

1 Mixed-cultivated grasslands enhance runoff generation and reduce soil loss in the restoration of
2 degraded alpine hillsides

3 Yulei Ma¹, Yifan Liu^{1,2}, Jesús Rodrigo-Comino³, Manuel López-Vicente⁴, Gao-Lin Wu^{1,2,5,*}

4 ¹ *State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, College of Soil
5 and Water Conservation Science and Engineering (Institute of Soil and Water Conservation),
6 Northwest A & F University, Yangling, Shaanxi 712100, China*

7 ² *Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water
8 Resource, Yangling, Shaanxi 712100, China*

9 ³ *Departamento de Análisis Geográfico Regional y Geografía Física, Facultad de Filosofía y Letras,
10 Campus Universitario de Cartuja, University of Granada, Granada, Spain*

11 ⁴ *Group Aquaterra, Interdisciplinary Centre of Chemistry and Biology, CICA-UDC, Universidade da
12 Coruña, 15071 A Coruña, Spain*

13 ⁵ *CAS Center for Excellence in Quaternary Science and Global Change, Xi'an, 710061, China*

14 ***Correspondence author:** Gao-Lin Wu, e-mail: wugaolin@nwsuaf.edu.cn (G.L. Wu).

15 **Correspondence address:** State Key Laboratory of Soil Erosion and Dryland Farming on the Loess
16 Plateau, Northwest A & F University, No 26, Xinong Road, Yangling, Shaanxi 712100, P.R. China

17 Phone: +86- (29) 87012884 Fax: +86- (29) 87016082

18 **ABSTRACT**

19 Vegetation restoration is among the most effective measures for controlling runoff and soil erosion
20 resulting from human activity. Nevertheless, few studies have been undertaken to analyze the effects
21 of grassland restoration on maintaining local runoff, especially, in alpine degraded hillsides where
22 mixed-cultivated grasslands predominate. In this research, runoff plots were established to investigate
23 the impact of three mixed-cultivated grasslands, each sowing two grass species per plot: *Deschampsia*
24 *cespitosa* and *Elymus nutans* (*DE*), *Poa pratensis* L.cv. Qinghai and *Elymus nutans* (*PE*), and *Poa*
25 *pratensis* L.cv. Qinghai and *Deschampsia cespitosa* (*PD*); on a 20-degree slope, assessing the
26 activation and volume of surface runoff and the magnitude of soil loss in alpine degraded hillsides
27 over three years: 2019, 2020 and 2022. A severely degraded meadow (*SDM*) plot was used as control.
28 The findings indicated that mixed-cultivated grasslands can effectively maintain runoff and reduce
29 soil loss as planting age increases. Between 2019 and 2022, the values of the average runoff depth
30 for *DE*, *PE*, *PD* and *SDM* were 0.47, 0.55, 0.45 and 0.27 mm, respectively. Despite the increase in
31 runoff, grassland restoration favored soil conservation: the net soil loss per unit area of *SDM* was 1.4,
32 1.3 and 1.9 times greater than that in *DE*, *PE* and *PD*, respectively. The key factors affecting soil loss
33 and runoff were rainfall amount, duration and intensity (60-min intensity). We conclude that the
34 results of this study can serve as scientific guides to design efficient policy decisions for planning the
35 most effective vegetation restoration in the severely degraded hillside alpine meadows. To improve
36 the effectiveness of grassland restoration, we suggest that protective measures should be prioritized
37 during the initial planting stage of cultivated grasslands.

38 **Keywords:** Alpine meadow; Degraded hillside; Mixed-cultivated grassland; land management; runoff;
39 soil erosion.

40 **1 Introduction**

41 Grasslands are an essential component of terrestrial ecosystems and habitats for the development of
42 animal livestock (O'Mara, 2012). They make significant contributions to biodiversity conservation,
43 climate mitigation, carbon sequestration, and water supply and regulation (Bardgett et al., 2021).
44 Despite the importance of grasslands, about half of them are degraded globally –5% of them
45 undergoing severe degradation (based on net primary productivity)–, and this issue has become a
46 major concern for landscape conservation (Gang et al., 2014; Török et al., 2021). Global grassland
47 net primary productivity (NPP) has declined by 58.84 Tg C per year. Grassland degradation causes
48 the loss of up to 90% of the soil structure that facilitates water movement (infiltration) and retention
49 (water-holding capacity) in soils (Wick et al., 2016), reduces carbon storage potential (Liebig et al.,
50 2013), and impedes soil functioning. Moreover, degraded grasslands are prone to severe soil erosion,
51 especially in mountainous areas. For example, in the Swiss alpine uplands, water erosion ranges from
52 0.14 to 1.25 t ha⁻¹ month⁻¹ according to the phenological stage of the grasses (Schmidt et al., 2019);
53 and in the gully slope of the Loess Plateau, the average amount of soil erosion was 306.7 t ha⁻¹ month⁻¹
54 during the 2018–2020 grass growing season (Zhu et al., 2021).

55 Precipitation is the main water source of soil moisture supply in semi-arid areas and the
56 conversion of precipitation to runoff is one of the major contributors to river streamflow (Leung et al.
57 2015; Li et al., 2024). In some previous experiences, it was observed that vegetation restoration
58 reduced surface runoff and decreased sediment production, which led to lower river levels,
59 threatening the health of river ecosystems (Dijk et al., 2007). A recent study conducted by Wu et al.
60 (2020) proposed sustainable management strategies for semi-arid areas with a positive trade-off
61 between surface runoff maintenance and erosion control. However, very few studies have addressed
62 to date the effects of restored grasslands in maintaining surface runoff and preventing soil erosion

63 (Minea et al., 2022). This topic is particularly important for alpine grasslands, which play a vital role
64 in the supply of fresh water and the development of livestock husbandry (Cui et al., 2022). Therefore,
65 it is necessary to assess the impacts of grassland restoration on runoff generation and soil protection.

66 Vegetation restoration is widely considered as one of the most effective methods for controlling
67 runoff and soil erosion worldwide (Anache et al., 2018; Vanacker et al., 2022). The effects of
68 vegetation cover properties on runoff and soil loss reduction are strongly connected to plant species,
69 leaf and branch coverage, above-ground biomass, litter biomass, and root systems (Liu et al., 2022;
70 Freschet and Roumet, 2017; Gyssels et al., 2005; Zhu et al., 2021). Furthermore, the processes of
71 runoff and soil loss are significantly influenced by the improvement of soil characteristics with
72 vegetation restoration (Schwarz et al., 2015; Gyssels et al., 2005). The interaction between vegetation
73 and soil could stabilize the topsoil and alter soil properties (Saxton and Rawls, 2006; Ma et al., 2023a).
74 Vegetation restoration promotes the formation of soil aggregates, decreases soil bulk density,
75 enhances organic matter and nutrients and improves soil porosity, resulting in high soil hydraulic
76 conductivity and field capacity (Qiu et al., 2022; Saxton and Rawls, 2006). The above-interlinked soil
77 properties alter soil hydrological properties and ultimately influence hillslope and watershed
78 hydrology, such as runoff and soil erosion (Lu et al., 2020; Qiu et al., 2022). While vegetation
79 restoration holds the potential to be a key method of environmental restoration under human
80 management, the inappropriate selection of species can negatively impact the sustainability of local
81 economic and environmental development (Huang et al., 2017; 2019). For example, cultivated
82 grasslands were already advocated as a sensible solution for the conservation of soil and water, as
83 well as the regrowth of vegetation in semi-arid mountain areas (Liu et al., 2022; Wu et al., 2010).
84 Grass communities with multiple stratified structures are better at maintaining surface runoff and
85 decreasing soil loss than those with a single composition and structure (Mohammad and Adam, 2010).

86 Surface runoff –also known as stormwater runoff or overland flow– reaches the stream in the form
87 of sheet, rill and gully flow (Rumynin, 2015). The conversion of rainfall to overland flow depends on
88 the rainfall intensity, the soil hydrological properties, such as (non-)saturated hydraulic conductivity,
89 matrix flux potential and field capacity, and initial soil water content (López-Vicente and Navas, 2012;
90 Gyssels et al., 2005; De Baets et al., 2007). Because runoff is the primary driver of water erosion on
91 hillslopes and serves as the main agent for sediment transport, reducing the conversion of rainfall to
92 runoff is regarded as an effective way to control water erosion, through vegetation restoration (Zhou
93 et al., 2016; Zhu et al., 2021). On the other hand, in arid and semi-arid regions, surface runoff is the
94 major water supply source to the river streamflow, thereby it is vital for ensuring the sustainability of
95 ecosystems and human activities (Liu et al., 2020; Robinson et al., 2003). Therefore, restoration
96 efforts in areas with low rainfall should be oriented to maintain runoff while reducing its level of
97 sediment concentration.

98 Soil erosion can be reduced by various factors, including the above- and below-ground biomass
99 of grasses, litter cover, and root systems (De Baets et al., 2007; Durán Zuazo and Rodríguez
100 Pleguezuelo, 2008; Gyssels and Poesen, 2003; Wen et al., 2024). Grasslands can control water erosion
101 relying on the role of the aboveground biomass in dissipating flow energy (Bochet and García-Fayos,
102 2004), living roots in decreasing soil detachment capacity (Zhang et al., 2013), grass plant cover in
103 intercepting rainfall (Liu et al., 2019), and litter cover in enhancing rainwater infiltration (Liu et al.,
104 2022). Moreover, the interweaving of plant roots can remarkably alter the physical properties of the
105 topsoil, enhancing its resistance to erosion (Schwarz et al., 2015; Wang et al., 2018). The impact of
106 grassroots on the soil characteristics can be summarized as follows: i) increasing the stability of soil
107 aggregates through aggregating fine soil particles into macroaggregates; ii) enhancing soil cohesion
108 through interweaving with the soil; and iii) decreasing soil bulk density through increasing soil

109 porosity (Wu et al., 2019; Gyssels et al., 2005). For example, numerous recent studies have confirmed
110 that a grass with shallow yet dense fibrous root system appears to be more effective at controlling
111 water erosion than grass with good ground cover but low root density (De Baets et al., 2007; Bochet
112 et al., 2006).

113 Alpine meadows, especially in the Qinghai-Tibetan Plateau, constitute the predominant
114 ecosystem in China and the world, accounting for 44% and 6% of total grassland areas, respectively
115 (Wang et al., 2016). Over 50% of the alpine meadows have been subject to an increasing degree of
116 degradation (Bardgett et al., 2021), with the extent of degradation depending on the meadow patch
117 coverage resulting from the fragmentation of alpine meadows (Fig. 1b). Severely degraded meadows
118 (also known as “black beach” and “black soil-type degraded meadow”) formed after the mattic
119 epipedon, typically 10 to 15 cm deep, was fully removed by overgrazing and rodent activity exposing
120 the sub-soil (Fig. 1c; Ma et al., 2023a; Shang et al., 2008). Severely degraded meadows amounted to
121 about 30% of the total area of alpine meadows on the Qinghai-Tibetan Plateau (Shang et al., 2008).
122 Recent studies by Niu et al. (2021) and Ma et al. (2023b) have observed that fragmentation of alpine
123 meadows and severely degraded meadows could reduce surface runoff and enhance soil erosion.

124 The Qinghai-Tibetan Plateau serves as the headwaters for many of Asia's major rivers (Xu, 2018).
125 The eastern and southern parts of the Qinghai-Tibet Plateau are influenced by the monsoon, and
126 rainfall is the primary source of streamflow (Cuo et al., 2014). The long-term and widespread
127 degradation of hillside alpine meadows has disrupted the soil water balance, reducing surface runoff
128 (Niu et al., 2019; Ma et al., 2023b). This, in turn, diminishes river streamflow, ultimately constraining
129 the sustainable development of both local and downstream regions. The importance of artificial
130 grassland in restoring alpine degraded meadow is widely accepted (Li et al., 2018; Wu et al., 2010).
131 Artificial grassland –also known as tamed grassland, sowed grassland and cultivated grassland– refers

132 to fields that have been broken up and replanted with exotic grasses and forbs and utilized for hay
133 crop production or cattle grazing (Fisher et al., 2018). The establishment of artificial grassland on
134 severely degraded areas provides a dual benefit by boosting productivity and improving the ecological
135 environment of alpine grasslands (Shang et al., 2008; Liu et al., 2022).

136 While previous studies have often focused on carbon sequestration capacity, vegetation
137 characteristics, soil quality and productivity of cultivated grassland (Wang et al., 2013; Bai and
138 Cotrufo et al., 2022), there has been a limited examination of the impacts of mixed-cultivated
139 grasslands on the provision of runoff and prevention of soil erosion on the alpine hillsides. Recently,
140 Liu et al. (2022) evaluated the effects of plant morphological characteristics on runoff and soil erosion
141 in different mixed-cultivated grassland under natural rainfall events. Here, we present novel research
142 to examine the ability of cultivated grasslands to regulate runoff and soil loss and evaluate the effect
143 of three different mixed-cultivated grasslands: *Deschampsia cespitosa* and *Elymus nutans* (*DE*), *Poa*
144 *pratensis* L.cv. Qinghai and *Elymus nutans* (*PE*), and *Poa pratensis* L.cv. Qinghai and *Deschampsia*
145 *cespitosa* (*PD*), compared to a severely degraded meadow (*SDM*) by a three-year field experiment.
146 In particular, this study aimed to (1) assess the temporal variations in soil and water loss of *DE*, *PE*
147 and *PD* grasslands during the growing season and under natural rainfall; and (2) determine the key
148 factors influencing the mixed-cultivated grasslands in controlling runoff and soil erosion. This study
149 has realistic implications for understanding the contribution of mixed-cultivated grasslands
150 restoration on soil erosion control in degraded alpine hillsides.

151

152 **2 Materials and methods**

153 **2.1 Study area**

154 This study was carried out in the representative area of Zhique Village (33°40'01" N and 99°43'06" E,
155 elevation over 4200 m a.s.l), Dari County, Qinghai province, which served as a field experimental
156 site and model area for the restoration of severely degraded alpine meadow on the Qinghai-Tibetan
157 Plateau (Fig. 1a). The climate conditions correspond to a typical highland one with low temperatures
158 throughout the year, i.e., not showing the typical four-season pattern (spring, summer, autumn, winter),
159 but rather just two main seasons: cold and warm. In the study region, the average annual temperature
160 is -3.1 °C, with monthly variations from -14.7 °C in January to 7.5 °C in July (values corresponded
161 to the period 1981-2018; data source: European Centre for Medium-Range Weather Forecasts). The
162 average annual precipitation is 416 mm, with the majority of it falling from July to September, based
163 on Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS). The majority of the
164 precipitation and the warm season falls during the vegetation growth period (from May to September),
165 favoring optimal conditions for the development of plants. The soil type in the study area is classified
166 as Mat Cryi-gelic Cambisols (IUSS-WRB, 2015). Currently, the remnant vegetation in this site is
167 composed of an alpine shrub (*Salix cupularis* and *Potentilla fruticose*), alpine meadow (*Kobresia*
168 *pygmaea*, *Kobresia humilis* and *Kobresia capillifoli*) and swamp meadow (*Carex atrofusca*, *Poa*
169 *annua* and *Carex parva*).

170 Soil erosion in the degraded alpine meadows is severe, becoming the primary source of sediment
171 delivered to streams in the study area (Liu et al., 2022). The mattic epipedon of alpine meadow has
172 experienced fragmentation and even disappearance (Fig. 1b), eventually forming a severely degraded
173 meadow (Fig. 1c). Before implementing the grassland restoration project, i.e., Subsidy and Incentive
174 System for Grassland Conservation, the average soil erosion rate and the total erosion in the study
175 area were 13.63 t ha⁻¹ y⁻¹ and 323.58 × 10⁶ t y⁻¹, respectively (Zhao et al., 2021). Severely degraded
176 meadows were restored via mixed-cultivated grasslands –fields were ploughed and replanted with

177 two grass species— and moderately degraded meadows were restored by broadcast sowing on the
178 hillslopes during the implementation of the grassland restoration project. The grass species used for
179 the projects have excellent characteristics like strong trampling tolerance, good palatability, abundant
180 leaf quantity and developed rhizome, such as *Poa pratensis* L. cv. Qinghai, *Deschampsia cespitosa*
181 and *Elymus nutans* (Shang et al., 2008).

182

183 **2.2 Experimental design and measurement**

184 The degraded hillslopes are the main component of runoff generation and confluence areas on the
185 Qinghai-Tibetan Plateau. Hence, the grass species chosen for mixed-cultivated grasslands not only
186 must it be grazing-tolerant and good forage, but also prevent soil loss and maintain surface runoff.
187 Potential grass species should also be fully acclimated to harsh alpine climate and have
188 complementary morphological characteristics and living habits (Liu et al., 2022). The community
189 established by matching of grasses morphological characteristics and habits has a hierarchical vertical
190 cover structure and little inter- or intraspecific competition. Following the above-mentioned
191 guidelines for choosing grass species, we ultimately decided on three species (*Deschampsia cespitosa*,
192 *Poa pratensis* L. cv. Qinghai and *Elymus nutans*) from the most widely utilized grass species.
193 *Deschampsia cespitosa* is a cool-season bunching grass native to alpine environments. It typically
194 forms a low, dense tussock (to 30–50 cm tall) of very thin (0.5 cm wide), arching, flat to inrolled,
195 dark green grass blades (to 5 cm long). *Deschampsia cespitosa*, a common bottom grass, has 70% of
196 its grass stems growing between 0 and 30 cm tall. *Elymus nutans* is a common and important plant
197 species in the alpine meadows of the Qinghai-Tibetan Plateau (Chen et al., 2009). It is a valuable
198 fodder grass in alpine locations that has been extensively employed for animal production, disturbed
199 grassland restoration, and artificial grassland construction due to its resilience to cold, drought and

200 pests (Ren et al., 2010). *Elymus nutans* is a herbaceous perennial species with sparsely tufted culms
201 that can grow to heights of 70 to 100 cm (Liu et al., 2022). *Poa pratensis* L. cv. *Qinghai* is the common
202 and dominant species native to the Qinghai-Tibetan Plateau. It is an excellent species that has been
203 selected and cultivated to restore degraded alpine meadows. Also, *Poa pratensis* L. cv. *Qinghai* is an
204 herbaceous perennial species with erect or geniculate base culms that grow 20–60 cm tall.

205 To reveal the effects of mixed-cultivated grasslands in controlling runoff and soil loss on hillsides,
206 field observation of mixed grass plots designed by us was conducted from the 2019 to 2022 growing
207 seasons. Therefore, one plot with severely degraded meadow (*SDM*) as a control and three plots with
208 two mixed grass seeds per plot of *Deschampsia cespitosa* and *Elymus nutans* (*DE*), *Poa pratensis*
209 L.cv. *Qinghai* and *Elymus nutans* (*PE*), and *Poa pratensis* L.cv. *Qinghai* and *Deschampsia cespitosa*
210 (*PD*) were selected as the testing site (Fig. 1d). All four runoff plots were spaced 1m apart and were
211 located on the same hillside with the same elevation and soil texture. All plots were bounded by steel
212 plates (30 cm high and 2 mm thick sheet) and built during May 2019, with an area of 10 m² (2 m wide
213 and 5 m long parallel to the maximum slope gradient). To collect only runoff and soil loss from the
214 runoff plot, the steel plate was put vertically into the soil to a depth of about 10 cm, with the remainder
215 sticking out from the soil surface. At the outlet of each plot, a steel runoff collection and calibrated
216 tank (75 L) were set up to gather sediment and runoff. To prevent the collected runoff from being lost
217 to evaporation, the calibrated tank was set inside a sealed vat (Fig. 1d).

218 In addition, the grass seeding for each runoff plot was completed in May 2019. For the runoff
219 plots, grass seeds were distributed to a depth of less than 1 cm in strips at 20 cm intervals following
220 plowing. The seeding rate was set at 6.0 g m⁻² for *Poa pratensis* L.cv. *Qinghai* and *Deschampsia*
221 *cespitosa* and 4.5 g m⁻² for *Elymus nutans* to ensure a constant number of plants based on germination
222 and seedling emergence rates. None of the runoff plots experienced any human disturbance during

223 the observation period (2019–2022), including grazing, harvesting, and excavation.

224

225 **2.3 Rainfall, runoff and soil loss measurement**

226 A Vantage pro 2TM weather station (Davis Instruments Corp., USA) with a measurement accuracy of
227 4% was positioned next to the experimental plots to monitor precipitation intensity and duration (Fig.
228 1). A precipitation event was defined by the occurrence of a no-rain interval lasting more than 3 h
229 between them. A total of 42 precipitation events were recorded from 2019 to 2022 throughout the
230 growing season. Snow was not collected, and only rainfall was recorded during the growing season
231 (from June 15 to August 25). Precipitation characteristics of each event, including amount (*P*),
232 duration (*RD*), and maximum intensities of 60 minutes (*RI*₆₀) were recorded. Average rainfall intensity
233 (*ARI*) was calculated by dividing the total rainfall amount by the duration of the rainfall event. After
234 each rainfall-runoff event, both runoff and sediment were collected right away. The water level in the
235 calibrated tank was first measured to calculate the runoff volume. Then, runoff was fully mixed inside
236 the calibrated tank using a stirring bar to thoroughly whirl, and two 500 ml bottles were used to obtain
237 mixture samples of sediment and runoff. When the calibrated tank had less than 1000 ml of runoff
238 sample, all runoff was collected. Lastly, the calibrated tank was cleaned in order to collect sediment
239 and runoff for the subsequent rainfall-runoff event. The mixture samples in the bottle were transported
240 back to the lab to be filtered on filter paper with a pore size of 30–50 µm. The filter paper with
241 sediment was oven-dried to a consistent weight at 105 °C. The ratio of soil loss amount to runoff
242 volume in the mixed samples was applied to calculate the sediment concentration. Finally, runoff
243 volume and sediment concentration were multiplied to calculate soil loss in each plot.

244 We collected runoff and soil erosion data during the growing season for the years 2019 to 2022.

245 Data for 2021 could not be collected due to the prevention and control strategies for coronavirus

246 (COVID-19). Soil erosion and runoff were portrayed in this work by soil erosion per unit area (g m^{-2}) and runoff depth (mm). The runoff depth (R) and soil erosion per unit area (S) could be calculated
247 using the following formulas:
248

$$R = \frac{V_R}{A} \times 10^3 \quad (1)$$

$$S = \frac{S_T}{A} \quad (2)$$

249 where V_R is the volume of runoff from runoff plots (m^3), S_T is the total amount of soil erosion from
250 runoff plots (g), and A is the area of runoff plot (m^2).
251

252 **2.4 Vegetation and soil properties measurement**

253 Vegetation cover (VC), including dead (standing litter) and living vegetation, was measured monthly
254 from 2019 to 2022 growing seasons using a steel wire frame ($50 \text{ cm} \times 50 \text{ cm}$) subdivided into 25
255 plots of $10 \text{ cm} \times 10 \text{ cm}$. Fig. 2 exhibited the change in vegetation coverage for all runoff plots from
256 2019 to 2022. After collecting runoff samples each year, the quadrats ($50 \text{ cm} \times 50 \text{ cm}$) were positioned
257 in the up-, mid-, and down-slope areas. Litter in each quadrant was collected and oven-dried to
258 determine litter biomass (LB) (Zhu et al., 2021). The litter collection for 2019 was not completed due
259 to the seeding of mixed-cultivated grasslands in May 2019, and the litter collection for 2020 and 2021
260 was collected at the end of the runoff collection for the current year. Undisturbed soil samples were
261 taken in the 0–10 cm soil layers using steel rings in 2022. All soil samples were saturated and then
262 weighed (W_{sat}). Then the saturated soil samples were placed on the dry sand layer to drain water for
263 about 2 h and 8 h, and weighed (W_{2h} and W_{8h}). Finally, soil samples were dried in an oven at $105 \text{ }^\circ\text{C}$
264 for 24 h and then weighed (W_{dr}). Based on the above measurement, soil bulk density (BD , g cm^{-3}),
265 total porosity (TP , %), capillary porosity (CP , %), non-capillary porosity (NCP , %), and soil water
266 content at field capacity (FC , %) were determined as follows:

$$FC = \frac{(W_{8h} - W_{dr})}{(W_{dr} - W_{sr})} \quad (3)$$

$$BD = \frac{(W_{dr} - W_{sr})}{V} \quad (4)$$

$$TP = \left(1 - \frac{BD}{ds}\right) \times 100 \quad (5)$$

$$CP = \frac{(W_{2h} - W_{dr})}{V} \quad (6)$$

$$NCP = TP - CP \quad (7)$$

267 where W_{sr} is the weight of the steel ring (g), ds is the soil particle density (generally being 2.65 g
268 cm^{-3}), and V is the volume of the ring (100 cm^3).

269 In addition, root mass density (*RMD*) was obtained using a root drill, followed by washing with
270 water and drying in the oven. Four undisturbed samples were collected in each quadrat using a steel
271 ring (6.18 cm diameter and 2.0 cm height), and they were applied to a direct shear (ZJ type). The soil
272 cohesion was obtained by the Mohr–Coulomb theory (Labuz and Zang, 2012).

273

274 **2.5 Calculating the reduction effect of runoff and soil loss**

275 Four metrics were employed to assess the efficiencies of the mixed-cultivated grasslands in regulating
276 runoff and soil loss, which were: The runoff reduction benefit (*RRB*, %), sediment concentration
277 reduction benefit (*CRB*, %), soil erosion reduction benefit (*SRB*, %), and the percentage of runoff
278 reduction ratio to soil loss reduction ratio (*RRSR*) (Zhao et al., 2014). High values of *RRB*, *SRB* or
279 *CRB* indicated that vegetation was able to reduce runoff, soil erosion or sediment concentration
280 compared to the rates observed in the control plot (severely degraded meadow). In addition, a low
281 *RRSR* implied that vegetation was more beneficial in minimizing soil erosion than in minimizing
282 runoff (Liu et al., 2020). These indices were calculated as follows:

$$RRB = \frac{R_c - R_v}{R_c} \times 100 \quad (8)$$

$$SRB = \frac{S_c - S_v}{S_c} \times 100 \quad (9)$$

$$CRB = \frac{C_c - C_v}{C_c} \times 100 \quad (10)$$

$$RRSR = \frac{RRB}{SRB} \times 100 \quad (11)$$

283 where R_c and R_v are the runoff depths of the degraded meadow plot and plots covered by mixed-
 284 cultivated grasslands; S_c and S_v are the soil loss per unit area of the degraded meadow plot and
 285 plots covered by mixed-cultivated grasslands; C_c and C_v are the sediment concentrations of the
 286 degraded meadow plot and plots covered by mixed-cultivated grasslands, respectively.

287

288 **2.6 Statistical analyses**

289 All data were analyzed using SPSS statistics software (IBM, USA, version 26.0). The Kolmogorov–
 290 Smirnov test was used to test the normality of data. Duncan’s multiple range tests of one-way analysis
 291 of variance (ANOVA) were applied to test for significant differences between soil and vegetation
 292 characteristics, runoff depth, soil erosion amount, and runoff and soil loss reduction ratio under
 293 various mixed-cultivated grasslands at 0.05 significance levels. Also, path analysis is a form of
 294 multiple regression statistical analysis that is used to evaluate causal models by examining the
 295 relationships between runoff, soil loss and soil and vegetation properties. By using this method, one
 296 can identify the major factors influencing runoff and soil loss and determine the direct and indirect
 297 effects of soil and vegetation properties on runoff and soil loss.

298

299 **3 Results**

300 **3.1 Mixed-cultivated grasslands modified runoff amount and soil loss**

301 Mixed-cultivated grasslands increased runoff and reduced soil erosion. One-way analysis of variance

302 (ANOVA) revealed that runoff significantly ($p < 0.05$) increased after the severely alpine degraded
303 hillside was restored by the mixed-cultivated grassland (Fig. 3). During the three evaluated growing
304 seasons (2019, 2020 and 2022), the average runoff depth for *DE*, *PE*, *PD* and *SDM* was 0.47, 0.55,
305 0.45 and 0.27 mm, respectively. The average runoff depths of *SDM* in 2019, 2020, and 2022 were
306 0.23, 0.34 and 0.25 mm, respectively, all significantly ($p < 0.05$) lower than (except for 2020) the
307 average runoff of mixed-cultivated grassland *DE* *PE* and *PD*, which measured 0.44, 0.59 and 0.50
308 mm in 2019, 0.55, 0.51 and 0.38 mm in 2020, 0.43, 0.54 and 0.40 mm in 2022 (Fig. 3a). Regarding
309 soil conservation, the amount of soil loss in grasslands was significantly influenced by planting age.
310 As depicted in Fig. 3b, soil loss in *DE*, *PE* and *PD* (except for *DE* in 2019) were significantly ($p <$
311 0.05) higher in 2019 and 2020 (the first and second years of planting) than those in the fourth year of
312 planting (2022). In 2020, soil loss produced by *DE*, *PE*, and *PD* was significantly higher ($p < 0.05$)
313 than that of *SDM*. Satisfactorily, the three mixed-cultivated grasslands did exhibit a clear reduction
314 in soil loss compared to *SDM* in 2022 (albeit not significantly), with soil loss per unit area for *SDM*
315 being 1.4, 1.3 and 1.9 times higher than those for *DE*, *PE* and *PD*, respectively. No significant
316 difference ($p > 0.05$) was observed in runoff depth and soil loss between *DE* *PE* and *PD* in 2019,
317 2020 and 2022. The results showed that any of the three mixed-cultivated grasslands (*DE*, *PE* and
318 *PD*) could be effective in controlling soil loss and maintaining runoff.

319

320 **3.2 Specific runoff and soil loss reduction ratios of the cultivated grasslands**

321 Fig. 4 illustrates the runoff, soil loss and sediment concentration reduction ratio after planting various
322 mixed-cultivated grasslands. Lower *RRB* values indicated a better ability to maintain runoff for
323 mixed-cultivated grasslands, while higher *SRB* and *CRB* values indicated better effectiveness of
324 grasslands in soil loss reduction. The mean *RRB* values of the grass community *DE*, *PE* and *PD* were

325 -79.3%, -130.4% and -48.5% in 2019, -36.9%, -53.5% and -21.5% in 2020, and -115.4%, -156.1%
326 and -87.6% in 2022, respectively (Fig. 4a). Regardless of the combination of the above-mentioned
327 grass species, the average increase ratio of runoff in 2022 (the fourth years of planting) was
328 significantly ($p < 0.05$) higher than that in 2019 and 2020 (the first and second years of planting). The
329 *SRB* of the three mixed-cultivated grasslands (*DE*, *PE* and *PD*) increased with increasing planting
330 age. It is worth noting that the average *SRB* values in the grassland communities of *DE*, *PE* and *PD*
331 were 18.0%, 24.3% and 31.9% in 2022, respectively (Fig. 4b). The *SRE* values of *DE*, *PE* and *PD* in
332 2022 were significantly ($p < 0.05$) higher than those of 2019, whereas *SRE* values between 2020 and
333 2022 was significant ($p < 0.05$) for *DE* but not ($p > 0.05$) for *PE* and *PD*. Additionally, *CRB* for all
334 mixed-cultivated grasslands in 2022 was significantly ($p < 0.05$) higher than that in 2019 and 2020.
335 The mean *CRB* values of the cultivated-grassland communities *DE*, *PE* and *PD* increased from -120.9%
336 to 55.8%, from -112.4% to 59.7%, and from -94.3% to 62.1% from 2019 to 2022, respectively (Fig.
337 4c). Regardless of the age of the grasslands, the value of *RRSR* was less than 1, suggesting that the
338 soil erosion reduction effect of the grasslands was higher than its runoff reduction effect (Fig. 4d). No
339 significant differences ($p > 0.05$) appeared in *RRB*, *SRB*, *CRB* and *RRSR* between *DE* *PE* and *PD* in
340 2019, 2020 and 2022.

341

342 **3.3 Key factors affecting runoff and soil loss**

343 Precipitation characteristics and vegetation features played a significant role in influencing the
344 hydrological response of the soil. In this study, path analysis was applied to identify the key factors
345 affecting soil loss. The results of this analysis indicated that the sum of path coefficients of *RI*₆₀, *RD*,
346 *P* and *VC* were 0.31, 0.36, 0.40 and 0.32, respectively (Table 1). This suggests that *P*, *RD*, *VC* and
347 *RI*₆₀ had positive effects on runoff amount, with *P* being the most influential factor. Direct influences

348 on runoff were primarily attributed to *ARI* and *RD*, with direct path coefficients of 0.37 and 0.67,
349 respectively. Meanwhile, the influences of *P* and *LB* on runoff were mainly indirect, with indirect
350 path coefficients of 0.57 and 0.25, respectively. For instance, *P*, in combination with other factors,
351 particularly *RI₆₀* and *RD*, contributed significantly to runoff.

352 Soil loss was significantly influenced by *R*, *RI₆₀*, *ARI* and *LB*. The sum of path coefficients of *R*,
353 *RI₆₀*, *ARI* and *LB* were 0.52, 0.20, 0.28 and -0.25, respectively (Table 2). These results show that *R*,
354 *RI₆₀* and *ARI* had a promotional effect, whereas *LB* had an inhibitory effect on soil loss. Meanwhile,
355 *R* and *P* had a direct positive influence on soil erosion, with direct path coefficients of 0.60 and 0.28,
356 whereas *RI₆₀* and *RD* had a direct negative influence on soil erosion, with direct path coefficients of
357 -0.29 and -0.41 (Table 2). In addition, the direct and indirect path coefficients both indicated that *LB*
358 had an inhibitory influence on the soil loss per unit area, with values of -0.10 and -0.25, respectively.

359

360 **4 Discussion**

361 **4.1 Benefits of mixed-cultivated grasslands on soil conservation and runoff maintenance**

362 The mixed-cultivated grasslands (*DE*, *PE* and *PD*) effectively maintained runoff and minimized soil
363 loss (Fig. 4). This finding is similar to those of some previous studies (Liu et al., 2019; Liu et al.,
364 2022). In this study, the mixed-cultivated grasslands significantly increased surface runoff compared
365 to the *SDM*. The difference in runoff between mixed-cultivated grasslands and *SDM* may be attributed
366 to the soil infiltration rate. Mixed-cultivated grasslands had more abundance of fibrous roots in the
367 topsoil compared with *SDM* (Fig. 5), and those fine roots reduced infiltration by occupying the soil
368 pore (Leung et al., 2015). In comparison to *SDM*, soil non-capillary porosity (*NCP*) and field capacity
369 (*FC*) of *DE*, *PE* and *PD* significantly decreased by 46%, 32% and 48%, and increased by 55%, 59%

370 and 48%, respectively (Fig. 5). This implied that *SDM* was restored to mixed-cultivated grasslands
371 with lower permeability and better water retention.

372 Soil loss in all three mixed-cultivated grassland communities (*DE*, *PE* and *PD*) was higher than
373 that in the *SDM* during the first- and second years following planting. However, by the fourth year,
374 the *SDM* exhibited higher soil loss than the three mixed-cultivated grasslands (Fig. 3). These changes
375 in soil erosion were dominantly attributed to the developing of the root system and improvement of
376 soil structure (Zhu et al., 2021). The seeding method of plowing led to a disruption of soil structure,
377 resulting in increased soil loss in the three mixed-cultivated grasslands during the initial stages of
378 planting. We confirmed that the age of plantation was a key factor in understanding the inter-annual
379 changes of soil erosion. This idea was also demonstrated in other types of primary land uses such as
380 woody crops or young forests (Rodrigo-Comino et al., 2018). Nevertheless, we hypothesize that
381 grassland topsoil demonstrated a stronger resilience to erosion as its root system grew, which had a
382 reinforcement impact on the soil and led to lower soil loss in the fourth year of planting than that of
383 the *SDM*. The topsoil (0–10 cm) of the grasslands had significantly different soil properties from the
384 *SDM* in the fourth year after planting, as detailed in Table 3. In comparison to *SDM*, the root mass
385 density and soil cohesion of grasslands *DE*, *PE* and *PD* increased by 672%, 890% and 589%, and by
386 379%, 282% and 315%, respectively.

387

388 **4.2 Effect of rainfall and vegetation characteristics on runoff and soil loss**

389 Surface runoff and erosion process is influenced and constrained by rainfall depth, intensity and
390 duration, and by vegetation cover (*VC*) as well (Mohamadi and Kavian, 2015; Bochet et al., 2006).
391 In this study, the *VC* had a directly promoted effect on surface runoff. Moreover, this result was in
392 line with the finding of Niu et al. (2021), who reported that the surface runoff increased with the

393 grassland coverage. Our results also indicated that rainfall amount (P) could have an indirect effect
394 on surface runoff through rainfall duration (RD) and maximum intensities of 60 minutes (RI_{60}). This
395 implies that heavier and longer-lasting rainfall events were more likely to lead to surface runoff
396 generation (Dos Santos et al., 2017). The findings demonstrated that runoff depth (R) and the average
397 rainfall intensity (ARI) were the most and second most influential factors in promoting soil erosion
398 (Table 2). The primary cause for this is that runoff velocity increases with higher precipitation
399 intensity (Wang et al., 2013), which likely enhances the capacity of soil detachment and transport by
400 surface runoff (Zhu et al., 2021). Furthermore, litter biomass (LB) had a direct and negative impact
401 on soil loss (Table 2), indicating that the effectiveness of grasslands in reducing soil loss increased as
402 litter biomass increased. Liu et al. (2022) found that the soil loss rate decreased with increasing litter
403 biomass in grassland. Plant litter can intercept precipitation, reducing rainfall kinetic energy and
404 splash erosion, while also increasing surface roughness (Liu et al., 2017; Xia et al., 2019) All these
405 processes favor a reduction in runoff yield and soil loss rates.

406 Grass combinations with different morphological characteristics can effectively reduce soil loss
407 (Liu et al., 2022). In this study, the reduction in soil loss in the early stages of mixed-cultivated
408 grassland planting (2019 and 2020) was attributed to grassland cover and plant morphological
409 characteristics. *Deschampsia cespitosa*, *Poa pratensis* L.cv. Qinghai and *Elymus nutans* are dense
410 clump type, rhizomatic-sparse clump type, and sparse clump perennial grasses, respectively. In
411 addition, *Deschampsia cespitosa* and *Poa pratensis* L.cv. Qinghai are bottom grasses, while *Elymus*
412 *nutans* belongs to the top grass. The mix of dense and sparse grasses (DE and PD), and mix of top
413 and bottom grasses (DE and PE) can complement each other morphologically and structurally,
414 thereby more effectively reducing the kinetic energy of raindrops (Liu et al., 2022). *Poa pratensis*
415 *L.cv. Qinghai*, a rhizomatic grass, also has abundant root systems intertwined with the soil, increasing

416 soil cohesion and consequently reducing soil detachment capacity (Wang et al., 2018). Overall, in
417 this study, the morphological and root characteristics of mixed-cultivated grasslands reduced runoff
418 velocity, influenced water infiltration process and decreased soil erodibility.

419

420 **4.3 Implications for grasslands restoration on degraded alpine hillsides**

421 Our findings demonstrated that mixed-cultivated grasslands with complementing morphological
422 features and habits can be effective at maintaining runoff and reducing soil erosion. Three mixed-
423 cultivated grasslands (*DE*, *PE* and *PD*) exhibited an effective role in controlling soil loss on the
424 degraded alpine hillside. However, at the start of planting, the mixed planted grassland had a greater
425 soil erosion than the severely degraded meadow, whereas soil loss was reduced in the 4th year of
426 planting (Figs. 2 and 3). This suggested that protection measures, such as mesh covering and anti-
427 trampling, may be taken into account to reduce soil loss in the initial planting stage of cultivated
428 grassland in alpine hillsides (Liu et al., 2022). Moreover, grass may also be planted with a no-till
429 system to avoid the initial increase of soil erosion at the initial phases of cultivated grassland by
430 destroying soil structure (Karayel and Sarauskis, 2019). In addition, spring meltwater is the main
431 driver of soil erosion in degraded alpine meadows in alpine regions, which greatly increases turbidity
432 of rivers (Shi et al., 2020). The restoration of severely degraded hillslope meadows increased
433 vegetation cover and soil ability, both of which could have an inhibitory impact against meltwater
434 erosion (Liu et al., 2022). To better understand the effects of cultivated grassland on meltwater erosion,
435 future experiments under natural freezing and thawing conditions need to be conducted and monitored.

436 Cultivated grasslands, considered a crucial component of vegetation restoration, have been
437 extensively utilized in the rehabilitation of degraded alpine hillsides (Shang et al., 2008). Nevertheless,
438 plant restoration is not necessarily beneficial to the long-term viability of on- and off-site ecosystems'

439 functions, including natural succession and river ecosystems. Therefore, the selected vegetation types
440 ought to be advantageous for the ecosystem's sustainability, both on- and off-site, such as maintaining
441 river streamflow and unrestricted natural succession. The seed prices of cultivated grass communities
442 of *Deschampsia cespitosa* and *Elymus nutans*, *Poa pratensis* L.cv. Qinghai and *Elymus nutans*, and
443 *Poa pratensis* L.cv. Qinghai and *Deschampsia cespitosa* were about \$690, \$750 and \$480 per ha,
444 respectively, in Xining, Qinghai Province, in 2019. Planting properly mixed-cultivated grassland on
445 the alpine degraded hillsides can achieve both environmental and economic benefits. This study
446 proved that mixed-cultivated grasslands could maintain runoff and decrease soil loss.

447 **5 Conclusions**

448 Based on the measured data during the 2019, 2020 and 2022 growing seasons, the planting of mixed-
449 cultivated grassland on severely degraded hillside alpine meadow effectively maintained surface
450 runoff and decreased soil loss, especially after the mixed-cultivated grassland played a positive role
451 in consolidating the soil surface. The benefits were statistically significant compared with the control
452 plot, but differences between the three types of cultivated grasslands were not significant. Planting
453 the mixed-cultivated grasslands after ploughing loosened the soil structure and thus increased
454 sediment concentration in runoff during the first stage after planting. Subsequently, sediment
455 concentration decreased with the growth of the root system of the mixed-cultivated grasslands,
456 improving root-soil cohesion due to the root architecture. To guarantee that mixed-cultivated
457 grasslands can perform the aforementioned functions, protective measures should be implemented
458 during the initial planting stage to support their healthy growth. Our results also suggested that mixed-
459 cultivated grasslands with different but complementary morphology and structure and abundant fine
460 root systems were effective in maintaining surface runoff and reducing soil erosion. Precipitation

461 amount, duration, maximum 60-minute intensity, vegetation coverage and composition were the
462 predominant factors affecting surface runoff and soil loss. The erosion resistance contribution of the
463 above-ground community characteristics and below-ground roots along the cultivated time could
464 maintain a relatively high surface runoff and decrease sediment concentration. These findings have
465 potential implications for understanding the contribution of mixed-cultivated grasslands restoration
466 on soil erosion control in the degraded hillsides of alpine areas.

467

468 *Data availability.* The data that support the findings of this study are available on request from the
469 corresponding author.

470

471 *Author contributions.* Yulei Ma: Investigation, Formal analysis, Methodology, Software, Writing -
472 original draft. Yifan Liu: Investigation, Formal analysis, Writing - review & editing. Jesús Rodrigo-
473 Comino: Interpretation of data, Writing - review & editing. Manuel López-Vicente: Interpretation of
474 data, Writing - review & editing. Gao-Lin Wu: Conceptualization, Funding acquisition, Supervision,
475 Writing - original draft, review & editing.

476

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

479

480 *Disclaimer.* Publisher's note: Copernicus Publications remains neutral with regard to jurisdictional
481 claims in published maps and institutional affiliations

482 *Acknowledgments.* We thank Nunzio Romano, Gall Corinna, Vanacker Veerle and Qianjin Liu for

483 their constructive comments and suggestions on this manuscript.

484 *Financial support.* This research was funded by the National Natural Science Foundation of China
485 (NSFC41930755, NSFC32230068), the Strategic Priority Research Program of the Chinese Academy
486 of Sciences (XDB40000000), and the Second Stage's Research and Technique Extending Project of
487 Sanjiangyuan Ecological Protection and Building in Qinghai (2019-S-1).

488

489 **References**

490 Anache, J.A.A., Flanagan, D.C., Srivastava, A., and Wendland, E.C.: Land use and climate change
491 impacts on runoff and soil erosion at the hillslope scale in the Brazilian Cerrado, *Sci. Total*
492 *Environ.*, 622–623, 140–151, <https://doi.org/10.1016/j.scitotenv.2017.11.257>, 2018.

493 Bai, Y., Cotrufo, M.F.: Grassland soil carbon sequestration: Current understanding, challenges, and
494 solutions, *Science*, 377(6606), 603–608. <https://doi.org/10.1126/science.abo2380>, 2022.

495 Bardgett, R.D., Bullock, J.M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M.,
496 Durigan, G., Fry, E.L., Johnson, D., Lavallee, J.M., Le Provost, G., Luo, S., Png, K., Sankaran,
497 M., Hou, X.Y., Zhou, H.K., Ma, L., Ren, W.B., Li, X.L., Ding, Y., Li, Y.H., and Shi, H.X.:
498 Combatting global grassland degradation, *Nat. Rev. Earth Env.*, 2(10), 720–735,
499 <https://doi.org/10.1038/s43017-021-00207-2>, 2021.

500 Bochet, E., and García-Fayos, P.: Factors controlling vegetation establishment and water erosion on
501 motorway slopes in Valencia, Spain, *Restor. Ecol.*, 12(2), 166–174, <https://doi.org/10.1111/j.1061-2971.2004.0325.x>, 2004.

503 Bochet, E., Poesen, J., and Rubio, J.L.: Runoff and soil loss under individual plants of a semi-arid

504 Mediterranean shrubland: influence of plant morphology and rainfall intensity, *Earth Surf. Proc.*
505 *Land.*, 31(5), 536–549, <https://doi.org/10.1002/esp.1351>, 2006.

506 Chen, S., Ma, X., Zhang, X., and Chen, Z.: Genetic variation and geographical divergence in *Elymus*
507 *nutans* Griseb. (Poaceae: Triticeae) from West China, *Biochem. Syst. Ecol.*, 37(6), 716–722,
508 <https://doi.org/10.1016/j.bse.2009.12.005>, 2009.

509 Cui, Z., Liu, Y.F., Liu, Y., Leite, P.A.M., Shi, J.J., Shi, Z.H., and Wu, G.L.: Fragmentation alters the
510 soil water conservation capacity of hillside alpine meadows on the Qinghai-Tibetan Plateau,
511 *Geoderma*, 428, 116133, <https://doi.org/10.1016/j.geoderma.2022.116133>, 2022.

512 Cuo, L., Zhang, Y.X., Zhu, F.X., and Liang, L.Q.: Characteristics and changes of streamflow on the
513 Tibetan Plateau: A review, *J. Hydrol-Reg. Stud.*, 2, 2014, 49–68,
514 <https://doi.org/10.1016/j.ejrh.2014.08.004>, 2014

515 De Baets, S., Poesen, J., Knapen, A., Barberá, G.G., and Navarro, J.A.: Root characteristics of
516 representative Mediterranean plant species and their erosion-reducing potential during
517 concentrated runoff, *Plant Soil*, 294(1–2), 169–183, [https://doi.org/10.1007/s11104-007-9244-](https://doi.org/10.1007/s11104-007-9244-2)
518 2, 2007.

519 Dijk, A. I. J. M., and Keenan, R. J: Planted forests and water in per spective, *Forest Ecol. Manag.*,
520 251, 1–9, <https://doi.org/10.1016/j.foreco.2007.06.010>, 2007.

521 Dos Santos, J.C.N., de Andrade, E.M., Medeiros, P.H.A., Guerreiro, M.J.S., and de Queiroz Palácio,
522 H.A.: Effect of Rainfall Characteristics on Runoff and Water Erosion for Different Land Uses
523 in a Tropical Semiarid Region, *Water Resour. Manag.*, 31(1), 173–185, [https://doi.org/](https://doi.org/10.1007/s11269-016-1517-1)
524 10.1007/s11269-016-1517-1, 2017.

525 Durán Zuazo, V.H., and Rodríguez Pleguezuelo, C.R.: Soil-erosion and runoff prevention by plant
526 covers. A review. *Agron. Sustain. Dev.*, 28(1), 65–86, <https://doi.org/10.1051/agro:2007062>,

527 2008.

528 Fisher, R.J., Sawa, B., and Prieto, B.: A novel technique using LiDAR to identify native-dominated
529 and tame-dominated grasslands in Canada, *Remote Sens. Environ.*, 218, 201–206,
530 <https://doi.org/10.1016/j.rse.2018.10.003>, 2018.

531 Freschet, G.T., and Roumet, C.: Sampling roots to capture plant and soil functions, *Funct. Ecol.*, 31(8),
532 1506–1518, <https://doi.org/10.1111/1365-2435.12883>, 2017.

533 Gang, C.C., Zhou, W., Chen, Y.Z., Wang, Z.Q., Sun, Z.G., Li, J.L., Qi, J.G., and Odeh, I.:
534 Quantitative assessment of the contributions of climate change and human activities on global
535 grassland degradation, *Environ. Earth Sci.*, 72(11), 4273–4282, [https://doi.org/10.1007/s12665-](https://doi.org/10.1007/s12665-014-3322-6)
536 014-3322-6, 2014.

537 Gyssels, G. and Poesen, J.: The importance of plant root characteristics in controlling concentrated
538 flow erosion rates, *Earth Surf. Proc. Land.*, 28, 371–384. <https://doi.org/10.1002/esp.447>, 2003.

539 Gyssels, G., Poesen, J., Bochet, E., and Li, Y., Impact of plant roots on the resistance of soils to
540 erosion by water: a review, *Progr. Phys. Geogr.*, 29(2), 189–217, [https://doi.org/10.1191/](https://doi.org/10.1191/0309133305pp443ra)
541 0309133305pp443ra, 2005.

542 Huang, Z., Tian, F.P., Wu, G.L., Liu, Y., and Dang, Z.Q.: Legume grasslands promote precipitation
543 infiltration better than gramineous grasslands in arid regions, *Land Degrad. Dev.*, 28(1), 309–
544 316, <https://doi.org/10.1002/ldr.2635>, 2017.

545 Huang, Z., Liu, Y.F., Cui, Z., Liu, Y., Wang, D., Tian, F.P., and Wu, G.L.: Natural grasslands
546 maintain soil water sustainability better than planted grasslands in arid areas, *Agr. Ecosyst.*
547 *Environ.*, 286(1), 106683, <https://doi.org/10.1016/j.agee.2019.106683>, 2019.

548 Karayel, D., and Šarauskis, E.: Environmental impact of no-tillage farming, *Environ. Res. Eng.*
549 *Manag.*, 75(1), 7–12, <http://dx.doi.org/10.5755/j01.erem.75.1.20861>, 2019.

- 550 Labuz, J.F., and Zang, A. Mohr–Coulomb Failure Criterion, *Rock Mech. Rock Eng.*, 45, 975–979,
551 <https://doi.org/10.1007/s00603-012-0281-7>, 2012.
- 552 Leung, A.K., Garg, A., Coe, J.L., Ng, C.W.W., and Hau, B.C.H.: Effects of the roots of *Cynodon*
553 *dactylon* and *Schefflera heptaphylla* on water infiltration rate and soil hydraulic conductivity,
554 *Hydrol. Process.*, 29(15), 3342–3354. <https://doi.org/10.1002/hyp.1045>, 2015.
- 555 Liebig, M.A., Kronberg, S.L., Hendrickson, J.R., Dong, X., and Gross, J.R.: Carbon dioxide efflux
556 from long-term grazing management systems in a semiarid region, *Agr. Ecosyst. Environ.*, 164,
557 137–144, <https://doi.org/10.1016/j.agee.2012.09.015>, 2013.
- 558 Li, J., Wu, J., Yu, J., Wang, K., Li, J., Cui, Y., Shanguan Z.P., and Deng, L.: Soil enzyme activity
559 and stoichiometry in response to precipitation changes in terrestrial ecosystems. *Soil Biol.*
560 *Biochem.*, 191, 109321, <https://doi.org/10.1016/j.soilbio.2024.109321>, 2024.
- 561 Liu, W.J., Luo, Q.P., Lu, H.J., Wu, J.E., and Duan, W.P.: The effect of litter layer on controlling
562 surface runoff and erosion in rubber plantations on tropical mountain slopes, SW China, *Catena*,
563 149, 167–175, <https://doi.org/10.1016/j.catena.2016.09.013>, 2017.
- 564 Liu, Y., Li, S.Y., Niu, Y.L., Cui, Z., Zhang, Z.C., Wang, Y.L., Ma, Y.S., López-Vicente, M., and
565 Wu, G.L.: Effectiveness of mixed cultivated grasslands to reduce sediment concentration in
566 runoff on hillslopes in the Qinghai-Tibetan Plateau, *Geoderma*, 422, 115933, <https://doi.org/10.1016/j.geoderma.2022.115933>, 2022.
- 568 Liu, Y.F., Dunkerley, D., López-Vicente, M., Shi, Z.H., and Wu, G.L.: Trade-off between surface
569 runoff and soil erosion during the implementation of ecological restoration programs in semiarid
570 regions: A meta-analysis, *Sci. Total Environ.*, 712, 136477, [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.scitotenv.2019.136477)
571 [scitotenv.2019.136477](https://doi.org/10.1016/j.scitotenv.2019.136477), 2020.
- 572 Liu, Y.F., Liu, Y., Wu, G.L., and Shi, Z.H.: Runoff maintenance and sediment reduction of different

573 grasslands based on simulated rainfall experiments., *J. Hydrol.*, 572, 329–335, [https://doi.org/10.](https://doi.org/10.1016/j.jhydrol.2019.03.008)
574 [1016/j.jhydrol.2019.03.008](https://doi.org/10.1016/j.jhydrol.2019.03.008), 2019.

575 Liu, Y., Zhao, L.R., Liu, Y.F., Huang, Z., Shi, J.J., Wang, Y.L., Ma, Y.S., Lucas-Borja, M.E., L'opez-
576 Vicente, M., and Wu, G.L.: Restoration of a hillslope grassland with an ecological grass species
577 (*Elymus tangutorum*) favors rainfall interception and water infiltration and reduces soil loss on
578 the Qinghai-Tibetan Plateau, *Catena*, 219, 106632, [https://doi.org/10.1016/j.catena.2022.](https://doi.org/10.1016/j.catena.2022.106632)
579 [106632](https://doi.org/10.1016/j.catena.2022.106632), 2022.

580 Li, W., Wang, J.L., Zhang, X.J., Shi, S.L., Cao, W. X.: Effect of degradation and rebuilding of artificial
581 grasslands on soil respiration and carbon and nitrogen pools on an alpine meadow of the
582 Qinghai-Tibetan Plateau, *Ecol. Eng.*, 111, 134–142,
583 <https://doi.org/10.1016/j.ecoleng.2017.10.013>, 2018.

584 López-Vicente, M., and Navas, A.: A new distributed rainfall-runoff (DR2) model based on soil
585 saturation and runoff cumulative processes, *Agricultural Water Management*, 104, 128–141.
586 <https://doi.org/10.1016/j.agwat.2011.12.007>, 2012.

587 Lu, J.R., Zhang, Q., Werner, A.D., Li, Y.L., Jiang, S.Y., and Ta, Z.Q.: Root-induced changes of soil
588 hydraulic properties – a review, *J. Hydrol.*, 589, 125203 [https://doi.](https://doi.org/10.1016/j.jhydrol.2020.125203)
589 [org/10.1016/j.jhydrol.2020.125203](https://doi.org/10.1016/j.jhydrol.2020.125203), 2020.

590 Ma, Y.L., Liu, Y.F., López-Vicente, M., and Wu G.L.: Divergent shift of normal alpine meadow
591 towards shrub and degraded meadows reduces soil water retention and storage capacity, *J.*
592 *Hydrol.*, 625, 130109, <https://doi.org/10.1016/j.jhydrol.2023.130109>, 2023a.

593 Ma, Y.L., Liu, Y.F., López-Vicente, M., and Wu, G.L.: Divergent shift of normal alpine meadow
594 exacerbated soil loss of hillslope alpine meadows based on field experiments, *Int. Soil Water*
595 *Conserv. Res.*, In Press, <https://doi.org/10.1016/j.iswcr.2023.11.007>, 2023b.

596 Minea, G., Mititelu-Ionuș, O., Gyasi-Agyei, Y., Ciobotaru, N., and Rodrigo-Comino, J.: Impacts of
597 grazing by small ruminants on hillslope hydrological processes: A review of European current
598 understanding, *Water Resour. Res.*, 58, e2021WR030716, <https://doi.org/10.1029/2021WR>,
599 2022.

600 Mohamadi, M.A., and Kavian, A.: Effects of rainfall patterns on runoff and soil erosion in field plots,
601 *Int. Soil Water Conse.*, 3(4), 273–281, <http://dx.doi.org/10.1016/j.iswcr.2015.10.001>, 2015.

602 Mohammad, A.G., and Adam, M.A.: The impact of vegetative cover type on runoff and soil erosion
603 under different land uses, *Catena*, 81(2), 97–103, <http://dx.doi.org/10.1016/j.catena.2010.01.008>,
604 2010.

605 Niu, Y.L., Li, S.Y., Liu, Y., Shi, J.J., Wang, Y.L., Ma, Y.S., and Wu, G.L.: Regulation of alpine
606 meadow patch coverage on runoff and sediment under natural rainfall on the eastern Qinghai-
607 Tibetan Plateau, *J. Hydrol.*, 603, 127101, <https://doi.org/10.1016/j.jhydrol.2021.127101>, 2021.

608 O'Mara, F.P.: The role of grasslands in food security and climate change, *Ann. Bot-London* 110(6),
609 1263–1270, <https://doi.org/10.1093/aob/mcs209>, 2012.

610 Qiu, D.X., Xu, R.R., Wu, C.X., Mu, X.M., Zhao, G.J., and Gao P.: Vegetation restoration improves
611 soil hydrological properties by regulating soil physicochemical properties in the Loess Plateau,
612 China, *J. Hydrol.*, 609, 127730, <https://doi.org/10.1016/j.jhydrol.2022.127730>, 2022.

613 Ren, F., Zhou, H.K., Zhao, X.Q., Han, F., Shi, L.N., Duan, J.C., and Zhao, J.Z.: Influence of simulated
614 warming using OTC on physiological–biochemical characteristics of *Elymus nutans* in alpine
615 meadow on Qinghai-Tibetan plateau, *Acta Ecol. Sinica*, 30(3), 166–171, <https://doi.org/10.1016/j.chnaes.2010.04.007>, 2010.

617 Robinson, M., Cognard-Plancq, A.L., Cosandey, C., David, J., Durand, P., Führer, H.W., Hall, R.,
618 Hendriques, M.O., Marc, V., McCarthy, R., McDonnell, M., Martin, C., Nisbet, T., O’Dea, P.,

619 Rodgers, M., and Zollner, A.: Studies of the impact of forests on peak flows and baseflows: a
620 European perspective, *For. Ecol. Manag.*, 186, 85–97. [https://doi.org/10.1016/s0378-](https://doi.org/10.1016/s0378-1127(03)00238-x)
621 1127(03)00238-x, 2003.

622 Rodrigo-Comino, J., Brevik, E.C., and Cerdà, A.: The age of vines as a controlling factor of soil
623 erosion processes in mediterranean vineyards, *Sci. Total Environ.*, 616–617, 1163–1173,
624 <https://doi.org/10.1016/j.scitotenv.2017.10.204>, 2018.

625 Rumynin, V.G.: *Surface Runoff Generation, Vertical Infiltration and Subsurface Lateral Flow*. In:
626 Overland flow dynamics and solute transport. Theory and Applications of Transport in Porous
627 Media, vol 26. Springer, Cham, https://doi.org/10.1007/978-3-319-21801-4_1, 2015.

628 Saxton, K.E., and Rawls, W.J.: Soil water characteristic estimates by texture and organic matter for
629 hydrologic solutions, *Soil Sci. Soc. Am. J.*, 70(5), 1569–1578,
630 <https://doi.org/10.2136/sssaj2005.0117>, 2006.

631 Schwarz, M., Rist, A., Cohen, D., Giadrossich, F., Egorov, P., Büttner, D., Stolz, M., and Thormann,
632 J.J.: Root reinforcement of soils under compression, *J. Geophys. Res-Earth*, 120(10), 2103–2120,
633 <https://doi.org/10.1002/2015JF003632>, 2015.

634 Shang, Z.H., Ma, Y.S., Long, R.J., and Ding, L.M.: Effect of fencing, artificial seeding and
635 abandonment on vegetation composition and dynamics of ‘black soil land’ in the headwaters of
636 the Yangtze and the Yellow Rivers of the Qinghai-Tibetan Plateau, *Land Degrad. Dev.*, 19(5),
637 554–563, <https://doi.org/10.1002/ldr.861>, 2008.

638 Schmidt, S., Alewell, C., and Meusburger, K.: Monthly RUSLE soil erosion risk of Swiss grasslands,
639 *J. Maps*, 15, 247–256, <https://doi.org/10.1080/17445647.2019.1585980>, 2019

640 Török, P., Brudvig, L.A., Kollmann, J., Price, J., and Tóthmérész, B.: The present and future of
641 grassland restoration, *Restor. Ecol.*, 29(S1), e13378, <https://doi.org/10.1111/rec.13378>, 2021.

642 Wick, A.F., Geaumont, B.A., Sedivec, K.K., and Hendrickson, J.: *Grassland degradation*. In:
643 Shroder, J.F., Sivanpillai, R. (Eds.), *Biological and environmental hazards, risks, and disasters*.
644 Elsevier, pp. 257–276, 10.1016/B978-0-12-394847-2.00016-4, 2016.

645 Wang, B., Zhang, G., Yang, Y., Li, P., and Liu, J.: Response of soil detachment capacity to plant root
646 and soil properties in typical grasslands on the Loess Plateau, *Agr. Ecosyst. Environ.*, 266, 68–
647 75, <https://doi.org/10.1016/j.agee.2018.07.016>, 2018.

648 Wang, C.T., Wang, G.X., Liu, W., Wang, Y., Hu, L., and Ma, L.: Effects of establishing an artificial
649 grassland on vegetation characteristics and soil quality in a degraded meadow, *Isr. Ecol. Evol.*,
650 59(3), 141–153, <http://dx.doi.org/10.1080/15659801.2013.863669>, 2013.

651 Wang, L., Liang, T., and Zhang, Q.: Laboratory experiments of phosphorus loss with surface runoff
652 during simulated rainfall, *Environ. Earth Sci.*, 70(6), 2839–2846, [http://dx.doi.org/10.1007/
653 s12665-013-2344-9](http://dx.doi.org/10.1007/s12665-013-2344-9), 2013.

654 Wang, Z.Q., Zhang, Y.Z., Yang, Y., Zhou, W., Gang, C.C., Zhang, Y., Li, J.L., An, R., Wang, K.,
655 Odeh, I., and Qi, J.G.: Quantitative assess the driving forces on the grassland degradation in the
656 Qinghai–Tibet Plateau, in China, *Ecol. Inform.*, 33, 32–44, [http://dx.doi.org/10.1016/j.ecoinf.
657 2016.03.006](http://dx.doi.org/10.1016/j.ecoinf.2016.03.006), 2016.

658 Wen, Y.R., Liu, B., Lin, L.T., Hu, M.M., Wen, X., Li, T.Y., Rong, J.D., and Yao, S.H.: Shelterbelt
659 effects on soil redistribution on an arable slope by wind and water, *Catena*, 241, 108044.
660 <https://doi.org/10.1016/j.catena.2024.108044>, 2024.

661 Wu, G. L., Huang, Z., Liu, Y.F., Cui, Z., Chang, X.F., Tian, F.P., López-Vicented, M., and Shi, Z.H.:
662 Soil water response of plant functional groups along an artificial legume grassland succession
663 under semi-arid conditions, *Agr. Forest Meteorol.*, 278, 107670.
664 <https://doi.org/10.1016/j.agrformet.2019.107670>, 2019.

665 Wu, G.L., Liu, Y.F., Cui, Z., Liu, Y., Shi, Z.H., Yin, R., and Kardol, P.: Trade-off between vegetation
666 type, soil erosion control and surface water in global semi-arid regions: A meta-analysis, *J. Appl.*
667 *Ecol.*, 57, 875–885. <https://doi.org/10.1111/1365-2664.13597>, 2020.

668 Wu, G.L., Liu, Z.H., Zhang, L., Hu, T., and Chen, J.: Effects of artificial grassland establishment on
669 soil nutrients and carbon properties in a black-soil-type degraded grassland, *Plant Soil*, 333(1–
670 2), 469–479, <https://doi.org/10.1007/s11104-010-0363-9>, 2010.

671 Vanacker, V., Molina, A., Rosas, M. A., Bonnesoeur, V., Román-Dañobeytia, F., Ochoa-Tocachi, B.
672 F., and Buytaert, W.: The effect of natural infrastructure on water erosion mitigation in the Andes,
673 *Soil*, 8(1), 133–147, <https://doi.org/10.5194/soil-8-133-2022>, 2022.

674 Xia, L., Song, X.Y., Fu, N., Cui, S.Y., Li, L.J., Li, H.Y., and Li, Y.L.: Effects of forest litter cover on
675 hydrological response of hillslopes in the Loess Plateau of China, *Catena*, 181, 104076,
676 <https://doi.org/10.1016/j.catena.2019.104076>, 2019.

677 Xu, J.: A cave $\delta^{18}\text{O}$ based 1800-year reconstruction of sediment load and streamflow: The Yellow
678 River source area, *Catena*, 161, 137–147, <http://dx.doi.org/10.1016/j.catena.2017.09.028>, 2018.

679 Zhang, G.H., Tang, K.M., Ren, Z.P., and Zhang, X.C.: Impact of grass root mass density on soil
680 detachment capacity by concentrated flow on steep slopes, *T. ASABE*, (56), 927–934, 2013.

681 Zhao, X., Huang, J., Wu, P., Gao, X.: The dynamic effects of pastures and crop on runoff and
682 sediments reduction at loess slopes under simulated rainfall conditions, *Catena*, 119, 1–7,
683 <https://doi.org/10.1016/j.catena.2014.03.001>, 2014.

684 Zhao, Y.T., Pu, Y.F., Lin, H.L., and Tang, R.: Examining soil erosion responses to grassland
685 conversation policy in Three-River Headwaters, China, *Sustainability*, 13(5), 2702,
686 <https://doi.org/10.3390/su13052702>, 2021.

687 Zhou, J., Fu, B.J., Gao, G.Y., Lü, Y.H., Liu, Y., Lü, N., and Wang, S.: Effects of precipitation and

688 restoration vegetation on soil erosion in a semi-arid environment in the Loess Plateau, China,
689 *Catena*, 137, 1–11, <https://doi.org/10.1016/j.catena.2015.08.015>, 2016.

690 Zhu, P.Z., Zhang, G.H., Wang, H.X., Yang, H.Y., Zhang, B.J., and Wang, L.L.: Effectiveness of
691 typical plant communities in controlling runoff and soil erosion on steep gully slopes on the
692 Loess Plateau of China, *J. Hydrol.*, 602, 126714. <https://doi.org/10.1016/j.jhydrol.2021.126714>,
693 2021.

694 **Table 1.** Results of path analysis of the factors affecting runoff depth.

Influence factor	Direct path coefficient	Indirect path coefficient						Sum of path coefficient	
		<i>RI</i> ₆₀	<i>ARI</i>	<i>RD</i>	<i>P</i>	<i>VC</i>	<i>LB</i>		Total
<i>RI</i> ₆₀	0.24*		0.25	-0.09	-0.11	0.02	0.00	0.07	0.31
<i>ARI</i>	0.37**	0.16		-0.34	-0.05	0.02	0.02	-0.19	0.18
<i>RD</i>	0.67**	-0.03	-0.18		-0.08	0.03	-0.03	-0.31	0.36
<i>P</i>	-0.18**	0.14	0.10	0.31		0.02	0.00	0.57	0.40
<i>VC</i>	0.29**	0.01	0.03	0.06	-0.01		-0.06	0.03	0.32
<i>LB</i>	-0.12	0.01	-0.09	0.18	0.00	0.15		0.25	0.13

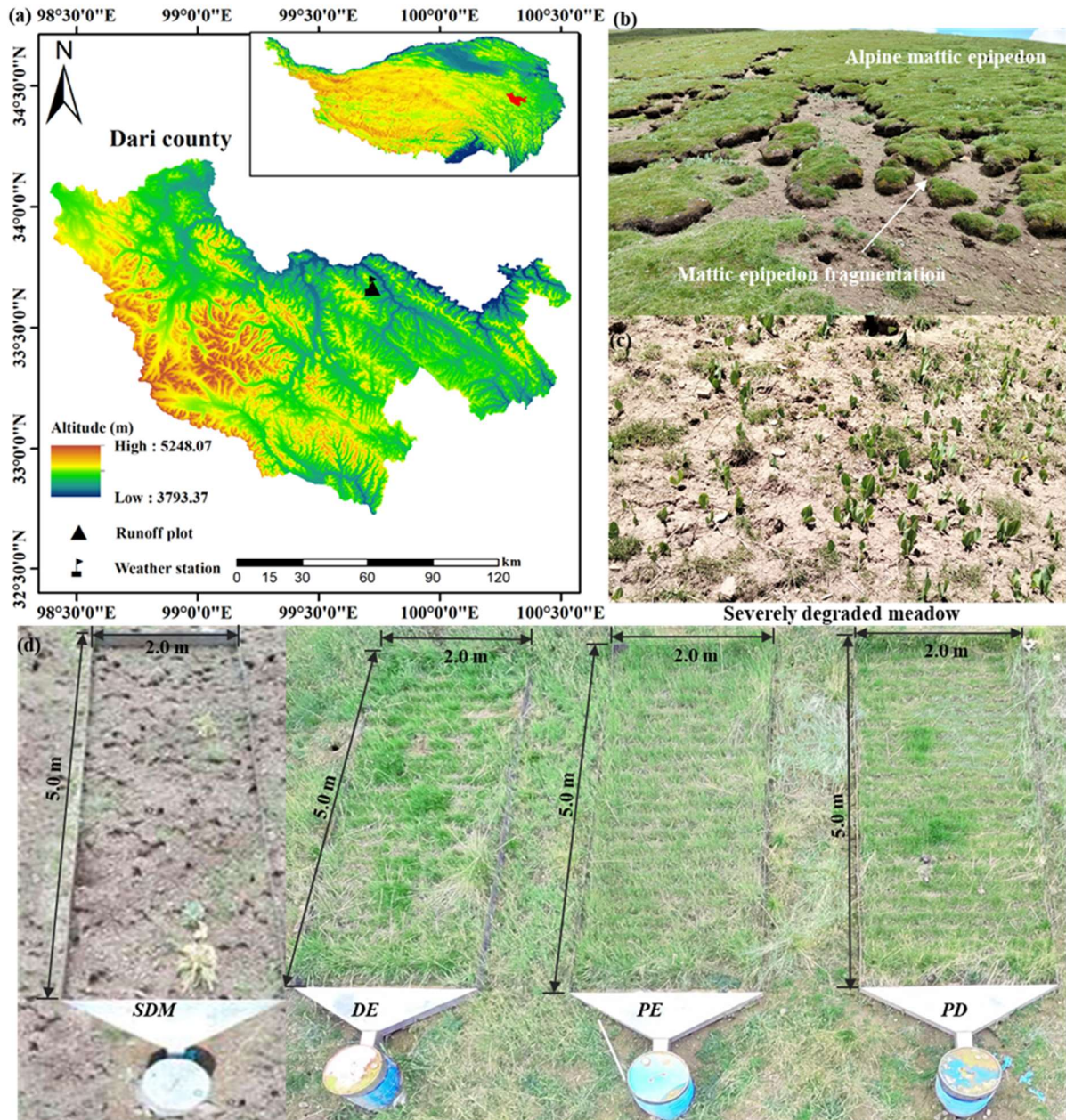
695 Note: *RI*₆₀ is maximum 60-minute intensity (mm h⁻¹), *ARI* is average rainfall intensity (mm h⁻¹), *RD*
696 is rainfall duration (h), *P* is rainfall amount (mm), *VC* is vegetation coverage (%), *LB* is litter biomass
697 (g m⁻²). * means the correlation is significant at 0.05 significance level, and ** means the correlation
698 is significant at 0.01 significance level.

699

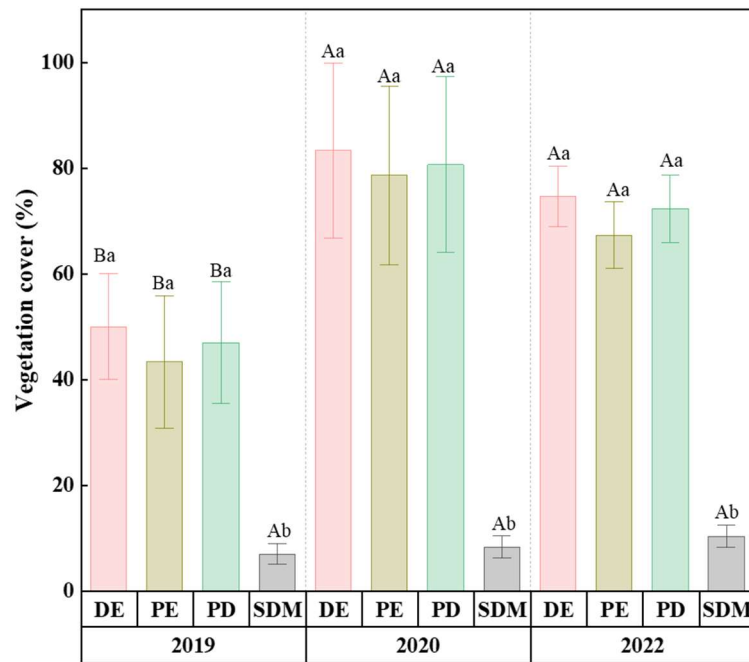
700 **Table 2.** Results of path analysis of the factors affecting soil loss per unit area.

Influence factor	Direct path coefficient	Indirect path coefficient								Sum of path coefficient
		<i>R</i>	<i>RI</i> ₆₀	<i>ARI</i>	<i>RD</i>	<i>P</i>	<i>VC</i>	<i>LB</i>	Total	
<i>R</i>	0.60**		-0.12	0.01	-0.10	0.11	0.01	0.01	-0.08	0.52
<i>RI</i> ₆₀	-0.29**	0.24		0.02	0.07	0.16	0.00	0.00	0.49	0.20
<i>ARI</i>	0.04	0.13	-0.19		0.21	0.07	0.01	0.02	0.25	0.28
<i>RD</i>	-0.41**	0.15	0.05	-0.02		0.13	0.00	-0.04	0.27	-0.13
<i>P</i>	0.28**	0.24	-0.17	0.01	-0.19		0.00	-0.01	-0.11	0.17
<i>VC</i>	0.03	-0.04	-0.04	0.01	-0.03	0.03		-0.06	-0.12	-0.10
<i>LB</i>	-0.10	-0.01	-0.01	-0.01	-0.16	0.03	0.02		-0.15	-0.25

701 Note: *R* is surface runoff (mm), *RI*₆₀ is maximum 60-minute intensity (mm h⁻¹), *ARI* is average rainfall
702 intensity (mm h⁻¹), *RD* is rainfall duration (h), *P* is rainfall amount (mm), *VC* is vegetation coverage
703 (%), *LB* is litter biomass (g m⁻²). ** means the correlation is significant at 0.01 significance level.



704 **Figure 1.** The location of the study area on the Qinghai-Tibetan Plateau, and the location of runoff
 705 plots in the study area. (a) The location of the study area, (b) the fragmenting mattic epipedon on the
 706 alpine hillslope and (c) severely degraded meadows formed by the disappearance of mattic epipedon
 707 and (d) four runoff plots of severely degraded meadows (*SDM*) and mixed-cultivated grasslands. A
 708 typical severely degraded meadow with a slope of 20° was selected to plant mixed grasses. Runoff
 709 plots were photographed with a drone in the early stages of the 2022 growing season. *DE*,
 710 *Deschampsia cespitosa* and *Elymus nutans*; *PE*, *Poa pratensis* L.cv. Qinghai and *Elymus nutans*; and
 711 *PD*, *Poa pratensis* L.cv. Qinghai and *Deschampsia cespitosa*.



712

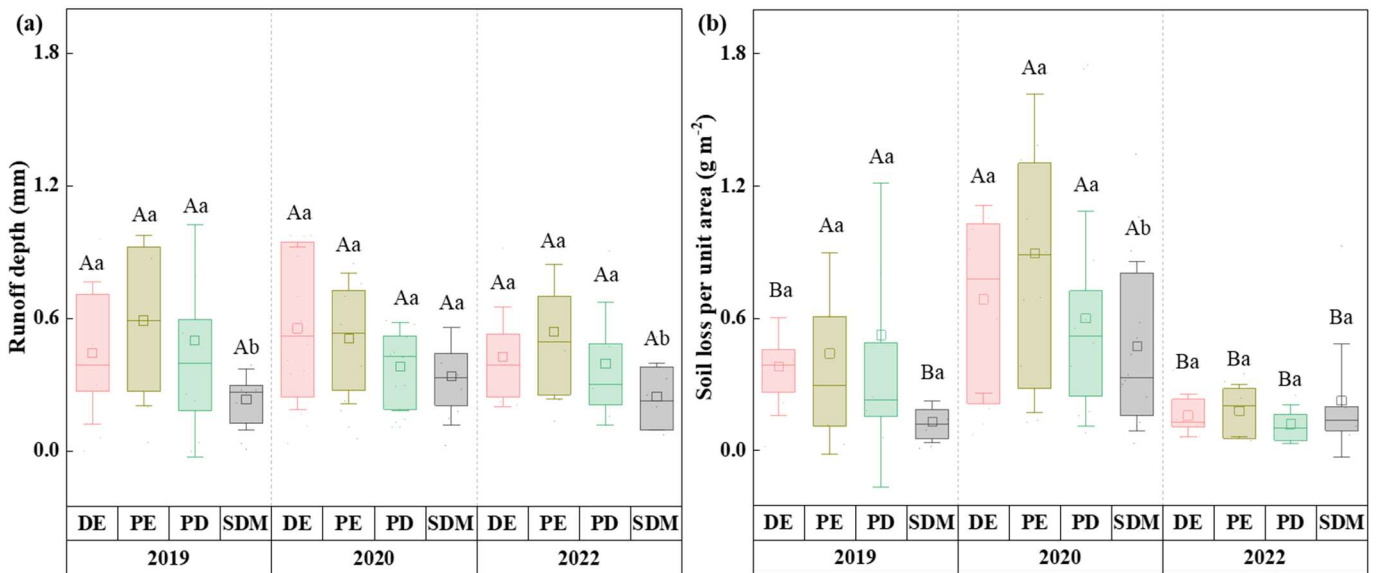
713 **Figure 2.** Changes in vegetation cover under various mixed-cultivated grasslands from 2019 to 2022.

714 Different capital letters mean that differences were significant in different years for the same

715 grassland community, and different lowercase letters mean that differences were significant between

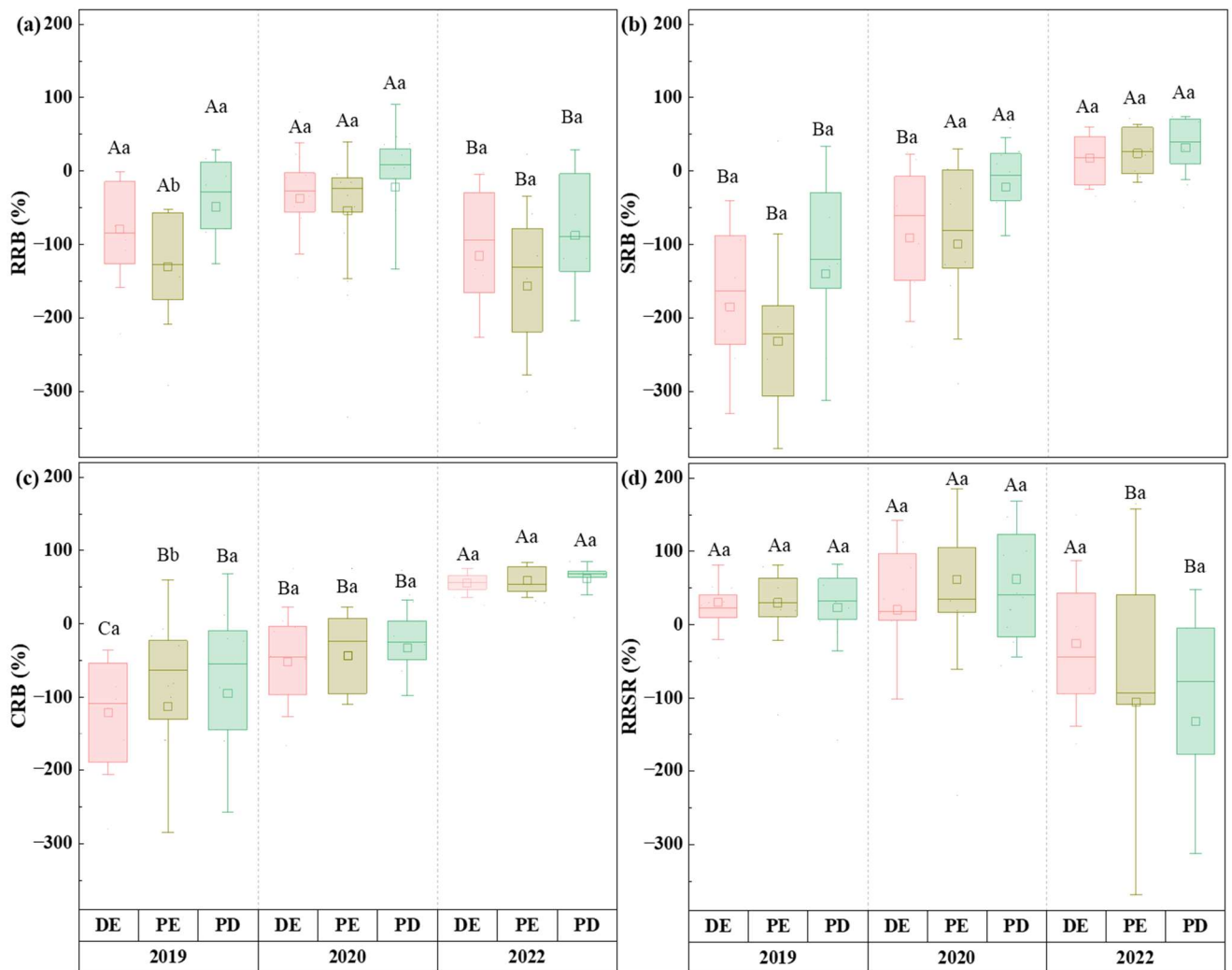
716 different communities in the same year.

717

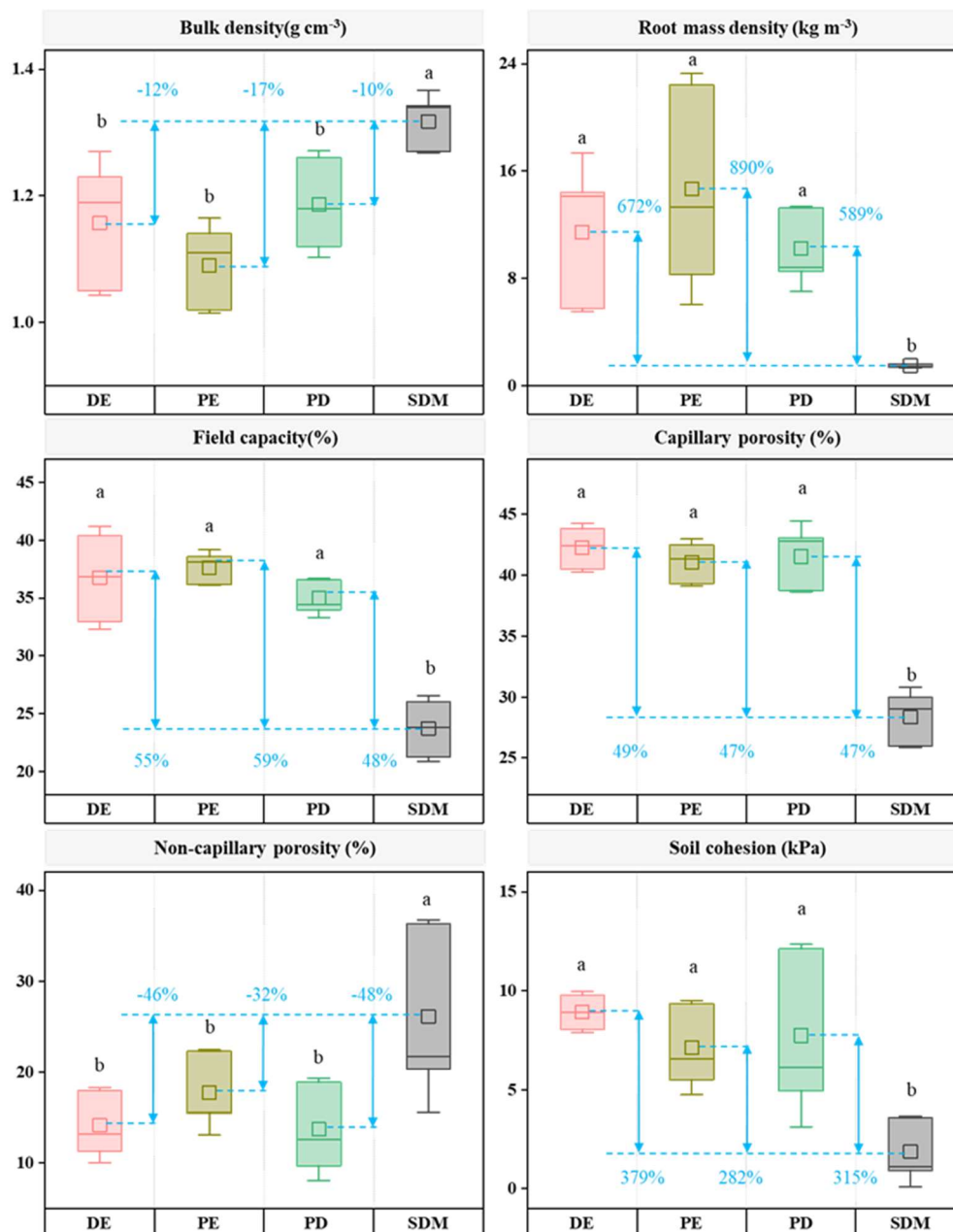


718 **Figure 3.** Changes in soil erosion and runoff under various mixed-cultivated grasslands from 2019 to
 719 2022. (a) Runoff depth and (b) soil loss per unit area. Note: For the four treatment runoff plots, runoff
 720 and sediment were measured 14, 18, and 10 times, respectively, during the growing season of 2019,
 721 2020, and 2022. Different capital letters mean that differences were significant in different years for
 722 the same grassland community, and different lowercase letters mean that differences were significant
 723 between different communities in the same year. *SDM*, severely degraded meadows, *DE*,
 724 *Deschampsia cespitosa* and *Elymus nutans*; *PE*, *Poa pratensis* L.cv. Qinghai and *Elymus nutans*; and
 725 *PD*, *Poa pratensis* L.cv. Qinghai and *Deschampsia cespitosa*. The lines in the middle of the box
 726 represent the median values. The squares in the box represent the average value.

727



728 **Figure 4.** Runoff, soil loss and sediment concentration reduction ratio under different mixed-
729 cultivated grasslands from 2019 to 2022. (a) Runoff reduction ratio (*RRB*), (b) soil loss reduction
730 ratio (*SRB*), (c) sediment concentration reduction ratio (*CRB*) and (d) the percent of runoff reduction
731 ratio to soil loss reduction ratio (*RRSR*). Note: Different capital letters mean that differences were
732 significant in different years for the same grassland community, and different lowercase letters mean
733 that differences were significant between different communities in the same year. The lines in the
734 middle of the box represent the median values. The squares in the box represent the average value.
735



736 **Figure 5.** Changes in bulk density, root mass density, field capacity, capillary capacity, non-capillary
 737 porosity and soil cohesion in 0-10 cm soil layer when severely degraded meadow (*SDM*) were
 738 restored to mixed-cultivated grassland for 4 years. *DE*, *Deschampsia cespitosa* and *Elymus nutans*;
 739 *PE*, *Poa pratensis L.cv. Qinghai* and *Elymus nutans*; and *PD*, *Poa pratensis L.cv. Qinghai* and
 740 *Deschampsia cespitosa*. Percentages represent the increased rate of soil properties (increased rate =
 741 $(V_{DE}$ or V_{PE} or $V_{PD} - V_{SDM})/V_{SDM}$), where V_{SDM} , V_{DE} , V_{PE} and V_{PD} are the mean values of soil
 742 characteristics of *SDM*, *DE*, *PE* and *PD*. Different lowercase letters mean that differences were
 743 significant between different communities. The lines in the middle of the box represent the median
 744 values. The squares in the box represent the average value.