001	76
Growing degree days	Fall	0.783	<.001	76
Drought	Spring	<0.001	1.000	45
Precipitation	Spring	0.999	<.001	45
Growing degree days	Spring	0.985	<.001	45

Note: Magnitude of sensitivity was the parameter estimate for the interaction term of plant cover × the climate variable. See Methods: *Phylogenetic signal* for additional details. Separate analyses were conducted for each climate variable in spring and in fall. *N* = number of plant species in the analysis.

(a) Fall species
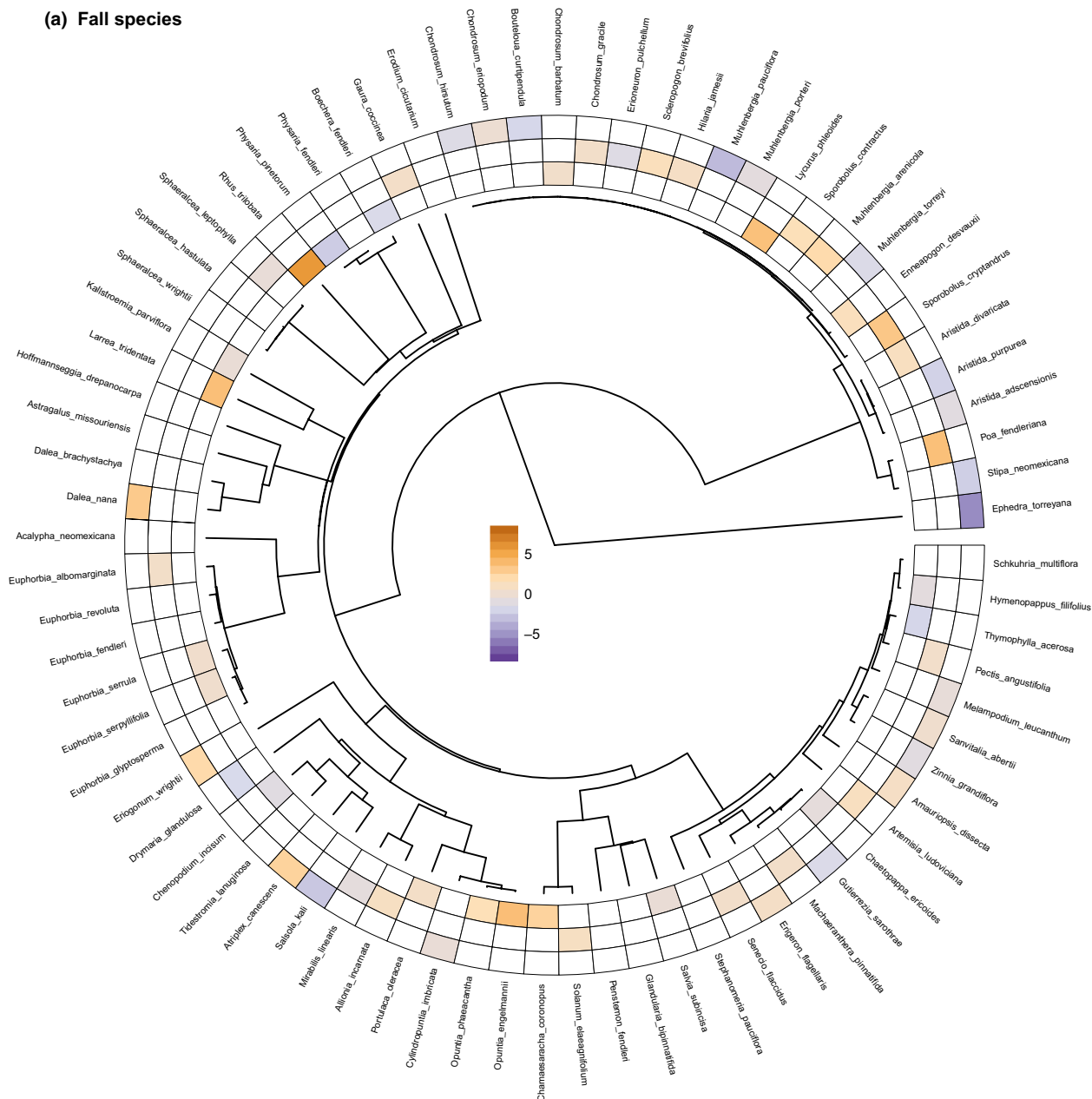
FIGURE 2 Plant species-specific sensitivities of biomass allometry to climate variables plotted against the phylogeny derived from Qian and Jin (2016). Each colour shows the magnitude and direction of sensitivity to climate (*I*) for the outer ring = temperature (GDD); middle ring = *SPEI* drought index; inner ring = precipitation (PPT). A colour was not plotted for species with climate-insensitive allometry. (a) Fall species (*N* = 76); (b) Spring species (*N* = 45). Note that sensitivity to *SPEI* of the spring species, *Artemesia ludoviciana*, was very large (−23.4) and was not plotted to improve readability of the remaining data

for 83% of grasses, 75% of forbs and 63% of shrubs. Of just the cover-biomass allometries, ~76% were sensitive to climate (92 of 121 cases).

2. *Is the sensitivity of allometry to climate predictable from plant phylogenetic relatedness, functional group identity, life history strategy, or photosynthetic pathway?*

The magnitude of sensitivity of allometry to climate had strong phylogenetic signal (Table 2, Figure 2) in five of six analyses. The exception was drought in spring, for which sensitivity was not predictable from plant relatedness. Phylogenetic signal was strongest for sensitivity to precipitation in fall-collected species and weakest for sensitivity to temperature (GDDs) in fall-collected species (Figure 2a). Occurrence of sensitivity (insensitive vs. sensitive) had strong phylogenetic signal for fall species (*s2* = 3.85, *p* < .001, *N* = 76) but not spring species (*s2* = 0.00, *p* = .50, *N* = 45).

Grasses and shrubs were more likely than forbs to have size-biomass allometry that was sensitive to climate (Figure 3a, X^2 = 12.0, *p* = .0025). Functional groups differed in allometry more strongly in
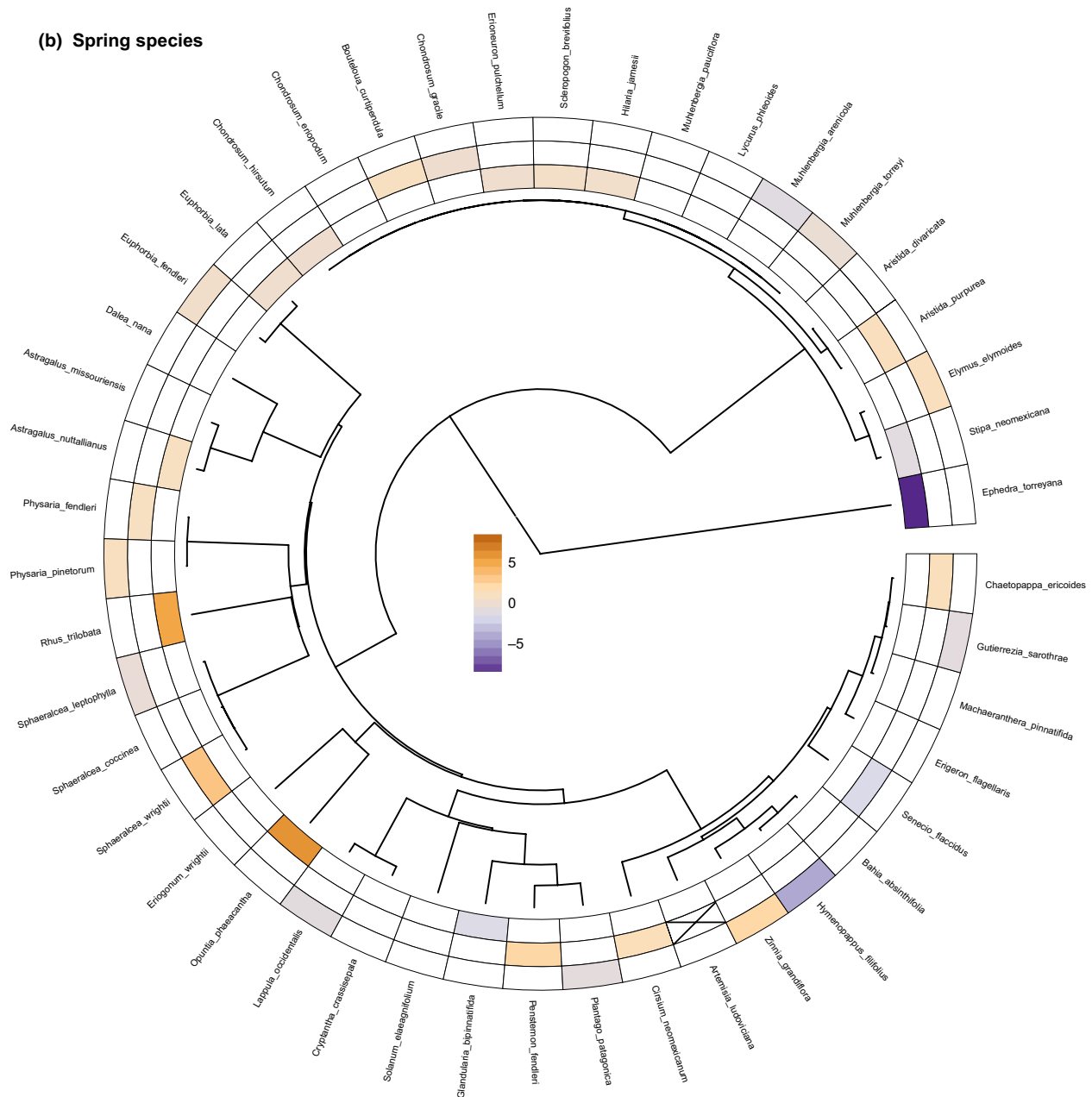
(b) Spring species

FIGURE 2 Continued

fall than in spring (season × functional group, X^2 = 8.4, p = .0152). In fall, all shrub and grass species had cover-biomass allometries that were sensitive to climate, while 64% of forb species were climate sensitive. In spring, 83% of shrubs were sensitive to climate, while 73% of grasses and 67% of forb species were sensitive. Results were consistent when we selected the best allometry from among both cover and volume models (functional group, p < .0228). However, phylogenetic logistic regression did not detect relationships between plant functional group and the *occurrence* of sensitivity (fall, p > .99; spring, p > .48). Phylogenetically independent contrasts to detect potential relationships between the *magnitude* of sensitivity and functional group showed no significant difference between functional groups (Fall, $F_{1,74}$ = 0.04, p > .83; Spring, $F_{1,43}$ = 0.122, p > .72).

Perennial plants were more likely than annuals to have climate-sensitive allometries (Figure 3b, life history, X^2 = 3.8, p = .0500). In fall, 84% of perennials and 65% of annuals were climate-sensitive. In spring, 73% of perennials were sensitive to climate, but annuals were poorly represented (2 of 4 annual species were sensitive). Life-history differences in sensitivity did not differ between seasons (season × life history, X^2 = 0.0, p > .98). Results were qualitatively similar when we selected the best allometry from both cover- and volume-biomass relationships but were non-significant (life history, p = .24). Phylogenetic logistic regression did not detect relationships between plant life history and the *occurrence* of sensitivity (fall, p > .26; spring, p > .34). In *PIC* analyses, the *magnitude* of sensitivity did not differ between annuals and perennials (Fall, $F_{1,74}$ = 1.148, p > .28; Spring, $F_{1,43}$ = 0.001, p > .97).
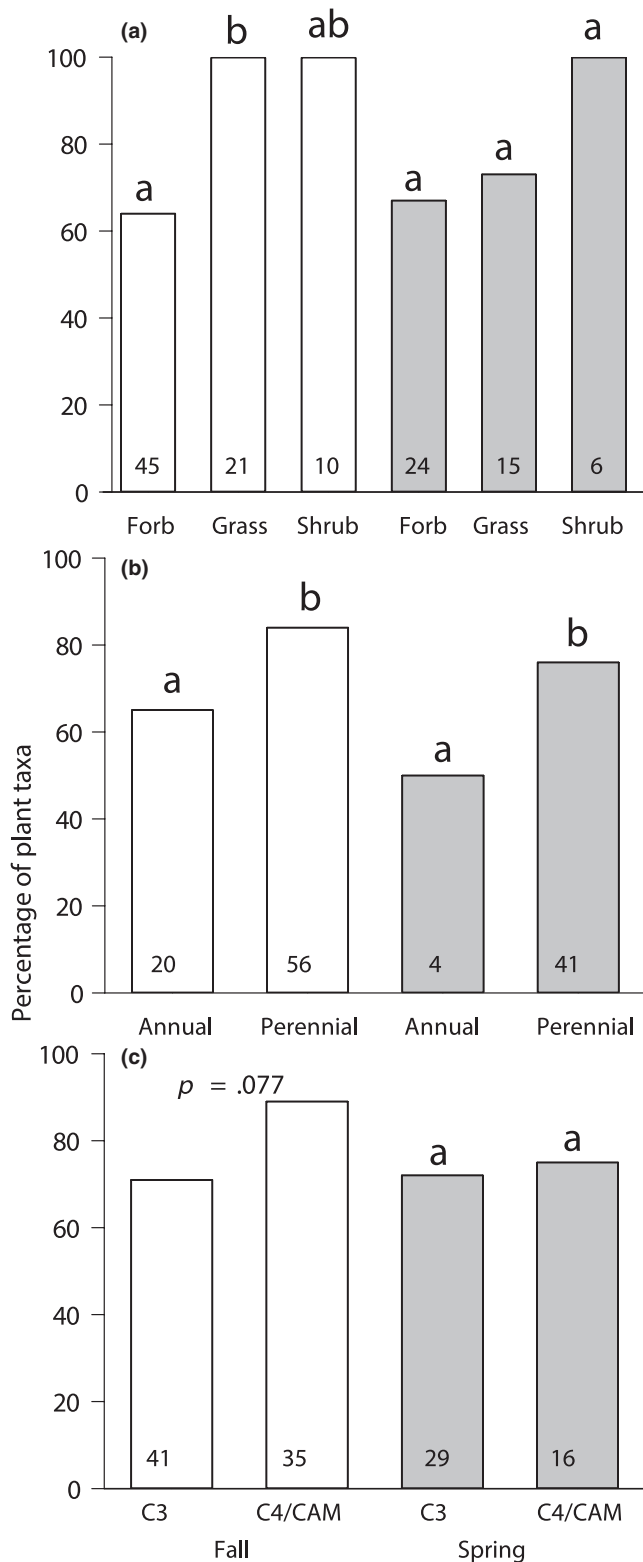
FIGURE 3 Percentage of plant taxa for which cover-biomass allometry was sensitive to climate, separated by season (fall = open bars, spring = filled bars) and for (a) plant functional groups, (b) plant life history, or (c) plant photosynthetic pathway. Different letters indicate that groups were statistically significantly different in pairwise contrasts within a generalized linear model for each season. Numbers on each bar indicate the number of plant species in each group

Plants with water-conservative photosynthetic pathways (C_4/ CAM) were somewhat more likely than C_3 plants to adjust allometry in response to climate (Figure 3c, X^2 = 3.1, p = .0769). Season did not interact with photosynthetic pathway to influence sensitivity (X^2 = 0.8, p = .36). In fall, 89% of C_4/CAM species had allometries that were sensitive to climate, but 71% of C_3 species were sensitive. In spring, 75% of C_4/CAM species and 69% of C_3 species had climate-sensitive allometries, respectively. Selecting the best allometry from cover or volume models returned similar results. Phylogenetic logistic regression did not detect differences in the *occurrence* of sensitivity for plants with different photosynthetic pathways (fall, p > .34; spring, p > .66), nor did phylogenetically independent contrasts detect an influence of photosynthetic pathway on the *magnitude* of sensitivity (Fall, $F_{1,74}$ = 0.030, p > .86; Spring, $F_{1,43}$ = 0.044, p > .83).

3. *To which climate variables is allometry most sensitive: temperature, precipitation, or drought?*

Of the 92 plant species × season combinations for which including climate sensitivity improved the estimate of size-biomass allometry, similar percentages of species were most sensitive to each of the three climate variables. In fall, 26% of species were most sensitive to drought, 28% to temperature as GDDs, and 25% to precipitation. In spring, 24% of species were most sensitive to temperature or precipitation, and 22% to drought. Plant species differed in the climate variable to which they were most sensitive, and meta-analysis revealed that the *magnitude* of the influence of different climate variables on allometry differed between spring and fall seasons (climate × season, X^2 = 1,455.8, p < .0001; Figure 4).

In the fall, 21 plant species had allometries that, on average, invested less biomass per unit cover under more arid climates, indicated by a more negative *SPEI* effect and supported by significantly positive interaction effect sizes (*I*) between *SPEI* and plant cover (Figure 4a). A different set of 18 species were most sensitive to precipitation in fall (e.g. Figure 1b), but the average effect size for this group did not significantly differ from zero (Figure 4b). A further set of 21 species invested less biomass per unit cover under warmer temperatures (as in example, Figure 1b), as indicated by the negative interaction effect size (*I*) for fall GDD (Figure 4c). In fall, woody and herbaceous plants that were sensitive to climate had similar average effect sizes for sensitivity (p > .29; herbaceous × season, X^2 = 197.8, p < .0001), as did C_4/CAM versus C_3 (p > .99). In both seasons, the magnitude of sensitivity did not differ between annuals and perennials (X^2 = 1.44, p > .23).

In the spring, plant allometry was significantly sensitive to drought and precipitation (Figure 4d,e; i.e. the magnitude of *I* was significantly greater than zero) with 9 plant species investing less biomass per unit cover under drier *SPEI* (Figure 4d) and 10 species that either increased or decreased biomass per unit cover with increasing spring precipitation (Figure 4e). Temperature did not substantially alter plant allometry in the spring (Figures 4f and 2b, 95% confidence intervals for (*I*) overlapped zero). In spring, the magnitude
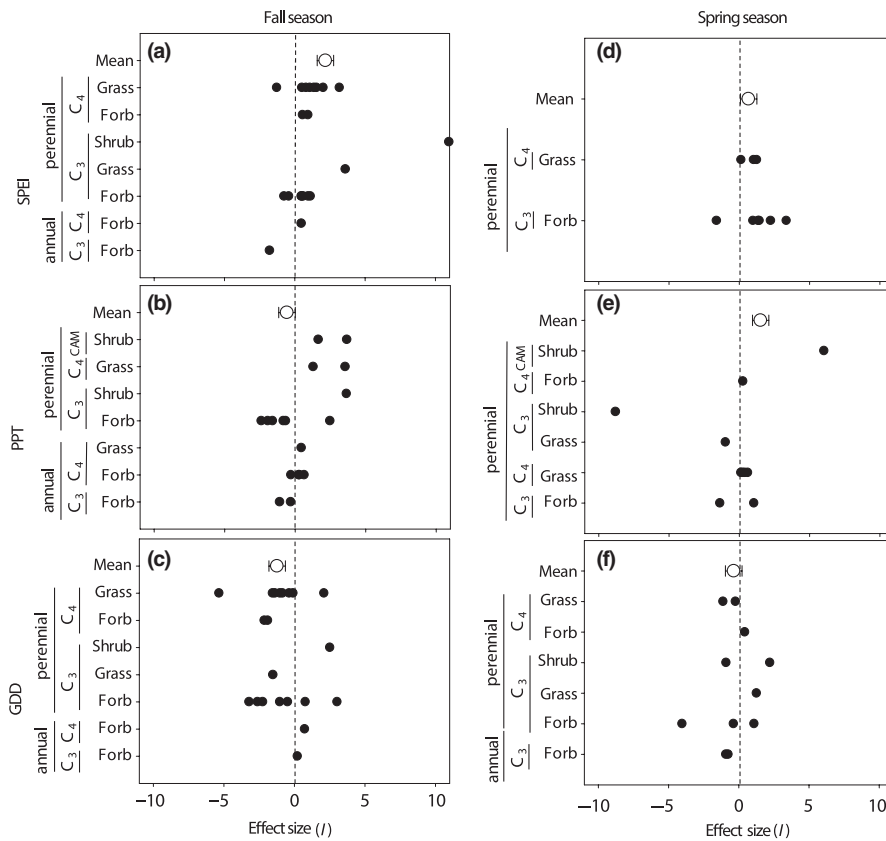
FIGURE 4 The magnitude and direction of sensitivity to climate (*I*) for species with cover-biomass allometry that was sensitive to climate, graphed separately for each season: fall (a-c) or spring (d-f) and for the *SPEI* drought index (a, d), precipitation (PPT) (b, e) or growing degree days (GDD) (c, f). Open symbols show mean effect size (*I*) ± 95% CI across species in each group. Filled symbols show individual effect sizes (*I*) for each species. In plot (d), *Artemesia ludoviciana* was excluded to improve the ability to visualize the other species, due to its large effect size (*I* = −23.4)

of climate sensitivity (for sensitive species only) was stronger for woody shrubs (mean [95% CI], 2.14 [0.77–3.51]) than herbaceous grasses/forbs (1.1 [−0.29 to 2.44]; *p* = .017). Also, the magnitude of sensitivity was larger for the C_4/CAM plant species than for C_3 plants (*p* = .002; photosynthetic pathway × season, X^2 = 1,087.2, *p* < .0001). C_4/CAM plants were most different from C_3 in their sensitivity to precipitation (photosynthetic pathway × climate variable, X^2 = 489.0, *p* < .0001; Figure 4b,e).

4. How much does climate-sensitive allometry influence estimates of aboveground primary production?

Accounting for climate sensitivity of allometry increased the precision of above-ground primary production estimates in some ecosystems (Figure 5). The strongest increases occurred in spring (Figure 5a), when accounting for climate sensitivity in allometry significantly changed total biomass estimates in all ecosystems (allometry method X^2 range 8.1–780.9, *p* < .0001; method × year X^2 range 5.6–512.3, *p* < .0001) except for the understorey community of piñon-juniper woodlands (*p* > .18). In fall, climate sensitivity significantly changed total biomass estimates for desert shrubland (Figure 5b, allometry method X^2 = 22.5, *p* < .0001; method × year X^2 = 25.1, *p* = .12) and desert grassland (allometry method X^2 = 26.6, *p* < .0001; method × year X^2 = 62.0, *p* < .0001) but was non-significant in plains grassland (*p* > .5) and woodland (*p* > .7).

4 | DISCUSSION

A majority of dryland plant species from annual forbs to perennial grasses and dominant shrubs exhibited changes in cover-biomass allometry with natural spatiotemporal variation in climate. Among the 85 plant species, ~70% (conservatively, 65%) had allometries that were significantly climate-sensitive. The large percentage of species with climate-sensitive allometry suggests that one-time measures of allometry can be inaccurate in long-term or cross-site studies that extrapolate to years or sites in which size-biomass relationships were not directly measured. Furthermore, application of climate-sensitive allometries to estimate above-ground primary production can substantially alter productivity estimates; in ecosystems studied here, this improvement was strongest in spring seasons and in grassland rather than woody ecosystems (Figure 5).

4.1 | Phylogenetic signal in sensitivity of allometry to climate

Evidence for phylogenetic signal in allometric sensitivity to climate was strong, indicating that closely related species are likely to have similar changes in cover-biomass relationships with changes in climate. From a practical perspective, the detection of phylogenetic signal means that the sensitivity of allometry for unstudied species may be predictable using plant phylogenies such as Qian and Jin (2016). This application could be useful for investigating

FIGURE 5 Estimates of total above-ground biomass averaged over 40–100 1 × 1 m quadrats per year per ecosystem type for either climate-sensitive (dark grey) or climate-insensitive (light grey) allometry methods for biomass estimation in four ecosystem types in (a) spring or (b) fall
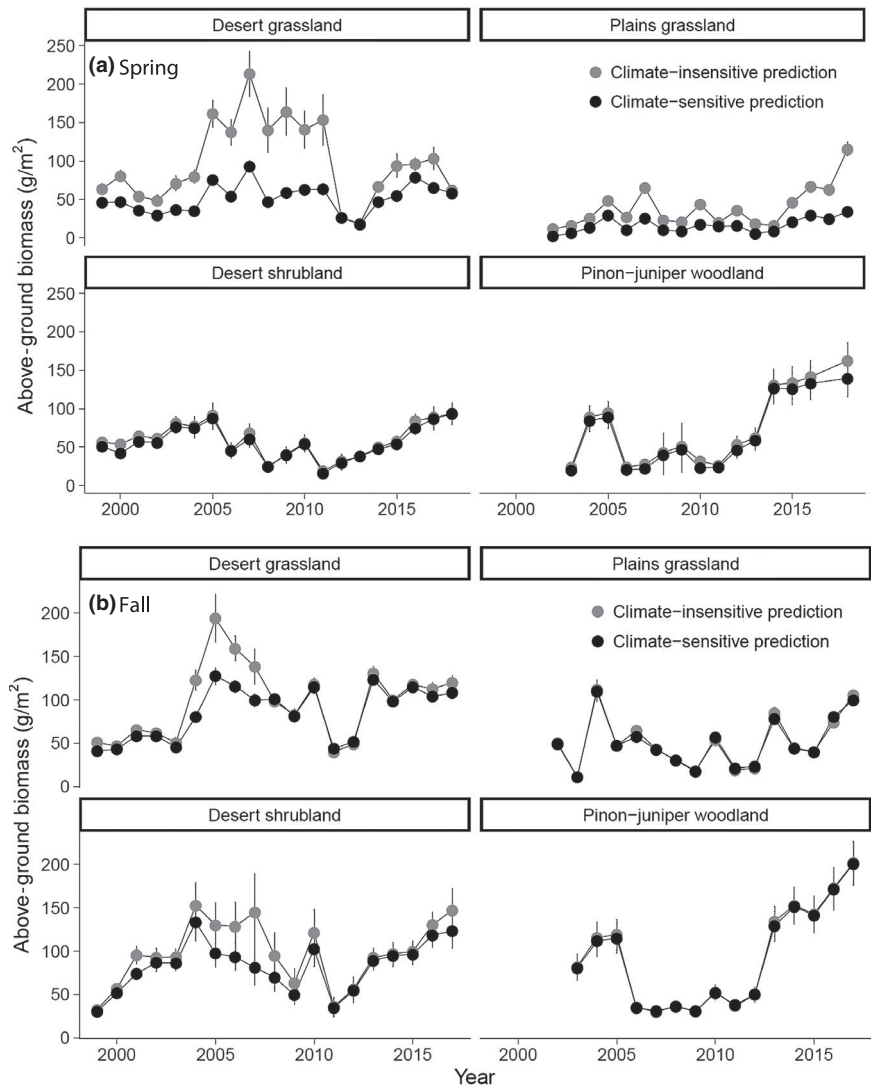
the accuracy of cases in which a single estimate of allometry was used to predict biomass across different climates, years or sites. The wide range of observed sensitivities in our dataset means that, in practice, size-biomass allometry should be measured under different climate conditions for individual species whenever possible. However, because species were differentially sensitive to different climate variables (e.g. temperature vs. precipitation), there is not a simple solution to capturing the climate sensitivity of allometry across a variety of plant species. Similar to our results, close relatives also share patterns of *organ-specific* biomass partitioning (e.g. partitioning of total biomass among roots, leaves or stems, McCarthy, Enquist, & Kerkhoff, 2007). Phylogenetic signal may indicate that physiological mechanisms to adjust allometry have diverged across plant lineages. However, our result contrasts with global analyses of *organ-specific* allometry, where within-plant partitioning of biomass among roots, stems or leaves tracked plant functional group more than phylogeny (Poorter et al., 2015; see also Ackerly & Donoghue, 1998), suggesting the explanatory power

of plant relatedness may differ between whole-plant and tissue-specific scales.

4.2 | Potential mechanisms underlying species differences in allometric sensitivities

Our results raise new hypotheses about why the sensitivity of plant size-biomass allometry varies with plant phylogeny, traits or life-history strategies. First, in contrast to our initial prediction, annuals and forbs had allometries that were *less* sensitive to climate than perennials and woody species. Short-lived and short-statured plants like annual forbs may be more likely to have determinate growth patterns than perennials, limiting mechanisms for plastic adjustments in size-biomass allometry (e.g. Perrin & Sibly, 1993). Annuals are also more likely than perennials to grow over a narrow range of conditions that follow from their abiotic thresholds of seed germination and rapid growth cycles (Farnsworth, 2007). In our dataset, clonal, rhizomatous or stoloniferous species were not represented

in sufficient numbers to investigate whether plants with vegetative reproduction strategies could adjust size-biomass allometry more than species that lack clonality. However, this could be an interesting hypothesis for future study. Second, size-biomass allometries of C_3 plants trended towards less sensitivity to climate than C_4/CAM plants. Larger sample sizes to separate C_4 and CAM strategies could be informative because CAM species use internally stored water (Tissue, Yakir, & Nobel, 1991), that should make their growth and growth form somewhat independent from short-term water availability. Altogether, our results align with recent meta-analysis of organ-specific plant allometries, which documented significant differences among annuals versus perennials and herbaceous versus woody plants in the patterns of biomass partitioning among roots, leaves or reproductive tissues under experimental drought (Eziz et al., 2017).

4.3 | Ecological and practical consequences of allometric sensitivities to climate

Substantial variation in plant size-biomass allometry under different abiotic conditions could have diverse ecological consequences. For example, altered above-ground plant tissue density could have cascading effects on consumers in resource-poor environments. Plant size-biomass allometries could affect the amount of resources available in a single foraging patch and thereby alter optimal foraging strategies of consumers, such as small mammals, which shift diet dramatically in response to climate in desert ecosystems (Noble et al., 2019). Similarly, shifts in biomass per unit cover could influence the pace of pathogen transmission among plant leaves and stems, affecting disease dynamics. Assuming a sparse versus dense size-biomass allometry could alter plants' competitive ability for sunlight or soil resources, affecting plant community dynamics. Finally, plant architecture has well-studied effects on nesting and perching sites for vertebrates and can also influence how predators capture herbivorous prey (Marquis & Whelan, 1996).

Our findings have an additional practical application for studies that use allometry to estimate biomass from non-destructive measures of plant size. As a non-destructive measure of size, plant cover was as good as volume for a majority of forb, grass and shrub species. Cover was adequate for more than three-fourths of forb and grass species, although volume was important for some species. Additional work in other ecosystem types would be needed to generalize the replacement of cover for volume. However, for drylands, our results suggest the extra labour of measuring plant height does not increase precision of biomass estimation, with the exception of tall shrub species and some dominant grasses.

4.4 | Future directions

Here, we focused on above-ground size – biomass allometries for plants in drylands, and the diversity of sensitivities we observed across species suggests that similar investigations could be useful for other aspects of plant morphology. For example, in a large study on plant rooting depths, rooting depth varied with mean annual precipitation (Schenk & Jackson, 2002). It could be interesting to investigate whether the sensitivity of below-ground allometry to climate rivals or exceeds above-ground sensitivities, and whether above- and below-ground allometries are most sensitive to different climate variables. We found that approximately one-third of species were most sensitive to each climate variable we investigated (precipitation, temperature, or drought), but below-ground allometry may be most sensitive to soil moisture, due to the temperature-buffering effect of soil. Additionally, recent work examined biomass partitioning among seed traits to characterize plant investment in seed dispersal, seed defence and seed endosperm provisioning (Chen & Giladi, 2018). Understanding the climate sensitivity of seed allometries could be useful for predicting whether climate change will alter dispersal distances, dispersal patterns or the dynamics of consumers that depend on the energy in seeds.

5 | CONCLUSIONS

Patterns of plant biomass partitioning are fundamental to estimates of primary productivity and ecosystem processes, such as carbon storage. We demonstrated that allometric relationships between above-ground plant biomass and measures of plant size varied considerably with spatiotemporal changes in precipitation, temperature and drought and that the sensitivity of allometry to climate tracked plant evolutionary history. Our results are important for the practical, functional use of allometry to estimate primary production and for understanding the cascading ecological consequences of climate-altered plant morphologies in dryland ecosystems.

AUTHORS' CONTRIBUTIONS

J.A.R., A.H., M.E.L., E.H.M., W.T.P., and K.D.W. conceived the ideas and designed methodology; S.R.B., E.H.M., L.B., and K.M.H. collected, curated and managed the plant and meteorological data; J.A.R., A.H., and K.D.W. analysed the data; J.A.R. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data packages are available from the Environmental Data Initiative Digital Repository (environmentaldatainiatiative.org) (Baker, Baur, Muldavin, & Rudgers, 2019; Hallmark et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.