Received: 21 June 2021 | Revised: 12 January 2022 | Accepted: 10 February 2022
DOI: 10.1002/ldr.4236

RESEARCH ARTICLE

WILEY

Precipitation regulates the livestock dung seed bank through above ground vegetation productivity in the Qaidam basin

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Funding information
National Natural Science Foundation of China, Grant/Award Numbers: 32161143028, U21A20242; National Key Research and Development Program of China, Grant/Award Number: 2021YFD1300504; The Program of National Science and Technology Assistance, Grant/Award Number: KY202002011; The Program for Innovative Research Team of Ministry of Education, Grant/Award Number: IRT17R50; The Technological Support for Grassland Ecological Management and 'Lanzhou City's Scientific Research Funding Subsidy to Lanzhou University'

Abstract

The livestock dung seed bank (DSB) plays an important role in the regeneration and sustainability of grasslands in grazing ecosystems. As global precipitation patterns change, the productivity of the above ground vegetation (AGV) in semiarid and arid regions may be substantially affected, as will both the size and composition of the livestock DSB. However, the effects of altered precipitation patterns remain to be determined. Dung was collected for three consecutive years (2018–2020) from horses, cattle and sheep in the desert region of the Qaidam basin, China. The seedling emergence method was used to examine species richness and seed density in the DSB, and the structure and composition of the DSB and the AGV were also investigated. Combined with precipitation data, a structural equation model was used to explore how precipitation affects the livestock DSB by quantifying changes in the AGV in the basin. The results showed that horses [seedling density 5.32 (2018), 6.30 (2019) and 7.44 (2020) g^{-1} dung] had greater seed dispersal potential than cattle (3.91, 5.08 and 6.42 g^{-1} dung) or sheep (0.88, 1.32 and 2.96 g^{-1} dung), indicating that horse dung contributes the most to the AGV in the Qaidam basin. Furthermore, the seed composition of the DSB differed substantially from species of the AGV, implying that the DSB can promote the diversification of grasslands. An increase in precipitation increased both the productivity of the AGV (and hence livestock forage) and the size and composition of the DSB. These results highlight that the DSB is an essential driver of the development of grasslands in arid areas and that the indirect effect of precipitation on the livestock DSB for the regeneration and conservation of grasslands should be considered in arid regions.

KEYWORDS
arid area, climate change, dung seedling, endozoochory, grazing ecosystem

1 | INTRODUCTION

When mature plant seeds are consumed by foraging livestock, some of these seeds survive passage through the digestive tract and are ultimately deposited in dung. These viable seeds in herbivore faeces constitute the dung seed bank (DSB) (Wang & Hou, 2021a). The composition of the DSB depends on the rangeland composition and the selective feeding by livestock and can benefit plant species in various ways (Wang & Hou, 2021b).

Seed dispersal through endozoochory is an important source of vegetation renewal and a supplement to the soil seed bank (SSB; Wang et al., 2021). Moreover, the nutrients and organic matter in livestock dung promote seedling emergence and growth (Nchanji & Plumptre, 2003; Traveset et al., 2001; Woldu & Saleem, 2000). Meanwhile, livestock dung can also hamper the germination of species characteristic to nutrient-poor environments, and in some cases the livestock avoids places with dung, so its deposition pattern can also influence future grazing patterns (MacLusky, 1960; Yu, Xu, Muhammad, & Long, 2013). Accordingly, the DSB can change the grassland vegetation composition and promote grassland patch formation by influencing the SSB composition and seedling density (Elisabeth & Han, 2003; Myers et al., 2004; Yu, Xu, Muhammad, & Long, 2013). Hence, an appreciation of the composition, size (e.g., the number of seeds that can germinate per unit weight of dung), and ecological characteristics of the DSB is essential for studies of grazing ecology (D'Hondt & Hoffmann, 2015).

Seed quantity and the range of seed species dispersed by herbivores can considerably influence the dynamics and species richness of grazed ecosystems (Pakeman et al., 2002). Faecal sedimentation, dung-borne seed germination, and seedling establishment in faeces increase plant species richness and influence the large-scale spatial community composition of grazed ecosystems (Malo & Suárez, 1995). Specifically, the similarity of plant communities between different types of grazed grasslands is increased, and diversity among grassland plants within local communities is fostered (Malo & Suárez, 1995). It is assumed that seed ingestion—specifically the seed quantity and the range of seed species—by livestock increases plant species richness and influences the large-scale spatial community composition of grazed ecosystems by intensifying the intercommunity seed flow. However, the relationship between the DSB and above ground vegetation (AGV) characteristics remains unclear, as does the mechanism by which this relationship is maintained (Albert et al., 2015).

In the context of global climate change, there will be fewer precipitation events in certain geographic regions yet larger per-event rainfall volumes, and the frequency of extreme precipitation events will also increase globally (Intergovernmental Panel on Climate Change, 2013). Precipitation correlates positively with grassland productivity (Gamoun, 2016; Song et al., 2019). Changes in precipitation patterns can have a notable impact on the structure and species dynamics of grassland ecosystems, as precipitation is the main limiting factor of grassland productivity, especially in semiarid and arid regions (Noy-Meir, 1973; Reynolds et al., 2004).

Grazing is the most commonly used and effective grassland management method (Hou & Yang, 2006). In grassland-grazing ecosystems, precipitation affects the food resources available to livestock by changing the composition and structure of the AGV and seed production, thereby regulating the size and composition of the DSB. Grazing management and precipitation patterns have been shown to alter the coverage of grassland species, the composition of plant communities and even the development of entire grassland ecosystems (Gamoun et al., 2011; Gamoun et al., 2012).

Located in northwestern China and the northeastern part of the Qinghai-Tibetan Plateau, the Qaidam basin (plateau-type basin) has been identified as the most climate-sensitive region across the entire Qinghai-Tibetan Plateau, which is the largest grazing ecosystem in Eurasia (Cai et al., 2014). The region is mainly characterised by an extremely arid desert climate (Zhao et al., 2020). Based on meteorological data, precipitation in the Qaidam basin increased continuously from 1980 to 2015 (an interannual increase of over 10%), indicating a change to a wetter yet still arid-type climate (Zhang et al., 2019). Increased precipitation will inevitably impact the production of local livestock. Previous studies of indigenous animals and livestock on the Qaidam basin have mostly focused on the impact of precipitation on the composition and structure of the AGV (Li, 2018; Xu & Yang, 2013). However, against the backdrop of changing precipitation patterns as well as the DSB as a potential force for grassland regeneration (Wang & Hou, 2021a; Yu et al., 2012), research on the effect of precipitation on the properties of the livestock DSB has largely lagged.

In this study, we collected dung from livestock (i.e., horses, cattle and sheep) in the Qaidam basin desert grassland during three continuous years (2018–2020) and determined the size and composition of the DSB as well as the characteristics of the AGV over the same period. Combining these factors with precipitation data, we hypothesised that precipitation indirectly promotes the size and composition of the livestock DSB by directly increasing the seed yield, richness and diversity of the AGV. The objectives of this research were to study: (i) the changing characteristics of the composition and structure of the AGV in the basin desert grassland under changing (e.g., increasing) precipitation conditions; (ii) the size and species composition of the DSB from different livestock species and the relationship between the DSB and AGV; and (iii) the mechanisms of precipitation effects on the livestock DSB by quantifying changes in the AGV characteristics. The results provide an improved understanding of the mechanisms of grass–animal interactions under climate change in semiarid and arid regions throughout the World.

2 | MATERIALS AND METHODS

2.1 | Study area

Covering an area of ~5000 ha, the study site is located in the northern part of the Qaidam basin (38°72′ N–38°84′ N, 94°46′ E–94°98′ E; ~3520 m a.s.l.; Figure 1) and is grazed by horses (*Equus caballus*, ca. 100 head), cattle (*Bos taurus*, ca. 200 head), and sheep (*Ovis aries*, ca. 400 head) year-round. The most common management method for grazing in this area is nomadic, where transhumant flocks move seasonally with their herders between fixed warm (May–October) and cold (November–April) season pastures. Wild ungulates are rarely seen in the sampling site, and livestock is evenly distributed across the landscape. Owing to an adjustment in the local government's grazing policy in recent years, the stocking rate in this area has remained at a moderate level (Wang et al., 2018). Furthermore, there are no large-scale enclosures in this area, given that fences undermine biodiversity targets (Sun et al., 2021). The climate type is inland, extremely arid and cold, with an annual average temperature of ~3.5°C (from −12°C in January to +16°C in July). The annual average sunshine duration is >3000 h, and the evaporation rate is high (~1500 mm).

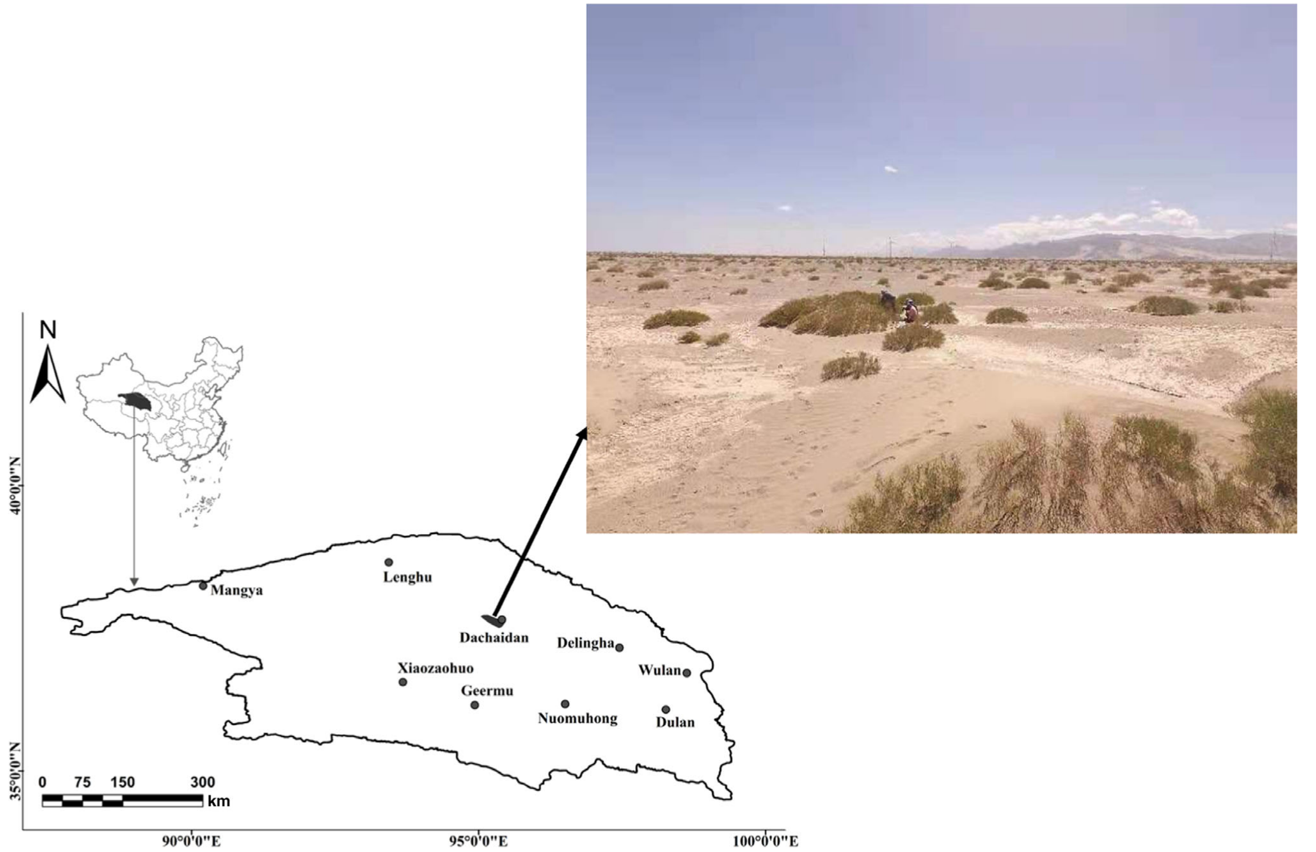

FIGURE 1 The study site in the Qaidam basin, China. Wiley acknowledges that the borders within the figure are subject to multiple territorial claims [Colour figure can be viewed at wileyonlinelibrary.com]

Vegetation is sparse and arid desert grassland, with single species and a simple structure consisting mainly of shrubs, semi-shrubs and herbs with high drought resistance, including a large proportion of halophytes. The semi-desert plant community is clustered, especially near shrubby and thorny patches, where a lower intensity of grazing occurs (Hadinezhad et al., 2021). The soil type is saline desert soil (Liu, 1962). The average annual precipitation is ~80 mm and is mostly concentrated from April to October (>90% of the annual precipitation), with the highest precipitation occurring in August (Figure 2a). Meteorological data provided by the local weather station revealed that, since 2018, precipitation at the study site (peak period from July to September) has increased annually (Figure 2b).

2.2 | Assessment of the AGV

The AGV was surveyed in mid-August of 2018, 2019 and 2020 at the study site. Owing to unique climatic conditions and vegetation phenology, the species richness, biomass and seed production of the AGV were at their peak (~35 species) during this period, which reflects the maximum productivity of the grassland at the study site (Li, 2018).

The transect sampling method was used to investigate the characteristics of AGV (Hu et al., 2019; Hu et al., 2020). At a site where livestock dung was densely distributed, three planting lines were selected (at 40-m intervals), and three quadrats (2 m × 2 m, at 40-m intervals) were established for each line. Therefore, each year comprised nine quadrats (9 replicates, 3 lines × 3 quadrats, $n = 9$). Species richness (the number of plant species) and density were recorded for each quadrat (2 m × 2 m) during each year, as well as mature seed mass (i.e., seed yield, the mass of mature seeds per square metre, g m^2) and AGV (i.e., biomass harvest not including seeds) were collected and dried to a constant weight at 65°C.

2.3 | Livestock dung collection

Mid-August to mid-September is the peak period of plant seed maturation at the study site. During this period, plants retain a large number of mature seeds, which constitute the canopy seed bank (Oudtshoorn & Rooyen, 1998). All livestock had access to seed-bearing vegetation because the grazing animals were evenly distributed across the landscape throughout the study.

From mid-August to mid-September of 2018, 2019 and 2020 (i.e., the peak of seed maturation), samples of fresh dung (newly defecated) from each horse (~3.5 kg, 82.40% water content), cattle (~3.5 kg, 84.29% water content) and sheep (~4.5 kg, 65.54% water content) were collected near the quadrat. Individual dung samples from each species were pooled evenly, placed in a clearly marked canvas bag, and transported to the laboratory. All samples were oven-dried at 35°C for ~72 hr to prevent decay and premature seed

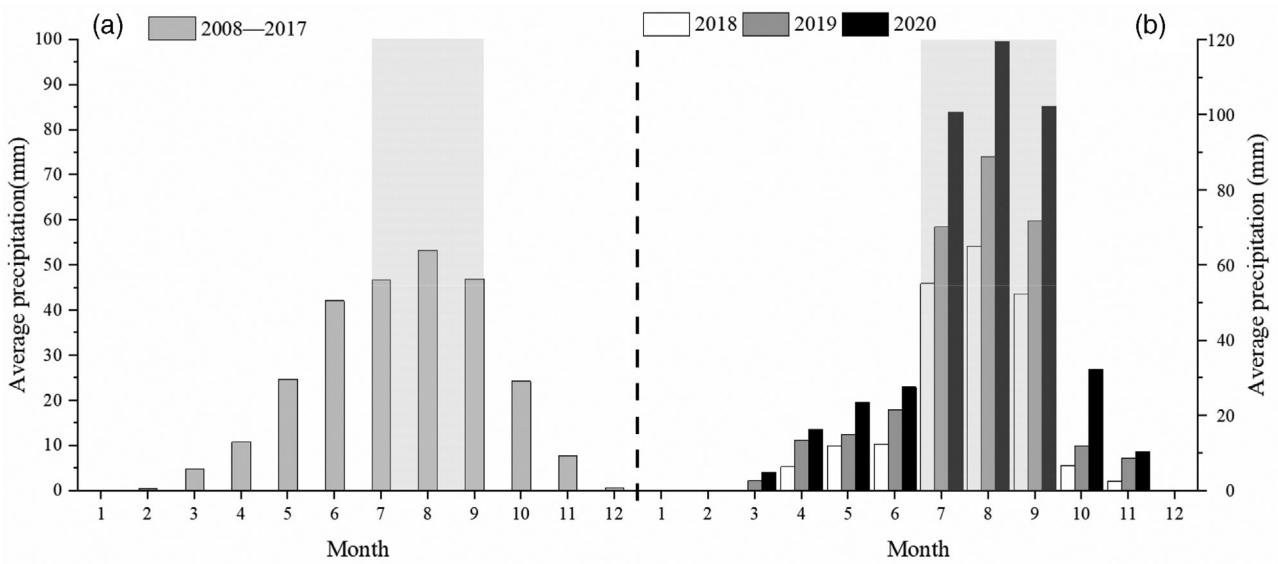

FIGURE 2 Mean precipitation from 2008 to 2017 (a), and monthly precipitation in 2018, 2019 and 2020 (b). The shaded section in each graph corresponds to the peak period of precipitation at the study site

germination. Importantly, drying at this temperature does not substantially affect the germination potential of seeds in dung (Wang et al., 2019). All dried dung samples for each livestock type during each year were then divided into nine equal subsamples (nine replicates, 300 g per subsample) and stored in the dark at room temperature before subjecting them to the germination assay.

2.4 | Germination to assess the livestock DSB

The seedling germination method (An et al., 2020; Ter Heerdt et al., 1996) was used to determine the species composition and size of the DSB. Dried dung (300 g, gently compressed without damage) was mixed with ~50 g of sterilised sand and potted in a 2-cm layer over 5 cm of vermiculite. Pots were placed in the yard of a local herdsman in Qaidam basin under natural conditions. Ten pots containing only sterilised sand and vermiculite were placed alongside the dung pots as controls for wind-blown seeds or other forms of seed contamination. A total of 91 pots (3 years $\times$ 3 livestock species$\times$ 9 replicates $+$10 controls) were obtained. Seedlings were watered twice daily from March until September 2020. The experiment ended 6 months later when no substantive new germination had been detected for 2 weeks (Malo, 2000). Emerging seedlings were recorded and removed as soon as they could be identified or were transplanted into separate pots for later identification. Whenever seedlings were removed, the dung/sand mix sample was gently stirred to facilitate additional germination of buried seeds (He et al., 2021).

2.5 | Diversity and similarity indices

The number of emerged seedlings (seedlings g^{-1} dung) and the species richness (species g^{-1} dung) were determined based on data collected from nine replicates of each dung sample. For each seedling pot or quadrat, a Shannon diversity index (H') was calculated as follows:

$$H' = -\sum_{i=1}^{S} p_i 1np_i, \quad (1)$$

Where: p_i is the relative proportion of species of the whole community (in this study, the community refers to the pot/quadrat), and s is the total number of species for each dung sample/quadrat.

The composition of both the DSB and AGV was compared between different years by a non-metric multidimensional scaling analysis (using PC–ORD 5.0 for Windows software: Gleneden Beach, OR) with a Raup–Crick dissimilarity matrix (Plue et al., 2020; Raup & Crick, 1979). The ordination result was considered acceptable for a stress value of <0.05.

2.6 | Data analysis

Data for AGV/dung seedling species density, richness and diversity were log10-transformed with the assumption of normality and homogeneity of variances. Precipitation (i.e., 2018, 2019 and 2020) and livestock type (i.e., horse, cattle, and sheep) were treated as fixed effects. A two-way analysis of variance was used to assess differences in dung seedling density and AGV density, species richness and the effects of precipitation and livestock type on species diversity. A Shapiro–Wilk test was used to test the normality of data before comparing mean values. The level of significance used was $p < 0.05$. Error bars and numbers following averages denote standard error (SE). Analysis of variance was conducted with the Statistical Package for the Social Sciences (SPSS) (version 26.0 for Windows; SPSS, Inc., Chicago, IL).

Structural equation modelling was used to estimate the effect of precipitation changes on the AGV biomass and DSB (based on dung seedling density). First, an a priori conceptual model was constructed assuming that precipitation indirectly promotes the size and composition of the livestock DSB by directly increasing the productivity (e.g., biomass) of the AGV. A chi-squared test was used to evaluate the model's fit where $0 \le \chi^2/df \le 2$ and $0.05 < p \le 1$ indicate a good fit. A large p-value (>0.05) indicated that the data's covariance structure did not differ significantly from the expected model (Grace, 2006). Structural equation modelling analyses were performed using AMOS 24.0 (Arbuckle, 2010).

3 | RESULTS

3.1 | AGV richness, density, biomass, diversity and seed yield

The species richness, density, biomass, diversity and seed yield of the AGV increased significantly during the 3-year study period (Figure 3). Furthermore, precipitation and the interaction between precipitation and livestock, but not livestock alone, had a significant impact on the characteristics of the AGV (Table 1).

3.2 | Species germinated from dung

Thirty-four herb species germinated from the DSB samples, representing 13 families (Poaceae, Leguminosae, Chenopodiaceae, Asteraceae, Zygophyllaceae, Brassicaceae, Tamaricaceae, Plumbaginaceae, Ephedraceae, Polygonaceae, Rosaceae, Plantaginaceae, Iridaceae; Table 2). Essentially, all the common plant species in the study area were detected in the DSB, suggesting that, in grazing ecosystems

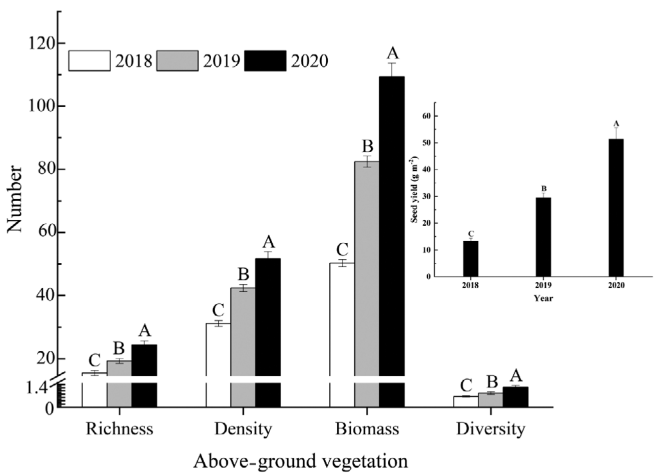

FIGURE 3 Above ground vegetation richness, density, biomass, diversity and seed yield during 2018–2020. For each category, columns with different upper-case letters are significantly different between different years ($p < 0.05$)

in arid regions, seeds from all plants (especially dominant/common species) may have the potential to survive transit through the livestock digestive tract and become dispersed.

During the 3-year study period, horse dung was found to contain the greatest number of germinated seeds, with an average density of viable (more likely to germinate) seeds of 5.32 (2018), 6.30 (2019) and 7.44 (2020) g^{-1} dung, which was significantly greater than the corresponding values for dung samples of cattle (3.91, 5.08 and 6.42 g^{-1} dung) and sheep (0.88, 1.32 and 2.96 g^{-1} dung) (Figure 4). Moreover, the horse dung seedling richness and diversity values were significantly greater than the corresponding values for cattle and sheep dung. For each livestock species, the dung seedling density, richness and diversity increased significantly over the three consecutive years. Both precipitation and individual livestock species, and their interaction, had significant effects on dung seedling properties (Table 1).

3.3 | Comparison of the DSB and AGV

An ordination diagram revealed differences in the plant species composition between dung seedlings and AGV for each year with distinct clustered point-clouds (Figure 5), as dung seedlings and AGV clustered together, respectively, implying that the DSB has the potential to increase the heterogeneity of the AGV near the microsites of the dung pieces.

3.4 | Relationship between precipitation, AGV and the livestock DSB

Precipitation had a significant direct effect on the production of AGV (standardised path coefficient = 0.88; $p < 0.0001$; Figure 6), and a significant indirect effect on livestock dung seedling density (0.32), richness (0.27) and diversity (0.24) (all $p < 0.05$). These findings verified our hypothesis that precipitation indirectly promotes the size and composition of the livestock DSB by directly increasing the biomass, richness and diversity of the AGV.

4 | DISCUSSION

4.1 | Effect of precipitation on AGV

Precipitation is the most important factor limiting grassland production in arid regions (Song et al., 2019). We found that, with an increase in precipitation, the abundance, density, biomass, diversity and seed yield of the AGV increased significantly. This phenomenon has also been verified in other arid regions (Gherardi & Sala, 2018; Huxman et al., 2004; Lehouerou et al., 1988). The reason may be that an increase in precipitation leads to the advancement of the greening period of plants and the postponement of the withering period (Ganjurjav et al., 2020); that is, precipitation can prolong the plant growth period and ultimately increases the aboveground biomass. In

TABLE 1 Effect of precipitation and livestock species on above ground vegetation and dung seed bank properties ($n = 9$)

	Precipitation		Livestock		Precipitation × livestock	
Item	*F*	*p*-value	*F*	*p*-value	*F*	*p*-value
Above ground vegetation						
Density	47.23	0.041*	29.71	0.0533	2.75	0.039*
Richness	8.33	0.029*	2.47	0.073	6.43	0.045*
Diversity	1.78	0.032*	64.26	0.061	8.66	0.043*
Seed yield	3.63	0.034*	33.74	0.056	4.76	0.036**
Biomass	5.32	0.00043***	57.73	0.058	37.256	0.0028**
Dung seedlings						
Density	19.00	0.00086***	32.17	0.023*	21.75	0.0031*
Richness	12.13	0.0063**	4.38	0.034*	1.43	0.041*
Diversity	7.43	0.0078**	64.26	0.047*	47.66	0.043*

***$p < 0.001$; **$p < 0.01$; *$p < 0.05$

addition, moisture is a prerequisite for seed germination (Wang et al., 2020). Hence, in arid regions, precipitation promotes the germination of seeds in the SSB, improves the efficiency of SSB conversion to AGV, and thereby increases the abundance and species diversity of the AGV (Figure 3) (Hu et al., 2019).

It is generally believed that, because of the compensatory growth strategy of plants, moderate grazing (i.e., at this study site) can increase grassland species diversity and maintain grassland health (intermediate disturbance hypothesis) (Gao & Carmel, 2020; Grime, 2006). However, we found that grazing did not significantly affect the composition and structure of the AGV during the observation period (Table 1). This may be because, in semiarid and arid regions, the impact of grazing on grasslands is offset by precipitation. It further shows that precipitation is the dominant factor affecting grassland stability in grazing ecosystems in semiarid and arid regions (Gherardi & Sala, 2018).

4.2 | Size and composition of the livestock DSB

In this study, the seedling density in dung increased significantly over the three consecutive years for each livestock species (Figure 4). As precipitation enhanced plant growth, it also increased seed production (Figure 3). Therefore, it would be expected that seed availability would correlate directly with the number of seeds found in herbivore dung.

The size of the DSB can be affected by livestock species, the amount of seed intake by livestock, and the physical and chemical properties of the faeces (Milotić & Hoffmann, 2016), in addition to seed traits (Pakeman et al., 2002). In this study, we found that the number of germinated seeds in the dung of horses (caecal digester) was greater than that in the dung of cattle (large ruminant) or sheep (small ruminant) during all 3 years (Table 2; Figure 4), which is consistent with the findings of Wang & Hou (2021a). Compared with horses and cattle, the chewing method of sheep causes the most severe damage to seeds. For example, in the central region of Spain, fragments of chewed seeds of the Mediterranean shrub *Retama sphaerocarpa* (seed mass of 77 mg) are often found in sheep dung (Manzano et al., 2005). In ruminants, plant seeds are affected not only by chewing and rumen digestion but also by the rumination process, which is quite destructive (Wang et al., 2017). In contrast, horses are monogastric animals in which the food is chewed particularly roughly (Zang, 2015), but there is no rumination-related damage to the seeds. However, Mouissie et al. (2005) reported that, in the heathlands in the northern Netherlands, the mean seedling density of cattle dung was greater than that of horse dung. Subtle variations in grazing behaviour and diet selection could explain some of the observed differences in germinating seed content between cattle and horse dung (Malo, 2000). In addition, herbivore species have interspecific differences in functional traits, such as habits, size, age, mating frequency, cognition and forage preferences, which may result in differences in dung seedling density and the seed dispersal service they provide (Zwolak, 2017).

4.3 | Comparison of the DSB and AGV

As a result of differences in the grazing regime (e.g., nomadic), animal species, environmental factors and the spatial distribution of species, the effects of grazing on the similarity between the DSB and AGV are debatable (Agra & Ne'eman, 2012; Peco et al., 1998; Ungar & Woodell, 1996). For example, Wang & Hou (2021a) found that the similarity index between the DSB and the corresponding AGV in alpine meadows was significantly lower than that in the desert grasslands. Wang et al. (2019) found that the relationship between the tan sheep DSB and AGV was weak on the Loess Plateau of China. The present study showed a high dissimilarity between the DSB for each of the three livestock species and the AGV during the 3-year experimental period (Figure 5), indicating that the DSB had the potential to increase the heterogeneity of the AGV near the microsites of the dung pieces (Wang & Hou, 2021b; Yu, Xu, Muhammad, & Long, 2013). Meanwhile, the livestock has long gut retention times and can move several kilometres every day (Manzano et al., 2005;

TABLE 2 Mean (± SE) germination density (seedlings g^{-1} dung) of species from livestock dung ($n = 9$) collected within the desert of the Qaidam basin during 2018–2020

		2018			2019			2020		
Family	Species	Horse	Cattle	Sheep	Horse	Cattle	Sheep	Horse	Cattle	Sheep
Poaceae	*Achnatherum splendens* (Trin.) Nevski	5.71 ± 0.23			6.73 ± 0.27			8.03 ± 1.32		
	Agropyron cristatum (L.) Gaertn.	6.32 ± 0.34			7.31 ± 0.73		1.98 ± 0.48	8.61 ± 1.03	7.55 ± 0.83	3.48 ± 0.54
	Stipa orientalis Trin.	6.01 ± 0.46			7.04 ± 0.74	4.98 ± 0.43		8.33 ± 0.67	6.31 ± 0.92	
Leguminosae	*Astragalus laxmannii* Jacquin	5.27 ± 0.21		0.78 ± 0.21	6.26 ± 0.62		1.57 ± 0.53	7.56 ± 0.83		3.07 ± 0.46
	Corethrodendron multijugum (Maximowicz) BH Choi & H Ohashi	4.32 ± 0.27	3.38 ± 0.45		5.31 ± 0.36	4.57 ± 0.34		6.71 ± 0.48	5.96 ± 0.74	4.32 ± 0.43
	Glycyrrhiza glabra L.			0.83 ± 0.22			1.13 ± 0.25		6.41 ± 0.23	2.63 ± 0.26
	Oxytropis aciphylla Ledeb.	5.12 ± 0.53			6.12 ± 0.23			7.42 ± 1.43		3.04 ± 0.23
	Sphaerophysa salsula (Pall.) DC.	5.23 ± 0.23	3.78 ± 0.54		6.23 ± 0.13	4.93 ± 0.54		7.35 ± 1.24	6.21 ± 0.47	
	Thermopsis lanceolata R. Br.		4.02 ± 0.34			5.24 ± 0.35		7.01 ± 1.27	6.64 ± 0.67	
Chenopodiaceae	*Agriophyllum squarrosum* (L.) Moq.			0.84 ± 0.43			0.99 ± 0.26			2.49 ± 0.52
	Bassia dasyphylla (Fisch. et Mey.) O. Kuntze	5.54 ± 0.23			6.57 ± 0.29			6.87 ± 0.78		
	Corispermum pamiricum Iljin		4.56 ± 0.17		6.51 ± 0.25	5.75 ± 0.26		6.82 ± 1.01	7.15 ± 0.63	
	Kalidium capsicum (L.) Ung.-Sternb.				6.04 ± 0.71		0.97 ± 0.14	7.34 ± 1.25		2.47 ± 0.71
	Kalidium foliatum (Pall.) Moq.		4.13 ± 0.71			5.32 ± 0.27			6.71 ± 0.52	3.11 ± 0.48
	Salsola affinis CA Mey.		4.78 ± 0.63			5.96 ± 0.42		7.75 ± 1.53	7.16 ± 0.73	
	Salsola heptapotamica Iljin		3.67 ± 0.26			4.87 ± 0.25		6.78 ± 1.47	6.25 ± 0.47	
	Salsola tragus Linnaeus	6.23 ± 0.23			7.23 ± 0.52			8.53 ± 0.68	5.55 ± 0.84	
	Sympegma regelii Bunge			1.07 ± 0.34			1.37 ± 0.41	6.73 ± 0.76		2.87 ± 0.64
Asteraceae	*Artemisia scoparia* Waldst. et Kit.	4.38 ± 0.42			5.37 ± 0.48			8.67 ± 0.79	6.23 ± 0.98	
	Cirsium arvense var. integrifolium C. Wimm. et Grabowski			0.78 ± 0.27			1.15 ± 0.43			2.65 ± 0.73
	Echinops gmelinii Turcz.	5.29 ± 0.27			6.11 ± 0.64			7.41 ± 0.78		
	Ixeris chinensis subsp. Versicolor (Fisch. ex Link) Kitam.		3.56 ± 0.23			4.76 ± 0.24		7.23 ± 0.68	6.16 ± 0.67	
Zygophyllaceae	*Nitraria roborowskii* Kom.	5.15 ± 0.42			6.13 ± 0.35			7.43 ± 0.86		
	Nitraria tangutorum Bobr.				6.38 ± 0.13		1.23 ± 0.26	7.68 ± 1.34		2.73 ± 0.28
	Peganum harmala L.							7.57 ± 1.27	6.13 ± 0.42	
Brassicaceae	*Lepidium latifolium* Linnaeus	4.78 ± 0.41		0.76 ± 0.26	5.78 ± 0.73		1.19 ± 0.24	7.12 ± 1.23		2.69 ± 0.17
	Smelowskia tibetica (Thomson) Lipsky		3.04 ± 0.28			4.22 ± 0.38		6.11 ± 0.96	5.62 ± 0.68	2.87 ± 0.32
Tamaricaceae	*Reaumuria soongarica* (Pallas) Maximowicz					5.01 ± 0.83			6.41 ± 0.53	

(Continues)

TABLE 2 (Continued)

Family	Species	2018 Horse	2018 Cattle	2018 Sheep	2019 Horse	2019 Cattle	2019 Sheep	2020 Horse	2020 Cattle	2020 Sheep
Plumbaginaceae	*Limonium aureum* (L.) Hill.		4.21 ± 0.33		6.29 ± 0.37	5.43 ± 0.27		7.59 ± 0.93	6.83 ± 0.85	
Ephedraceae	*Ephedra przewalskii* Stapf						1.43 ± 0.37		6.36 ± 0.58	2.93 ± 0.53
Polygonaceae	*Atraphaxis pungens* (Bieb.) Jaub. et Spach.				6.14 ± 0.62			7.43 ± 0.92		
Rosaceae	*Potentilla anserina* L.			1.12 ± 0.24		5.12 ± 0.23	1.47 ± 0.63		6.51 ± 0.46	2.97 ± 0.64
Plantaginaceae	*Plantago depressa* Willd.	5.17 ± 0.12			6.17 ± 0.25			7.47 ± 0.87		3.13 ± 0.27
Iridaceae	*Iris lacteal* Pall.					5.05 ± 0.29			6.28 ± 0.69	

Note: The Latin names of dung seedling species are cited on the Flora Reipublicae Popularis Sinicae (FRPS) website (http://www.iplant.cn/frps).

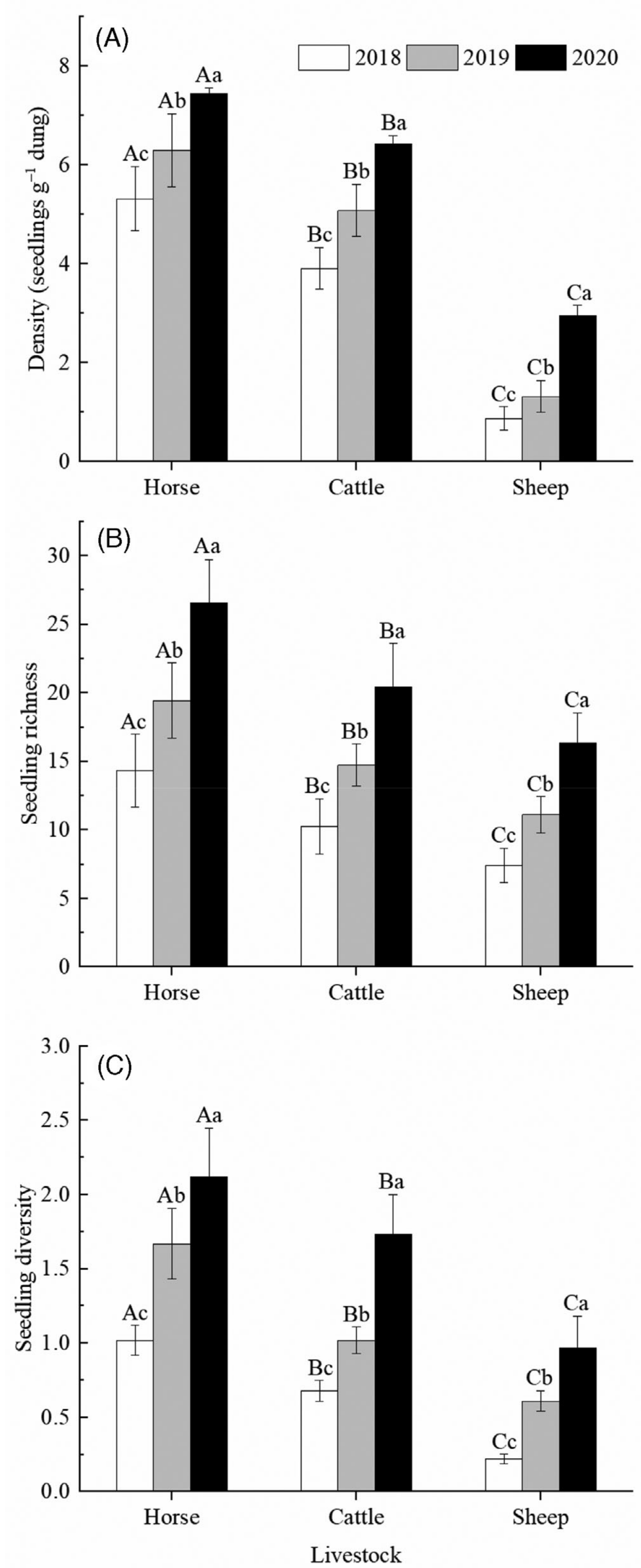

FIGURE 4 Dung seedling density (seedlings g^{-1} dung), richness and diversity among livestock species during 2018–2020. Columns with different lower-case (uppercase) letters are significantly different between years (livestock type) for each livestock type (year) ($p < 0.05$)

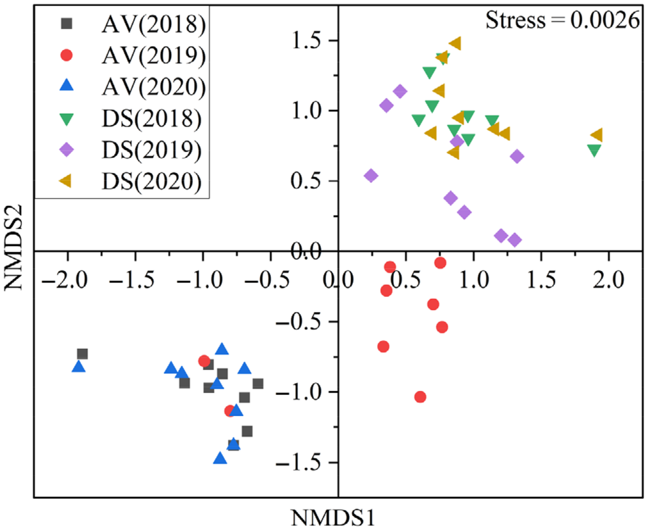

FIGURE 5 Ordination diagram of the nine quadrats for the density of the above-ground vegetation and dung seed bank over 3 years based on non-metric multidimensional scaling (NMDS). AV, composition of the above-ground vegetation; DS, composition of the dung seed bank. Stress value = 0.0026, n = 9 [Colour figure can be viewed at wileyonlinelibrary.com]

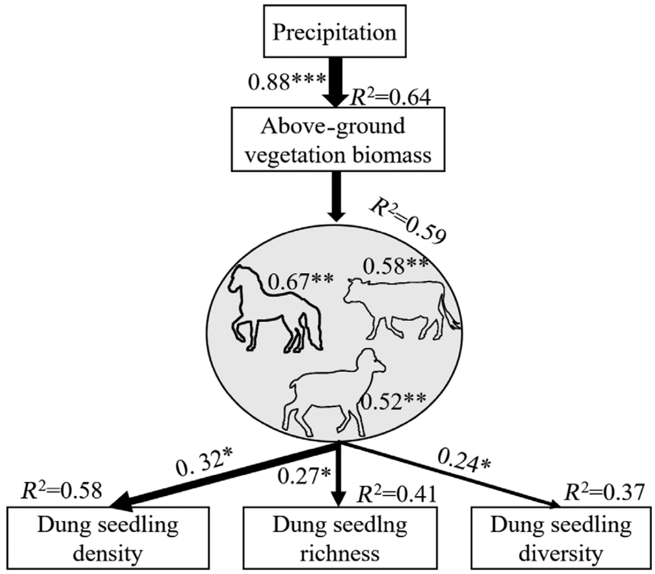

FIGURE 6 Structural equation modelling (SEM) of the effects of precipitation on the above ground vegetation biomass and livestock dung seedling density, richness and diversity. Species numbers were used for the calculations. Numbers on the arrows are standardised path coefficients indicating the effective sizes of the relationships. Arrow width is proportional to the strength of the relationship. The proportion of variance explained is given as R^2. *p < 0.05, **p < 0.01, ***p < 0.001. Results of model fitting: χ^2 = 6.54, df = 5, p = 0.18

Wang et al., 2016), so at least some of the dung seeds delivered near our quadrats would be expected to be from plants located several kilometres away—a potential explanation for the differences between the composition of the vegetation and that of the dung.

The relationship between the DSB and AGV can be influenced by the selective feeding of livestock (Bagchi & Ritchie, 2010), physical and chemical properties of faeces (Milotić & Hoffmann, 2016), and microhabitat properties at dung (and hence seeds) discharge sites (Calviño-Cancela & Martín-Herrero, 2009). For example, in grazing ecosystems, because of livestock feeding preferences, a large number of plant seeds accumulate in faeces (the 'fertile island effect') (Cai et al., 2020). The heterogeneity in the composition between the DSB and that of AGV indicates that the DSB is a potential driving force for the formation of grassland patching due to grazing (Fulgoni et al., 2020; Wang & Hou, 2021a, 2021b; Yu et al., 2012; Yu, Xu, Wang, Shang, & Long, 2013). Moreover, in arid environments such as the desert grassland of the study site, seed dispersal via dung pellets provides substantial protection for seeds until sufficient rainfall occurs to allow germination and seedling establishment, thus representing an adaptation for survival in this type of harsh environment.

4.4 | Precipitation modulates the DSB

This study found that precipitation increased the above-ground foraging resources for livestock by promoting the composition and structure of the AGV, thereby increasing the size and composition of the livestock DSB (Figure 6). In arid regions, precipitation accelerates the decomposition of livestock faeces (Sitters et al., 2014; Zhu et al., 2020). Therefore, the peak periods of precipitation and plant seed maturation are identical. In our study area, precipitation peaks in July, August and September (Figure 2). At this time, a large number of viable seeds collect in the faeces of livestock through ingestion and excretion until the right time (onset of consistent precipitation) to germinate (Table 2; Figure 4), eventually converting to the SSB, thus becoming an important potential resource for grassland vegetation renewal (Wang et al., 2019). This positive effect of livestock faeces on the grassland is also an adaptation strategy for plants to respond to livestock intake (i.e., grass-livestock interactions) as well as the changing environment (e.g., increasing precipitation) (Wang et al., 2019).

5 | CONCLUSIONS

In the desert grasslands of the Qaidam basin, plant seeds are consumed by grazing livestock and then accumulate in faeces after passage through the digestive tract, resulting in a large number of viable seeds in livestock dung after deposition. Precipitation promotes this process, as it increases the productivity of grasslands in arid regions, thereby increasing the availability of above-ground food resources to livestock. Both the diversity and abundance of dung seedlings were significantly greater for horses than for cattle or sheep, indicating that horse dung makes the greatest contribution to the SSB. Moreover, the composition of the DSB and AGV differed significantly, implying that the DSB may increase the heterogeneity of the AGV. This study demonstrates that the DSB is an essential driving factor for the development of grasslands in arid areas and that the indirect effect of precipitation on the livestock DSB for the regeneration and succession of grasslands should be considered in arid regions.

ACKNOWLEDGEMENTS

We are grateful to The Second Comprehensive Scientific Research Team of the Qinghai-Tibetan Plateau for collecting the experimental samples. Field investigation: You-Shun Jin, Hai-Ren Shi, Ze-Chen Peng, Sheng-Hua Chang and Qian-Min Jia. Funding: This study was supported by the National Natural Science Foundation of China (32161143028, U21A20242), the National Key Research and Development Program of China (2021YFD1300504), the Program of National Science and Technology Assistance (KY202002011), the Program for Innovative Research Team of Ministry of Education (IRT17R50), the Technological Support for Grassland Ecological Management and 'Lanzhou City's Scientific Research Funding Subsidy to Lanzhou University'.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Shu-Lin Wang collected and analysed the data and wrote the manuscript. Fu-Jiang Hou designed the research and assisted with manuscript revisions.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available from the corresponding author upon request.

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How to cite this article: Wang, S.-L., & Hou, F.-J. (2022). Precipitation regulates the livestock dung seed bank through above ground vegetation productivity in the Qaidam basin. *Land Degradation & Development*, *33*(10), 1637–1648. https://doi.org/10.1002/ldr.4236