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ABSTRACT

Reducing grass standing crop by grazing may increase forbs and benefit wildlife that depend on forbs. However, precipitation and soil texture also strongly influence forb standing crop. We determined if standing crop of forbs selected by white-tailed deer (*Odocoileus virginianus* Zimm.) is more strongly influenced by grazing or precipitation. Ungulates typically graze in patches with greater standing crop than the surrounding vegetation. Our second objective was to determine if predicted relationships of forb standing crop with grazing, precipitation, and percent sand were similar with less productive sites included or excluded from models. We estimated standing crop of grasses and forbs in 50 paired grazing exclosures and grazed plots on each of six 2 500-ha study sites. Standing crop of forbs selected by white-tailed deer (selected forbs) was strongly related to precipitation and percent sand but not estimated percent use of grasses. For our second objective, we examined grazing effects on forbs by removing pairs of exclosures and grazed plots from the data where grass standing crop in nongrazed exclosures exceeded the average standing crop of grass after grazing. Percent use of grasses did not influence selected forb standing crop when we included only productive patches. For overall forb standing crop in productive patches, percent use of grasses and percent sand interacted. Forbs declined with increasing percent use of grasses in less sandy soils and increased with percent use of grasses in sandy soils. Grazing is not useful to increase forbs selected by white-tailed deer in our study sites because standing crop of selected forbs is more strongly dependent on precipitation and soil texture than on grazing. Grazing did influence forb standing crop in productive areas, which suggests accounting for grazing effects in productive versus less productive areas of the landscape provides insight into herbivore-vegetation relationships.

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Introduction

Large herbivores are often a primary driver of vegetation dynamics on rangelands (Anderson et al. 2007; Frank et al. 2018). Grazing alters composition of vegetation, with the effect becoming more pronounced as grazing intensity increases (Briske et al. 2003). Aldo Leopold (1933) recognized the potential use of cattle (*Bos* spp.) to manipulate vegetation structure and composition to benefit wildlife. Altering vegetation composition through targeted grazing has the potential to enhance forage quality and quantity for a variety of wildlife species (Holechek et al. 1982; Bailey et al. 2019).

Cattle selectively forage on grasses, which can reduce competition between forbs and grasses, resulting in increased abundance of forbs (Collins and Barber 1985; Damhoureyeh and Hartnett 1997; Towne et al. 2005). Forbs are important for many wildlife species (Damhoureyeh and Hartnett 1997). Increased abundance of forbs in response to grazing may benefit wildlife species that use them as a resource (Damhoureyeh and Hartnett 1997; Ruthven 2007; Krausman et al. 2009). Forb standing crop in response to grazing, however, may vary depending on the forb species, life history guild, and precipitation (Damhoureyeh and Hartnett 1997; Hayes and Holl 2003; Van Coller et al. 2018; Hines et al. 2020). Soil

texture influences forb abundance and forb composition of white-tailed deer diets differs on sandy versus clay-textured soils (Drawe 1968).

The idea that forb standing crop increases in response to selective foraging on grasses by herbivores is based on traditional equilibrium models of vegetation dynamics (Dyksterhuis 1949; Vesk and Westoby 2001). In traditional models of vegetation dynamics, selective foraging causes palatable plants to decline in abundance. Less palatable or more grazing-resistant plants termed "increasers" become more abundant as grazing intensifies, peak at an intermediate grazing intensity, and then decline as grazing intensity becomes more severe (Dyksterhuis 1949). Traditional models of vegetation dynamics such as described by Dyksterhuis (1949) are based on the idea that grazing by large herbivores is a driver of community change away from climax plant composition. In systems with equilibrium vegetation dynamics, vegetation composition and structure change in response to herbivory because herbivores and plants are tightly coupled (Ellis and Swift 1988; Briske et al. 2003; Derry and Boone 2010). A change in forb standing crop in response to increasing intensity of grazing, whether an increase or a decrease, would be evidence of the tight coupling of herbivores and plants predicted to occur in equilibrium systems.

An alternative idea is that vegetation equilibrium rarely occurs, particularly in highly stochastic systems (Ellis and Swift 1988; Briske et al. 2003). Observations of the strong influence of variation in precipitation on vegetation composition on arid and semiarid rangelands led to development of the nonequilibrium model of vegetation dynamics (Illius and O'Connor 1999; Briske et al. 2003; Vetter 2005; Derry and Boone 2010; von Wehrden et al. 2012). In the nonequilibrium model, abiotic factors, primarily variation in precipitation, drive vegetation dynamics rather than herbivores. In contrast to equilibrium systems, herbivores and vegetation are weakly linked in nonequilibrium systems. Abiotic factors such as precipitation and soils, not herbivores, drive fluctuations in vegetation composition and abundance in these systems. Consequently, a strong influence of precipitation on forb standing crop and lack of influence of increasing intensity of grazing would be evidence of the absence of coupling of herbivores and plants predicted to occur in nonequilibrium systems. Forb abundance in these ecosystems depends on rainfall, not on herbivory. Nonequilibrium vegetation dynamics are likely to occur in areas where the coefficient of variation in annual precipitation exceeds 33% (Derry and Boone 2010), which is typical on rangelands such as those in southwestern Texas (Gann et al. 2019). Because precipitation rather than grazing drives vegetation dynamics in nonequilibrium systems, use of grazing as a management tool to increase forbs may be ineffective in nonequilibrium ecosystems.

Ruminants do not forage in a homogeneous fashion across the landscape. For example, Wilmshurst et al. (2000) suggested ruminants typically forage in areas with intermediate levels of biomass. Elk (*Cervus canadensis* Erxleben) in Canada selected areas with the maximum forage standing crop (Hebblewhite et al. 2008). Wallace et al. (1995) concluded that ungulates select feeding sites based on forage standing crop at the landscape scale. Vegetation on rangelands is typically a mosaic of productive patches of vegetation in a matrix of less productive patches or bare ground (Aguiar and Sala 1999). Patches are discrete components of the landscape that differ in structure and composition (Pickett and Cadenasso 1995). Ungulates may forage in productive patches and avoid less productive patches. If most grazing occurs in patches of intermediate or greater productivity, including less productive patches to predict effects of foraging may increase variation in statistical models, making it more difficult to detect grazing effects.

White-tailed deer (*Odocoileus virginianus* Zimm.) are an economically important ungulate species that select forbs, when they are available, over grasses and shrubs (Fulbright and Ortega 2013;

Gann et al. 2019). Forb availability is particularly important to white-tailed deer because forbs meet nutrient needs for reproduction more effectively than browse and grasses (Gann et al. 2019). Cattle grazing is recommended in the management literature as a tool for increasing forbs and enhancing the supply of forage for white-tailed deer (Harmel and Litton 1981; Lyons and Wright 2003). Despite these recommendations, unequivocal documentation that cattle grazing increases the abundance of forbs important to white-tailed deer diets in semiarid environments is lacking (Fulbright and Ortega-S. 2013). Varying effects of grazing on forb standing crop reported in the literature may occur because forb responses to cattle grazing are mediated in part by variation in precipitation and soil properties (Anderson et al. 2007).

Our primary objective was to determine if standing crop of forbs selected by white-tailed deer is more strongly influenced by grazing or precipitation. We hypothesized that standing crop of forbs selected by white-tailed deer and standing crop of all forbs increases with increasing grazing intensity, reaches a peak at an intermediate level of grazing, and then declines as grazing becomes more intense. We tested this hypothesis on six study sites in South Texas. Our alternative hypothesis was that precipitation and percent sand influence standing crop of forbs selected by white-tailed deer and all forbs more than grazing does. A second alternative hypothesis was that precipitation and percent sand interact with grazing. Our secondary objective was to determine if relationships of forb standing crop with grazing, precipitation, and percent sand were similar with less productive sites included and excluded from statistical models. We predicted that the effect of grazing on forb standing crop would be stronger in productive sites than in unproductive sites.

Methods

Study area

We conducted research on four ranches operated by the East Foundation, an Agricultural Research Organization that promotes the advancement of land stewardship through ranching, science, and education. We selected six 2 500-ha study sites on the East Foundation properties (Fig. 1). Three study sites were on the 60 034-ha San Antonio Viejo Ranch in Jim Hogg and Starr Counties (lat 27°1′44.4″N, long −98°47′13.2″W, lat 26°53′49.2″N, long −98°43′40.8″W, and lat 26°45′25.2″N, long −98°46′11.9″W). The other three study sites were on the 6 113-ha Buena Vista Ranch in Jim Hogg County (lat 26 °57′14.4″N, long −98°27′21.6″W), the 7 544-ha Santa Rosa Ranch in Kenedy County (lat 27°10′58.8″N, long −97°51′39.6″W), and the 10 984-ha East El Sauz Ranch in Willacy and Kenedy counties (lat 26°31′58.8″N, long −97°29′23.9″W). All study sites, except one site on the San Antonio Viejo, were in the Coastal Sand Plain ecoregion (Diamond and Fulbright 1990; Fulbright et al. 1990; Forman et al. 2009). The third site on the San Antonio Viejo ranch (lat 26°45′25.2″N, long −98°46′11.9″W) was in the Tamaulipan Thornscrub ecoregion (Fulbright 2001).

Two study sites on the San Antonio Viejo ranch and the site on the Buena Vista Ranch were on rolling sand plains dominated by mesquite (*Prosopis glandulosa* Torr.) with understory clusters of diverse shrub species. The site on the San Antonio Viejo Ranch that was in the Tamaulipan Thorn scrub ecoregion was underlain by caliche soils supporting blackbrush acacia (*Vachellia rigidula* [Benth.] Seigler & Ebinger). Santa Rosa Ranch was on rolling sand plains dominated by mesquite with areas of live oak (*Quercus fusiformis* Small) mottes. East El Sauz Ranch supported open prairies, scattered active sand dunes, live oak mottes, and coastal saline plant communities. Dominant soil series at the study sites include the Nueces-Sarita association, Delmita, Comitas, Galveston, Mustang, Palobia, Sauz, Yturria, Copita, McAllen, and Za-
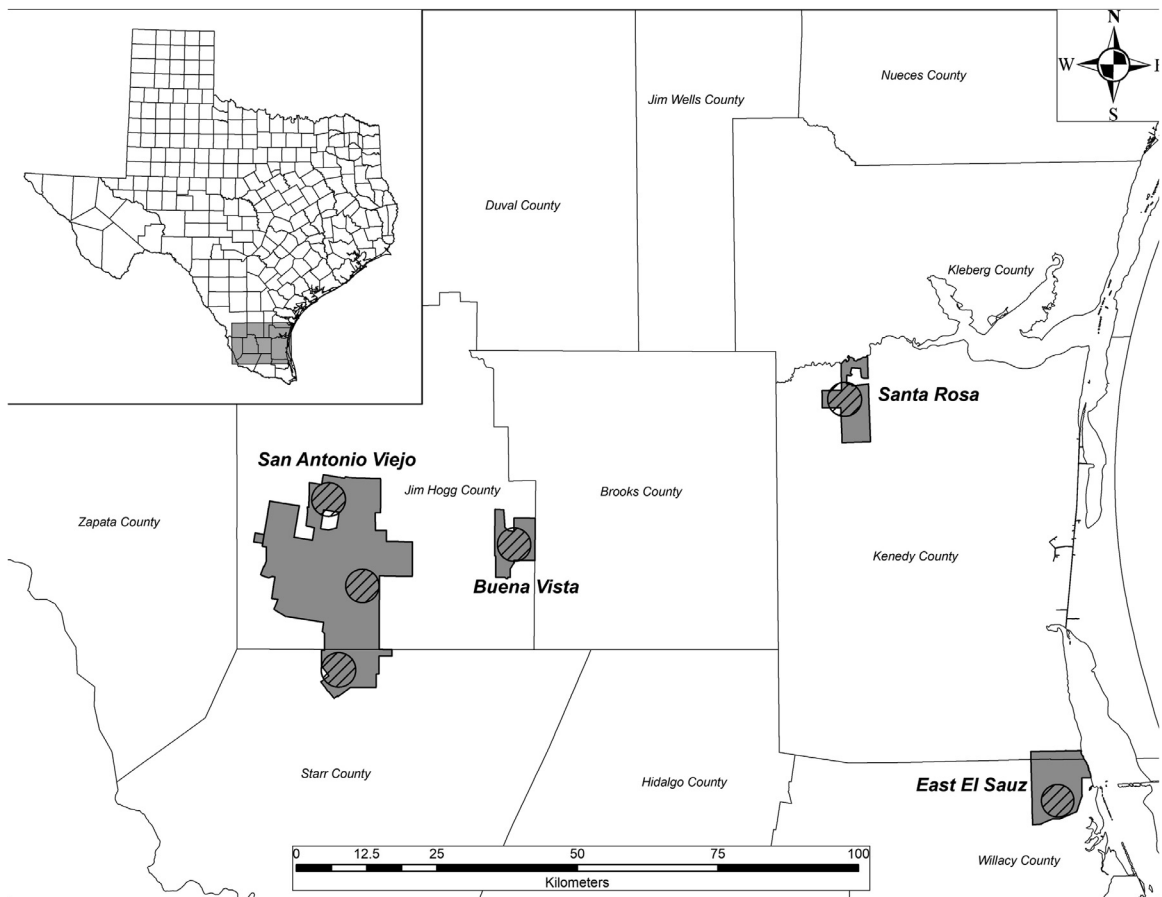
Figure 1. Location of six 2 500-ha study sites (circles with hatch marks; 10–134 km apart) located on 4 East Foundation ranches (gray in color) spanning the semiarid region from the Gulf Coast to western south Texas, United States, on Buena Vista, El Sauz, Santa Rosa, and San Antonio Viejo Ranches operated by the East Foundation, Jim Hogg, Kenedy, Star, and Willacy Counties, Texas, 2012–2019.

Table 1

Mean monthly precipitation (cm) averaged across six study sites on four ranches in southern Texas, Jim Hogg, Kenedy, Star, and Willacy Counties, Texas, 2011–2019. Shaded months are those when the Palmer Drought Severity Index indicated moderate to severe drought (National Integrated Drought Information System−NOAA 2020).

Yr	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
2011	4.4	0.2	0.9	0.0	2.4	5.4	3.4	0.5	3.8	2.8	0.2	4.9	28.9
2012	0.6	8.4	3.3	3.3	6.5	1.2	6.4	2.2	5.5	0.8	2.3	0.2	40.7
2013	3.9	0.5	0.0	5.8	10.6	2.6	3.1	2.4	16.8	1.3	4.5	5.3	56.6
2014	1.8	1.0	5.0	0.3	7.3	2.8	2.4	5.9	19.5	3.0	11.0	3.3	63.3
2015	3.5	3.0	12.0	12.4	12.3	8.2	1.1	2.4	8.4	17.2	2.7	1.2	84.5
2016	5.7	0.0	7.8	1.7	9.6	10.1	1.4	11.3	5.7	1.5	4.6	4.5	58.2
2017	1.5	2.7	9.9	4.0	6.6	5.4	2.2	4.9	2.6	4.1	2.8	6.7	53.3
2018	1.6	1.5	1.1	2.4	2.7	23.9	0.8	1.4	29.2	6.4	3.1	3.4	77.6
2019	2.8	0.7	2.5	5.2	5.5	7.3	3.3	1.0	10.3	2.6	6.0	1.8	49.0

Table 2

Estimated nilgai and white-tailed deer densities based on counts from helicopters corrected for visibility using distance sampling techniques on Buena Vista, El Sauz, Santa Rosa, and San Antonio Viejo Ranches operated by the East Foundation, Jim Hogg, Kenedy, Starr, and Willacy counties, Texas, 2013–2019 (East Foundation, San Antonio, Texas, 2019, unpublished data).

Ranch	Species	$\bar{x}$ (ha animal^{-1})	Range	Yr sampled
Buena Vista	Nilgai	0	0	2013–2015
	White-tailed deer	7	6–9	2013–2019
El Sauz	Nilgai	12	4–25	2013–2019
	White-tailed deer	17	13–23	2013–2019
Santa Rosa	Nilgai	13	6–22	2013–2019
	White-tailed deer	9	2–16	2013–2019
San Antonio Viejo	Nilgai	734	547–866	2013–2015
	White-tailed deer	10	7–13	2013–2019

pata (USDA-NRCS 2011a, 2011b). Percent sand for soils across the study sites ranged from 52 to 100 ($\bar{x} = 90$).

Rainfall in South Texas is sporadic with most falling during May−June and September−October (Fulbright et al. 1990). Monthly rainfall during our study ranged from none to 29.2 cm averaged across ranches (Table 1). Long-term coefficient of variation in annual (1932–2002) precipitation ranges from about 20% along the coast to 32% at Falfurrias near the Santa Rosa Ranch and 37% at Rio Grande City near the Buena Vista and San Antonio Viejo ranches (Parylak 2010).

Study sites on the four ranches were grazed by cattle, nilgai (*Boselaphus tragocamelus* Pallas), and white-tailed deer (Table 2).

Wild pigs (*Sus scrofa* L.) and collared pecarries (*Pecari tajacu* L.) were also present. Cattle were the dominant grazers in the study sites. Throughout the duration of the study, cattle operations on East Foundation ranches primarily employed cow-calves as animal units. However, East Foundation ranches have increasingly used stocker cattle as animal units to maximize flexibility given frequent and reoccurring droughts in South Texas (Ortega et al. 2013). In addition, East Foundation cattle were managed under a combination of continuous year-long and deferred-rotation grazing systems, depending on operational and experimental objectives. From 2013 to 2019, cattle stocking rate (ha AU^{-1}) on each of the four East Foundation ranches ranged from 14.9 to 25.1 ($\bar{x} = 19.2$) for Buena Vista, from 14.5 to 36.6 ($\bar{x} = 19.8$) for El Sauz, from 10.0 to 15.3

($\bar{x} = 13.0$) for Santa Rosa, and from 22.2 to 35.7 ($\bar{x} = 25.8$) for San Antonio Viejo. Herein, we considered all six study sites on the four ranches as grazed by cattle.

Nilgai are an introduced herbivore from India that consume primarily grass and browse (Sheffield 1983). Sheffield (1983) found that nilgai diets averaged 60% grass and 25% forbs in South Texas. In our study sites, grasses comprised 88% ± 1% ($\bar{x} \pm SE$) of cattle diets compared with 10% ± 1% of deer diets and about 21–38% ± 2% of nilgai diets during autumn 2012–2014 based on stable isotope analysis of feces (Hines et al. 2016, unpublished data). Forb standing crop responses to grazing that we report herein are therefore responses to a mix of herbivores with cattle as the dominant grazer.

Vegetation sampling

We randomly allocated 50, 1.5-m × 1.5-m grazing exclosures using ArcMap GIS (ArcGIS software v. 10, ESRI, Redlands, CA) software within each of the six 2 500-ha study sites during January to March 2012. Each grazing exclosure was constructed using 10 cm × 10 cm spacing, six-gauge galvanized utility panels and four t-posts. Cattle, white-tailed deer, and nilgai were excluded from grazing inside each grazing exclosure but all had access to consume forages outside of each grazing exclosure. Smaller herbivores such as lagomorphs were not excluded. We installed grazing exclosures in areas dominated by herbaceous vegetation. Concurrent to construction of an exclosure we selected a paired, grazed plot about 10 m from each exclosure. We selected paired plots that had visually similar vegetation and bare ground as plots within the exclosures.

Grazing exclosures were in place for 8–12 mo on each study site before samples were collected within and outside the exclosures. In South Texas, most of the herbaceous forage production occurs during two periods, April to June and September to October. Autumn is the only season when grasses and forbs are concurrently in their peak growing season in south Texas (Fulbright and Ortega-S. 2013). Thus, we sampled during autumn (October and November) 2012–2019.

We harvested standing crop of grasses and forbs at ground level within a 0.5-m × 0.5-m sampling frame in the center of each grazing exclosure and in each paired grazed sampling area. We separated forage samples into 1) grasses, 2) forbs selected by white-tailed deer, and 3) forbs not selected by white-tailed deer (Tables S1–S3; available online). We separated forb species into those selected and not selected by deer based on previous research regarding forb palatability to white-tailed deer in South Texas (Gann et al. 2019). Nonselected forbs consisted of 32 species that white-tailed deer would either not consume at all or only consumed when other forage was lacking. Because deer are opportunistic feeders (Fulbright and Ortega-S. 2013), we classed all other forbs as selected by white-tailed deer. We dried forage samples at 45°C until they reached a constant mass, and then we weighed them to the nearest 0.1 g. After we completed sampling, we moved grazing exclosures 10 m in a randomly assigned cardinal direction (previously sampled locations were avoided) and a new paired grazed area was selected and marked.

Precipitation and soils

We used historical rainfall records from PRISM Climate Data to determine monthly precipitation for each site. We included mean percent sand for each site as a covariate in analyses to account for the influence of soil texture on forb standing crop. We extracted values from National Resource Conservation Service data (USDA-NRCS 2011a, 2011b).

Statistical analyses

We tested normality of residuals using Shapiro–Wilks W-statistic (Shapiro and Wilk 1965) and log transformed the data to stabilize variation when necessary. We first compared selected forbs and all forbs in exclosures and grazed plots using mixed models with study site as the random effect (Littell et al. 1996). Means of standing crop of forbs selected by white-tailed and all forbs combined for each site and year combination were dependent variables in statistical models. Year and grazing treatment (nongrazed exclosure vs. grazed plots) were fixed effects.

We analyzed the data in two steps to test our hypotheses. In step 1, we screened percent sand and August and September precipitation covariates to determine the most influential covariates in predicting standing crop of forbs selected by white-tailed deer and of all forbs in plots exposed to grazing. In step 2, we included estimates of percent use of grass in response surface models with covariates that were selected in step 1. We calculated percent use of grasses for each study site and year combination as:

$$U = \left(\frac{Non-grazed \ minus \ Grazed}{Non-grazed} \right) \times 100 \qquad (1)$$

where U is the mean of 50 exclosures in each site for percent use of grasses, *Nongrazed* is the mean ($n = 50$ in each site) standing crop of grasses inside exclosures, and *Grazed* is the mean ($n = 50$ in each site) standing crop of grasses outside enclosures. We considered use of grasses to be a measure of the intensity of grazing on grasses in the study sites. Our objective in the second step was to determine relationships between forb standing crop and intensity of grazing of grasses in models that included soil and precipitation covariates and interactions of use of grasses with these covariates. We used response surface analysis in the second step because we wanted to examine linear and quadratic components to provide a test of our hypothesis of a quadratic relationship between use of grasses and forb standing crop (SAS Institute, Inc. 2013b). In addition, response surface analysis allowed us to compute the optimal response of the dependent variable to the combined influence of predictor variables in three-dimensional space.

In step 1, we determined the best combination of percent sand and precipitation covariates (August precipitation and September precipitation) to include in models to predict mean standing crop of forbs selected by white-tailed deer and of all forbs using the Schwarz Bayesian information criterion (SBC). The dependent variables in analyses were the mean standing crop of forbs selected by white-tailed deer and of all forbs in grazed plots within each study site and year combination. Covariates included in analyses were percent sand, August precipitation before vegetation sampling, and September precipitation before sampling for each site and year combination. We screened covariates using the GLMSELECT procedure in SAS 9.3 (SAS Institute, Inc. 2013a). We performed backwards selection that began with August and September precipitation and percent sand in the model. We specified use of the SBC in statistical models to control the entry and removal of covariates. We used the SBC in model selection because the Bayesian Information Criterion often performs better than Akaike Information Criterion or the Akaike Information Criterion corrected for small sample sizes when heterogeneity in the data set is large (Brewer et al. 2016). We included the hierarchy option to specify that only one covariate enter or leave the model at a time during model selection. We log transformed standing crop values for forbs selected by white-tailed deer and all forbs standing crop before analyses. We estimated condition indices and variance inflation factors (VIF) for all models to assess multicollinearity among covariates (Belsley et al. 1980). We used multiple regression models to estimate condition indices and VIF with the covariates identified in the best model (SAS Institute, Inc. 2014). In our models, variance inflation

was $\leq$ 1.1 and the condition index of the models was $\leq$ 40. A condition index near 10 suggests weak dependencies; an index value > 100 indicates that regression estimates may have a numerical error (Belsley et al. 1980).

In step 2, we included influential soil and precipitation covariates in a response surface analysis with use of grasses as a covariate. We used response surface analysis to determine relationships between mean forbs selected by white-tailed deer and all forbs standing crop in grazed plots with use of grasses, soil and precipitation covariates, and interactions between precipitation and soil covariates and use (SAS Institute, Inc. 2013b). We considered a covariate to be influential in predicting forb standing crop when the 95% confidence interval for the regression estimate did not overlap 0. In cases where the 95% confidence interval of the regression estimate of use and use^2 overlapped 0, we considered use and use^2 to not be influential in predicting forb standing crop and we did not include these covariates in further models. We then performed a second response surface analysis with covariates that entered the best model identified in step 1. When regression estimates for use did not overlap 0 and were included in models, we standardized regression estimates by multiplying the original estimate for a covariate by the standard deviation of the covariate and then dividing by the standard deviation of the dependent variable (SAS Institute, Inc. 2014). Standardization allowed us to compare the strength of the regression relationship among covariates measured with different units. We estimated model R^2, adjusted R^2, and prediction R^2 for each model. Estimating the predicted R^2 provides a means of validating the models. If the prediction R^2 is considerably smaller than the adjusted R^2, the model does not validate well (Montgomery et al. 2012).

Our secondary objective was to determine if relationships of forb standing crop with grazing, precipitation, and percent sand were similar with less productive sites included and excluded from statistical models. We examined models with less productive sites excluded because including them in models to predict effects of foraging may increase variation, thus making it more difficult to detect grazing effects. To include only the most productive patches in models and exclude less productive patches, we first determined the mean standing crop of grasses by study site and sampling date in unprotected plots (i.e., the grazed plots paired with protected plots in exclosures). Mean standing crop of grasses in unprotected plots averaged across study sites and sampling dates was 628 kg ha^{-1} (95% CI = 587–668). We termed this the *residual standing crop,* defined as the average standing crop of grass at the end of the grazing season in unprotected (grazed) plots. We then censored all pairs of plots from the data set where average grass standing crop inside the exclosures was < 628 kg ha^{-1} (the average residual standing crop in grazed plots). Censoring resulted in a 52% reduction in the number of pairs of protected and grazed plots used in

statistical analyses (2 400 pairs in the full data set compared with 1 145 pairs in the reduced data set). Of the 1 255 censored pairs of plots, there were 343 (27%) with no grass in the exclosure.

We censored pairs of plots from the data set where average grass standing crop inside the exclosures was < 628 kg ha^{-1} to test the prediction that the effects of grazing on forb standing crop would be stronger in productive patches. Our rationale was that the residual represents the standing crop remaining after grazing. We assumed that cattle and other herbivores avoid or spend less time grazing in patches supporting less than the residual standing crop (Wilmshurst et al. 2000). We then conducted the previously described statistical analyses using the reduced data set. We define the term *productive* in the forthcoming "Results and Discussion" as patches of vegetation where the standing crop of grasses within exclosures exceeded the mean of the residual standing crop of grasses across study sites and years.

Results

Our study began in 2012, one yr following the most intense drought in recorded Texas history (Nielsen-Gammon 2012). Drought continued in the study area from January 2012 to November 2013 (see Table 1; National Integrated Drought Information System−NOAA 2020). Drought occurred during 47 (44%) of the 108 mo from January 2011 to December 2019.

Full data set

Standing crop of grass and forbs varied annually during the eight years of study (Table 3). Averaged across sites and years, standing crop of forbs selected by white-tailed deer was 24% lower ($F = 48_{1,75\text{ df}}$, $P < 0.001$) in grazed plots than in plots protected from grazing. All forb standing crop was also greater in exclosures than in grazed plots ($F_{1,75\text{ df}} = 8.68$, $P = 0.004$). Year and grazing treatment did not interact for forbs selected by white-tailed deer forbs or for all forbs ($F_{7,75\text{ df}} = 2.43$, $P = 0.879$ and $F_{7,75\text{ df}} = 0.51$, $P = 0.822$, respectively).

The best regression model for predicting standing crop of forbs selected by white-tailed deer included percent sand ($\hat{\beta} = 0.114$, 95% CI = 0.072–0.156) and September precipitation ($\hat{\beta} = 0.061$, 95% CI = 0.035–0.086, $R^2 = 0.58$). The best model for predicting all forbs also included percent sand ($\hat{\beta} = 0.139$, 95% CI = 0.106–0.173) and September precipitation ($\hat{\beta} = 0.038$, 95% CI = 0.018–0.058, $R^2 = 0.68$).

We added percent use of grasses to response surface models with percent sand and September precipitation with forbs selected by white-tailed deer as the dependent variable and with all forbs as the dependent variable (Fig. 2). Parameter estimates for use of

Table 3
Means ($n = 300$; 50 plots × 6 sites) and 95% confidence intervals for grass standing crop, standing crop of forbs selected by white-tailed deer (selected forbs), all forb standing crop inside grazing exclosures and in grazed plots averaged across six study sites on Buena Vista, El Sauz, Santa Rosa, and San Antonio Viejo Ranches operated by the East Foundation, Jim Hogg, Kenedy, Star, and Willacy Counties, Texas, 2012–2019.

| Yr	Grass standing crop (kg ha^{-1})				Selected forb standing crop (kg ha^{-1})				All forbs standing crop (kg ha^{-1})			
	Exclosures		Grazed		Exclosures		Grazed		Exclosures		Grazed	
	$\bar{x}$	95% CI	$\bar{x}$	95% CI	$\bar{x}$	95% CI	$\bar{x}$	95% CI	$\bar{x}$	95% CI	$\bar{x}$	95% CI
2012	507	366–649	129	91–167	103	75–131	40	30–51	252	199–305	131	104–158
2013	496	405–587	245	195–296	298	241–355	227	181–274	611	516–707	459	392–525
2014	1 165	1 026–1 304	771	659–883	442	357–526	384	322–447	558	461–654	477	408–546
2015	1 695	1 476–1 915	1 216	1 028–1 405	214	171–258	142	108–176	395	321–468	266	216–316
2016	1 690	1 366–1 815	845	730–961	125	95–156	66	45–88	231	189–273	172	131–213
2017	847	697–998	473	383–563	82	61–104	64	31–97	153	123–183	136	95–177
2018	914	796–1 033	733	614–853	279	225–334	233	191–275	416	347–484	386	322–450
2019	762	668–855	607	522–692	131	104–158	123	97–148	181	135–226	165	127–204

CI indicates confidence interval.
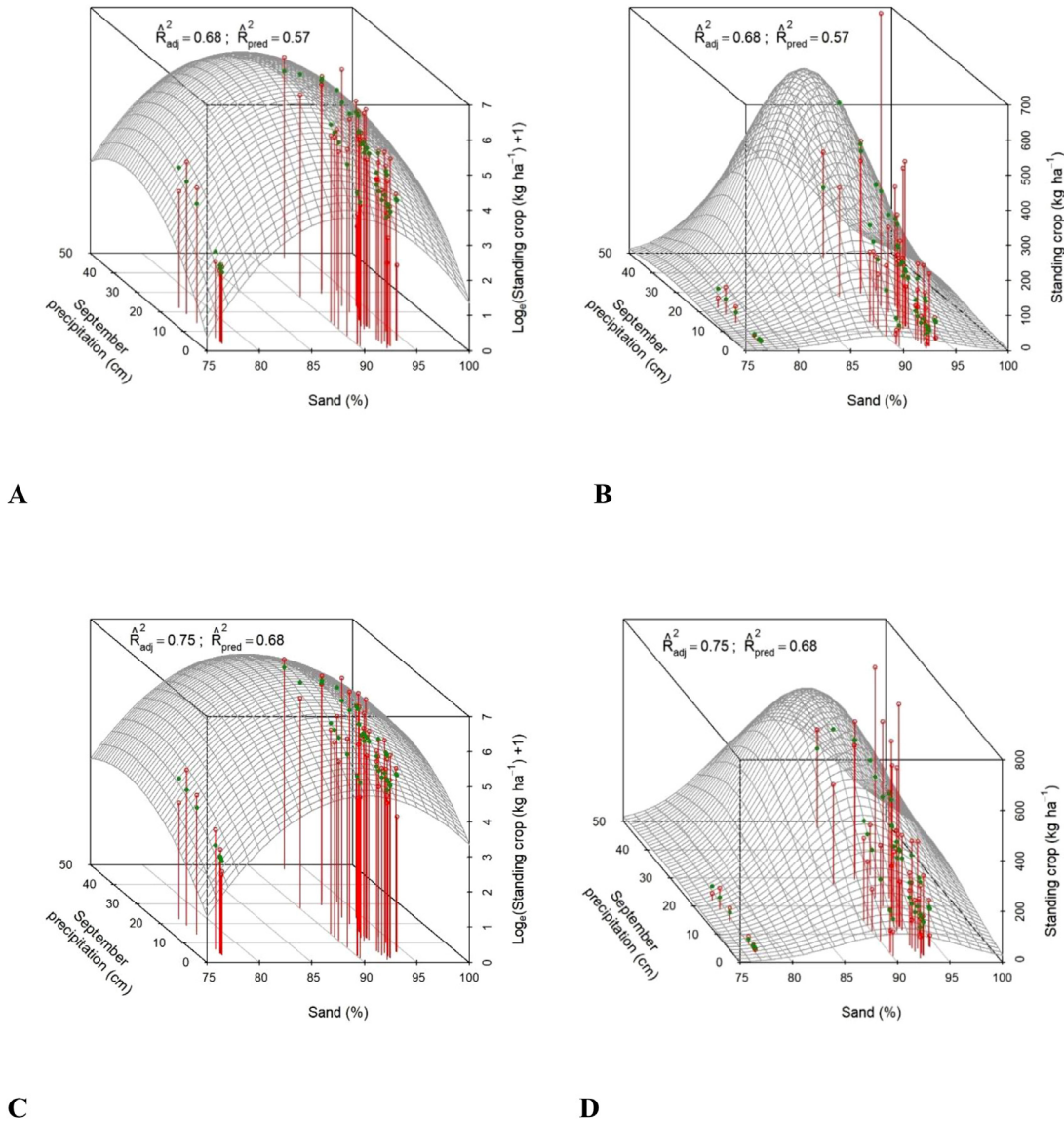
Figure 2. Response surface, adjusted R^2, and prediction R^2 for the relationship of log transformed (**A**) and observed scale (**B**) standing crop of forbs selected by white-tailed deer with September precipitation and percent sand and the relationship of log transformed all forbs (**C**) and observed scale (**D**) with September precipitation and percent sand (bottom) on Buena Vista, El Sauz, Santa Rosa, and San Antonio Viejo Ranches operated by the East Foundation, Jim Hogg, Kenedy, Star, and Willacy Counties, Texas, 2012–2019. Observed values are depicted by green dots with red tails.

grasses and cross products of other covariates with use of grasses overlapped 0 (Table 4). *P* values for parameter estimates for use of grasses and cross products with use of grasses and other covari-ates were not significant ($P > 0.05$). We interpreted these results to show standing crop of forbs selected by white-tailed deer and standing crop all forbs neither increased nor decreased with in-creased percent use of grasses.

In response surface models with only percent sand and Septem-ber precipitation included, both covariates were linearly and quadratically related to standing crop of forbs selected by white-tailed deer and all forbs (see Fig. 2, Table 4). Our response sur-face model predicted that standing crop of forbs selected by white-tailed deer was maximized at 88% sand and then declined (see Fig. 2A). Standing crop of forbs selected by white-tailed deer was maximized with 32 cm of September precipitation. During our study, precipitation > 32 cm occurred in a localized thunderstorm that included seven pairs of exclosure-grazed plot combinations on the East El Sauz Ranch in September 2014 and across all pairs of plots on the Buena Vista Ranch in September 2018.

Reduced data set

For the relationship between forbs selected by white-tailed deer and soil and precipitation covariates, as with the full data set, the best regression model selected using the SBC included percent sand ($\hat{\beta} = 0.143$, 95% CI = 0.085–0.20) and September precipitation ($\hat{\beta} = 0.066$, 95% CI = 0.031–0.101, $R^2 = 0.49$). For all forbs, the best model also included percent sand ($\hat{\beta} = 0.159$, 95% CI = 0.116–0.201) and September precipitation ($\hat{\beta} = 0.034$, 95% CI = 0.008–0.059, re-spectively, $R^2 = 0.61$).

We added percent use of grasses to response surface models with percent sand and September precipitation with selected forbs and all forbs as dependent variables. Percent use of grasses was unrelated to standing crop of forbs selected by white-tailed deer (Table 5). However, all forbs declined with increasing percent use of grasses. Based on standardized regression estimates, percent use of grasses had a stronger negative effect on standing crop of all forbs than September precipitation ($\hat{\beta} = -5.01$ vs. $\hat{\beta} = -3.48$, re-spectively) but a much weaker effect than the positive effect of

Table 4

P values for linear and quadratic effects; covariates; parameter estimates, lower and upper 95% confidence intervals of parameter estimates; *P* values for the test that parameter estimates and cross products are different ($P < 0.05$) from 0; model R^2; and *P* value for analysis of variance (ANOVA) of covariate effects for response surface models using the full data set with standing crop of forbs selected by white-tailed deer and all forb standing crop as dependent variables and percent sand (S), September precipitation (SP), and use of grasses (U) as covariates (model 1); and with percent sand and September precipitation as covariates (model 2), on Buena Vista, El Sauz, Santa Rosa, and San Antonio Viejo Ranches operated by the East Foundation, Jim Hogg, Kenedy, Star, and Willacy Counties, Texas, 2012–2019.

Model	P values for effects		Covariate	Parameter estimate	Lower confidence interval	Upper confidence interval	P-value for parameter estimates	Model R^2	P value ANOVA
	Linear	Quadratic							
Forbs selected by white-tailed deer									
1	< 0.001	< 0.001	S	3.549	1.418	5.680	0.002	0.72	< 0.001
			SP	0.097	−0.416	0.610	0.705		< 0.001
			U	−0.039	−0.224	0.147	0.674		0.482
			S · S	−0.020	−0.033	−0.008	0.002		
			SP · S	0.000	−0.005	0.006	0.893		
			SP · SP	−0.002	−0.004	−0.001	0.006		
			U · S	0	−0.002	0.002	0.762		
			U · SP	0.001	−0.001	0.002	0.383		
			U · U	0	0	0	0.900		
			Intercept	−151.17					
2	< 0.001	< 0.001	S	3.282	1.211	5.353	0.003	0.72	< 0.001
			SP	0.219	−0.226	0.664	0.327		< 0.001
			S · S	−0.019	−0.031	−0.006	0.004		
			SP · S	−0.001	−0.006	0.004	0.807		
			SP · SP	−0.003	-0.004	-0.001	0.002		
			Intercept	−141.54			0.003		
All forbs									
1	<0.001	0.002	S	2.660	0.947	4.373	0.003	0.80	< 0.001
			SP	−0.026	−0.439	0.386	0.898		< 0.001
			U	−0.134	−0.283	0.016	0.078		0.355
			S · S	−0.015	−0.025	−0.005	0.004		
			SP · S	0.001	−0.003	0.006	0.553		
			SP · SP	−0.002	−0.003	0.000	0.015		
			U · S	0.001	0	0.003	0.076		
			U · SP	0	−0.001	0.001	0.737		
			U · U	0	0	0	0.889		
			Intercept	−111.47					
2	< 0.001	0.001	S	2.649	0.965	4.333	0.003	0.77	< 0.001
			SP	0.168	−0.194	0.530	0.354		< 0.001
			S · S	−0.015	−0.025	−0.005	0.005		
			SP · S	−0.001	−0.005	0.003	0.749		
			SP · SP	−0.002	−0.003	0	0.009		
			Intercept	−114.85					

increasing percent sand ($\hat{\beta} = 13.55$). Percent use of grasses and percent sand interacted; the 95% confidence interval of the regression estimate for the percent use × percent sand interaction did not overlap 0. The response surface model predicted that standing crop of all forbs was maximized at 89% sand, 12.5 cm of September precipitation, and 22% percent use of grasses. When September precipitation was set to the mean across study sites and years (12.3 cm), all forbs declined with increasing use of grass in soils with less sand, were unaffected by use of grasses at intermediate levels of sand, and increased slightly with increasing use of grasses in extremely sandy soils (Fig. 3**A** and 3**B**).

Discussion

Grazing and forb response

Our results did not support the hypothesis of a quadratic relationship between forbs selected by white-tailed deer and percent use of grasses. Instead, results supported the alternative hypothesis that standing crop of forbs selected by white-tailed deer varies with precipitation and percent sand. Although standing crop of forbs selected by white-tailed deer did not vary in relation to percent use of grasses, grazing did result in an overall reduction in standing crop of forbs selected by white-tailed deer when averaged across years of study and study sites. Manipulating intensities of grazing of grasses does not appear to be a strategy to increase

forbs for deer on rangelands in South Texas with a long history of intensive livestock grazing.

On the basis of our results and those of other studies, grazing grasses appears more likely to increase forbs in humid and subhumid environments than in semiarid areas (Fig. 4; Hines et al. 2020). For example, in the more mesic environment of southeastern Oklahoma and southwestern Arkansas, white-tailed deer diets in areas grazed by cattle were higher in forbs during summer than in areas not grazed by cattle (Jenks et al. 1996). Cattle grazing resulted in an increase in wood sorrel (*Oxalis dillenii* Jacq.), a forb selected by deer, in the subhumid Texas Gulf Prairies and Marshes region (Ortega et al. 1997). However, generalizations are difficult to make because there is considerable variation among published studies in semiarid regions. In semiarid environments outside the range of white-tailed deer, forb responses to cattle grazing have ranged from no response (Brady et al. 1989; Smith et al. 1996), reduction in perennial forbs (Smith and Schmutz 1975), to greater forb canopy cover on moderately grazed than lightly grazed rangeland (Nelson et al. 1997). In semiarid rangelands in Wyoming, forbs increased under heavy compared with light grazing (Manley et al. 1997). Some published studies reporting forb response to grazing are based on canopy cover rather than standing crop (Damhoureyeh and Hartnett 1997; Hayes and Holl 2003; Koerner and Collins 2013), making comparisons with our results less clear.

Standing crop of grasses in our study area was low in part because of a long history of intensive grazing. Past intensive grazing

Table 5

P values for linear and quadratic effects; covariates; parameter estimates, lower and upper 95% confidence intervals of parameter estimates; *P* values for the test that parameter estimates and cross products are different ($P > 0.05$) from 0; model R^2; and P-value for analysis of variance (ANOVA) of covariate effects for response surface models using the reduced data set with standing crop of forbs selected by white-tailed deer as the dependent variable and percent sand (S), September precipitation (SP), and use of grasses (U) as covariates (model 1); and with percent sand and September precipitation as covariates (model 2), and with all forbs as the dependent variable and percent sand, September precipitation, and August precipitation (AP) as covariates on Buena Vista, El Sauz, Santa Rosa, and San Antonio Viejo Ranches operated by the East Foundation, Jim Hogg, Kenedy, Star, and Willacy Counties, Texas, 2012–2019.

Model	P values for effects		Covariates	Parameter estimates	Lower confidence interval	Upper confidence interval	P value for parameter estimates	Model R^2	P value ANOVA
	Linear	Quadratic							
Forbs selected by white-tailed deer									
1	< 0.001	0.035	S	3.227	0.855	5.599	0.009	0.67	< 0.001
			SP	−0.132	−0.920	0.656	0.737		0.011
			U	−0.154	−0.454	0.147	0.308		0.149
			S · S	−0.018	−0.033	−0.004	0.014		
			SP · S	0.002	−0.007	0.011	0.652		
			SP · SP	-0.002	−0.004	0.000	0.071		
			U · S	0.001	−0.002	0.005	0.403		
			U · SP	0.002	−0.001	0.004	0.173		
			U · U	0	−0.001	0.001	0.803		
			Intercept	−137.19					
2	< 0.001	< 0.001	S	3.108	0.949	5.266	0.006	0.79	< 0.001
			SP	0.065	−0.620	0.750	0.849		< 0.001
			S · S	−0.017	−0.030	−0.005	0.009		
			SP · S	0.001	−0.006	0.009	0.765		
			SP · SP	−0.003	−0.005	0	0.021		
			Intercept	−136.92					
All forbs									
			S	3.023	1.404	4.643	0.001	0.78	< 0.001
			SP	−0.470	−1.008	0.068	0.085		0.024
			U	−0.329	−0.534	−0.123	0.003		0.008
			S · S	−0.018	−0.028	−0.008	0.001		
			SP · S	0.005	−0.001	0.012	0.073		
			SP · SP	−0.002	−0.003	0	0.041		
			U · S	0.004	0.001	0.006	0.003		
			U · SP	0.001	−0.001	0.003	0.213		
			U · U	0	−0.001	0	0.336		
			Intercept	−122.03					

may have resulted in standing crop of grasses in our study sites being too low for grass reduction to competitively release forbs. For example, forb standing crop increased in response to grazing in the Tall Grass Prairie of Kansas (Towne et al. 2005). Residual grass standing crop in their study was more than threefold higher (2 020 kg ha^{-1}) than in our study. Grazing may have a more substantial release effect for forbs in ecosystems where grass standing crop is greater.

In our response surface model with the full data set, maximum standing crop of forbs selected by white-tailed deer occurred following high precipitation amounts that rarely occur. Precipitation > 30 cm during September, for example, occurred in only 9 of 110 yr between 1901 and 2011 at Sarita, Texas, in Kenedy County near the Santa Rosa Ranch (Western Regional Climate Center 2020).

Consumption of forbs

A potential reason that we did not detect an effect of grazing intensity on forbs selected by white-tailed deer and on all forbs with the full data is that consumption of forbs by cattle, nilgai, and deer masked effects of grazing intensity on forbs. Whether or not consumption of forbs by cattle, nilgai, and white-tailed deer masked forb standing crop response is unclear. We speculate that masking of forb standing crop in response to grazing minimally influenced our results because cattle diets in the study sites were predominantly grass. Nilgai likely had little overall influence on forb standing crop because they were absent (or present in low numbers) on four of our six study sites. We also speculate that white-tailed deer consumption of forbs did not have a strong influence on forb standing crop. We base our speculation on results of research in the western portion of South Texas (Crider et al. 2015;

Gann et al. 2019). In those studies, grazing by white-tailed deer in the absence of cattle did not strongly influence the standing crop of forbs during a 9-yr period at deer densities higher than in the present study. White-tailed deer depend more on forbs in the eastern portion of South Texas than in the western portion (Fulbright and Ortega 2013) and may have affected our results on our two eastern study sites. Whether or not white-tailed deer may have affected our results is unclear, however, because effects of deer foraging on forbs in the absence of cattle has not been documented in the eastern Texas Coastal Sand Plain.

Drought effects and vegetation dynamics

Other potential reasons that we did not detect an effect of grazing intensity on forbs selected by white-tailed deer and on all forbs with the full data are the effects of drought and the stochastic nature of the environment of our study area. Frequent droughts are typical of our study area and may be a more important driver of variation in forb abundance than grazing (Gann et al. 2019). Stronger influence of variation in precipitation on vegetation composition and production than grazing intensity on semiarid rangelands has been reported by other researchers (Milchunas et al. 1994; Ryerson and Parmenter 2001; Vermeire et al. 2008). In our environment, substantial growth of forbs occurs in pulses during periods when moisture is abundant (Gann et al. 2019). These pulses of production may have a swamping effect such that forage is so abundant that foraging by herbivores does not have a measurable effect on palatable forbs. Similarly, herbivores will have little effect on forbs during drought when forbs are virtually absent.

Frequent severe droughts are characteristic of rangelands where vegetation follows nonequilibrium dynamics (Ellis and Swift 1988;
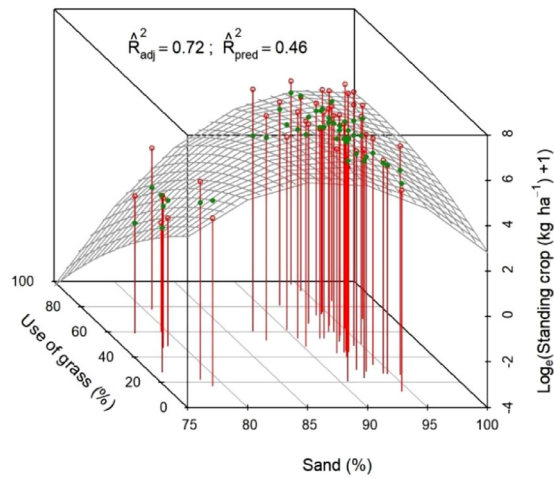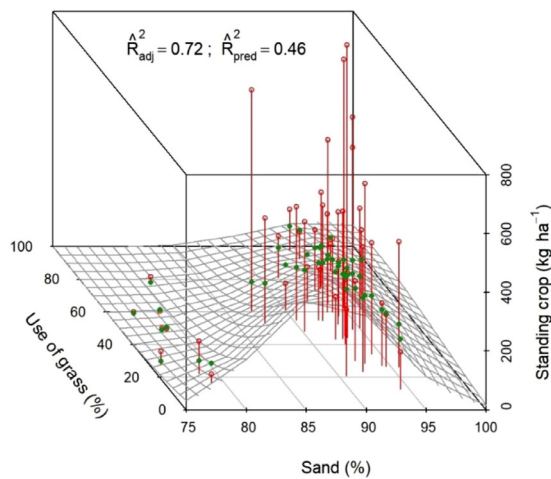
Figure 3. Response surface, adjusted R^2, and prediction R^2 for the relationship of log transformed standing crop of all forbs (selected by white-tailed deer and not selected combined) with percent use of grasses and percent sand with September precipitation set at 12.3 cm on Buena Vista, El Sauz, Santa Rosa, and San Antonio Viejo Ranches operated by the East Foundation, Jim Hogg, Kenedy, Star, and Willacy Counties, Texas, 2012–2019. Observed values are depicted by green dots with red tails.

Derry and Boone 2010; Sullivan and Rohde, 2002; Silcock and Fensham 2013). Our finding that grazing did not influence standing crop of forbs selected by white-tailed deer could in part have resulted because vegetation dynamics in our study area do not follow traditional equilibrium models. The coefficient of variation of precipitation on our study sites, except along the coast, exceeds the 33% threshold beyond which nonequilibrium vegetation dynamics are expected to occur (Ellis and Swift 1988; Derry and Boone 2010).

There are characteristics of our system that differ from pastoral systems in Africa, where research on non-equilibrium dynamics has been centered. In the African studies, livestock populations have negligible impacts on the vegetation because their numbers decline during periodic droughts (Ellis and Swift 1988; Derry and

Boone 2010, von Wehrden et al. 2012). Population declines during drought prevent livestock numbers from increasing to levels that alter vegetation composition. Dynamics of livestock in our system are not analogous to systems in the African nonequilibrium literature in part because livestock in our system are not free-ranging. For example, in our study sites, livestock are supplementally fed during drought. If drought conditions persist, cattle are removed.

In contrast to cattle, wild herbivores in our study sites were free-ranging and not supplementally fed. Dynamics of wild herbivore populations in our study sites, consequently, provide a better comparison to livestock in African studies described by Ellis and Swift (1988) and Derry and Boone (2010). White-tailed deer are only weakly density dependent in South Texas (Cook et al. 2019), which is a prediction of nonequilibrium models for plant-herbivore interactions (Ellis and Swift 1988). Cook et al. (2019) found that density dependence in South Texas white-tailed deer was more related to social pressures than food availability. Results of Cook et al. (2019) suggested that white-tailed deer and vegetation dynamics in South Texas are weakly linked, which is one of the predictions of nonequilibrium models.

Theories of vegetation dynamics provide the conceptual underpinning for the application of grazing to manipulate vegetation by natural resource managers. For example, the idea that grazing by cattle changes forb abundance is based on an assumption of tight coupling of plant-herbivore interactions, a prediction of equilibrium vegetation dynamics (Ellis and Swift 1988; Briske et al. 2003). Our results showed that coupling of plants and herbivores was relatively weak on our study sites, a characteristic of nonequilibrium systems. Consequently, we suggest that equilibrium vegetation dynamic theory does not provide a one-size-fits-all paradigm for making decisions when using grazing to manipulate vegetation. Instead, particularly in stochastic ecosystems, outcomes based on nonequilibrium dynamics should be considered in decision making. Further, equilibrium and nonequilibrium vegetation dynamics are not mutually exclusive theories. Briske et al. (2003) suggested that ecosystems are distributed along a continuum from equilibrium to nonequilibrium dynamics; therefore, a given system can express characteristics of both equilibrium and nonequilibrium dynamics in time or space. We speculate that expression of either equilibrium or nonequilibrium dynamics within a particular ecosystem may depend on factors such as site productivity and climatic trends. For example, in our study grazing caused a decline in total forb standing crop when more productive sites were considered, indicating a stronger coupling between plants and herbivores on more productive sites than within the system as a whole. Briske et al. (2003) speculated that the combined effects of grazing and climate variation may superimpose periods of nonequilibrium dynamics within an otherwise directional response of plant composition to long-term grazing. The duration of our study was insufficient to capture trends in responses of vegetation to grazing, such as those suggested by Briske et al. (2003) that may require decades to become evident.

Vegetation heterogeneity

Grazing influenced standing crop of all forbs when we only considered sites where standing crop of grasses exceeded the mean residual. Other researchers have reported that productivity of an area influences response to grazing (Milchunas and Lauenroth 1993; Travers and Berdugo 2020). Grazing animals are not randomly or uniformly distributed across the landscape; rather, they select sites with higher quantity or quality of forage (Wallace et al. 1995; Wilmshurst et al. 2000; Bailey and Provenza 2008; Hebblewhite et al. 2008). We did not examine the spatial distribution of grazing animals in our study. Therefore, the idea that animals were more likely to forage in patches with greater standing
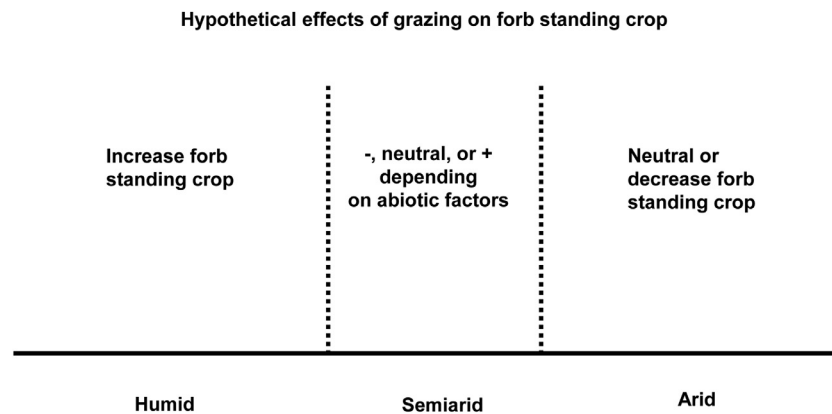
Hypothetical effects of grazing on forb standing crop

Figure 4. Hypothetical relationships among forb standing crop, grazing intensity, and climatic zones. Adapted from Fulbright (2011).

crop of grasses and avoid less productive sites is an assumption that we made based on the literature. However, because our results were different when we considered only the more productive sites, we suggest that investigators take into account vegetation heterogeneity and spatial distribution of animals in vegetation sampling schemes. Random vegetation sampling may not fully reflect effects of nonrandom foraging. We speculate that sampling patches herbivores are more likely to feed in may provide insights that are missed by random sampling. Patches with high standing crop of vegetation are highly important in ecosystem function on arid and semiarid rangelands because they serve as sinks for water and nutrients (Aguiar and Sala 1999). Understanding how grazing impacts their composition and productivity may be critical to maintaining patch function on rangeland landscapes.

Implications

Grazing does not result in increased standing crop of forbs selected by white-tailed deer in our study sites in South Texas. On the basis of a thorough review of the literature on cattle grazing and wildlife, Krausman et al. (2009) concluded that continuous grazing at light stocking rates has the best possibility of achieving wildlife management objectives. Our results support their conclusions because in our reduced model, 22% use of grasses was the predicted optimum grazing intensity for standing crop of all forbs and standing crop of all forbs declined with increasing percent use of grasses. A second finding that lends support to lighter stocking rates is the lower standing crop of forbs selected by white-tailed deer in grazed plots compared with nongrazed plots averaged across years and study sites.

Precipitation and soil texture appear to be more important drivers of forb standing crop than grazing by wild and domestic herbivores in our study sites. In areas with high annual variation in precipitation, pulses of moisture result in abundant forbs, but droughts, which occurred 40% of the time in our study, severely reduce forbs. Extreme variation in forb availability has a decoupling effect on the interaction between herbivores and forbs. Lyons and Wright (2003) recognized that grazing by livestock is unlikely to have a positive effect on forbs in areas with low precipitation. They suggested a threshold of 56 cm of annual precipitation, below which grazing will not increase forbs. Our results support their conclusion based on mean annual precipitation in our study sites from 2011–2019 (see Table 1). We speculate, on the basis of our results and previous research (Thill and Martin 1986, 1989; Brady et al. 1989; Jenks et al. 1996; Smith et al. 1996; Ortega et al. 1997; Towne et al. 2005; Ruthven 2007; Koerner and Collins 2013), that grazing of grasses may increase forbs in more humid environ-

ments, but as the environment becomes more arid, grazing is more likely to have a neutral effect or reduce forbs (see Fig. 4).

Standing crop of forbs in response to grazing may differ between sites with high vegetation standing crop and less productive sites. Accounting for patch productivity and distribution may provide greater insight into herbivore-vegetation interactions. Forb standing crop responses to grazing may not be detectable on the entire landscape but may be localized in the most productive areas of the landscape.

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