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Title: Rainfall pulses mediate long-term plant community compositional dynamics in a semi-arid rangeland

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Abstract

1. Semi-arid rangelands, comprising more than 40% of the Earth's land surface, provide critical ecosystem services. Worldwide, these ecosystems are experiencing rapid degradation due to overgrazing and precipitation changes. However, how plants respond to these interacting factors remains relatively unexplored, and precisely which and how rainfall factors determine plant community dynamics in rangelands has not been well developed.
2. We used a long-term (1953–2018) dataset from semi-arid rangeland to investigate coupled effects of grazing intensity and rainfall intensity (the total amount of precipitation) on different groups of plant cover (herbaceous, woody, and cacti plants) using linear mixed-effects models, redundancy analysis and structural equation models. We examined how rainfall intensity influenced plant cover dynamics according to pulse size (intensity over time) categories, which we analyzed at three scales: yearly, within the wet season only (June to September), and within the dry season only (October to May).
3. Plant community cover showed a humpbacked trend in the last six decades, mostly through changes in woody plants. Although both grazing intensity and rainfall presented similar humpbacked trends with plant community cover, our models demonstrated that the reduction of plant cover from the 1990s has been mainly caused by a decrease of rainfall rather than grazing intensity, particularly due to profound reductions of the intensity of relatively small rainfall pulses (e.g., $5.1 \sim 15 \text{ mm} \cdot \text{day}^{-1}$) during the dry season. Specifically, these small rainfall pulses can increase plant cover of all subgroups of woody and herbaceous species, thereby increasing plant community cover. Moreover, rainfall pulses during the wet season had negative effects on herbaceous species and positive effects on woody plants. These results suggest a phenological niche partitioning between woody plants and herbaceous in subtropical rangelands.
4. *Synthesis and applications.* Our results show how critical seasonal rainfall pulses are for regulating plant community compositional dynamics, which has significant implications for rangeland management and our ability to adapt and mitigate amplified climate influences in semi-arid ecosystems.

Keywords: climate change, drylands, interspecific relationships, plant life-forms, plant-animal interactions, rainfall seasonality, rainfall event size, synusiae

Introduction

Rangelands occupy ~40 % of the Earth's land surface and provide indispensable services worldwide (Herrero et al., 2013; Fetzel, Havlik, Herrero, & Erb, 2017). Livestock grazing plays a critical role in altering ecosystem functioning and services (McNaughton, Oesterheld, Frank, & Williams, 1989; Asner, Elmore, Olander, Martin, & Harris, 2004), which mainly has been driven by plant composition shifts in response to herbivory (Koerner et al., 2018; Collins, Knapp, Briggs, Blair, & Steinauer, 1998). These responses to herbivory are generally related to two central attributes: plant functional traits and grazing intensity (Augustine & McNaughton, 1998). Herbivores generally prefer tall to short, erect to prostrate, and perennial to annual or biennial plants (Díaz et al., 2007). And, this foraging selectivity is associated with grazing intensity. Increasing grazing pressure (overgrazing) leads to a high selectivity for favored plants (e.g., herbaceous) in a given pasture with certain plant compositions, potentially increasing opportunities for unfavored plants (e.g., woody plants) (Archer et al., 2017; Van Auken, 2000). Understanding the mechanisms of how grazing shapes plant composition can help guide management actions and improve the predictions of ecosystem functioning and services in rangelands. Thus, there is still a need for further exploration of how different plant functional groups respond to a long-term gradient of grazing intensity.

Rangelands are sensitive to rainfall variability (Sloat et al., 2018), particularly in arid and semi-arid regions (Liang & Gornish, 2019). For example, grazing effects can be enhanced both in a dry year (Liang et al., 2018; Stampfli, Bloor, Fischer, & Zeiter, 2018) and in relatively drier regions (Dangal et al., 2016; Eldridge, Poore, Ruiz-Colmenero, Letnic, & Soliveres, 2016), and these coupled effects of grazing and rainfall on plants are primarily dependent on plant functional groups (Liang et al., 2018; Stampfli et al., 2018). Additionally, the responses of plants to rainfall variability vary with plant functional groups. Specifically, increasing variability of rainfall intensity might not affect herbaceous species but can increase woody plant productivity (Gherardi & Sala, 2015) and canopy circumference (Kulmatiski & Beard, 2013). Importantly, a seasonal shift in precipitation contributes to the global rainfall variability in rangeland ecosystems (Sloat et al., 2018). Previous work indicates that seasonal shifts in rainfall could influence plant community dynamics more than livestock grazing (Brown, Valone, & Curtin, 1997); identifying these rainfall regulations may mitigate climate impacts

in rangelands. However, it remains unclear how the responses of plants of different functional groups to grazing will be regulated by rainfall intensity and seasonality in changing rangelands.

Rainfall pulse size – the size of rainfall events – is an important element of directing plant relationships and plant communities in drylands (Sala & Lauenroth, 1982). Previous studies show that small rainfall events negatively affect ecosystem carbon balance in drylands due to a trigger of microbial respiration (Huxman et al., 2004), whereas larger rainfall events maintained net carbon uptake, due to increased soil water availability that promotes plant photosynthesis and aboveground productivity (Heisler-White, Knapp, & Kelly, 2008; Parton et al., 2012). A very recent study indicates that the variability in the size of rainfall events within years could mediate rainfall use efficiency of ANPP in response to growing season precipitation (Felton, Slette, Smith, & Knapp, 2020). Rainfall pulse size has been generally recognized in Noy-Meir's 'pulse-reserve' paradigm, which describes how different rainfall sizes can produce different biologically-significant 'pulses' of soil water recharge for plants in arid ecosystems (Noy-Meir, 1973), in particular in herbaceous and woody plant communities. Specifically, herbaceous plants are expected to absorb water by dense fine roots at shallow soil layers (e.g., small rainfall pulses), whereas woody roots can reach more distant water both laterally and vertically (e.g., large rainfall pulses) (Archer et al., 2017; Schenk & Jackson, 2002). These niche separations between species can maintain a variety of distinct resource-acquisition strategies to facilitate their coexistence (Walter, 1971; Scholes & Archer, 1997), which could maintain plant diversity and may eliminate the pressure of grazing selectivity in rangelands. Furthermore, woody plants are expected to develop 'islands of fertility' that accumulate nutrients under their canopies via accelerating litterfall decomposition (D'Odorico, Bhattachan, Davis, Ravi, & Runyan, 2013; Schlesinger et al., 1990). These islands can not only provide a canopy 'shelter' for herbaceous plants to avoid herbivores, but they can also support herbaceous nutrient demands (Allington & Valone, 2014). Thus, in attempting to investigate how rainfall pulses regulate plant-plant or plant-animal interactive relationships via 'triggering' plant activities, understanding the importance of rainfall pulse size and how plants in different functional groups respond to these pulse sizes is critical.

The Santa Rita Experimental Range (SRER), in the southwest US, has supported grazing since the 1900s (<https://cals.arizona.edu/srer/>) is an ideal location for exploring how plants in different

functional groups respond to grazing and rainfall factors. Hereafter, we employ the ‘synusiae’ terminology referring to ‘vegetation layers of the community’, which consist of the same life-form plants (Barkman, 1978), such as herbaceous, woody plants, and cacti. Using a six-decade (1953–2018) plant cover dataset from SRER, we asked: (1) do grazing and rainfall have different impacts for different plant functional groups?; (2) what rainfall factors are most important as regulators of plant cover across functional groups in response to grazing? (3) what ecological mechanisms (facilitation vs. competition) mediate responses of plant species to rainfall variability and grazing intensity?

Materials and methods

Study site

The SRER is 21,500 ha, is characterized as desert grassland vegetation (Fig. S1), and is located ~50 km south of Tucson, Arizona USA (McClaran, Browning, & Huang, 2010). Mean annual temperature is approximately 16 °C. Mean annual precipitation ranges from ~200 to ~600 mm, and averaged 367.5 mm (CV = 0.25) during 1953 – 2018 (Fig. 1e). The soil is largely coarse sandy loam (McClaran & Wei, 2014).

Grazing intensity

Cattle grazing is the primary management practice that occurs on ~90 % of the SRER. The number of cattle changes across pastures monthly, seasonally, and annually. Generally, an animal unit per year per hectare ($\text{AUY} \cdot \text{ha}^{-1}$) in each pasture plots is used as an index of grazing intensity, which is the averaged value based on 12-month livestock rates.

Transect plant cover data

Plant cover data (%) was collected over a 65-yr period (1953–2018) on multiple same-size transects in nine pastures at SRER, including pasture 8, 12B, 2N, 3, 5N, 5S, 6A, 6B, and 2S. Eleven transects have been monitored in pasture 8 since 1953. Ten, six, ten, ten, eight, and 20 transects have been monitored in pastures 12B, 2N, 3, 5N, 5S, and 6A since 1957, respectively. Sixteen transects have been monitored in pasture 6B since 1959. And 8 transects have been monitored in pasture 2S since

1975. Cover data is collected every 0.03 m along the transect. Each transect was 30.48 m. Details of the geographic locations and data collections can be found at <https://cals.arizona.edu/srer/data.html>.

Multi-synusiae classification

Synusiae have been used to recognize vegetation layers of the community, which is a group of plant species having the same life or growth forms (Barkman, 1978). We classified 80 recorded plant species from the SRER dataset into three main synusiae based on life-form: woody plants, herbaceous, and cacti. We divided synusiae into management-relevant subgroups. For example, woody synusiae include tall trees and small shrubs, and was further divided into subgroups legume and non-legume groups. *Prosopis velutina* (Velvet mesquite) was the dominant species in woody legumes; and *Haplopappus tenuisectus* (Burroweed) was the dominant species in woody non-legumes. Herbaceous synusiae was comprised of perennial grasses, and was further divided into the subgroups of introduced and native grasses. *Eragrostis lehmanniana* (Lehmann lovegrass) is an invasive grass, which dominates native grasses in the herbaceous synusia, including *Aristida* spp., *Bouteloua* spp. (Grama grass), *Digitaria californica* (Arizona cottontop), *Muhlenbergia porter* (Porter's muhly), and *Heteropogon contortus* (Tanglehead). Cacti synusiae was divided into two subgroups groups: cholla and other cacti. Cholla largely consists of *Cylindropuntia* spp. (Cholla) and *Opuntia engelmannii* (Prickly pear) is the most widespread of other cacti. For each synusiae and its subgroups, plant cover was an average value of all species that were characterized in the given classification. Due to a lack of data on annual grasses and forbs, we did not include plants from these groups in our analysis.

Ground precipitation gauge data

Seventy-five gauges, located through the SRER (<https://cals.arizona.edu/srer/precip/rainstautm.txt>) have been collecting monthly precipitation data since June 1922, each with a precision of 0.25 mm. Mean annual precipitation is a yearly averaged value of the accumulated amount of monthly measurements by the gauges. Precipitation during a wet season was the total amount of precipitation from June to September (McClaran & Wei, 2014). To consider the lagged effects of precipitation, particularly after the wet season in the last year, we used the total amount of precipitation (mm)

during October and May to characterize the rainfall intensity during the dry season (Browning, Archer, Asner, McClaran, & Wessman, 2008; Brown et al., 1997).

We also used daily measurements for precipitation to calculate rainfall pulses from another seven gauges at the SRER, which started collecting data in July 1975 (Goodrich et al., 2008). Based on Sala and Lauenroth's rainfall pulses classifications (Sala & Lauenroth, 1982), we classified rainfall pulses into five levels, including I: $0.1 \sim 5.0 \text{ mm} \cdot \text{day}^{-1}$; II: $5.1 \sim 10 \text{ mm} \cdot \text{day}^{-1}$; III: $10.1 \sim 15 \text{ mm} \cdot \text{day}^{-1}$; IV: $15.1 \sim 20 \text{ mm} \cdot \text{day}^{-1}$; and V: $>20 \text{ mm} \cdot \text{day}^{-1}$. For each rainfall pulse, we also calculated the total amount of precipitation (mm) and the total number of each rainfall pulse as their intensity and frequency, respectively, calculated over the entire year, within the wet season each year, and within the dry season each year. The intensity of rainfall pulses was strongly correlated to their frequencies (Fig. S4), thus we used the intensity in all further statistical models; hereafter, the rainfall pulse denotes rainfall pulse size (mm) throughout.

Data analysis

To investigate whether grazing effects on plant community dynamics are related to grazing intensity or the types of multi-synusiae, we ran linear regression models between grazing intensity (i.e., explanatory variable, $n = 214$) and plant cover (i.e., response variable) through each subgroup of woody, herbaceous, and cacti synusiae.

To examine the effects of rainfall on plant community dynamics, we conducted first-order autoregressive (AR(1)) linear mixed-effects models between rainfall factors (i.e., explanatory variable) and plant cover (i.e., response variable), with pasture sites ($n = 9$) as a random factor. The LMMs were implemented for different rainfall factors (e.g., the intensity of all rainfall events and the intensity of rainfall pulses), different plant subgroups (woody, herbaceous, and cacti synusiae), and different time periods (entire year, dry season, and wet season). The sampling sizes of rainfall factors were according to yearly measurements of plant cover (e.g., 29 censuses), and the intensity of all rainfall events observed across 29 censuses between 1953 and 2018. The intensity of rainfall pulses was derived from 13 censuses between 1978 and 2018 because the daily precipitation measurements started in 1975. Analyses were conducted in R v 3.6.0 (R Development Core Team, 2019), using *lme4* (Bates, Mächler, Bolker, & Walker, 2015). We used redundancy analysis (RDA) to assess the effects

of grazing intensity rainfall factors on multi-synusiae, and we evaluated the significant ordination axes by permutation tests using *vegan* (Oksanen et al., 2019).

Plant cover data were averaged across transects conducted in the same pasture and year, and plant cover at the community level was used as an accumulative value of all synusiae. Grazing intensity was given for each pasture yearly. We averaged rainfall factors across all gauges in each year. All these data have been standardized ($\frac{v_i - \mu_{vi}}{\sigma_{vi}}$) to compare effects sizes; plant cover and grazing intensity were standardized at pasture level, and rainfall factors standardized yearly, where v_i denote the observed value of variables, μ_{vi} and σ_{vi} represent the mean and standard deviation of plant cover variables and grazing intensity at pasture level or rainfall variables yearly.

To explore direct and indirect effects of rainfall pulse in different seasons and grazing intensity on plant community via shifting the plant-plant relationships or regulating the contribution of changes in cover of synusiae to changes in total plant cover, we employed two partial least squares-based structural equation modeling (PLS-SEM) using *plspm* (Sanchez, Trinchera, & Russolillo, 2015), with the rainfall pulse during the entire year and during the wet and dry seasons ($n = 117$). The model fit was based on the good-of-fit index (GoF). Each PLS-SEM consists of inner models (formative structural models) and outer models (reflective measurement models), which present pathway correlations between measurable variables and latent variables. In our PLS-SEM, we used four latent variables, including rainfall pulse, woody plants, herbaceous, and cacti. Each latent variable consists of several measurable variables. For example, rainfall pulse has five different rainfall event sizes ($0.1 \sim 5.0 \text{ mm} \cdot \text{day}^{-1}$; $5.1 \sim 10 \text{ mm} \cdot \text{day}^{-1}$; $10.1 \sim 15 \text{ mm} \cdot \text{day}^{-1}$; $15.1 \sim 20 \text{ mm} \cdot \text{day}^{-1}$; and $>20 \text{ mm} \cdot \text{day}^{-1}$) during the entire year, during the wet season, and during the dry season, respectively; woody plants include non-legume and legume subgroups; herbaceous includes introduced perennial grasses (IPG) and native perennial grasses (NPG); cacti includes cholla and other cactus plants.

Results

Plant community dynamics

Plant cover at the community level in SRER showed a humpbacked trend from 1953 to 2018 (Fig. S2a), which were also evident in the trends of legume, non-legume, and introduced perennial grasses (IPG). However, this trend was not identified for native perennial grasses (NPG), cholla, and other

cacti groups (Fig. 1). Woody synusiae (both legume and non-legume) contributed ~ 78% to community cover (Fig. S2b).

Grazing effects

Grazing intensity has declined at SRER since 1953 (Fig. 1d). An increase of grazing intensity had a negative effect on plant community cover (Fig. 2a, $P < 0.0001$), which was also evident in the negative effects of grazing intensity on legume and non-legume groups (Fig. 2b, $P < 0.0001$ and $P = 0.009$, respectively). Grazing was not significantly ($P > 0.05$) related to IPG, NPG, nor cholla and other cacti groups (Fig. 2 and Table S1).

Rainfall regulations

Rainfall intensity had no apparent trends at SRER from 1953 to 2018, through the entire year (Fig. 1e, $P = 0.216$) or in the wet season (Fig. 1f, $P = 0.669$); but it showed a humpbacked trend during the dry season (Fig. 1e, $P = 0.005$). Rainfall intensity during the dry season positively affected plant community cover (Fig. 2a, $P < 0.0001$), which was possibly due to its substantial positive effects on non-legumes (Fig. 2b, $P < 0.0001$). Moreover, these rainfall variabilities through different temporal periods influenced multi-synusiae ($P < 0.0001$). Specifically, rainfall intensity during the entire year increased non-legumes and slightly decreased NPG. Rainfall intensity during the wet season also positively affected non-legumes, but it decreased IPG and NPG (Fig. 2 and Table S2).

Size-dependent effects of seasonal rainfall pulse

The intensity and frequency of rainfall pulses of all five levels declined during the entire year from 1978 to 2018 (Fig. S3a and Fig. S3b), which may have resulted from a decline of all pulses during the dry season (Fig. S3e and Fig. S3f, $P < 0.05$ and $slope < 0$ for all pulse levels) but no changes occurred during the wet season (Fig. S3c and Fig. S3d, $P > 0.05$ for all pulse levels). Thus, the intensity of relatively small rainfall pulses (i.e., $5.1\text{--}10 \text{ mm}\cdot\text{day}^{-1}$ and $10.1\text{--}15 \text{ mm}\cdot\text{day}^{-1}$) during the entire year had positive effects on plant community cover, which may have resulted from the positive effects of these pulses during the dry season on plant community cover (Fig. 2a, $P < 0.0001$). Redundancy analysis also indicated that plant community cover was positively driven by the intensity of relatively small rainfall pulses, such as $5.1\text{--}10 \text{ mm}\cdot\text{day}^{-1}$ during the entire year and both $5.1\text{--}10 \text{ mm}\cdot\text{day}^{-1}$ and $10.1\text{--}15 \text{ mm}\cdot\text{day}^{-1}$ during the dry season (Fig. 3).

Furthermore, the effects of rainfall pulse intensity on plant cover varied with multi-synusiae, pulse size, and seasonality (Fig. 2, Table S3, Table S4, and Table S5). All pulse effects on legumes were positive both during the wet and dry seasons, whereas relatively large pulse sizes (i.e., 15.1~20 mm·day⁻¹ and > 20 mm·day⁻¹) on non-legumes were negative both during the entire year and the dry season (Fig. 2b, $P < 0.05$ in all cases). All pulse effects on herbaceous (both IPG and NPG) were negative during the wet season. During the dry season, smaller rainfall pulses (5.1~10 mm·day⁻¹ and 10.1~15 mm·day⁻¹) increased plant cover of both IPG and NPG ($P < 0.0001$), while larger pulse sizes decreased IPG (Fig. 2c, $P < 0.05$ in all cases). Cacti exhibited a more conservative response to an increase in rainfall pulse intensity (in particular for the other cacti group) except for the relatively large pulse size (> 20 mm·day⁻¹), which may have suppressed the cholla group both during the wet and dry seasons (Fig. 2d).

Intrinsic ecological factors

The partial least squares-based structural equation modeling (PLS-SEM) confirmed the seasonality of rainfall pulse intensity regulations on multi-synusiae (Fig. 4, Table S6, and Table S7). By increasing woody plant cover, rainfall pulse intensity increased plant community cover during the entire year (Fig. 4a and Table S6, total effects: TES = 0.42); however, rainfall pulse intensity decreased herbaceous species during the wet season (Fig. 4b and Table S7, TES = -0.38) and increased their cover during the dry season (Fig. 4b and Table S7, TES = 0.40). Grazing intensity indirectly decreased plant community cover (Table S6, TES = -0.18; Table S7, TES = -0.18) by reducing woody plants (Table S6, TES = -0.22; Table S7, TES = -0.21) and increasing herbaceous species (TES = 0.20), because woody plants (Table S6, TES = 0.97; Table S7, TES = 1.00) contributed more to plant community than herbaceous species (Table S6, TES = 0.28; Table S7, TES = 0.25).

The PLS-SEMs also revealed that the relationships between plants essentially regulated plant community dynamics in our study, and the relationships among herbaceous, woody, and cacti plants could either impact or be impacted by grazing and rainfall factors (Fig. 4, Fig. S6 and Fig. S7). Cover of wood plants positively related to cover of herbaceous plants (Fig. 4a, $r = 0.26$, $P = 0.005$; Fig. 4b, $r = 0.24$, $P = 0.016$), potentially indicating facilitation. Specifically, IPG positively correlated with woody legumes ($r = 0.27$, $P < 0.0001$) and non-legumes (Fig. S8, $r = 0.33$, $P < 0.0001$). Alternatively, cover of cacti plants negatively related to cover of herbaceous plants (Fig. 4a, $r = -0.31$, $P = 0.001$;

Fig. 4b, $r = -0.23$, $P = 0.014$); similarly, IPG negatively correlated with other cacti (Fig. S8; $r = -0.40$, $P < 0.0001$), indicating possible competition.

Discussion

Synusiae-dependent responses to grazing

Our results suggest that cattle grazing in the Santa Rita Experimental Range (SRER) could decrease plant community cover by reducing woody plants' canopy cover. These results contradict previous work that shows that woody plants generally gain an advantage from livestock grazing (Archer et al., 2017; Van Auken, 2000; Cipriotti, Aguiar, Wiegand, Paruelo, & Toit, 2019). Presumably, leaves of woody plants (for legumes, in particular) have higher nutrient content than other plant types. An increase of livestock grazing could result in substantial browsing of all leaves and damage apical meristems, limiting growth. Moreover, our PLS-SEMs demonstrate that grazing intensity had positive effects on herbaceous species via increasing plant cover of introduced perennial grasses (IPG), suggesting that grazing may cause alien species invasion. This likely occurred because grazing reduces native grasses while additional resources (nutrients, space, and light, etc.) become available to support new species (Koerner et al., 2018; Liang et al., 2018). And one of the dominant species in IPG – *Eragrostis* – is a C₄ plant that could sufficiently use these “surplus” resources for growing and colonization.

Seasonal rainfall regulations

Our findings demonstrate that seasonal rainfall intensity regulates plant community dynamics in this semi-arid rangeland; showing a positive relationship of plant community cover to rainfall intensity during the dry season. This may have happened due to woody non-legumes being significantly affected by precipitation during the dry season. Previous studies have shown that woody plants exhibit no response to summer precipitation (Ehleringer, Phillips, Schuster, & Sandquist, 1991), but large increases in woody cover can occur during increased winter precipitation (Brown et al., 1997; Reynolds, Kemp, Ogle, & Fernández, 2004). During the dry season, precipitation can percolate more deeply due to cold temperatures and relatively low evaporation rates. This water can then preferentially benefit woody plants characterized by deep-root systems (Walter, 1971; Schenk & Jackson, 2002). Additionally, woody non-legumes (e.g., *Larrea*) could shift their temporal growth

patterns to take advantage of water availability (Reynolds, Virginia, Kemp, De Soyza, & Tremmel, 1999). Our results highlight the importance of considering seasonal rainfall regulations (and not just annual rainfall variability) on plant community dynamics via altering multi-synusiae in these ecosystems.

Size-dependent influences of rainfall pulses

Our results demonstrate that rainfall pulse regulates plant community dynamics, mainly depending upon their size and seasonality. Specifically, an increase of intensity of small rainfall pulses consistently increased plant community cover, in particular for herbaceous synusiae during the dry season. Small rainfall pulses are typically high frequency and could recharge soil moisture at 0~30 cm depth in drylands (Sala & Lauenroth, 1982), and perennial grasses have a dense-root system consisting of fine roots in the shallow soil layer that support a greater capacity of water use from small rainfall pulses. Also, most of the dominant herbaceous species are C₄ grasses, which have a higher capacity for water use efficiency than C₃ plants (e.g., woody plants). This may help herbaceous species gain more advantages from small rainfall pulses than other synusiae. Moreover, we found that large rainfall pulses negatively affect herbaceous species, especially during the wet season. At SRER, precipitation is considerably greater during the wet season than during the dry season (McClaran & Wei, 2014), which could keep a relatively high saturation of soil moisture that may exceed the threshold for herbaceous synusia. Consequently, it suppresses herbaceous regrowth by inhibiting root respiration and mineral uptake under anoxic environments.

Our findings also highlight how the effects of rainfall pulses on plant cover vary with subgroups of both woody and cacti synusiae. This might have occurred because of their growth forms, rooting patterns, and physiological responses to water availability. Both legume and non-legume woody plants have more vertically extensive root systems than other synusiae, which can take up water at deeper soil depths (Schenk & Jackson, 2002; Archer et al., 2017). Generally, the amount of water that plants can exploit is primarily dependent on how much rainfall deposits on the soil at each rainfall event (i.e., size of rainfall pulses). Large rainfall events optimize water infiltration into deeper layers and end up being stored longer during the dry season with cold temperature, low evaporation demands, and low evapotranspiration rates (Brown et al., 1997; Sala & Lauenroth, 1982); thereby, the size of rainfall pulse could indicate water availability. Woody legumes (e.g., *Prosopis*) are capable of

shifting their growth and physiological activities temporally to adjust water demands and would be more resilient to changing water availability than woody non-legumes (Reynolds et al., 1999; Ogle & Reynolds, 2004). Lastly, cacti have widely-spread root systems that can acquire and store water very rapidly (within the first few hours after rainfall events), providing access to the stored water in the following days or weeks (Walter, 1971). This could explain our findings that increased rainfall pulse intensity reduced the cover of cacti synusiae, especially the profoundly negative effects of large rainfall pulse on cholla. Thus, if the soil is saturated by large rainfall events or a coincidentally clustered small rainfall event, this may result in cacti root damage under anoxic environments that inhibit root respiration, mineral uptake, and subsequently, plant regrowth.

Niche partitioning in multi-synusiae

Niche partitioning has long described how water-use strategies may explain woody-herbaceous coexistence (Scholes & Archer, 1997; Archer et al., 2017), but an empirical understanding of this mechanism remains elusive. Our results not only indicate the differential water-demands for rainfall size among multi-synusiae, but also suggest a seasonal partitioning (or phenological niche partitioning) of these demands between woody plants and herbaceous species, which may be related to their phenology shifts. A previous study reported that plants could shift their growth towards both earlier spring emergence and delayed autumn senescence to offset the drought-induced reduction of plant cover in summer, and this was predicted to be widespread and consistent with increasing aridity of North American grasslands in future climate scenarios (Hufkens et al., 2016). In general, herbaceous species grow in summer but need water for germination before spring, and they typically exploit water at shallow soil depths with their dense fine roots. The water at deep soil depths is used more by woody roots, and the water stored in cacti stems can persist long after a rainfall event (Scholes & Archer, 1997). Additionally, herbaceous plants generally can grow with much lower annual precipitation than is necessary for woody plants (Walter, 1971), therefore a relatively low annual rainfall could be sufficient for herbaceous plants in drylands, but not for encroaching woody plants. Thus, our findings could help explain how plants in different life-forms adapt to rainfall variability in different seasons.

Moreover, our results describe positive correlations between woody and herbaceous species, which may result from phenological niche partitioning. Woody plants can facilitate herbaceous

species (Maestre, Bautista, Cortina, & Bellot, 2001), and this facilitation becomes more common under stress (Maestre, Callaway, Valladares, & Lortie, 2009). In nutrient-poor and harsh-climate drylands, grazing stress could amplify positive relationships between woody and herbaceous plants. Grazing interferences could optimize ‘islands of fertility’, where woody plants accumulate nutrients under their canopies (D’Odorico et al., 2013; Schlesinger et al., 1990; Allington & Valone, 2014). For example, woody plants can provide a canopy ‘shelter’ where herbaceous plants can ‘hide’ to avoid livestock. Below the crown, solar radiation is low, inhibiting evaporation and creating a microclimate condition that is an ideal location for microbes to accelerate decomposition. Thus, our findings may be helpful for understanding how plants in different life-forms adapt to rainfall variability in different seasons in a way that considers plant-plant and plant-animal interactions.

Implications for rangeland management

Rangeland management has become a critical issue for mitigating climate change worldwide. Understanding rainfall regulations on plant community dynamics is crucial for rangeland management in a changing world (Sloat et al., 2018). Increasing the intensity or variability of rainfall could increase woody plant encroachment (Kulmatiski & Beard, 2013; Gherardi & Sala, 2015), which has become a vexing problem in rangelands globally (Van Auken, 2000; Archer et al., 2017). In this study, our novel findings highlight that these ecosystems may be more vulnerable to climate change than livestock management policy in the long-term, especially as the dry season becomes much drier and the wet season becomes much wetter in the southwestern U.S. More than the magnitude of total precipitation, the size of rainfall events (i.e., rainfall pulse sizes) and its seasonality can significantly drive plant community dynamics. These results could both help to understand how livestock intensity and climate change factors interactively affect plant community dynamics globally and guide local livestock management and decision making.

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Authors’ contributions

ML and ESG conceived the idea. ML, XF, and ESG analyzed the data, wrote the first draft, and developed the manuscript. All authors gave final approval for publication.

Data availability statement

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.r4xgxd29r> (Liang, Feng, & Gornish, 2020).

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FIGURE LEGENDS

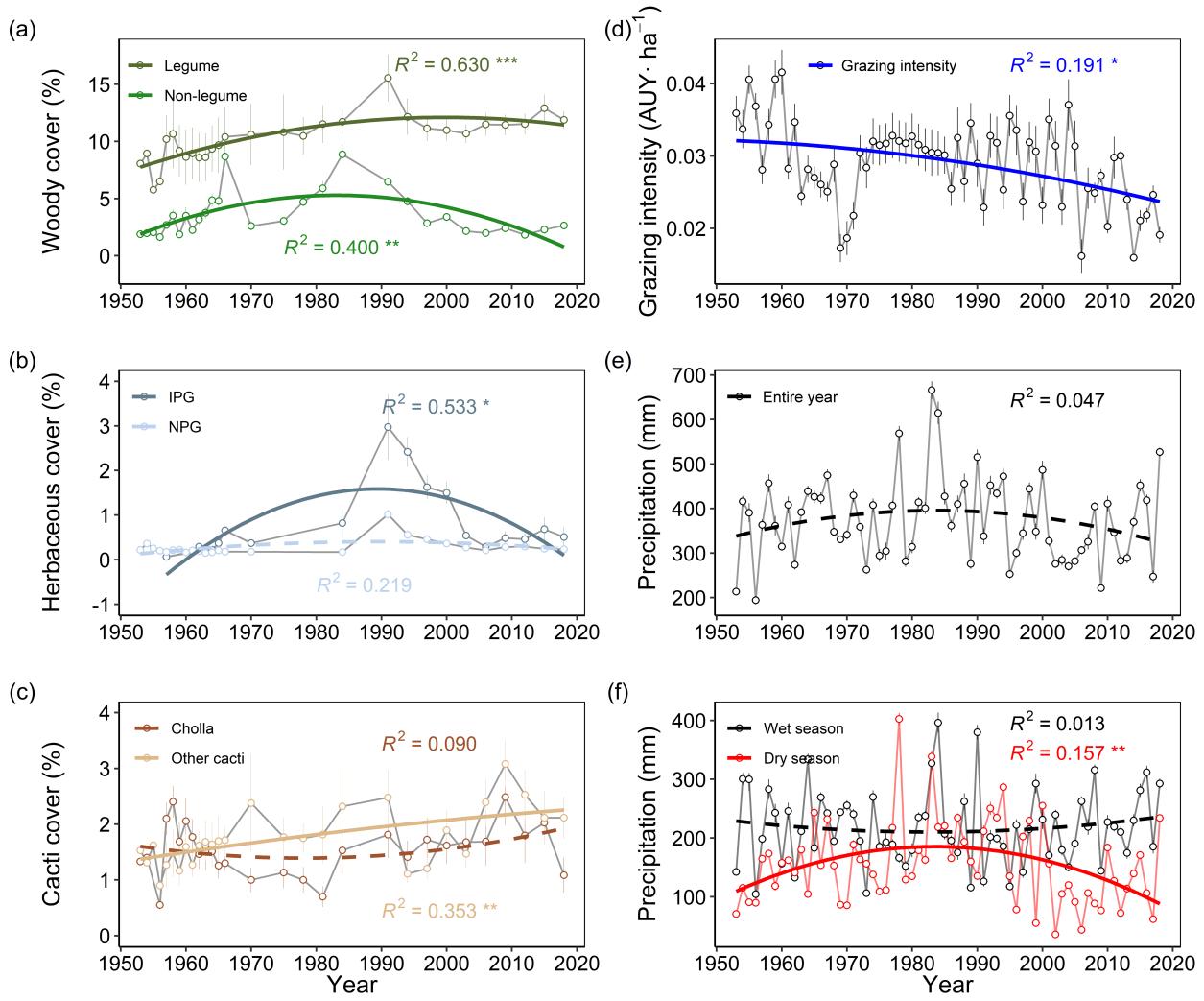
FIGURE 1 Dynamics of the plant community, grazing intensity, and precipitation during 1953–2018 in the Santa Rita Experimental Range (SRER), USA. Shown are the trends of plant cover among (a) woody, (b) herbaceous, and (c) cacti synusiae, (d) grazing intensity, and the amount of precipitation during (e) the entire year and (f) different seasons (wet season: June to September; dry season: October to May), respectively. The bold lines indicate the quadratic regressions with “year” as a predictor. Solid and dashed lines represent significant and insignificant ($P \geq 0.05$), respectively. Significant level: “*”: $P < 0.05$; “**”: $P < 0.001$; “***”: $P < 0.0001$. Key: Legume = legume woody plants; Non-legume = non-legume woody plants; IPG = introduced perennial grasses; NPG= native perennial grasses; CHOLLA = cholla plants; OTHCACTUS = other cacti plants.

FIGURE 2 The effects of grazing intensity and rainfall intensity on plant cover in the Santa Rita Experimental Range (SRER), USA. Shown are the standardized regression coefficients (\pm SE) of the linear models (LM) and the linear mixed-effects models (LMMs) on plant cover of (a) community, (b) woody, (c) herbaceous, and (d) cacti synusiae, respectively. The effects of grazing intensity (GI: $AUY \cdot ha^{-1}$) and rainfall variables on plant cover (both of the plant community and multi-synusiae) are given based on LM and LMMs (i.e., pasture sites as a random factor), respectively. Rainfall intensity (mm) includes the total amount of precipitation for all rainfall events and the total amount of precipitation for each of five rainfall pulse sizes (I: $0.1 \sim 5.0 \text{ mm} \cdot \text{day}^{-1}$; II: $5.1 \sim 10 \text{ mm} \cdot \text{day}^{-1}$; III: $10.1 \sim 15 \text{ mm} \cdot \text{day}^{-1}$; IV: $15.1 \sim 20 \text{ mm} \cdot \text{day}^{-1}$; V: $> 20 \text{ mm} \cdot \text{day}^{-1}$) during the entire year (Entire year, YEAR-1, YEAR-2, YEAR-3, YEAR-4, and YEAR-5), during the wet season (Wet season, WET-1, WET-2, WET-3, WET-4, and WET-5), and during the dry season (Dry season, DRY-1, DRY-2, DRY-3, DRY-4, and DRY-5), respectively. Filled dots indicate the significant effects; significant levels and multi-synusiae acronyms are the same as in FIGURE 1, except for Community = plant community. See Table S1-S5 for the full results of the models.

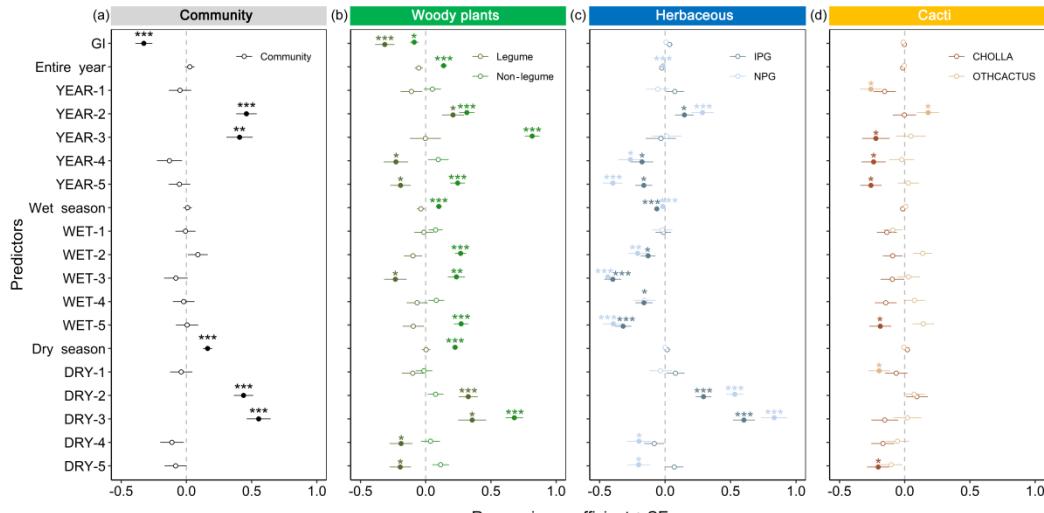
FIGURE 3 Redundancy analysis of grazing intensity and rainfall pulses for plant cover in the Santa Rita Experimental Range (SRER), USA. Shown the intensity of rainfall pulses (a, $R^2 = 0.280$, $df = 6$, $F\text{-value} = 7.142$, $P < 0.0001$; RDA1 $F\text{-value} = 21.527$, $P < 0.0001$; RDA2 $F\text{-value} = 15.093$, $P < 0.0001$) during the entire year and (b, $R^2 = 0.417$, $df = 11$, $F\text{-value} = 6.833$, $P < 0.0001$; RDA1 $F\text{-value} = 44.196$, $P < 0.0001$; RDA2 $F\text{-value} = 23.189$, $P < 0.0001$.) during the wet and dry seasons for plant cover of both

community and multi-synusiae, respectively. The acronyms are the same as in FIGURE 2.

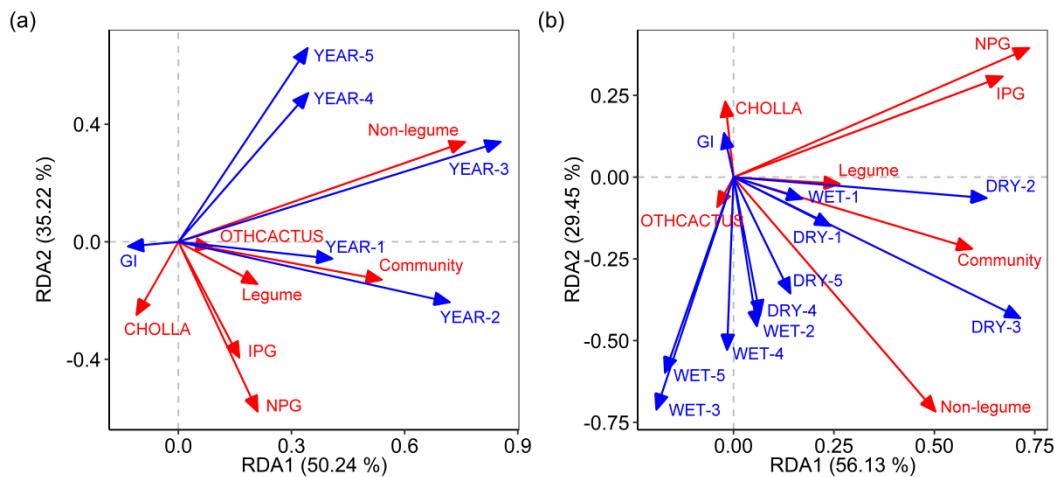
FIGURE 4 Partial least squares based structural equation modeling (PLS-SEM) of the effects of grazing intensity and the intensity of rainfall pulse on plant community cover via direct and indirect shaping multi-synusiae (woody plants – herbaceous – cacti) in the Santa Rita Experimental Range (SRER), USA. The full-loading PLS-SEMs are given (**a**) during the entire year ($GoF = 0.461$) and (**b**) during the wet and dry seasons ($GoF = 0.499$), respectively. GoF is the Goodness-of-Fit index; the numbers denote the standardized path correlation coefficients (Pearson's r); the R^2 denotes the proportion of variance explained by factors; the red and black arrows represent the significantly ($P < 0.05$ at 95% confidence level) negative and positive pathways, respectively; $n = 117$ in all three PLS-SEMs. Rainfall pulse, woody plants, herbaceous, and cacti are latent variables, see FIGURE S3-S5 for their outer model loadings and Table S6-S7 for total effects.



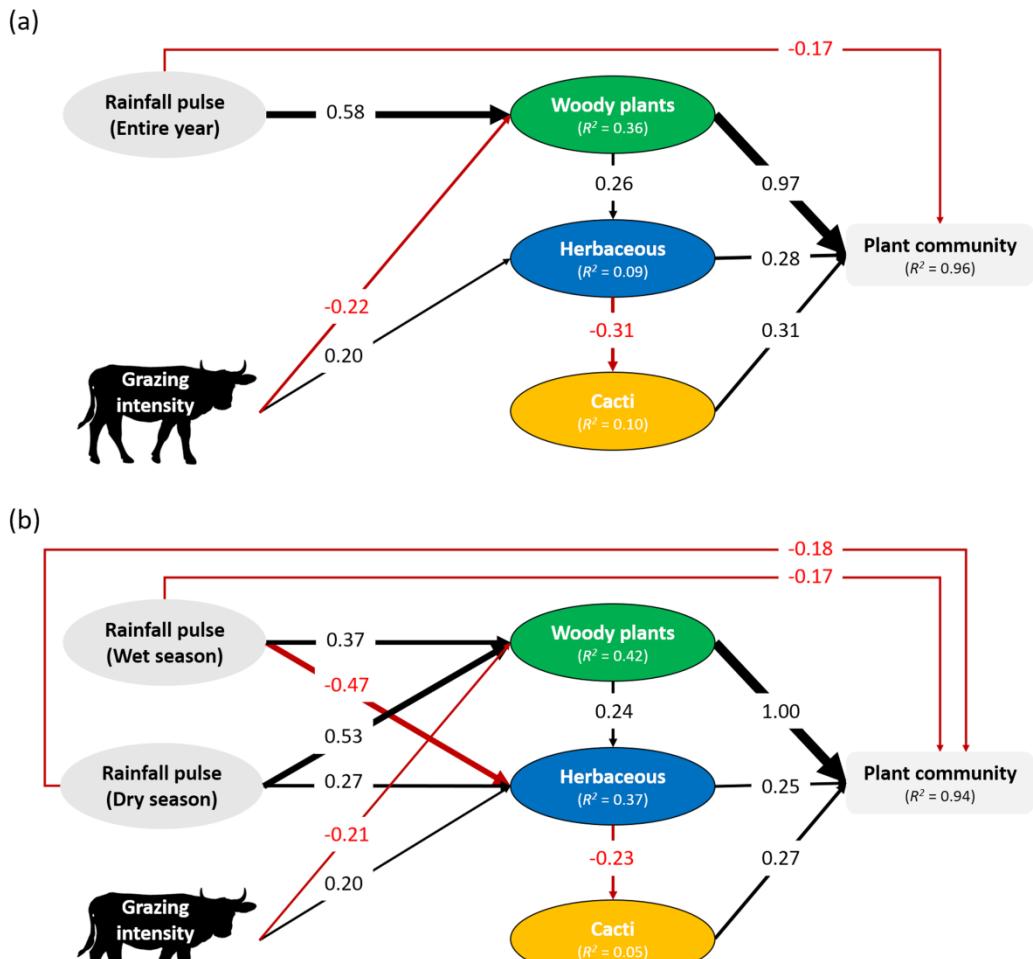
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