Journal of Environmental Management 323 (2022) 116167

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Ecological thresholds of toxic plants for sheep production and ecosystem multifunctionality and their trade-off in an alpine meadow

Yingxin Wang [a,b], Yi Sun [a], Yang Liu [a], Zhaofeng Wang [a], Shenghua Chang [a], Yongqiang Qian [b], Jianmin Chu [c], Fujiang Hou [a,*]

[a] State Key Laboratory of Grassland Agro-ecosystems, Key Laboratory of Grassland Livestock Industry Innovation, Ministry of Agriculture and Rural Affairs, College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou, 730020, China

[b] Grassland Research Center of National Forestry and Grassland Administration, Institute of Ecological Conservation and Restoration, Chinese Academy of Forestry, Beijing, 100091, China

[c] Research Institute of Forestry, Chinese Academy of Forestry, Beijing, 100091, China

ARTICLE INFO

Keywords:
Toxic plants
Thresholds
Livestock production
Ecosystem function
Trade-off
Alpine meadow

ABSTRACT

Toxic plants are a natural component of alpine meadow which co-evolved with Tibetan sheep for thousands of years. One challenge for indigenous herders is to know the ecological thresholds of toxic plants and maintain their vital functions in ways that are compatible with economic income and ecological conservation. To achieve this, field trials with Tibetan sheep grazing in alpine meadow were conducted to examine the ecological thresholds of toxic plants for sheep production and ecosystem functions and their trade-offs. Our results demonstrated that the changing point values of biomass proportion of toxic plants for dry matter intake and liveweight gain of sheep were 17% and 22%, respectively. The changing point value of biomass (richness) proportion of toxic plants for soil carbon accumulation index was 31% (59%), for soil nutrient cycling index was 38% (42%), and for ecosystem multifunctionality index was 28% (50%). The trade-off between liveweight gain of sheep and ecosystem multifunctionality first decreased and then increased along the gradient of biomass proportion of toxic plants (the value of changing point was 37%), and had a significant negative correlation with richness of toxic plants. In addition, structural equation modeling indicated that toxic plants can affect the trade-off between liveweight gain of sheep and ecosystem multifunctionality though increasing acid detergent fiber of plant and decreasing plant species richness, belowground biomass and soil total phosphorus. Consequently, opinions towards toxic plants should shift from the conventional view that they are serious threat to grassland ecosystem health to an inclusive understanding that they are beneficial to livestock and ecosystem functions under certain ecological thresholds.

1. Introduction

Toxic plants are traditionally defined as those plant species which are noxious, exotic, injurious or poisonous to domesticated livestock, wild animals and human (Ralphs, 2005; Zhao et al., 2012). In the natural grassland of China, the toxic plants are about 1,300 species belong to 140 botanical families (Zhang et al., 2020). Previous studies always paid attention to the adverse impact of toxic plants, such as how they suppress neighbor species growth, poison livestock, cause habitat degradation, and limit the economic productivity of local herders (Hierro and Callaway, 2003; Li et al., 2014; Welch et al., 2018; Ralphs and Sharp, 2019). However, the lopsided views (only focus on the negative effects) may lose sight of the potentially positive ecological function of toxic plants on plant diversity (e.g., conservation of biodiversity), soil nutrients (e.g., sand fixation and fertile island effect), co-existing plant (e.g., provide biotic refuge) and livestock production (Xie et al., 2020; Wang et al., 2014; Zhang et al., 2020). Hence, quantitative evaluation of the trade-off between negative and positive effects of toxic plants are essential to adopt strategic management practices disposing the issues of toxic plants in alpine meadow on the Qinghai-Tibet Plateau (QTP).

Toxic plants are often perceived as triggers and indicators for grassland degradation (Li et al., 2014; Wu et al., 2015). The first indicator of grassland degradation is a rise in the percentage of toxic plants to the detriment of desirable plants (Kemp et al., 2018). As over-grazing

* Corresponding author.
E-mail address: cyhoufj@lzu.edu.cn (F. Hou).

https://doi.org/10.1016/j.jenvman.2022.116167
Received 25 April 2022; Received in revised form 31 August 2022; Accepted 31 August 2022
Available online 15 September 2022

continues, desirable plant species are preferentially grazed, to the point from which they are unable to recover, allowing the toxic plants with lower nutritional value (e.g., with highly fibrous leaves and stems, thorns, and toxins) to become dominant (Kemp et al., 2018). In degraded alpine grassland, the toxic plants (e.g., *Anemone rivularis* Buch.-Ham, *Anemone trullifolia* Hook. f. et Thoms, *Ligularia virgaurea* Maxim. and *Stellera chamaejasme* Linn.) reduce overall forage quality and quantity and poison livestock, potentially leading to huge economic losses and hindering the healthy development of animal husbandry (Lu et al., 2012). For example, the economic losses were more than 20.3 million RMB, which resulted from killing about 1.03 million livestock by grazing toxic locoweed in Ali area of QTP (Zhao et al., 2012). Likewise, in the Tianzhu county, livestock foraged and ingested *Oxytropis kansuensis* Bunge, resulting in morbidity, abortion, and mortality rates of 89.1%, 29.0% and 21.9%, respectively (Li et al., 1987).

The standpoint that toxic plants are all bad is often based on emotional judgment, for example in alpine grassland, where they can cause immeasurable economic loss to local herders (Wang et al., 2014). From an ecological perspective, toxic plants in degraded grassland contribute to the survival of other neighbor plants, preventing them further to degenerate in the severe weather (Callaway et al., 2005; Zhang et al., 2020). These toxic plants are more tolerant of grazing pressure than desirable plants, as livestock consume them only when other palatable plants are tightly circumscribed (Wang et al., 2010). Moreover, the physiological and morphological traits of toxic plants (e.g., well-developed root systems) are beneficial for resisting drought and cold environments (Winter et al., 2011). Some toxic plants are rich in nutrients and are therefore a potential feed resource (Wang et al., 2010). For example, locoweeds (*Astragalus* spp. and *Oxytropis* spp.) have a crude protein content of 11–20%, so have the potential to be fed after processing for detoxification (Ralphs et al., 2002; Cook et al., 2009; Liu et al., 2020). The palatability of Larkspur (*Delphinium* spp.) increases with the toxicity declines in the mature stage (Pfister et al., 2002). Contrarily, livestock have a potentially fatal injure when they feed Larkspur between flowering and early pod stage (Pfister et al., 1996). Furthermore, toxic plants (e.g., *Oxytropis ochrocephala* Bunge. and *Stellera chamaejasme* Linn.) have definite potential to improve soil fertility by fixing nitrogen (Xu et al., 2013), reducing nitrate leaching and N_2O emissions (Ma et al., 2020). From the perspective of livestock, they also have the ability to detoxify a certain degree of ingested poisons or rendering the toxins ineffective (Callaway et al., 2005; Bergvall et al., 2006). Diversified diet of herbivores can dilute the toxicology of a toxic plant (Freeland and Saladin, 1989; Parikh et al., 2017). Likewise, mouth, gut and rumen environment of sheep, such as microbes, and antioxidant (i.e., SOD and T-AOC) may modify and degrade the plant toxin (Cheeke, 1994; Xie et al., 2020). For instance, the saliva of deer (a browsing ruminant) inactivates tannin toxic effects of tannin-rich shrubs essentially because of the proline-rich proteins they secrete in the saliva (Austin et al., 1989).

Alpine meadow has a rich and varied flora which includes a wide variety of toxic plants (Wu et al., 2015). In traditional view, the occurrence of toxic plants is equated with poor grassland condition and resulted in livestock loss (Keeler et al., 2013). However, the coevolution of toxic plants, livestock, and rumen microflora offers possibilities for toxic plants to become valuable at certain thresholds. For example, the threshold of phenolic content of toxic plant (*Acer pseudoplatanus* Linn.) was 56.5 mg/g DM for horses (Aboling et al., 2019). Thus, one challenge for indigenous herders and policymakers is to know the ecological thresholds of toxic plants and maintain their vital functions in ways that are compatible with economic income and ecological conservation. The toxicity threshold assessment is central to manage toxic plant resources (Sasaki et al., 2008), but threshold analysis of toxic plants for livestock production and ecosystem functions in alpine meadow remains unclear. Moreover, the trade-off between livestock production and ecological multifunctionality (EMF) in this region have not been assessed, particularly, the influence paths of toxic plants regulate the trade-offs are still not yet fully understood. Here, we conducted a field experiment under various Tibetan sheep grazing regimes to examine the objectives as follows: (1) to analyze and identify the thresholds (turning points) of toxic plants for liveweight gain (LWG) of sheep, Dry matter (DM) feed intake, and ecosystem functions; and (2) to explore the relationship between trade-offs of sheep production and EMF, and the driving mechanisms associated with environmental factors induced by toxic plants. The study site used for sheep grazing experiment was in Gannan, Gansu, on a representative and well-used alpine meadow as a part of the ACIAR project since 2004 (Kemp, 2020). The results of this study enrich our understanding of the function of toxic plants in ways that are compatible with sheep production and ecological conservation of Ganan alpine meadow. To our knowledge, this is the first analysis and report addressing the threshold's toxicity of plants to Tibetan sheep production under grazing conditions in grassland systems.

2. Methods and materials

2.1. Site description

The study site located in Maqu county (latitude 33°42′21″N, longitude 102°07′02″E), Gansu province in the east of QTP (Fig. 1a). The average elevation is 3650 m. The climate type of this region is typical plateau continental climate, which is characterized by cool, dry cold season and wet, humid warm season (Wang et al., 2020). The mean annual precipitation and temperature are 620 mm and 1.3 °C, respectively. 75% of the rainfall is distributed from June to September. The grassland type is alpine meadow, which consisted of sedges (*Kobresia graminifolia* C. B. Clarke.), legumes (*Oxytropis kansuensis* Bunge.), grasses (*Elymus nutans* Griseb. and *Poa pratensis* Linn.) and forbs (*Saussurea* species and *Anemone* species). The soil type is classified as alpine meadow soil. The common toxic plants of the site are *Ligularia virgaurea* Maxim, *Euphorbia esula* Linn, *Oxytropis kansuensis* Bunge, *Ranunculus tanguticus* Maxim, *Delphinium grandiflorum* Linn. and *Gentiana macrophylla* Pall. *etc.* (Table S1; Wu et al., 2015). The biomass (dry weight) of toxic plants ranged from 4.45 to 70.57 g/m^2 (Fig. S1) and richness of toxic plants ranged from 8 to 22 species per 0.25 m^2 (Fig. S1).

2.2. Field grazing experiment, sampling and measurements

Data was collected from the Tibetan sheep grazing experiment in alpine meadow conducted from 2010 to 2014. The detailed design of grazing experiment was provided in our previous studies (Sun et al., 2015; Wang et al., 2018). The key information linked to this study are given here (Table S2). The dimensions of the grazing experimental area were 24 ha. In each year, warm season grazing lasted for three months from the beginning of July to the later of September (Fig. 1b). The grazing regimes are included rotational grazing (two grazing intensity at 8 and 16 sheep/ha), and continuous grazing with grazing intensity of 8 sheep/ha. Eight sheep were stocked in each grazing plot at any time in rotational grazing and continuous grazing regimes. For rotational grazing, the grazing plot sizes were 1.0 and 0.5 ha with six replicates. For continuous grazing, the grazing plot size was 1.0 ha with three replicates (Table S2). Within each replicate of rotational grazing, the grazing plots were subdivided into three subdivisions and sheep were moved between the subdivisions every 10 days. The grazing plots of continuous grazing were not sub-divided and sheep were continuously stocked for 3 months. In total, there was 15 replicate grazing plots which used for measured plant characteristics, soil properties, liveweight gain (LWG) of sheep and dry matter (DM) feed intake. The terminology used here for describing grazing regimes were internationally accepted (Allen et al., 2011).

Plant characteristics. In aforementioned replicate grazing plots, three quadrats (0.5 m × 0.5 m) were randomly set to investigate the plant characteristics from July to September each year. In each quadrat, we measured the height of each species, then further to obtain

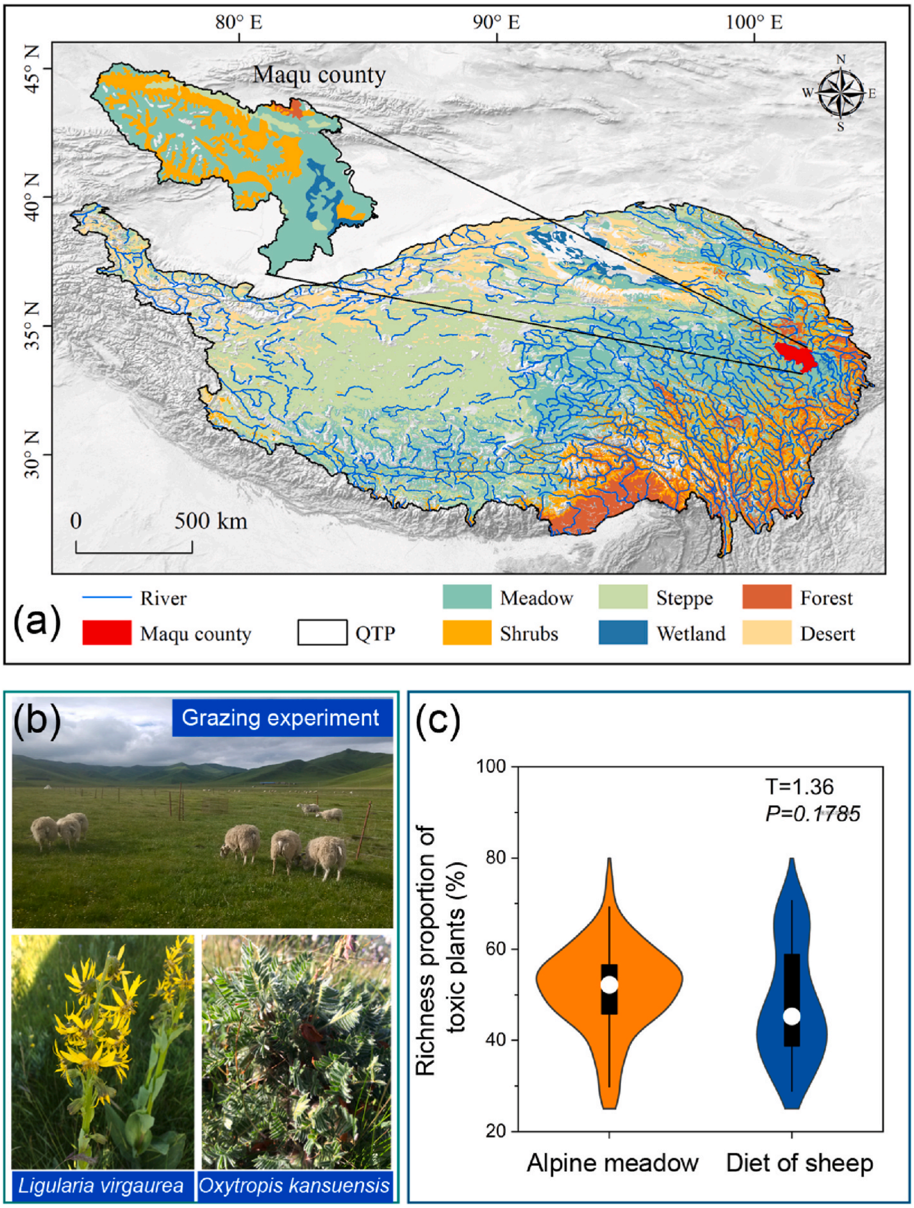

Fig. 1. Geographical location of the study site on the QTP (a); Sheep grazing experiment conducted in Maqu alpine meadow from 2010 to 2014. The typical toxic plants of the site are *Ligularia virgaurea* Maxim, and *Oxytropis kansuensis* Bunge (b). The photographs in Fig. 1b were taken by Yingxin Wang; The richness proportion of toxic plants in alpine meadow community (violin plot in orange) and diet composition of sheep (violin plot in blue). The significant difference with Tukey test estimated at 95% of confidence (c). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

community plant average height (PH). Plant species richness (SR) was indicated with total number of species. All aboveground parts of plants were cut away to separate each plant species, then oven-dried, weighed and summed as aboveground biomass (AGB). Likewise, biomass or richness of toxic plants was represented by the sum from biomass or richness of each toxic plants. In this study, four variables to assess toxic plants included biomass of toxic plants, biomass proportion of toxic plants, richness of toxic plants and richness proportion of toxic plants. Plant samples were ground using a mill (MM400, Retsch) and then sieved through a 100-mesh sample screen. Plant total nitrogen was determined with An Element Analyzer (Vario Macro CHNS) and then gain the crude protein (CP) content. Ankom 200 Fiber Analyzer (Ankom Technology) was used for analyze neutral detergent fiber (NDF) and acid detergent fiber (ADF) of plant.

Soil properties. In each quadrat which used for measured plant characteristics, we used TDR-300 soil moisture meter (Spectrum Technologies, Plainfield, IL, USA) to measure soil temperature (ST) and soil moisture (SM) of surface layer (0–10 cm). Soil was sampled at depth of 0–10 cm with soil auger (9 cm diameter). Root and soil fractions were separated. The root fractions were washed and weighed as belowground biomass (BGB) after drying. The soil fractions were sieved through a 100-mesh sample screen, then stored in a refrigerator at 4 °C for soil properties analyzing. The values of soil total nitrogen (STN) and soil total phosphorus (STP) were directly obtained from Element Analyzer. The traditional potassium dichromate oxidation method was used to measure soil organic carbon (SOC).

Liveweight gain (LWG) of sheep. At the beginning of the study, the average liveweights of sheep were 29.1 ± 3.0, 26.6 ± 2.2, 27.7 ± 2.4, 23.7 ± 1.2 and 33.1 ± 2.6 kg in 2010, 2011, 2012, 2013 and 2014, respectively. Values of original average liveweights were similar among the grazing regimes. The growth of sheep is described as an increase in live weight gain per unit of time (Blaxter et al., 1982). Each year and during the warm season, sheep were weighed at the beginning and end of each month (June to September). LWG of sheep per day in each replicate grazing plot was calculated by the difference between liveweights in the end of month and in the beginning of month then divided 30 days.

DM feed intake of sheep. For each replicate grazing plot, the difference of plant biomass after and before sheep grazing, corrected for plant biomass accumulation during restricted grazing period (5 days) was applied to estimate the DM feed intake of sheep (Smit et al., 2005; Du et al., 2017). Specifically, three buckle cages (1 × 1 × 1 m^3) were placed on the grassland in each grazing plots. On day 0, plant samples were collected from three quadrats (0.5 m × 0.5 m) randomly placed on the area outside of cage. On day 5, three plant samples were collected of both outside, and inside of the cage.

In addition, foraging activities of sheep included feeding behaviors and diet composition were recorded by us (trained observers) using telescopes (Du et al., 2017). Three sheep per grazing plot were randomly chosen and marked with a colored ribbon for observing diet composition of sheep in three consecutive days. The diet of each marked sheep was recorded at 30s intervals by direct observation methods (Harrington, 1986). First, we recorded the first plant was eaten by sheep within the first 5s of any 30s interval. Three sheep in each grazing plot were studied in rotation and each sheep was observed 2 times per day. In total, 270 observations (15 grazing plots × 3 sheep/plot × 3 days × 2 times/day) were recorded to analyze the diet composition of sheep. Second, the diet composition of sheep was separated three groups as desirable plants, toxic plants and shrubs, then calculated the richness proportion of toxic plants in the diet composition of sheep (Harrington, 1986).

2.3. Index calculation

Ecosystem multifunctionality (EMF). Four ecosystem functions including plant growth, plant quality, soil nutrient cycle and soil carbon sink to estimate EMF. Concretely, plant NDF, ADF and CP have been shown forage quality, while PH, SR, AGB and BGB represent vegetation structure (plant growth). ST, STN and STP represent soil nutrient cycling, while SOC, soil C: P and soil C: N represent soil carbon accumulation. We adopted the average approach (Maestre et al., 2012) to calculate the EMF, forage quality index (FQI), plant growth index (PGI), soil nutrient cycling index (SNI) and soil carbon accumulation index (SCI) (Wagg et al., 2014).

Trade-offs between LWG of sheep and EMF. As shown in Fig. S2, relative benefit for a single object (LWG of sheep/EMF) is defined as the deviation from the mean for a given observation (Bradford and D'Amato, 2012; Liu et al., 2022). The value of relative benefit (RB_i) for object A (LWG of sheep/EMF) is calculated by the following formula:

$$RB_i = \frac{X_i - minX_i}{maxX_i - minX_i}$$

where RB_i represents the relative benefit of i; X_i, $X_{\min}$, and $X_{\max}$ are the values of observed, minimum, and maximum for specified indicator (LWG of sheep or EMF), respectively.

The value of the trade-off between LWG of sheep and EMF was obtained via calculating RMSE of the individual *RB*. The detailed calculation method can see Sun and Wang (2016).

2.4. Statistical analysis

First, a Tukey's test with the "*agricolae*" package in R version 4.1.2 (R Development Core Team, 2021) was used to verify the differences for richness percentage of toxic plants between alpine meadow community and diet composition of sheep. The normality and distribution of data was checked with the Shapiro-Wilk goodness-of-fit test. Second, we performed partial correlation analyses by control year (to eliminate the heterogeneous effects of year on relationships analysis) through the "*ppcor*" package in R to compute the relationships between ecosystem functions and the variables of toxic plants, the relationships between LWG of sheep, EMF, their trade-offs and plant, soil properties (i.e., AGB, BGB, SR, PH, CP, ADF, NDF, SOC, STN and STP). Third, the linear piecewise quantile regression analysis was performed in Origin (2021b) (Origin Lab Corporation, Northampton, Massachusetts, USA) and "*chngpt*" package (Fong et al., 2017) was used in R to obtain the change points in LWG of sheep, DM feed intake, SR, PGI, FQI, SNI, SCI, EMF and the trade-offs between LWG of sheep and EMF along the gradient of biomass (richness) of toxic plants. Finally, structural equation model in IBM® SPSS® Amos™ 21 was constructed to examine the effects of toxic plants on the trade-off between LWG of sheep and EMF directly and indirectly via mediating multiple components (SR, ADF, BGB and STP). All graphs were constructed in Origin 2021b (OriginLab Corporation) and "*ggplot 2*" package in R software.

3. Results

3.1. Thresholds analysis of toxic plants for LWG of sheep and DM feed intake

Both LWG of sheep and DM feed intake increased first and then decreased along the gradient of toxic plants properties (Fig. 2). LWG of sheep was peaked when biomass of toxic plants was about 62 g/m^2 and richness of toxic plants was about 14 species per 0.25 m^2 (Fig. 2a and c). The threshold values of biomass proportion and richness proportion of toxic plants were 22% and 45% when LWG of sheep was the highest (Fig. 2b and d). Sheep DM feed intake reached the maximum when biomass of toxic plants was about 81 g/m^2 and richness of toxic plants was about 14 species per 0.25 m^2 (Fig. 2e and g). The changing point value of biomass proportion of toxic plants for sheep DM feed intake was 17% (Fig. 2g).

3.2. Thresholds analysis of toxic plants for ecosystem functions

Partial correlation analyses showed that both PGI and FQI (Fig. 3) were positively correlated with characteristic index of toxic plants ($P < 0.05$). The SCI and SNI were peaked when biomass of toxic plants was about 100 g/m^2 and 99 g/m^2 (Fig. 3m, q), and richness of toxic plants were about 14 and 13 species per 0.25 m^2 (Fig. 3o, s). The changing point value of biomass proportion and richness proportion of toxic plants for SCI were 31% (Fig. 3n) and 59% (Fig. 3p), and for SNI were 38% (Fig. 3r) and 42% (Fig. 3t). EMF reached the maximum when biomass of toxic plants was about 99 g/m^2 (Fig. 3u). The changing point value of biomass proportion and richness proportion of toxic plants for EMF were 28% (Fig. 3v) and 50% (Fig. 3x), respectively.

3.3. The trade-offs between LWG of sheep and EMF and their relationships with toxic plants

The value of trade-offs between LWG of sheep and EMF distributed from −0.3798 to 0.4316, and the mean value was 0.0462 ± 0.1830 (Fig. 4a). Linear piecewise quantile regression analysis indicated that the trade-offs first decreased and then increased along the gradient of biomass proportion of toxic plants (Fig. 4b). The turning value was 37% for biomass proportion of toxic plants (Fig. 4b). Also, there was a negative significant correlation ($P < 0.05$) between the trade-offs and richness of toxic plants (Fig. 4c).

3.4. Direct and indirect influences of toxic plant on the trade-off between LWG of sheep and EMF

LWG of sheep was significantly and positively correlated to CP (P < 05, R^2 = 0.32) (Fig. 5a). EMF was significantly related to SR ($P < 0.05$, R^2 = 0.52) and STP ($P < 0.05$, R^2 = 0.29) of alpine meadow (Fig. 5a). Results of SEM analysis indicated that standardized total effect coefficients of toxic plants on trade-off between LWG of sheep and EMF was −0.032 (Fig. 5b and c), which could be attributed to indirect affects through SR, BGB, ADF and STP rather than its direct affects (see Fig. 5c). Toxic plant had a significant positive correlation with SR and BGB (Fig. 5b), and in turn these had significant negative correlations with the trade-offs between LWG of sheep and EMF (Fig. 5b). In addition, toxic plants had a significantly ($P < 0.05$) indirect effect on the trade-off between LWG of sheep and EMF through its positive direct effect on

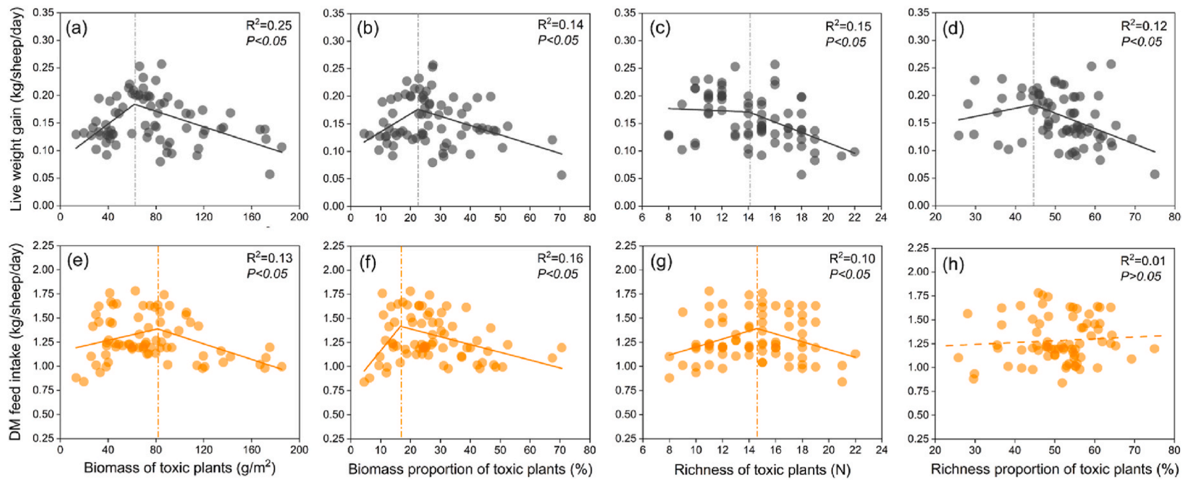

Fig. 2. Relationships between liveweight gain (LWG) of sheep and the variables of toxic plants (grey scatter plots) (a) biomass of toxic plants, (b) biomass proportion of toxic plants, (c) richness of toxic plants, (d) richness proportion of toxic plants. Relationships between DM feed intake and the variables of toxic plants (orange scatter plots) (e) biomass of toxic plants, (f) biomass proportion of toxic plants, (g) richness of toxic plants, (h) richness proportion of toxic plants. The relationships were analyzed through linear piecewise quantile regression analysis (a–g) and partial correlation analyses (h). The solid and dashed lines represent $P < 0.05$ and $P >$ 0.05, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

ADF with the standardized effect coefficient was 0.45 (Fig. 5b and c).

4. Discussion

4.1. Toxic plants and sheep production

Thresholds may represent the "maximum level of sheep production" to toxic plants, and comprised two parts: (1) the maintenance of sheep liveweight gain at moderate levels of toxic plants, and (2) the loss of sheep liveweight gain once toxic plants exceeds the threshold zone. Our finding indicated that the threshold value of biomass percentage of toxic plants for DM feed intake and LWG of sheep were 17% and 22%, respectively (Fig. 2a and c); the threshold of richness percentage of toxic plants for LWG of sheep was 45% (Fig. 2g). These salient findings are differed from traditional views that toxic plants damage sheep breeding, reduce sheep weights and poison even kill sheep (Zhao et al., 2012). We further found that there was no significant difference ($P = 0.1785$) for richness percentage of toxic plants in the diet composition of sheep and community composition of alpine meadow (Fig. 1c). Therefore, our results suggested that toxic plants within a certain threshold are benefited for improving sheep feed intake and promoting sheep body weight in alpine meadow. Likewise, numerous feeding experiments in shed demonstrated that beneficial effects of toxic plants addition on livestock's feed intake, immune function, rumen fermentation ability and production (Qiao et al., 2012; Liang et al., 2013). For example, addition levels of at 4% and 6% of *C. deserticola* Ma. promoted average live weight gain by 215.71 g/day and 142.86 g/day, respectively; and increased the ratio of feed conversion by 0.20 and 0.14, respectively (Liu et al., 2020). The mechanisms that regulate these phenomena included the reaction pathways in both domestic livestock and plant.

From the perspective of livestock, sheep have several behavioral and physiological strategies to degrade or detoxify certain plant toxins of toxic plants, and thus increase their feed intake in their diet (Callaway et al., 2005). First, the sheep can combine toxins in the mouth and gut through microbial action, or the absorbed toxins can be detoxed by various reactions in the stomach wall or liver (James et al., 1992). The complex formed in the mouth may protect against the impacts of plant toxins (Cheeke, 1994). Second, rumen environment of sheep (e. g, nearly neutral pH, massive microbes, antioxidant and secondary metabolite) may modify and degrade the plant toxin (Fig. 6; Xie et al., 2020). Third, sheep can dilute the toxicology of toxic plants by having diversified diet intake (Freeland and Saladin, 1989; Wang et al., 2010). For example, the ability of deer rumen microbiota to deal with plant secondary compounds from various sources higher than that from an individual source (Jean et al., 2016). Also, sheep might lick various clays for minerals and some clays naturally bind to various toxins. Therefore, geophagy may help deactivate plant toxins (Gilardi et al., 1999).

From the perspective of plant, toxic plants contain varying amounts of nutrients which are easily absorbed by sheep, and also contains kinds of pharmacological substances to improve the sheep disease resistance, then enhance nutrient absorption of sheep (Zhao et al., 2012). The results of this study indicated that LWG of sheep was driven by CP of plant (Fig. 5a). Compared with other plant species (e. g, *Kobresia graminifolia* C. B. Clarke. and *Elymus nutans* Griseb.), *Ligularia virgaurea* Maxim. and *Stellera chamaejasme* Linn. are more labile and have lower lignin and higher available nitrogen (An et al., 2016; Ma et al., 2019). For example, Qiao et al. (2012) reported that addition of *Fructus Ligustri Lucidi* (FLL, Nuzhenzi in Chinese) with the level of 300 or 500 mg/kg promoted DM digestibility of sheep by changing rumen microflora diversity and size. Then, greater nutrient absorption ability of sheep may result in higher sheep live weight gain. Consequently, we put forward a new category system of toxic plants based on both the livestock forage preference (Provenza, 2003; Allen et al., 2011) and seasonal toxicity of toxic plants (Fig. S3).

4.2. Toxic plants and ecosystem multifunctionality

Toxic plants are key components of alpine meadow ecosystem that support multiple ecological functions, such as pest control, attract pollinators and soil stability (Gaba et al., 2020). However, we still lack comprehensive insight about the effects of toxic plants on ecosystem multifunctionality of grassland ecosystem. Our results indicated that SR, SCI, SNI and EMF were positive when the ratio of biomass (richness) percentage of toxic plants was more than about 20% and less than about 50% (Fig. 3; Fig. 6). Unlike previous study (Zhang et al., 2017), our results indicated that plant growth index and forage quality index increased with biomass (richness) percentage of toxic plants increased (Fig. 3; Fig. 6). Toxic plants are rich in protein and trace elements, for example, the crude protein contents of *Oxytropis ochrocephala* Benth. was 15.3% (Bin et al., 2014). To the best of our knowledge, the results of this study were the first to explore the ecological thresholds of toxic plants to ecosystem multifunctionality in alpine meadow (Fig. 6). Our findings do not support the conventional opinions that toxic plants are uniformly deleterious and the main driver of grassland degradation (Gao

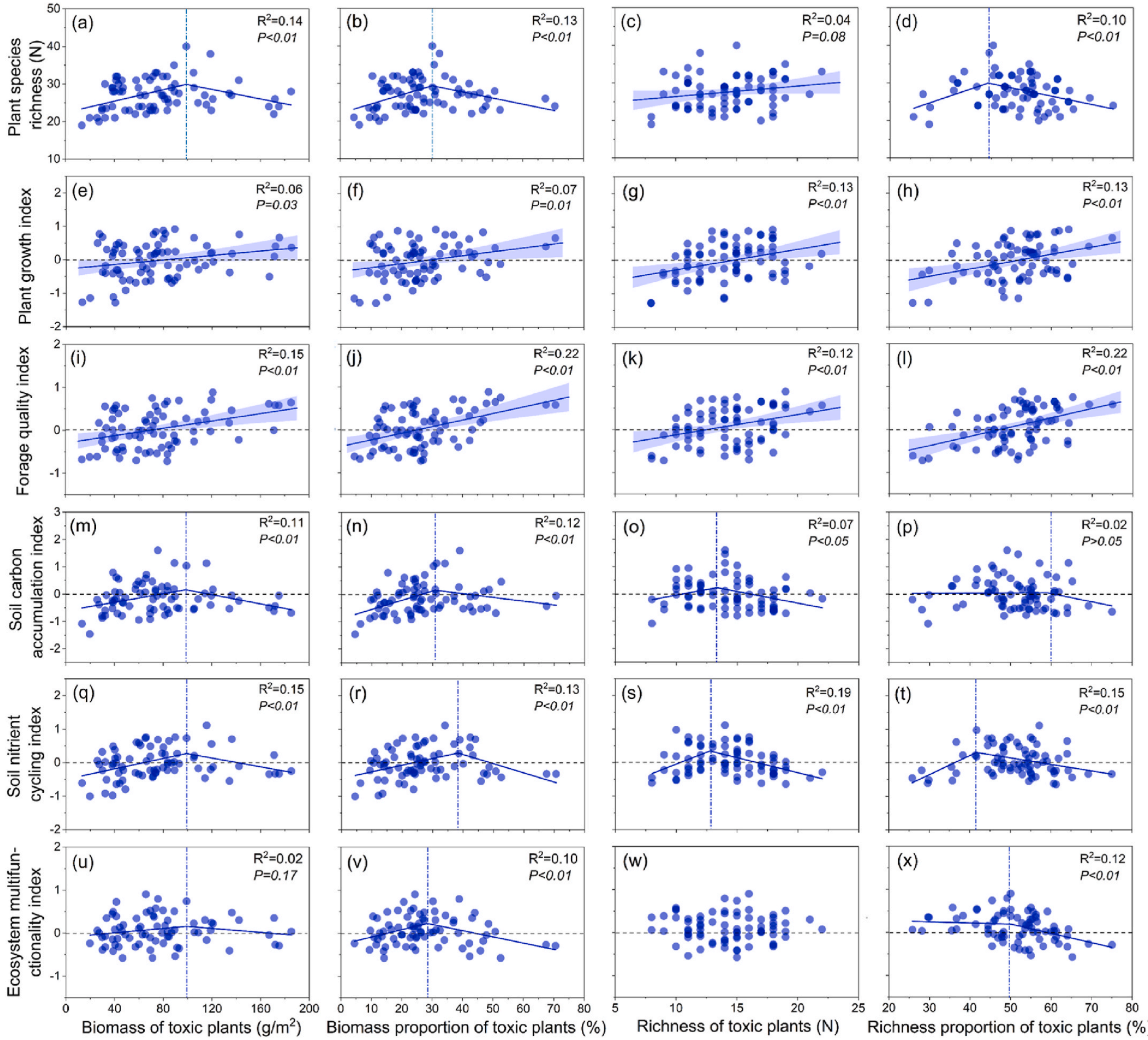

Fig. 3. Relationships between plant species richness (a, b, c & d), plant growth index (e, f, g & h), forage quality index (i, j, k & l), soil carbon accumulation index (m, n, o & p), soil nutrient cycling index (q, r, s & t), ecosystem multifunctionality index (u, v, w & x) and biomass (richness) of toxic plants, biomass (richness) proportion of toxic plants (blue scatter plots). The relationships were analyzed through linear piecewise quantile regression analysis and partial correlation analyses. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

et al., 2013). On the contrary, toxic plants can provide several ecological benefits by enhancing soil quality, providing biotic refuge for co-occurring plants and conservation of biodiversity (Callaway et al., 2005; Smit et al., 2006).

Majority of toxic plants have the ability to persist live in the nutrient-limited soils with their well-developed root system (Song et al., 2018). In the degraded sandy grassland, toxic plants can survive barren soils and wind erosion to establish their dominance vigorously (Zuo et al., 2009). For example, soil characteristics (e. g, soil nutrients, soil pH) have close relations to the presence of toxic plants (Li et al., 2014). Also, the decomposition and turnover of litter were increased through stimulating microbial activities by fertile island effect of toxic plants (Sun et al., 2009; Wan et al., 2021). As biological anti-herbivore refuges for desirable plants, toxic plants realize the goal through the following two aspects (Estapé et al., 2013). First, herbivores are difficult to forage the desirable plants or rejecting them directly on account of the toxins and odor of toxic plant (the neighbors of desirable plants) (McNaughton, 1978; Callaway et al., 2005). Second, micro-environmental conditions surrounding the patch of toxic plants are altered (Fig. 6). For example, soil nitrogen availability, microhabitat and litter turnover rates were promoted by *Stellera chamaejasme* Linn, and these changes provide a better microclimates and soil environment for co-occurring plant to growth (Sun et al., 2009). Besides, there are closely relationship between richness of toxic plants and pollinator diversity because of the greater temporal and spatial availability of pollen and nectar resources from toxic plants (Russell et al., 2021). The purple, blue and lavender flower colors of *Gentiana* Tourn., *Delphinium grandiflorum* Linn. and *Iris lacteal* Pall. raise the reproductive rate of plant by attracting more pollinators (Zhang et al., 2020), Simultaneity, the increases of insects and invertebrate's diversity facilitate the biodiversity maintenance (Wang

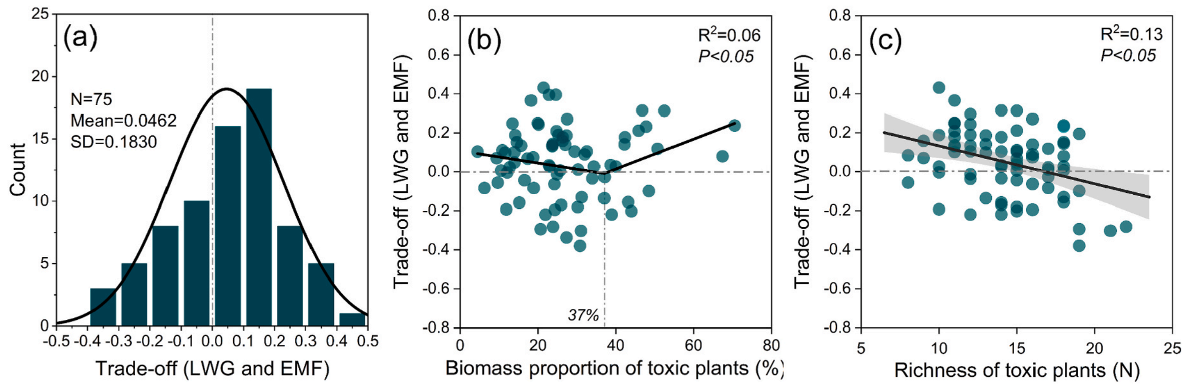

Fig. 4. Trade-offs between LWG of sheep and EMF (a), and their relations to biomass proportion of toxic plants (b) and richness of toxic plants (c). The relationships were analyzed through linear piecewise quantile regression analysis (b) and partial correlation analyses (c).

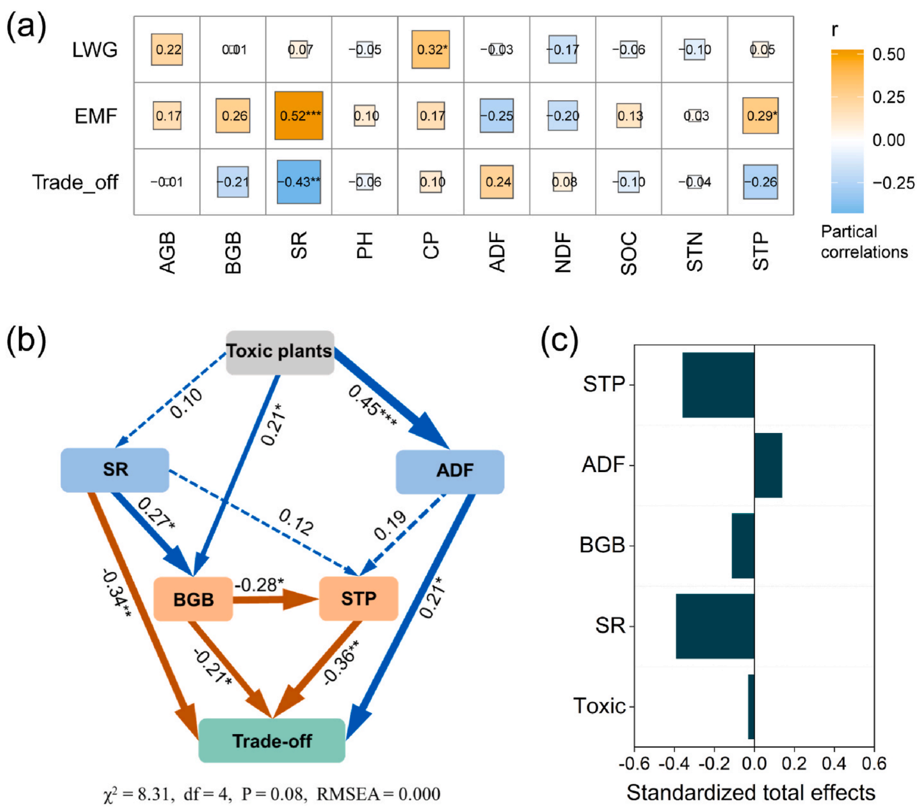

Fig. 5. Partial correlations among LWG, EMF and their trade-off with plant and properties (a). The numbers and colors in the square represent the correlation strengths. *: P < 0.05, **: P < 0.01, ***: P < 0.001. Structural equation model exhibits the connections between the toxic plant, SR (species richness), ADF (acid detergent fiber), BGB (belowground biomass), STP (soil total phosphorus) with Trade-off (trade-off between LWG of sheep and EMF) in alpine meadow (b & c). Orange and blue arrows indicate negative and positive relations, respectively. The arrows width indicates the strength of relationships. Value adjacent to the arrows are standardized path coefficients. Dashed arrows represent no significant relationships ($P > 0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

et al., 2014). Overall, the improvement of soil physicochemical properties and protection of co-occurring plant by toxic plants probably provide the explanations and evidences for toxic plants within an ecological threshold promote plant diversity and ecosystem multifunctionality in alpine meadow.

4.3. Toxic pant and trade-offs between LWG of sheep and EMF

Managing alpine meadow ecosystems for multiple service functions and balancing the interests of diverse stakeholders involves various trade-offs (Daw et al., 2015), such as the trade-off between LWG of sheep and EMF. In this study, we considered the crucial roles of toxic plants on the trade-off between LWG of sheep and EMF and elucidated that there was a concave-down relationship between them (Fig. 4b). Furthermore, plant and soil parameters (e.g., ADF, SR, BGB and STP) probably were the regulatory factors that affecting the relationships (Fig. 5). Thus, the economic threshold and ecological threshold of toxic plants were inconsistent. Toxic plants do not endanger the ecological balance of alpine meadow when that reach the maximum capacity of sheep production. That is, the economic thresholds should be taken as the control index to manage toxic pant in alpine meadow. A previous study reported that EMF was determined by plant species richness and soil nutrients (Jing et al., 2015). Our results also indicated that SR were positively related to toxic plants (Fig. S4). This further provide the explanation that toxic plants can influence the trade-off between LWG of sheep and EMF via reducing the SR of grassland.

4.4. Limitations of this study

Our study demonstrates that toxic plants at certain rates affect positively liveweight gain of sheep, ecosystem multifunctionality. However, this work was conducted in an “alpine meadow-Tibetan

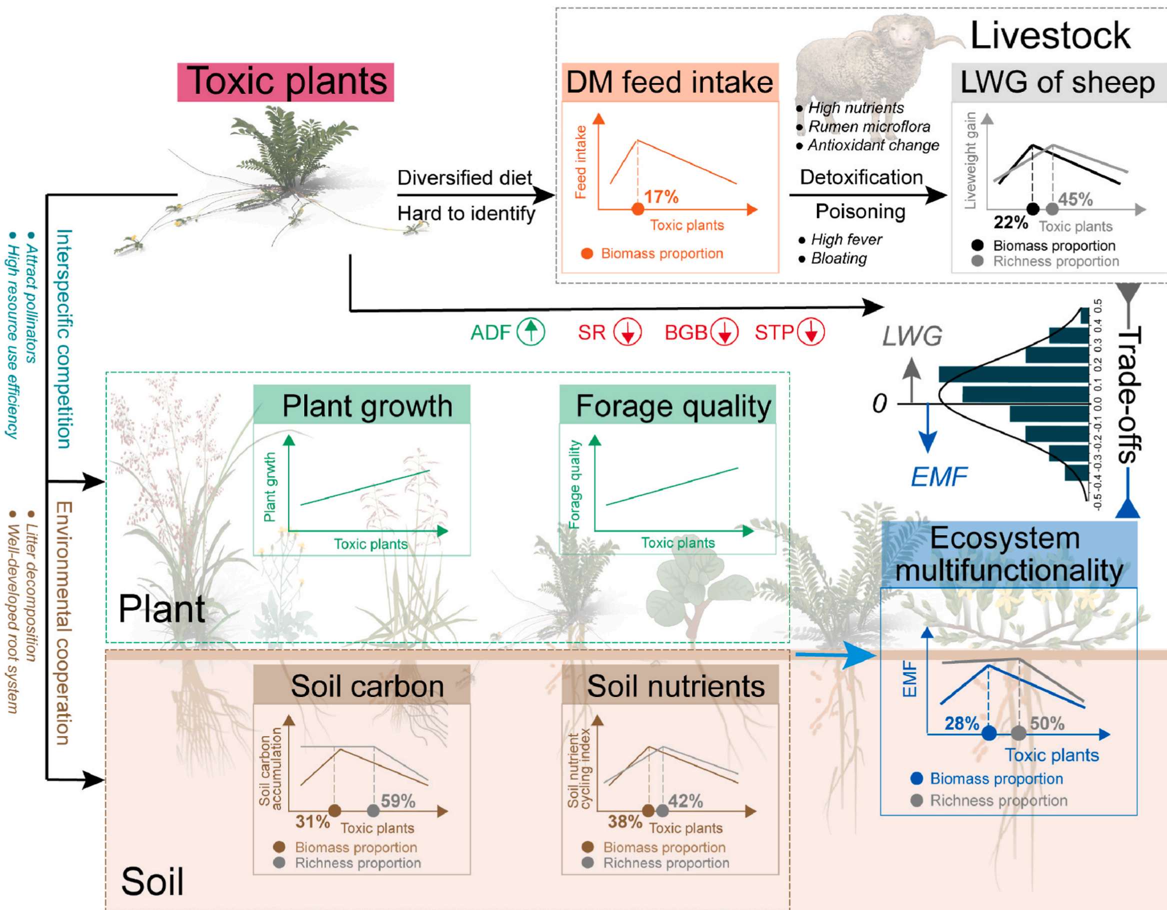

Fig. 6. Schematic diagram illustrating the effects (threshold analysis) of toxic plants on livestock production, grassland ecosystem functions and their trade-offs. From the perspective of livestock, toxic plants contribute to sheep production through the balance of detoxification and poisoning progresses. The adaptive strategies of toxic plants for grassland ecosystem functions were included interspecific competition and environmental cooperation. Trade-offs between LWG of sheep and EMF was regulated by toxic plants via increasing the ADF content of plant and decreasing plant species richness, belowground biomass and total phosphorus of soil.

sheep" grazing system. Whether the findings of the study are applicable to other grassland types and livestock still need further to be verified because of because of the feeding behaviors and nutritional ecology (Gordon and Prins, 2008) are different among different livestock (such as cows and horses). Considering the toxic plants with the same level of toxicity will certainly reduce the quality of the information, each plant has its specificities. Feed experiments in the pen are necessary to conduct to obtain the toxicology thresholds with supplementing different levels of toxic plants. Thresholds management of toxic plants for multiple functions is central for sustainable development of grassland. More wide-spread assessment of toxic plants thresholds for multiple services and functions across diverse grasslands worldwide are need in future.

5. Conclusions

Taken together, our study provided novel evidence that toxic plants at certain thresholds can improve sheep production, and facilitate ecosystem functions of alpine meadow. Specially, we identified and captured the turning point values of toxic plants for DM feed intake, LWG of sheep, EMF and their trade-off. Our result indicated that the sensitivity of livestock indicators to toxic plants were greater than that of ecological indicators to toxic plants. Moreover, the trade-offs between LWG of sheep and EMF was regulated by toxic plants via altering the key plant and soil parameters (e.g., ADF, SR, BGB and STP). The findings of this study suggest that opinions towards toxic plants should shift from the conventional view that they are serious threat to grassland ecosystem health to an inclusive understanding that they are beneficial to sheep and ecosystem functions under certain ecological thresholds.

Credit author statement

Yingxin Wang, **Yi Sun** and **Fujiang Hou** conceived the ideas and designed the methodology; **Yingxin Wang, Yi Sun, Yang Liu, Zhaofeng Wang** and **Shenghua Chang** collected the data; **Yingxin Wang** and **Yongqiang Qian** analyzed the data; **Yingxin Wang Jianmin Chu** and **Fujiang Hou** led the writing of the manuscript. All of the authors contributed critically to the drafts and gave their final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests of personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This study was jointly supported by the National Natural Science Foundation of China (32161143028); the Program of National Science and Technology Assistance (KY202002011); the Program for Innovative Research Team of Ministry of Education (IRT17R50) and the Basic Research Fund of National Non-profit Research Institutions (No. CAFYBB2019ZE001). We thank Shuaijun Hou, Yuhui Tan and Zhe Wu for their substantial assistance. Special thanks Ken Hodgkinson and Roger Davies for providing valuable comments and fruitful help.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2022.116167.

References

Aboling, S., Scharmann, F., Bunzel, D., Kulling, S., 2019. Negative Selection of Sycamore Maple Seedlings (*Acer Pseudoplatanus*) in Pasture Horses Is Mediated through Phenolic Compounds (in preparation).

Allen, V.G., Batello, C., Berretta, E.J., Hodgson, J., Kothmann, M., Li, X.L., Mclvor, J., Milne, J., Peter, A., Sanderson, M., 2011. An international terminology for grazing lands and grazing animals. Grass Forage Sci. 66, 2–28. https://doi.org/10.1111/j.1365-2494.2010.00780.x.

An, D.Y., Han, L., Ju-Ying, W.U., Chen, J., Jiang, Y.Y., Liu, Y., Amp, B., 2016. Effects of *Stellera chamaejasme* on soil properties of grassland in farming-pastoral zone in North China. Acta Agrestia Sinica 24, 559–567. https://doi.org/10.11733/j.issn.1007-0435.2016.03.012.

Austin, P.J., Suchar, L.A., Robbins, C.T., Hagerman, A.E., 1989. Tannin-binding proteins in saliva of deer and their absence in saliva of sheep and cattle. J. Chem. Ecol. 15 (4), 1335–1347. https://doi.org/10.1007/BF01014834.

Blaxter, K.L., Fowler, V.R., Gill, J.C., 1982. A study of the growth of sheep to maturity. J. Agric. Sci. 98 (2), 405–420. https://doi.org/10.1017/S0021859600041952.

Bradford, J.B., D'Amato, A.W., 2012. Recognizing trade-offs in multi-objective land management. Front. Ecol. Environ. 10 (4), 210–216. https://doi.org/10.1890/110031.

Bergvall, U.A., Rautio, P., Kesti, K., Leimar, T.O., 2006. Associational effects of plant defences in relation to within- and between-patch food choice by a mammalian herbivore: neighbour contrast susceptibility and defence. Oecologia 147 (2), 253–260. https://doi.org/10.2307/20445822.

Bin, Z.J., Wang, J.J., Zhang, W.P., Xu, D.H., Cheng, X.H., Li, K.J., Cao, D.H., 2014. Effects of N addition on ecological stoichiometric characteristics in six dominant plant species of alpine meadow on the Qinghai-Xizang Plateau, China. Chin J Plant Ecol 38 (3), 231–237. https://doi.org/10.3724/SP.J.1258.2014.00020.

Callaway, R.M., Kikodze, D., Chiboshvili, M., Khetsuriani, L., 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. Ecology 86 (7), 1856–1862. https://doi.org/10.1890/04-0784.

Cheeke, P.R., 1994. A review of the functional and evolutionary roles of the liver in the detoxification of poisonous plants, with special reference to pyrrolizidine alkaloids. Vet. Hum. Toxicol. 36 (3), 240–247. https://doi.org/10.1016/0041-0101(94)90344-1.

Cook, D., Ralphs, M., Welch, K., Stegelmeier, B., 2009. Locoweed poisoning in livestock. Rangelands 31 (1), 16–21. https://doi.org/10.2111/1551-501X-31.1.16.

Daw, T.M., Coulthard, S., Cheung, W.W.L., Brown, K., Munyi, L., 2015. Evaluating taboo trade-offs in ecosystems services and human well-being. P Natl Acad Sci USA 112 (22), 6949–6954. https://doi.org/10.1073/pnas.1414900112.

Du, W.C., Yan, T.H., Chang, S.H., Wang, Z.F., Hou, F.J., 2017. Seasonal hogget grazing as a potential alternative grazing system for the Qinghai-Tibetan Plateau: weight gain and animal behaviour under continuous or rotational grazing at high or low stocking rates. Rangel. J. 39 (5), 329–339. https://doi.org/10.1071/RJ16119.

Estapé, S.E.N., Semmartin, M., Paruelo, J.M., 2013. Refuge effect of an unpalatable forb on community structure and grass morphology in a temperate grassland. Plant Ecol. 214 (3), 363–372. https://doi.org/10.1007/s11258-013-0173-2.

Fong, Y., Huang, Y., Gilbert, P.B., Permar, S.R., 2017. *chngpt*: threshold regression model estimation and inference. BMC Bioinf. 18 (1), 1–7. https://doi.org/10.1186/s12859-017-1863-x.

Freeland, W.J., Saladin, L.R., 1989. Choice of mixed diets by herbivores: the idiosyncratic effects of plant secondary compounds. Biochem. Systemat. Ecol. 17 (6), 493–497. https://doi.org/10.1016/0305-1978(89)90029-X.

Gaba, S., Cheviron, N., Perrot, T., Piutti, Séverine, Gautier, J., Bretagnolle, V., 2020. Weeds enhance multifunctionality in arable lands in south-west of France. Front. Sustain. Food Syst. 4, 71. https://doi.org/10.3389/fsufs.2020.00071.

Gao, X.L., Zhao, M.L., Jing, W., Han, B., Willms, W., 2013. Strategies on Poisonous Plants Problem in China. Revitalising Grasslands to Sustain Our Communities: Proceedings, 22nd International Grassland Congress, 15-19 September, 2013. New South Wales Department of Primary Industry, Sydney, Australia.

Gilardi, J.D., Duffey, S.S., Munn, C.A., Tell, L.A., 1999. Biochemical functions of geophagy in parrots: detoxification of dietary toxins and cytoprotective effects. J. Chem. Ecol. 25 (4), 897–922. https://doi.org/10.1023/A:1020857120217.

Gordon, I.J., Prins, H., 2008. The Ecology of Browsing and Grazing. Springer Berlin Heidelberg.

Harrington, G.N., 1986. Herbivore diet in a semi-arid *Eucalyptus populnea* woodland. 1. Merino sheep. Aust. J. Exp. Agric. 26 (4), 413–421. https://doi.org/10.1071/EA9860413.

Hierro, J.L., Callaway, R.M., 2003. Allelopathy and exotic plant invasion. Plant Soil 256, 29–39. https://doi.org/10.1023/A:1026208327014.

James, L.F., Panter, K.E., Nielsen, D.B., Molyneux, R.J., 1992. The effect of natural toxins on reproduction in livestock. J. Anim. Sci. 70 (5), 1573–1579. https://doi.org/10.2527/1992.7051573x.

Jean, P.O., Bradley, R.L., Berthiaume, R., Tremblay, J.P., 2016. Evaluating old and novel proxies for in vitro digestion assays in wild ruminants. Wildl. Soc. Bull. 40 (2), 359–367. https://doi.org/10.1002/wsb.663.

Jing, X., Sanders, N.J., Shi, Y., Chu, H., Classen, A.T., Zhao, K., Chen, L.T., Shi, Y., Jiang, Y.X., He, J.S., 2015. The links between ecosystem multifunctionality and above- and belowground biodiversity are mediated by climate. Nat. Commun. 6 (6), 8159 https://doi.org/10.1038/ncomms9159.

Keeler, R.F., Van Kampen, K.R., James, L.F. (Eds.), 2013. Effects of Poisonous Plants on Livestock. Elsevier.

Kemp, D., Han, G.D., Hou, F.J., Hou, X.Y., Li, Z.G., Sun, Y., 2018. Sustainable management of Chinese grasslands-issues and knowledge. Frontiers of Agricultural Science and Engineering 5, 9–23. https://doi.org/10.15302/J-FASE-2018204.

Kemp, D.R., 2020. Sustainable Chinese Grasslands. Australian Centre for International Agricultural Research, Canberra.

Li, J.K., Yang, J.T., Pan, H.P., Tang, Z.X., 1987. Investigation on livestock poisoning of *Oxytropis kansuensis* Bunge and *Oxytropis ochrocephala* Bunge. Vet. Sci. Commun. 5, 22–23.

Li, Y.Y., Dong, S.K., Wen, L., Wang, X.X., Wu, Y., 2014. Soil carbon and nitrogen pools and their relationship to plant and soil dynamics of degraded and artificially restored grasslands of the Qinghai-Tibetan Plateau. Geoderma 213, 178–184. https://doi.org/10.1016/j.geoderma.2013.08.022.

Liang, X., Yamazaki, K., Kamruzzaman, M., Bi, X., Panthee, A., Sano, H., 2013. Effects of Chinese herbal medicine on plasma glucose, protein and energy metabolism in sheep. J. Anim. Sci. Biotechnol. 4, 51–57. https://doi.org/10.1186/2049-1891-4-51.

Liu, X.L., Liu, F.Y., Yan, T.H., Chang, S.H., Wanapat, M., Hou, F.J., 2020. *Cistanche deserticola* addition improves growth, digestibility, and metabolism of sheep fed on fresh forage from alfalfa/tall fescue pasture. Animals 10, 668. https://doi.org/10.3390/ani10040668.

Liu, M., He, W., Zhang, Z.C., Sun, J., Cong, N., Nie, X.W., Wang, Y.F., Zhang, L., Yang, B., Chen, Y.C., Zhou, H.K., Shao, X.Q., Wang, Y.X., 2022. Mutual feedback between above- and below-ground controls the restoration of alpine ecosystem multifunctionality in long-term grazing exclusion. J. Clean. Prod. 333, 130184 https://doi.org/10.1016/j.jclepro.2021.130184.

Lu, H., Wang, S.S., Zhou, Q.W., Zhao, Y.N., Zhao, B.Y., 2012. Damage and control of major poisonous plants in the western grasslands of China - a review. Rangel. J. 34, 329–339. https://doi.org/10.1071/RJ12057.

Ma, J.G., Hou, F.J., Bowatte, S., 2019. Effects of toxic plants on soil physicochemical properties and soil microbial abundance in an alpine meadow on the Qinghai-Tibetan Plateau. Pratacult. Sci. 36 (12), 3033–3040. https://doi.org/10.11829/j.issn.1001-0629.2019-0405.

Ma, J.G., Bowatte, S., Wang, Y.F., Newton, P., Hou, F.J., 2020. Differences in soil ammonia oxidizing bacterial communities under unpalatable (*Stellera chamaejasme* L.) and palatable (*Elymus nutans* Griseb.) plants growing on the Qinghai Tibetan Plateau. Soil Biol. Biochem. 144, 107779 https://doi.org/10.1016/j.soilbio.2020.107779.

Maestre, F.T., Castillo-Monroy, A.P., Bowker, M.A., Ochoa-Hueso, R., 2012. Species richness effects on ecosystem multifunctionality depend on evenness, composition and spatial pattern. J. Ecol. 100 (2), 317–330. https://doi.org/10.1111/j.1365-2745.2011.01918.x.

McNaughton, 1978. Stability and diversity of ecological communities. Nature 274, 251–253. https://doi.org/10.1038/274251a0.

Parikh, G.L., Forbey, J.S., Robb, B., Peterson, R.O., Vucetich, L.M., Vucetich, J.A., 2017. The influence of plant defensive chemicals, diet composition, and winter severity on the nutritional condition of a free-ranging, generalist herbivore. Oikos 126 (2), 196–203. https://doi.org/10.1111/oik.03359.

Pfister, J.A., Manners, G.D., Gardner, D.R., Price, K.W., Ralphs, M.H., 1996. Influence of alkaloid concentration on acceptability of tall larkspur (delphinium spp.) to cattle and sheep. J. Chem. Ecol. 22 (6), 1147–1168. https://doi.org/10.1007/BF02027951.

Pfister, J.A., Ralphs, M.H., Gardner, D.R., Stegelmeier, B.L., Manners, G.D., Panter, K.E., Lee, S.T., 2002. Management of three toxic Delphinium species based on alkaloid concentrations. Biochem. Systemat. Ecol. 30 (2), 129–138. https://doi.org/10.1016/S0305-1978(01)00124-7.

Provenza, F.D., 2003. Foraging Behavior: Managing to Survive in a World of Change: Behavioral Principles for Human, Animal, Vegetation, and Ecosystem Management. Utah State Univ., Department of Forest, Range, and Wildlife Sciences.

Qiao, G.H., Zhou, X.H., Li, Y., Zhang, H.S., Li, J.H., Wang, C.M., Lu, Y., 2012. Effect of several supplemental Chinese herb's additives on rumen fermentation, antioxidant function and nutrient digestibility in sheep. J Anim Physiol An N 96 (5), 930–938. https://doi.org/10.1111/j.1439-0396.2011.01211.x.

R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/.

Ralphs, M.H., 2005. Conditioning sheep to graze duncecap larkspur (*delphinium occidentale*). Rangel. Ecol. Manag. 58 (6), 628–631. https://doi.org/10.2111/05-014R2.1.

Ralphs, M.H., Greathouse, G.A.R.Y., Knight, A.P., Doherty, D., Graham, J.D., Stegelmeier, B.L., James, L.F., 2002. Prior feeding practices do not influence locoweed consumption. J. Range Manag. 55 (4), 390–393.

Ralphs, M.H., Sharp, L.A., 2019. Management to reduce livestock loss from poisonous plants. In: The Ecology and Economic Impact of Poisonous Plants on Livestock Production. CRC Press, pp. 391–405.

Russell, A.L., Fetters, A.M., James, E.I., Ashman, T.L., 2021. Pollinator effectiveness is affected by intraindividual behavioral variation. Oecologia 197 (1), 189–200. https://doi.org/10.1007/s00442-021-05016-4.

Sasaki, T., Okayasu, T., Jamsran, U., Takeuchi, K., 2008. Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. J. Ecol. 96 (1), 145–154. https://doi.org/10.1111/j.1365-2745.2007.01315.x.

Smit, H.J., Taweel, H.Z., Tas, B.M., Tamminga, S., Elgersma, A., 2005. Comparison of techniques for estimating herbage intake of grazing dairy cows. J. Dairy Sci. 88, 1827–1836. https://doi.org/10.3168/jds.S0022-0302(05)72857-5.

Smit, C., Den Ouden, J., Müller-Schärer, H., 2006. Unpalatable plants facilitate tree sapling survival in wooded pastures. J. Appl. Ecol. 43 (2), 305–312. https://doi.org/10.1111/j.1365-2664.2006.01147.x.

Sun, G., Luo, P., Wu, N., Qiu, P.F., Gao, Y.H., Chen, H., Shi, F.S., 2009. *Stellera chamaejasme* L. increases soil N availability, turnover rates and microbial biomass in an alpine meadow ecosystem on the eastern Tibetan Plateau of China. Soil Biol. Biochem. 41, 86–91. https://doi.org/10.1016/j.soilb io.2008.09.022.

Sun, J., Wang, H.M., 2016. Soil nitrogen and carbon determine the trade-off of the above- and below-ground biomass across alpine grasslands, Tibetan Plateau. Ecol. Indicat. 60, 1070–1076. https://doi.org/10.1016/j.ecolind.2015.08.038.

Song, A.Y., Dong, L.S., Liu, S.R., Liu, J.T., 2018. Soil infiltration characteristics and its influencing factors in different subalpine meadow communities. Res. Soil Water Conserv. 25, 41–45.

Sun, Y., Angerer, J.P., Hou, F.J., 2015. Effects of grazing systems on herbage mass and liveweight gain of Tibetan sheep in eastern Qinghai-Tibetan Plateau, China. Rangel. J. 37, 181–190. https://doi.org/10.1071/RJ14062.

Wagg, C., Bender, S.F., Widmer, F., van der Heijden, M.G.A., 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. P Natl Acade Sci USA 111 (14), 5266–5270. https://doi.org/10.1073/pnas.1320054111.

Wan, W., Gadd, G.M., Yang, Y., Yuan, W., Liu, W., 2021. Environmental adaptation is stronger for abundant rather than rare microorganisms in wetland soils from the Qinghai-Tibet Plateau. Mol. Ecol. 30 (10), 2390–2403. https://doi.org/10.1111/mec.15882.

Wang, L., Wang, D.L., He, Z., Liu, G.F., Hodgkinson, K.C., 2010. Mechanisms linking plant species richness to foraging of a large herbivore. J. Appl. Ecol. 47 (4), 868–875. https://doi.org/10.1111/j.1365-2664.2010.01837.x.

Wang, Y.X., Wang, Z.F., Chang, S.H., Hou, F.J., 2014. The roles of toxic and harmful grass in grassland Agro-ecosystems. Pratacult. Sci. 31 (3), 381–387. https://doi.org/10.11829/j. issn.1001-0629.2013-0720.

Wang, Y.X., Hodgkinson, K.C., Hou, F.J., Wang, Z.F., Chang, S.H., 2018. An evaluation of government-recommended stocking systems for sustaining pastoral businesses and ecosystems of the Alpine Meadows of the Qinghai-Tibetan Plateau. Ecol. Evol. 8 (8), 4252–4264. https://doi.org/10.1002/ece3.3960.

Wang, Y.X., Zhang, X.L., Sun, Y., Chang, S.H., Wang, Z.F., Li, G., Hou, F.J., 2020. Pika burrow and zokor mound density and their relationship with grazing management and sheep production in alpine meadow. Ecosphere 11 (5), e03088. https://doi.org/10.1002/ecs2.3088.

Welch, K.D., Lee, S.T., Cook, D., Gardner, D.R., Pfister, J.A., 2018. Chemical analysis of plants that poison livestock: successes, challenges, and opportunities. J. Agric. Food Chem. 66 (13), 3308–3314. https://doi.org/10.1021/acs.jafc.8b00337.

Winter, S., Penker, M., Kriechbaum, M., 2011. Integrating farmers' knowledge on toxic plants and grassland management: a case study on Colchicum autumnalein Austria. Biodivers. Conserv. 20 (8), 1763–1787. https://doi.org/10.1007/s10531-011-0060-x.

Wu, J.S., Yang, P.W., Zhang, X.Z., Shen, Z.X., Yu, C.Q., 2015. Spatial and climatic patterns of the relative abundance of poisonous vs. non-poisonous plants across the Northern Tibetan Plateau. Environ. Monit. Assess. 187, 491. https://doi.org/10.1007/s10661-015-4707-z.

Xie, K.L., Wang, Z.F., Wang, Y.J., Wang, C.M., Chang, S.H., Zhang, C., Zhu, W.H., Hou, F. J., 2020. Effects of *Allium mongolicum* regel supplementation on the digestibility, methane production, and antioxidant capacity of Simmental calves in northwest China. Anim. Sci. J. 91 (1), e13392 https://doi.org/10.1111/asj.13392.

Xu, L., Zhang, Y., Deng, Z.S., Zhao, L., Wei, X.L., Wei, G.H., 2013. *Rhizobium qilianshanense* sp. nov., a novel species isolated from root nodule of *Oxytropis ochrocephala* Bunge in China. Antonie Leeuwenhoek 103 (3), 559–565. https://doi.org/10.1007/s10482-012-9840-x.

Zhang, H.X., Zhang, M.L., Wang, Y., 2017. Distribution pattern of poisonous plant species in arid grasslands: a case from Xinjiang, Northwestern China. Rangel. J. 39 (3), 279–287. https://doi.org/10.1071/RJ16018.

Zhang, Z.C., Sun, J., Liu, M., Xu, M., Wang, Y., Wu, G.L., Zhou, H.K., Ye, C.C., Tsechoe, D., Wei, T.X., 2020. Don't judge toxic weeds on whether they are native but on their ecological effects. Ecol. Evol. 10, 9014–9025. https://doi.org/10.1002/ece3.6609.

Zhao, M.L., Gao, X.L., Wang, J., He, X.L., Han, B., 2012. A review of the most economically important poisonous plants to the livestock industry on temperate grasslands of China. J. Appl. Toxicol. 33 (1), 9–17. https://doi.org/10.1002/jat.2789.

Zuo, X.A., Zhao, X.Y., Zhao, H.L., Zhang, T.H., Guo, Y.R., Li, Y.Q., Huang, Y.X., 2009. Spatial heterogeneity of soil properties and vegetation-soil relationships following vegetation restoration of mobile dunes in Horqin Sandy Land, Northern China. Plant Soil 318 (1–2), 153–167. https://doi.org/10.1007/s11104-008-9826-7.