
Jiao Juying (Orcid ID: 0000-0001-9663-1883)

**SEEDLING AND RAMET RECRUITMENT AT THE COMMUNITY
LEVEL ON RECENT LANDSLIDE SCARS ON THE CHINESE
HILLY-GULLIED LOESS PLATEAU**

Shu Hu¹, Juying Jiao^{2*}, Yujin Li², Na Deng², Duoyang Wu³, Yifeng Zhang²

1 Key Laboratory of Resource Biology and Biotechnology in Western China, Ministry of Education, Northwest University, Xi'an, PR China

2 State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A & F University, Yangling, PR China

3 College of Forestry, Northwest A & F University, Yangling, PR China

*Correspondence to: J. Y. Jiao, Institute of Soil and Water Conservation, No. 26, Xinong Road, Yangling, Shaanxi Province, PR China. E-mail: jyjiao@ms.iswc.ac.cn

CONFLICT OF INTEREST STATEMENT – We would like to declare that no conflicts of interest exist in the submission of this manuscript.

ABSTRACT

In this study, we aimed to provide a comprehensive insight into seedling and ramet recruitment at the community level on recent landslide scars (i.e., the sliding surfaces regarded as the most difficult zones of landslides to restore), which may cast new light on landslide ecology and enhance theoretical support for interventions on landslide restoration. Through seedling and ramet monitoring and adult survey on 12 three-year-old landslide scars on the Chinese hilly-gullied Loess Plateau, we characterized seedling and ramet recruitment in terms of their trade-off, processes and amounts, and we also assessed compositional correspondence between the adult and young (all seedlings and ramets combined) layers. We found that seedling recruitment was employed in tandem with ramet recruitment, which might maximize colonists' fitness. Moreover, seedlings and ramets emerged constantly and were followed by low mortality rates. However, there were problems of emergence limitation and constant

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/ldr.3437

death and, as a result, seedlings and ramets remained low densities. Therefore, there appeared to be a slow and limited recruitment process of plant colonists on the scars. In addition, there was a high degree of compositional uncoupling between the adult and young layers, implying future potential changes of plant communities driven by *Poa sphondylodes* Trin., *Stipa bungeana* Trin., *Ixeridium sonchifolium* (Maxim.) Shih, *Astragalus discolor* Bunge ex Maxim. and *Artemisia scoparia* Waldst. et Kit. on shady scars and *I. sonchifolium* (Maxim.) Shih on sunny scars. We also proposed that the first three species can be used to restore landslide scars in the study area.

KEYWORDS: Landslide scar; vegetation restoration; seedling recruitment; ramet recruitment; recruitment limitation

Accepted Article

INTRODUCTION

Landslides, the rapid down-slope movement of soil and vegetation, have been regarded as a severe form of disturbance to mountain ecosystems (Restrepo et al., 2003, 2009; Sidle & Bogaarda, 2016; Neto et al., 2017; Yang et al., 2018). They often leave a great number of scars (i.e., the sliding surfaces) onto mountain slopes and few biological materials (e.g., seeds and sprouters) on the scars (Restrepo et al., 2009). Moreover, landslide scars are typically the steepest and most infertile relative to the depositional and adjacent undisturbed zones, and they are accompanied by post-landslide erosion (Adams & Sidle, 1987; Guariguata, 1990; Walker & Shiels, 2008; Restrepo et al., 2009). Accordingly, restoration is thought to be difficult on landslide scars (Walker et al., 2009).

During the restoration process, plants are generally faced with the challenges of seed dispersal and germination, vegetative expansion, resprouting, establishment, population recruitment, interspecific interactions and responses to stresses or disturbance (Walker et al., 2009). Studying these biological processes can help uncover plant community succession and assembly rules on landslides and thus provide theoretical support for interventions on landslide restoration, and an increasing number of studies have reported these processes over the last few decades (Lundgren, 1978; Guariguata, 1990; Chaudhry et al., 1996; Restrepo & Vitousek, 2001; Walker et al., 2010; Walker & Shiels, 2013; Neto et al., 2017; Gonzalez-Ollauri & Mickovski, 2017; Li et al., 2017; Hu et al., 2018; Pang et al., 2018). Population recruitment of plant species is a dynamic process by which seedlings or ramets emerge from seeds or clonal organs and survive to become new recruits to their populations (Harper, 1977; Molles, 2016). Efficient recruitment is critical for colonists to enhance their population persistence (Weiher et al., 1999; Bond & Midgley, 2001). However, this critical process on landslide scars has not been well studied (Hupp, 1983; Guariguata, 1990; Chaudhry et al., 1996; Myster, 2002; Mourya et al., 2019).

To recruit populations, plant species must take on two common challenges, i.e., seedling (or ramet) emergence and survival (Aicher et al., 2011; Marques & Burslem, 2015) and thus have evolved different patterns of recruitment. For example, some species produce young individuals in relatively high densities, but the young die at high rates, such as *Olea europaea* var. *sylvestris*. Brot. in the dense scrubland at Sierra Sur de Jaén of southern Spain (Rey & Alcantara, 2000) and *Phyteuma betonicifolium* Vill. in the dry grassland Poma of southern Switzerland (Zeiter et al., 2006). Conversely, some other species produce a few young individuals, but the young survive at high rates, such as *Rhododendron arboreum* Sm. in a

humid subtropical forest of northeast India (Barik et al., 1996). Moreover, some dominant herbs in woodland or fertile, tall-herb communities germinate at low temperatures (during early spring), probably because they need to grow rapidly prior to the closing of tree canopies or the growth of neighboring competitors (Grime et al., 1981). Some other species inhabiting alpine region germinate during late spring or early summer in order to prevent seedlings from dying of cold (Baskin & Baskin, 1998). In addition, many perennial plants are able to produce not only seedlings but also ramets (Fenner & Thompson, 2005). Ramet recruitment can play an important role in population recruitment in the situation of seedling recruitment limitation (Pérez-Harguindeguy et al., 2013; Lin et al., 2016) or in less-productive or disturbed environments (Grime, 2001; Bellingham & Sparrow, 2009; Wang et al., 2016). The trade-off between seedling and ramet recruitment has been well studied at the species level in response to different stresses or disturbance (Eriksson, 1986; Nobel, 1992; Ronsheim & Bever, 2000; García & Zamora, 2003; Travis et al., 2004; Yang et al., 2009; Wang et al., 2016; Li et al., 2018). However, little is known about seedling and ramet recruitment at the community level in severely disturbed environments such as landslide scars (Guariguata, 1990; Mourya et al., 2019). Furthermore, studying community-level recruitment can help predict future succession orientation of plant communities (Pérez-Ramos & Marañón, 2012; Fernandez-Lugo et al., 2015).

Landslides have been frequently occurring in the hilly-gullied region of the Chinese Loess Plateau for millennia (Liu & Wu, 1996; Cao et al., 2015). This region has also suffered from thousands of years of drought, soil infertility and other types of soil erosion such as sheet, rill and gully erosion (Li et al., 2008). Numerous landslide scars were left on gully slopes because of the continuous rainstorms in July 2013 in this region (Cao et al., 2015), and over half of plant colonists on the landslide scars were of clonality (Hu et al., 2018), thus providing us with a good opportunity to study seedling and ramet recruitment at the community level on the landslide scars characterized by not only less productivity but also post-landslide erosion.

In this study, we aimed to gain a comprehensive insight into seedling and ramet recruitment at the community level on recent landslide scars in the hilly-gullied region of the Chinese Loess Plateau. Through seedling and ramet monitoring and adult survey on 12 shallow landslide scars (selected out of the hundreds of landslide scars produced by the continuous rainstorms in July 2013 in this region and occurred on both shady and sunny gully slopes), we 1) identified the trade-off between seedling and ramet recruitment, 2)

characterized seedling and ramet recruitment processes, 3) analyzed if there was recruitment limitation, and 4) estimated compositional correspondence between the adult and young (all seedlings and ramets combined) layers in plant communities on both shady and sunny scars. Finally, we predicted future restoration progress and community changes on the scars, and we also proposed potential species for interventions on landslide restoration in the study area.

MATERIALS AND METHODS

Study Area

This study was conducted in the Fangta (36°47'–36°49' N, 109°14'–109°16' E), Yaozigou (36°47'–36°49' N, 109°15'–109°20' E) and Majiagou (36°49'–36°56' N, 109°09'–109°18' E) watersheds located in the hilly-gullied region of the Chinese Loess Plateau. Within the watersheds, the climate is cold and semi-arid (BSk; Köppen, 1884), with annual average temperatures of around 9 °C and annual precipitation of around 500 mm (50–70 % occurring from July to September and mostly in the form of rainstorms) (Li et al., 2008). The soils are generally silt loam and approximately homogeneous along the profile (Guo et al., 1992), with internal friction angles around 25° (Liu & Wu, 1996). The vegetation is characteristic of a transition between deciduous forests and typical steppe, and it is dominated by herbs (*Stipa bungeana* Trin., *Poa sphondylodes* Trin., *Cleistogenes caespitosa* Keng, *Leymus secalinus* (Georgi) Tzvel., *Bothriochloa ischaemum* (L.) Keng, *Heteropappus altaicus* (Willd.) Novopokr., *Patrinia heterophylla* Bunge and *Artemisia scoparia* Waldst. et Kit.), subshrubs (*Artemisia gmelinii* Web. ex Stechm., *Artemisia giraldii* Pamp. and *Lespedeza daurica* (Laxm.) Schindl.) and shrubs (*Syringa oblate* Lindl., *Sophora davidii* (Franch.) Skeels, *Periploca sepium* Bunge and *Buddleja alternifolia* Maxim.) (Li et al., 2008). *Robinia pseudoacacia* L., *Salix matsudana* Koidz., *Populus simonii* Carr., *Hippophae rhamnoides* L. and *Caragana korshinskii* Kom. have also been used for afforestation on a large scale to fight against serious soil erosion since 1999 (Li et al., 2008). There are also economic forests of *Malus pumila* Mill. and *Cerasus pseudocerasus* (Lindl.) G. Don according to our watershed-wide investigation. Landslides are common events due to the geomorphic, climatic, edaphic and vegetation characteristics as well as intense human activities (Liu & Wu, 1996), and they occur mostly in the form of shallow-seated slides (< 2 m erosion depth; Sidle & Ochiai, 2006).

Landslide Scars

Within the study area, we selected 12 landslides out of the hundreds caused by the continuous rainstorms in July 2013. The selected landslides occurred on both shady (0–89° & 271–359°)

and sunny (91–269°) gully slopes and were shallow-seated (Table SI). Then we carried out seedling and ramet monitoring and adult survey on the landslide scars, i.e., the sliding surfaces regarded as the most difficult zones to restore (Restrepo et al., 2009; Walker et al., 2009; see Table SI for more basic information).

The Young Layers

On each landslide scar, we laid out three 1-m² permanent quadrats before March 28th, 2016 (since then air temperature had steadily passed 5 °C in the study area, implying the beginning of the growing season). The three quadrats were parallel to each other and spaced 1 m apart at the mid-scar position. Within each quadrat, we identified and marked all the newly emerged young individuals with bamboo sticks of a specific color in the middle of each month from April to October (within the growing season in the study area) of 2016 (i.e., April 16th, 2016, May 17th, 2016, June 18th, 2016, July 19th, 2016, August 19th, 2016, September 19th, 2016 and October 20th, 2016) and then on April 22nd, 2017; each time we recorded the respective numbers of the emerged and died seedlings and ramets of each species.

The Adult Layers

On the entire surface of each landslide scar, we identified all the adult plants and recorded the number of adult individuals of each species in mid-August 2017 (at the peak of the growing season in the study area).

Statistical Analyses

To identify the trade-off between seedling and ramet recruitment on shady (or sunny) scars, we compared seedlings and ramets in terms of emergence amount, the degree of death and density at different time scales on shady (or sunny) scars (Table I).

To characterize seedling (or ramet) recruitment process on shady (or sunny) scars, we analyzed seedling (or ramet) dynamics in terms of emergence amount, the degree of death and density within the study period on shady (or sunny) scars (Table I).

To know if there was recruitment limitation on the scars, we first compared seedlings (or ramets) on shady scars and those on sunny scars in terms of emergence amount, the degree of death and density at different time scales (Table I), then we compared the data with those on gully slopes within nearby watersheds or landslide scars under other climates. The above analyses were performed using SPSS (IBM SPSS Statistics 20.0; International Business Machines Corporation, Armonk, NY, US).

Table I. Analytical items, data (n=6) and statistical approaches

[Table I]

To know whether the adult layers were coupled to the young layers in terms of species composition on shady (or sunny) scars, we analyzed differences in species composition between the adult layers in mid-August 2017 and the young layers (all the seedlings and ramets combined) at the eight study times (T1–T8) using permutational multivariate analysis of variance (PERMANOVA; Anderson & Walsh, 2013), and we visualized the differences using non-metric multidimensional scaling (NMDS). In addition, we averaged the relative densities of each species in the adult layers across the six shady (or sunny) scars and then identified the most abundant species in the adult layers on shady (or sunny) scars. We also averaged the relative densities of each species in the young layers across the six shady (or sunny) scars each time and then across the eight study times, then we identified the most abundant species in the young layers on shady (or sunny) scars. For each of these species on shady (or sunny) scars, we compared the averaged relative densities of its adult and young individuals and also considered emergence density and mortality rate of its young individuals throughout the study period (Table SV). Finally, we identified the species that may drive future compositional changes of plant communities on shady (or sunny) scars.

RESULTS

Seedling vs. Ramet Recruitment

There were no significant differences between seedlings and ramets in the overall emergence density during each study period (P1–P8), the growing season (P1–7) and the whole study period (P1–8) on shady scars (fixed effect: $F_{1, 94/10/10} = 0.196, 2.535$ and 2.367 , respectively, and $p = 0.659, 0.142$ and 0.155 , respectively; Figure 1a, b) and also on sunny scars (fixed effect: $F_{1, 94/10/10} = 0.052, 0.181$ and 0.076 , respectively, and $p = 0.820, 0.680$ and 0.788 , respectively; Figure 1a, b).

There were no significant differences between seedlings and ramets in the overall mortality rate during each growing period (P2–P7), the growing season (P2–7), the winter (P8) and the whole study period (P2–8) on shady scars (fixed effect: $F_{1, 69/10/10/10} = 0.219, 1.355, 0.029$ and 0.352 , respectively, and $p = 0.641, 0.271, 0.869$ and 0.566 , respectively; Figure 1c, d) and also on sunny scars (fixed effect: $F_{1, 59/10/10/10} = 0.003, 0.002, 0.360$ and 0.365 , respectively, and $p = 0.960, 0.965, 0.562$ and 0.559 , respectively; Figure 1c, d).

There were no significant differences between seedlings and ramets in the overall density at each study time (T1–T8), the end of the growing season (T7) and the last study time (T8) on shady scars (fixed effect: $F_{1, 94/10/10} = 0.638, 2.470$ and 3.170 , respectively, and $p = 0.427,$

0.147 and 0.105, respectively; Figure 1e) and also on sunny scars (fixed effect: $F_{1, 94/10/10} = 0.122, 0.127$ and 0.040 , respectively, and $p = 0.727, 0.729$ and 0.845 , respectively; Figure 1e).

Recruitment Processes

There were no significant differences among the overall emergence densities of seedlings during the eight study periods (P1–P8) on whether shady or sunny scars (fixed effect: $F_{7, 40} = 1.146$ and 0.849 , respectively, and $p = 0.355$ and 0.554 , respectively; Figure 1a) and also among those of ramets during those periods on whether shady or sunny scars (fixed effect: $F_{7, 40} = 0.415$ and 0.345 , respectively, and $p = 0.887$ and 0.928 , respectively; Figure 1a) (see Table SII for other statistics).

There were no significant differences among the overall mortality rates of seedlings during the six growing periods (P2–P7) on whether shady or sunny scars (fixed effect: $F_{5, 29/21} = 0.585$ and 1.826 , respectively, and $p = 0.711$ and 0.151 , respectively; Figure 1c) and also among those of ramets during those periods on whether shady or sunny scars (fixed effect: $F_{5, 30/28} = 0.130$ and 0.168 , respectively, and $p = 0.984$ and 0.972 , respectively; Figure 1c) (see Table SIII for other statistics). There were also no significant differences between the overall mortality rates of seedlings during the growing season (P2–7) and those during the winter (P8) on whether shady or sunny scars (fixed effect: $F_{1, 10} = 0.384$ and 0.151 , respectively, and $p = 0.549$ and 0.706 , respectively; Figure 1d) and also between those of ramets during the two periods on whether shady or sunny scars (fixed effect: $F_{1, 10} = 0.003$ and 1.167 , respectively, and $p = 0.956$ and 0.305 , respectively; Figure 1d).

There was a significant difference among the overall densities of seedlings at the eight study times (T1–T8) on shady scars (fixed effect: $F_{7, 40} = 3.338$, and $p = 0.007$), and those of seedlings increased slightly within the growing season and then decreased slightly over the winter (Figure 1e). However, there were no significant differences among the overall density of seedlings at the eight study times on sunny scars and also among those of ramets at those times on whether shady or sunny scars (fixed effect: $F_{7, 40} = 0.956, 2.164$ and 0.514 , respectively, and $p = 0.476, 0.059$ and 0.818 , respectively; Figure 1e) (see Table SIV for other statistics).

Recruitment on Shady vs. Sunny Scars

There were significant differences between shady and sunny scars in the overall emergence densities of seedlings during each study period (P1–P8; Wald $\chi^2 = 108.099$, $df = 15$, and $p < 0.0001$), the growing season (P1–7; Wald $\chi^2 = 11.596$, $df = 1$, and $p = 0.001$) and the whole study period (P1–8; Wald $\chi^2 = 10.582$, $df = 1$, and $p = 0.001$), and those of seedlings were

significantly higher on shady scars than on sunny scars (Figures 1a, b). Moreover, there were significant differences between shady and sunny scars in the overall emergence densities of ramets during each study period and the growing season (Wald $\chi^2 = 31.782$ and 4.786 , respectively, $df = 15$ and 1 , respectively, and $p = 0.007$ and 0.029 , respectively), and those of ramets were significantly higher on shady scars than on sunny scars (Figures 1a, b), but there was no significant difference during the whole study period (Wald $\chi^2 = 3.124$, $df = 1$, and $p = 0.077$; Figure 1b).

There was a significant difference between shady and sunny scars in the overall mortality rates of seedlings during each growing period (P2–P7; Wald $\chi^2 = 51.599$, $df = 11$, and $p < 0.0001$), and those of seedlings were significantly higher on shady scars than on sunny scars (Figure 1c), but there were no significant differences during the growing season (P2–7; Wald $\chi^2 = 2.730$, $df = 1$, and $p = 0.098$; Figure 1d), the winter (P8; Wald $\chi^2 = 0.371$, $df = 1$, and $p = 0.542$; Figure 1d) and the whole study period (P2–8; Wald $\chi^2 = 0.090$, $df = 1$, and $p = 0.765$; Figure 1d). Moreover, there were significant differences between shady and sunny scars in the overall mortality rates of ramets during the winter and the whole study period (Wald $\chi^2 = 6.622$ and 5.926 , respectively, both $df = 1$, and $p = 0.010$ and 0.015 , respectively), and those of ramets were significantly higher on sunny scars than on shady scars (Figure 1d), but there were no significant differences during each growing period and the growing season (Wald $\chi^2 = 7.420$ and 0.028 , respectively, $df = 11$ and 1 , respectively, and $p = 0.764$ and 0.866 , respectively; Figures 1c, d).

There were significant differences between shady and sunny scars in the overall densities of seedlings at each study time (T1–T8; Wald $\chi^2 = 176.120$, $df = 15$, and $p < 0.0001$), the end of the growing season (T7; Wald $\chi^2 = 10.352$, $df = 1$, and $p = 0.001$) and the last study time (T8; Wald $\chi^2 = 11.269$, $df = 1$, and $p = 0.001$), and those of seedlings were significantly higher on shady scars than on sunny scars (Figure 1e). Moreover, there were significant differences between shady and sunny scars in the overall densities of ramets at each study time and the end of the growing season (Wald $\chi^2 = 73.298$ and 5.226 , respectively, $df = 15$ and 1 , respectively, and $p < 0.0001$ and $= 0.022$, respectively), and those of ramets were significantly higher on shady scars than on sunny scars (Figure 1e), but there was no significant difference at the last study time (Wald $\chi^2 = 3.016$, $df = 1$, and $p = 0.082$; Figure 1e).

Species Composition of the Adult vs. Young Layers

On shady scars, there were significant compositional differences between the adult layers in

mid-August 2017 and the young layers at T4–T8 ($F = 1.740, 1.898, 2.717, 2.721$ and 2.440 , respectively, all $df = 1$, $R^2 = 0.148, 0.160, 0.214, 0.214$ and 0.196 , respectively, and $p = 0.048, 0.046, 0.026, 0.014$ and 0.042 , respectively; Figure 2a) but no significant differences at T1–T3 ($F = 0.150, 1.469$ and 1.593 , respectively, all $df = 1$, $R^2 = 0.130, 0.128$ and 0.137 , respectively, and $p = 0.124, 0.100$ and 0.077 , respectively; Figure 2a). *S. bungeana* Trin. and *P. sphondylodes* Trin. were the most abundant in both adult and young layers. *A. gmelinii* Web. ex Stechm. and *P. heterophylla* Bunge were the most abundant in the adult layers and moderately abundant in the young layers. *Calamagrostis epigeios* (L.) Roth and *A. giraldii* Pamp. were the most abundant in the adult layers but not abundant in the young layers. *Astragalus discolor* Bunge ex Maxim. was the most abundant in the young layers and moderately abundant in the adult layers. *A. scoparia* Waldst. et Kit. and *Ixeridium sonchifolium* (Maxim.) Shih were the most abundant in the young layers but not abundant in the adult layers (Table SV).

On sunny scars, there were significant compositional differences between the adult layers in mid-August 2017 and the young layers at T6–T8 ($F = 1.542, 1.720$ and 1.605 , respectively, all $df = 1$, $R^2 = 0.134, 0.147$ and 0.138 , respectively, and $p = 0.037, 0.018$ and 0.034 , respectively; Figure 2b) but no significant differences at T1–T5 ($F = 1.023, 1.210, 1.065, 1.265$ and 1.161 , respectively, all $df = 1$, $R^2 = 0.102, 0.108, 0.096, 0.112$ and 0.104 , respectively, and $p = 0.447, 0.212, 0.369, 0.207$ and 0.274 , respectively; Figure 2b). *Sphaerophysa salsula* (Pall.) DC. was the most abundant in both adult and young layers. *A. giraldii* Pamp. and *P. sepium* Bunge were the most abundant in the adult layers but not abundant in the young layers. *S. bungeana* Trin. was the most abundant in the young layers and moderately abundant in the adult layers. *Convolvulus arvensis* L. and *I. sonchifolium* (Maxim.) Shih were the most abundant in the young layers but not abundant in the adult layers (Table SV).

DISCUSSION

Trade-off between Seedling and Ramet Recruitment

Seedling recruitment is not the only form of population recruitment in plants. Many plants, especially herbaceous perennials, may also employ ramet recruitment via vegetative organs such as stolons, rhizomes, corms and bulbs (Fenner & Thompson, 2005; Pérez-Harguindeguy et al., 2013). Ramet recruitment offers various unique ecological advantages, such as a low cost of energy, high survivorship and rapid growth (because of resource and risk sharing and economies of scale among ramets), niche specialization and inbreeding avoidance (Muir,

1995; Grime, 2001; Fenner & Thompson, 2005; Gómez & Stuefer, 2006; Yang et al., 2009; Dodd & Douhovnikoff, 2016). Therefore, ramet recruitment acts as a recruitment assurance in the situation of seedling recruitment limitation or in less-productive or disturbed environments. However, seedling recruitment can avoid genetic uniformity produced by ramet recruitment, which is thought to be problematic in the long term because it may render the species unable to adapt to any environmental change (Fenner & Thompson, 2005; Dodd & Douhovnikoff, 2016). Seedling recruitment also facilitates the domination of more distant sites.

In this study, we found no differences between seedlings and ramets in the overall emergence densities, mortality rates and densities at different time scales on both shady and sunny scars (Figure 1), indicating the strategy of employing both seedling and ramet recruitment of plant colonists on the both less-productive and erosion-disturbed scars. This strategy offers colonists both short-term and long-term fitness by combining the advantages of both recruitment forms.

Recruitment Processes

Seedling and ramet emergence on shady and sunny scars were all continuous and steady within the study period (Figure 1a), reflecting a constant emergence pattern of plant colonists on the scars. This is inconsistent with the germination pattern of many perennials and winter annuals (or biennials) under temperate climates that they germinate explosively in autumn in order to initiate or accelerate flowering processes in the next year over prolonged cold of winter (Wu, 2018). However, the emerged seedlings and ramets on shady and sunny scars were all followed by constant mortality rates (Figure 1c, d). Although the mortality rates were not very high (Figure 1 c, d), none of seedlings and ramets on shady and sunny scars accumulated significantly throughout the study period (Figure 1e), implying a slow population recruitment process of plant colonists on the scars.

During the prolonged cold winter in the study area (daily average air temperature $< 5^{\circ}\text{C}$), hardly any seedlings or ramets could emerge, and the emerged ones died continuously and did at similar rates with those during the growing season (Figure 1d). Therefore, winter appeared to be the most influential period in recruitment efficiency of plant colonists on the scars.

Recruitment Limitation

Recruitment limitation can be a barrier to ecosystem restoration and conservation (Vargas & Stevenson, 2013; Heydari et al., 2017; Lu et al., 2019). Our findings may prove the presence

of recruitment limitation on the scars.

In terms of emergence amount, more seedlings and ramets generally emerged on shady scars than on sunny scars (Figure 1a, b); compared with the overall emergence densities of young individuals on gully slopes within the nearby Songjiagou and Zhifanggou watersheds from early-April to early-October of 2012 (183.4 ± 41.4 individuals m^{-2} and 121.9 ± 74.5 individuals m^{-2} on shady and sunny gully slopes, respectively, $n = 3$; unpublished data of our research group), those on the scars during P1–7 (54.0 ± 22.2 individuals m^{-2} and 20.3 ± 11.7 individuals m^{-2} on shady and sunny scars, respectively) appeared much lower. Accordingly, there appeared to be emergence limitation on the scars, especially on sunny scars. Emergence limitation can be attributed to seed (or ramet) limitation (e.g., the limitation of seed production, dispersal and persistence and the lack of buds) and germination (or sprouting) limitation (due to poor germination traits, stresses, or disturbance) (Marques & Burslem, 2015; De la Pena-Domene et al., 2018). Most plant individuals on the scars were clonal and their seeds were of anchorage mechanisms and high germination speeds and rates but low production and limited mobility (Hu et al., 2018). Moreover, it was probably because soil seed banks of the scars were still at the primitive accumulation stage that the densities (298 ± 407 seeds m^{-2} and 883 ± 980 seeds m^{-2} at 0–5 cm soil layer of shady and sunny scars in late-March 2016, respectively; unpublished data of our research) were much lower than those of the relatively old gully slopes within the Zhifanggou watershed ($1425\text{--}5238$ seeds m^{-2} ; Yuan, 2009; Wang, 2013). Soils of the scars remained available water but low contents of organic matter (Table SI). These findings may suggest the limitation of seed production, dispersal and persistence and sprouting on the scars, and future research will be necessary to find out the main causes.

In terms of the degree of death, seedlings and ramets generally died at similar rates on shady and sunny scars (Figure 1c, d); compared with the overall mortality rates of young individuals on gully slopes within the Songjiagou and Zhifanggou watersheds (shady gully slopes: 78.1 ± 2.2 %, 74.9 ± 1.0 % and 93.4 ± 0.7 % from early-May to early-October of 2012, during the winter of 2012 and from early-May of 2012 to early-April of 2013, respectively, $n = 3$; sunny gully slopes: 77.1 ± 4.9 %, 64.6 ± 9.1 % and 90.5 ± 1.7 % during the same respective periods, $n = 3$; unpublished data of our research group), those on the scars (shady scars: 32.0 ± 7.4 %, 26.6 ± 11.7 % and 45.3 ± 9.4 % during P2–7, P8 and P2–8, respectively; sunny scars: 25.9 ± 11.8 %, 37.5 ± 15.0 % and 50.6 ± 16.5 % during the same respective periods, respectively) appeared much lower. By contrast, serious survival limitation was

found in *Inga vera* Willd. (100% mortality rate after 1 year) on landslides at age 10–15 years in the Luquillo Experimental Forest of Puerto Rico under a tropical rainforest climate (Myster, 2002) and *Olea europaea* var. *sylvestris*. Brot. (90.7% mortality rate until the sapling stage) in the dense scrubland at Sierra Sur de Jaén of southern Spain under a semi-arid climate (Rey & Alcántara, 2000). Accordingly, there appeared to be not too much survival limitation on the scars, which might be attributed to the large weight of seeds of most plant individuals on the scars (Hu et al., 2018) because this trait helps seedlings survive under stresses (Pérez-Harguindeguy et al., 2013). However, the steepness and infertility of the scars (Table SI) might be the main causes for the mortalities. The underlying mechanisms driving seedling and ramet survivorship on the scars are still worthy of further research.

As a result of emergence and death, more seedlings and ramets generally accumulated on shady scars than on sunny scars (Figure 1e). Compared with the overall densities of young individuals on gully slopes within the Zhifanggou watershed from late-June to mid-October of 2007 (12.5–119.0 individuals m⁻² and 5.5–140.0 individuals m⁻² on shady and sunny gully slopes, respectively, n = 2; Wang, 2008) and the Songjiagou and Zhifanggou watersheds from early-April to early-October of 2012 (55–75 individuals m⁻² and 40–53 individuals m⁻² on shady and sunny gully slopes, respectively, n = 3; Su, 2013), those on the scars during P1–7 (4.5–40.0 individuals m⁻² and 2.3–15.8 individuals m⁻² on shady and sunny scars, respectively) appeared much lower. Seedlings showed a lower density (1.2 individuals m⁻²) on a landslide scar at age 2–7 years in the Luquillo Experimental Forest (Guariguata, 1990) and a much lower density (106.7 individuals ha⁻¹) within an old landslide area in a mixed conifer forest of Indian Central Himalaya under a monsoon-influenced humid subtropical climate (Mourya et al., 2019), but they showed higher densities (158.3 ± 113.0 individuals m⁻² and 26.7 ± 10.3 individuals m⁻² in July of 1979 and 1980, respectively, n = 2) on landslide scars at age two years in a block-field cove on Massanutten Mountain of northwestern Virginia under a humid subtropical climate (Hupp, 1983).

Compositional Uncoupling between the Adult and Young Layers

Once colonized a certain site, plant species will be confronted with the challenge of population recruitment (Weiher et al., 1999). However, a number of plant species may have the problem of recruitment limitation in terms of emergence, survival, or both, thus resulting in compositional uncoupling between the adult and young layers in plant communities, while those recruitment-efficient species can be expected as key drivers of future community succession (Pérez-Ramos & Marañón, 2012). In this study, we found a high degree of the

uncoupling on the scars (Figure 2). In detail, on shady scars, although *C. epigeios* (L.) Roth and *A. giraldii* Pamp. were the most abundant in the adult layers but not abundant in the young layers, probably because they might have the problem of emergence limitation (see Table SV); *A. scoparia* Waldst. et Kit. and *I. sonchifolium* (Maxim.) Shih were not abundant in the adult layers but the most abundant in the young layers with relatively high emergence densities and low mortality rates (see Table SV). Likewise, on sunny scars, *A. giraldii* Pamp. and *P. sepium* Bunge were the most abundant in the adult layers but not abundant in the young layers, probably because they might have problems of both emergence and survival limitation (see Table SV); *I. sonchifolium* (Maxim.) Shih and *C. arvensis* L. were not abundant in the adult layers but the most abundant in the young layers with relatively high emergence density (see Table SV).

Furthermore, the uncoupling relationship can be used to speculate future compositional changes of plant communities (Pérez-Ramos & Marañón, 2012; Fernandez-Lugo et al., 2015). We thus speculate that on shady scars, *C. epigeios* (L.) Roth and *A. giraldii* Pamp. will have a difficulty in persisting or expanding their populations; although *A. gmelinii* Web. ex Stechm. and *P. heterophylla* Bunge were moderately abundant in the young layers with low mortality rates, they might have emergence limitation (see Table SV), thus they will also have a difficulty in population persistence or expansion; *P. sphondylodes* Trin., *A. discolor* Bunge ex Maxim., *A. scoparia* Waldst. et Kit., *I. sonchifolium* (Maxim.) Shih and *S. bungeana* Trin. were the most abundant in the young layers with relatively high emergence densities and low mortality rates (see Table SV), thus they may persist or expand their populations and drive future compositional changes of plant communities on shady scars. On shady gully slopes within the Songjiagou and Zhifanggou watersheds, high recruitment efficiency of *S. bungeana* Trin. and emergence limitation of *A. gmelinii* Web. ex Stechm. have also been identified; however, *P. heterophylla* Bunge was of high recruitment efficiency, and *I. sonchifolium* (Maxim.) Shih and *A. scoparia* Waldst. et Kit. might have the respective problems of emergence and survival limitation (Su et al., 2014). On sunny scars, *A. giraldii* Pamp. and *P. sepium* Bunge will have a difficulty in persisting or expanding their populations; although *S. salsula* (Pall.) DC. and *C. arvensis* L. were the most abundant in the young layers with relatively high emergence densities, the young died at high mortality rates, and *S. bungeana* Trin. was the most abundant in the young layers with a low mortality rate but might have emergence limitation (see Table SV), thus these three species will also have a difficulty in population persistence or expansion. Emergence limitation of *S. bungeana* Trin.

and both emergence and survival limitation of *A. giraldii* Pamp. have also been identified on sunny gully slopes within the Songjiagou and Zhifanggou watersheds (Su et al., 2014). However, *I. sonchifolium* (Maxim.) Shih was the most abundant in the young layers with a relatively high emergence density and a low mortality rate (see Table SV), thus it may persist or expand its population and drive future compositional changes of plant communities on sunny scars.

Additionally, *P. sphondylodes* Trin., *S. bungeana* Trin. and *I. sonchifolium* (Maxim.) Shih act as dominant or common native species in the study area, with longevity, both sexual and asexual reproduction mechanisms, and moderate seed production (100–999 seeds individual⁻¹) and germination rates (47.3–86.7 %) and speeds (1.0–4.7 days) (Chen et al., 2001; Wang, 2013; Wang, 2014), thus they may be applied to restore landslide scars in the study area.

CONCLUSIONS

There appeared to be a slow and limited recruitment process of plant colonists on recent landslide scars in the study area, although the strategy of employing both seedling and ramet recruitment might maximize colonists' fitness. In addition, there was a high degree of compositional uncoupling between the adult and young layers, implying future potential changes of plant communities driven by *P. sphondylodes* Trin., *S. bungeana* Trin., *I. sonchifolium* (Maxim.) Shih, *A. discolor* Bunge ex Maxim. and *A. scoparia* Waldst. et Kit. on shady scars and *I. sonchifolium* (Maxim.) Shih on sunny scars. We also proposed that the first three species can be used to restore landslide scars in the study area. This study may address the lack of knowledge about plant population recruitment on landslide scars and thus cast new light on landslide ecology and enhance theoretical support for interventions on landslide restoration. Future research will be necessary to find out the underlying mechanisms driving seedling and ramet recruitment.

ACKNOWLEDGEMENTS

This study was supported by National Natural Science Foundation of China (No. 41771319) and China Postdoctoral Science Foundation (No. 2019M653893XB). We would like to thank our colleagues Meng Kou, Binting Cao, Fangchen Yan, Yue Liang and Hang Li for their assistance with fieldwork and Yongfu Chai for his assistance with data analyses.

REFERENCES

- Adams, P. W., Sidle, R. C. (1987). Soil conditions in three recent landslides in Southeast Alaska. *Forest Ecology and Management* 18, 93–102. doi: 10.1016/0378-1127(87)90136-8
- Aicher, R. J., Larios, L., Suding, K. N. (2011). Seed supply, recruitment, and assembly: Quantifying

- relative seed and establishment limitation in a plant community context. *American Naturalist* 178, 464–477. doi: 10.1086/661900
- Anderson, M. J., Walsh, D. C. I. (2013). PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs* 83, 557–574. doi: 10.1890/12-2010.1
- Barik, S. K., Rao, P., Tripathi, R. S., Pandey, H. N. (1996). Dynamics of tree seedling populations in a humid subtropical forest of northeast India as related to disturbance. *Canadian Journal of Forest Research* 26, 584–589. doi: 10.1139/x26-067
- Baskin, C. C., Baskin, J. M. (1998). *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press: San Diego.
- Bellingham, P. J., Sparrow, A. D. (2009). Multi-stemmed trees in montane rain forests: their frequency and demography in relation to elevation, soil nutrients and disturbance. *Journal of Ecology* 97, 472–483. doi: 10.1111/j.1365-2745.2009.01479.x
- Bond, W. J., Midgley, J. J. (2001). Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution* 16, 45–51. doi: 10.1016/S0169-5347(00)02033-4
- Cao, B. T., Jiao, J. Y., Wang, Z. J., Wei, Y. H., Li, Y. J. (2015). Characteristics of landslide under the extreme rainstorm in 2013 in the Yanhe basin. *Research of Soil and Water Conservation* 22, 103–109. doi:10.13869/j.cnki.rswc.20151116.015 [In Chinese]
- Chaudhry, S., Singh, S. P., Singh, J. S. (1996). Performance of seedlings of various life forms on landslide-damaged forest sites in Central Himalaya. *Journal of Applied Ecology* 33, 109–117. doi: 10.2307/2405020
- Chen, S. H., Zhang, H., Wang, L. Q., Zhan, B. L., Zhao, M. L. (2001). *Root systems of plants in the grassland in northern China*. Jilin University Press: Changchun. [In Chinese]
- De la Peña-Domene, M., Martínez-Garza, C., Ayestarán-Hernández, L. M., Howe, H. F. (2018). Plant attributes that drive dispersal and establishment limitation in tropical agricultural landscapes. *Forests* 9. doi: 10.3390/f9100620
- Dodd, R. S., Douhovnikoff, V. (2016). Adjusting to global change through clonal growth and epigenetic variation. *Frontiers in Ecology and Evolution* 4. doi: 10.3389/fevo.2016.00086
- Eriksson, O. (1986). Survivorship, reproduction and dynamics of ramets of *Potentilla anserina* on a Baltic seashore meadow. *Vegetatio* 67, 17–25.
- Fenner, M., Thompson, K. (2005). *The ecology of seeds*. Cambridge University Press: New York.
- Fernández-Lugo, S., de Nascimento, L., Méndez, J., González-Delgado, G., Gomes, E. P. C., Otto, R., Arévalo, J. R., Fernández-Palacios, J. M. (2015). Seedling survival patterns in Macaronesian laurel forest: a long-term study in Tenerife (Canary Islands). *Forestry* 88, 121–130. doi: 10.1093/forestry/cpu035
- García, D., Zamora, R. (2003). Persistence, multiple demographic strategies and conservation in long-lived Mediterranean plants. *Journal of Vegetation Science* 14, 921–926. doi: 10.1658/1100-9233(2003)014[0921:PMDSAC]2.0.CO;2
- Gómez, S., Stuefer, J. F. (2006). Members only: induced systemic resistance to herbivory in a clonal plant network. *Oecologia* 147, 461–468. doi: 10.1007/s00442-005-0293-z
- Gonzalez-Ollauri, A., Mickovski, S. B. (2017). Shallow landslides as drivers for slope ecosystem evolution and biophysical diversity. *Landslides* 14, 1699–1714. doi: 10.1007/s10346-017-0822-y
- Grime, J. P. (2001). *Plant strategies, vegetation processes, and ecosystem properties*. Wiley: New York.
- Grime, J. P., Mason, G., Curtis, A. V., Rodman, J., Band, S. R., Mowforth, M. A. G., Neal, A. M., Shaw, S. (1981). A comparative study of germination characteristics in a local flora. *Journal of Ecology* 69, 1017–1059. doi: 10.2307/2259651
- Guariguata, M. R. (1990). Landslide disturbance and forest regeneration in the Upper Luquillo Mountains of Puerto Rico. *Journal of Ecology* 78, 814–832. doi: 10.2307/2260901
- Guo, Z., Huang, Z. L., Feng, L. X. (1992). *Shaanxi soils*. Science Press: Beijing. [In Chinese]
- Harper, J. L. (1977). *Population biology of plants*. Academic Press: London.
- Heydari, M., Prévosto, B., Abdi, T., Mirzaei, J., Mirab-Balou, M., Rostami, N., Khosravi, M., Pothiere, D. (2017). Establishment of oak seedlings in historically disturbed sites: Regeneration success as a function of stand structure and soil characteristics. *Ecological Engineering* 107, 172–182. doi: 10.1016/j.ecoleng.2017.07.016
- Hu, S., Jiao, J. Y., García-Fayos, P., Kou, M., Chen, Y. X., Wang, W. Z. (2018). Telling a different story: plant recolonization after landslides under a semi-arid climate. *Plant and Soil* 426, 163–178. doi: 10.1007/s11104-018-3612-y

- Hupp, C. R. (1983). Seedling establishment on a landslide site. *Castanea* 48, 89–98.
- Köppen, W. (1884). The thermal zones of the earth according to the duration of hot, moderate and cold periods and the impact of heat on the organic world. *Meteorologische Zeitschrift*, 215–226.
- Li, B., Zeng, T., Ran, J. H., Yue, B. S., Zhang, M., Shang, T., Zhu, D. H. (2017). Characteristics of the early secondary succession after landslides in a broad-leaved deciduous forest in the south Minshan Mountains. *Forest Ecology and Management* 405, 238–245. doi: 10.1016/j.foreco.2017.09.020
- Li, L., Lan, Z. C., Chen, J. K., Song, Z. P. (2018). Allocation to clonal and sexual reproduction and its plasticity in *Vallisneria spirulosa* along a water-depth gradient. *Ecosphere* 9. doi: 10.1002/ecs2.2070
- Li, R., Yang, W. Z., Li, B. C. (2008). *Research and future prospects for the Loess Plateau of China*. Science Press: Beijing. [In Chinese]
- Lin, C. H., Miriti, M. N., Goodell, K. (2016). Demographic consequences of greater clonal than sexual reproduction in *Dicentra Canadensis*. *Ecology and Evolution* 6, 3871–3883. doi: 10.1002/ece3.2163
- Liu, B. Z., Wu, F. Q. (1996). *Soil erosion*. Shaanxi People's Publishing House: Xi'an. [In Chinese]
- Lu, X. M., Liang, E. Y., Wang, Y. F., Babst, F., Leavitt, S. W., Camarero, J. J. (2019). Past the climate optimum: Recruitment is declining at the world's highest juniper shrublines on the Tibetan Plateau. *Ecology* 100. doi: 10.1002/ecy.2557
- Lundgren, L. (1978). Studies of soil and vegetation development on fresh landslide scars in the Mgeta Valley, Western Uluguru Mountains, Tanzania. *Geografiska Annaler: Series A, Physical Geography* 60, 91–127. doi: 10.2307/520435
- Marques, M. C. M., Burslem, D. F. R. P. (2015). Multiple stage recruitment limitation and density dependence effects in two tropical forests. *Plant Ecology* 216, 1243–1255. doi: 10.1007/s11258-015-0505-5
- Molles, M., C. (2016). *Ecology: Concepts and applications*. McGraw-Hill Education: New York.
- Mourya, N. R., Bargali, K., Bargali, S. S. (2019). Impacts of *Coriaria nepalensis* colonization on vegetation structure and regeneration dynamics in a mixed conifer forest of Indian Central Himalaya. *Journal of Forestry Research* 30, 305–317. doi: 10.1007/s11676-018-0613-x
- Muir, A. N. (1995). The cost of reproduction to the clonal herb *Asarum canadense* (wild ginger). *Canadian Journal of Botany* 73, 1683–1686. doi: 10.1139/b95-182
- Myster, R. W. (2002). Foliar pathogen and insect herbivore effects on two landslide tree species in Puerto Rico. *Forest Ecology and Management* 169, 231–242. doi: 10.1016/S0378-1127(01)00757-5
- Neto, C., Cardigos, P., Oliveira, S. C., Zêzere, J. L. (2017). Floristic and vegetation successional processes within landslides in a Mediterranean environment. *Science of the Total Environment* 574, 969–981. doi: 10.1016/j.scitotenv.2016.09.119
- Nobel, P. S. (1992). Annual variations in flowering percentage, seedling establishment, and ramet production for a desert perennial. *International Journal of Plant Sciences* 153, 102–107. doi: 10.1086/297011
- Pang, C. C., Ma, X. K. K., Lo, J. P. L., Hung, T. T. H., Hau, B. C. H. (2018). Vegetation succession on landslides in Hong Kong: Plant regeneration, survivorship and constraints to restoration. *Global Ecology and Conservation* 15. doi: 10.1016/j.gecco.2018.e00428
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J. G., Thompson, K., Morgan, H. D., ter Steege, H., van der Heijden, M. G. A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A. C., Aquino, S., Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61, 167–234. doi: 10.1071/BT12225
- Pérez-Ramos, I. M., Marañón, T. (2012). Community-level seedling dynamics in Mediterranean forests: uncoupling between the canopy and the seedling layers. *Journal of Vegetation Science* 23, 526–540. doi: 10.1111/j.1654-1103.2011.01365.x
- Restrepo, C., Vitousek, P. (2001). Landslides, alien species and the diversity of a Hawaiian montane mesic ecosystem. *Biotropica* 3, 409–420. doi: 10.1111/j.1744-7429.2001.tb00195.x
- Restrepo, C., Vitousek, P., Neville, P. (2003). Landslides significantly alter land cover and the distribution of biomass: an example from the Ninole ridges of Hawai'i. *Plant Ecology* 166, 131–143. doi: 10.1023/A:1023225419111
- Restrepo, C., Walker, L. R., Shiels, A. B., Bussmann, R., Claessens, L., Fisch, S., Lozano, P., Negi, G., Paolini, L., Poveda, G., Ramos-Scharrón, C., Richter, M., Velázquez, E. (2009). Landsliding and its multiscale influence on mountainscapes. *BioScience* 59, 685–698. doi: 10.1525/bio.2009.59.8.10

- Rey, P. J., Alcántara, J. M. (2000). Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology* 88, 622–633. doi: 10.1046/j.1365-2745.2000.00472.x
- Ronsheim, M. L., Bever, J. D. (2000). Genetic variation and evolutionary trade-offs for sexual and asexual reproductive modes in *Allium vineale* (Liliaceae). *American Journal of Botany* 87, 1769–1777. doi: 10.2307/2656827
- Sidle, R. C., Bogaarda, T. A. (2016). Dynamic earth system and ecological controls of rainfall-initiated landslides. *Earth-Science Reviews* 159, 275–291. doi: 10.1016/j.earscirev.2016.05.013
- Sidle R C, Ochiai H. 2006. Landslides: Processes, prediction, and land use. In *Water Resources Monograph* Vol 18. American Geophysical Union: Washington D.C.; 312
- Su, Y. (2013). Seedling bank and seedling survival characteristics in different soil erosion environments in the hilly-gullied Loess Plateau. MA Dissertation, Northwest A & F University [In Chinese]
- Su, Y., Jiao, J. Y., Wang, Z. J. (2014). Characteristics of seedling survival in habitats of hill and gully slopes in hill-gully Loess Plateau region of northern Shaanxi. *Chinese Journal of Plant Ecology* 38, 694–709. doi: 10.3724/SP.J.1258.2014.00065 [In Chinese]
- Travis, S. E., Proffitt, C. E., Ritland, K. (2004). Population structure and inbreeding vary with successional stage in created *Spartina alterniflora* marshes. *Ecological Applications* 14, 1189–1202. doi: 10.1890/03-5135
- Vargas, I. N., Stevenson, P. R. (2013). Seed and establishment limitation: Effects on plant diversity in an Amazonian rain forest. *Biotropica* 45, 737–746. doi: 10.1111/btp.12063
- Walker, L. R., Landau, F. H., Velázquez, E., Shiels, A. B., Sparrow, A. D. (2010). Early successional woody plants facilitate and ferns inhibit forest development on Puerto Rican landslides. *Journal of Ecology* 98, 625–635. doi: 10.1111/j.1365-2745.2010.01641.x
- Walker, L. R., Shiels, A. B. (2008). Post-disturbance erosion impacts carbon fluxes and plant succession on recent tropical landslides. *Plant and Soil* 313, 205–216. doi: 10.1007/s11104-008-9692-3
- Walker, L. R., Shiels, A. B. (2013). *Landslide ecology*. Cambridge University Press: Cambridge.
- Walker, L. R., Velázquez, E., Shiels, A. B. (2009). Applying lessons from ecological succession to the restoration of landslides. *Plant and Soil* 324, 157–168. doi: 10.1007/s11104-008-9864-1
- Wang, D. L. (2014). Seed life-history strategies of plants and restoration by seed addition in the hill-gully Loess Plateau region. PhD Dissertation, Northwest A & F University [In Chinese]
- Wang, N. (2008). Effects of slope-gully erosion environment on the propagule and seedling establishment—a case study in Zhifanggou Ansai on Loess Plateau. MA Dissertation, Northwest A & F University [In Chinese]
- Wang, N. (2013). The limiting factors in vegetation recruitment in the hilly-gullied region of the Loess Plateau: on species resources aspect. PhD Dissertation, University of Chinese Academy of Sciences [In Chinese]
- Wang, Y. C., Alberto, B. C., Jiang, D. M., Ala, M., Li, X. H., Zhou, Q. L., Lin, J. X., Ren, G. H., Jia, L. (2016). The role of sexual vs. asexual recruitment of *Artemisia wudanica* in transition zone habitats between inter-dune lowlands and active dunes in Inner Mongolia, China. *Solid Earth* 7, 621–629. doi: 10.5194/se-7-621-2016
- Weihner, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., Eriksson, O. (1999). Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10, 609–620. doi: 10.2307/3237076
- Wu, W. H. (2018). *Plant Physiology*. Science Press: Beijing. [In Chinese]
- Yang, H. L., Huang, Z. Y., Baskin, C. C., Baskin, J. M., Cao, Z. P., Zhu, X. W., Dong, M. (2009). Responses of caryopsis germination, early seedling growth and ramet clonal growth of *Bromus inermis* to soil salinity. *Plant and Soil* 316, 265–275. doi: 10.1007/s11104-008-9778-y
- Yang, W. T., Qi, W. W., Zhou, J. X. (2018). Effects of precipitation and topography on vegetation recovery at landslide sites after the 2008 Wenchuan earthquake. *Land Degradation & Development* 29, 3355–3365. doi: 10.1002/ldr.3098
- Yuan, B. N. (2009). Studies on characteristics of soil seed banks in the natural vegetation restoration in the typical valley of loess hilly gully. MA Dissertation, Northwest A & F University [In Chinese]
- Zeiter, M., Stampfli, A., Newbery, D. M. (2006). Recruitment limitation constrains local species richness and productivity in dry grassland. *Ecology* 87, 942–951. doi: 10.1890/0012-9658(2006)87[942:RLCLSR]2.0.CO;2

Table I. Analytical items, data (n=6) and statistical approaches

Analytical item	Data	Statistical approach		
		Model	Distribution family	Link function
The relative amounts of seedling and ramet emergence on shady (or sunny) scars during each study period, the growing season and the whole study period	The overall emergence densities of seedlings and ramets on shady (or sunny) scars during P1 (28/03/2016–16/04/2016), P2 (17/04/2016–17/05/2016), P3 (18/05/2016–18/06/2016), P4 (19/06/2016–19/07/2016), P5 (20/07/2016–19/08/2016), P6 (20/08/2016–19/09/2016), P7 (20/09/2016–20/10/2016) and P8 (21/10/2016–22/04/2017)	Generalized linear mixed model (GLMM) with site as a random factor and with repeated measures		Identity
	The overall emergence densities of seedlings and ramets on sunny scars during P1–7 (28/03/2016–20/10/2016)			Identity
	The overall emergence densities of seedlings and ramets on sunny scars during P1–8 (28/03/2016–22/04/2017)	GLMM with site as a random factor		
	The overall emergence densities of seedlings and ramets on shady scars during P1–7			Log
The relative degrees of seedling and ramet death on shady (or sunny) scars during each growing period, the growing season, the winter and the whole study period	The overall mortality rates of seedlings and ramets on shady (or sunny) scars during P2–P7	GLMM with site as a random factor and with repeated measures	Normal distribution	Identity
	The overall mortality rates of seedlings and ramets on shady (or sunny) scars during P2–7 (17/04/2016–20/10/2016)			
	The overall mortality rates of seedlings and ramets on shady (or sunny) scars during P8	GLMM with site as a random factor		Identity
	The overall mortality rates of seedlings and ramets on shady (or sunny) scars during P2–8 (17/04/2016–22/04/2017)			
The relative amounts of seedlings and ramets on shady (or sunny) scars at each study time, the end of the growing season and the last study time	The overall densities of seedlings and ramets on shady (or sunny) scars at T1 (16/04/2016), T2 (17/05/2016), T3 (18/06/2016), T4 (19/07/2016), T5 (19/08/2016), T6 (19/09/2016), T7 (20/10/2016) and T8 (22/04/2017)	GLMM with site as a random factor and with repeated measures		Identity
	The overall densities of seedlings and ramets on shady (or sunny) scars at T7	GLMM with site as a random factor		Log
	The overall densities of seedlings and ramets on shady (or sunny) scars at T8			
Seedling (or ramet) emergence dynamics on shady (or sunny) scars within the study period	The overall emergence densities of seedlings on sunny scars during P1–P8			Identity
	The overall emergence densities of ramets on shady (or sunny) scars during P1–P8			Power
	The overall emergence densities of seedlings on shady scars during P1–P8			
Seedling (or ramet) death dynamics on shady (or sunny) scars within the growing season	The overall mortality rates of seedlings on sunny scars during P2–P7			Identity
	The overall mortality rates of ramets on shady (or sunny) scars during P2–P7			Power
	The overall mortality rates of seedlings on shady scars during P2–P7			
The relative degrees of seedling (or ramet) death on shady (or sunny) scars during the growing season and the winter	The overall mortality rates of seedlings (or ramets) on shady (or sunny) scars during P2–7 and P8	GLMM with site as a random factor	Normal distribution	Identity
	The overall densities of seedlings on sunny scars at T1–T8			
Seedling (or ramet) density dynamics on shady (or sunny) scars within the study period	The overall densities of ramets on shady scars at T1–T8			Identity
	The overall densities of seedlings on shady scars at T1–T8			Power
	The overall densities of ramets on sunny scars at T1–T8			
	The overall densities of seedlings on sunny scars at T1–T8			
The relative amounts of seedling (or ramet) emergence on shady and sunny scars during each study period, the growing season and the whole study period	The overall emergence densities of seedlings (or ramets) on shady and sunny scars during P1–P8	Generalized linear model (GLM) with repeated measures		Identity
	The overall emergence densities of seedlings (or ramets) on shady and sunny scars during P1–7	GLM	Normal distribution	Identity
	The overall emergence densities of seedlings (or ramets) on shady and sunny scars during P1–8			
The relative degrees of seedling (or ramet) death on shady and sunny scars during each growing	The overall mortality rates of seedlings (or ramets) on shady and sunny scars during P2–P7	GLM with repeated measures		Identity
	The overall mortality rates of seedlings on shady and sunny scars during P2–7	GLM		Identity

Accepted Article

Analytical item	Data	Statistical approach		
		Model	Distribution family	Link function
period, the growing period, the winter and the whole study period	The overall mortality rates of seedlings (or ramets) on shady and sunny scars during P8			
	The overall mortality rates of seedlings (or ramets) on shady and sunny scars during P2–8			
	The overall mortality rates of ramets on shady and sunny scars during P2–7			Log
The relative amounts of seedlings (or ramets) on shady and sunny scars at each study time, the end of the growing season and the last study time	The overall densities of seedlings on shady and sunny scars at T1–T8	GLM with repeated measures		Identity
	The overall densities of ramets on shady and sunny scars at T1–T8			Power
	The overall densities of seedlings (or ramets) on shady and sunny scars at T7	GLM		Identity
	The overall densities of seedlings (or ramets) on shady and sunny scars at T8			

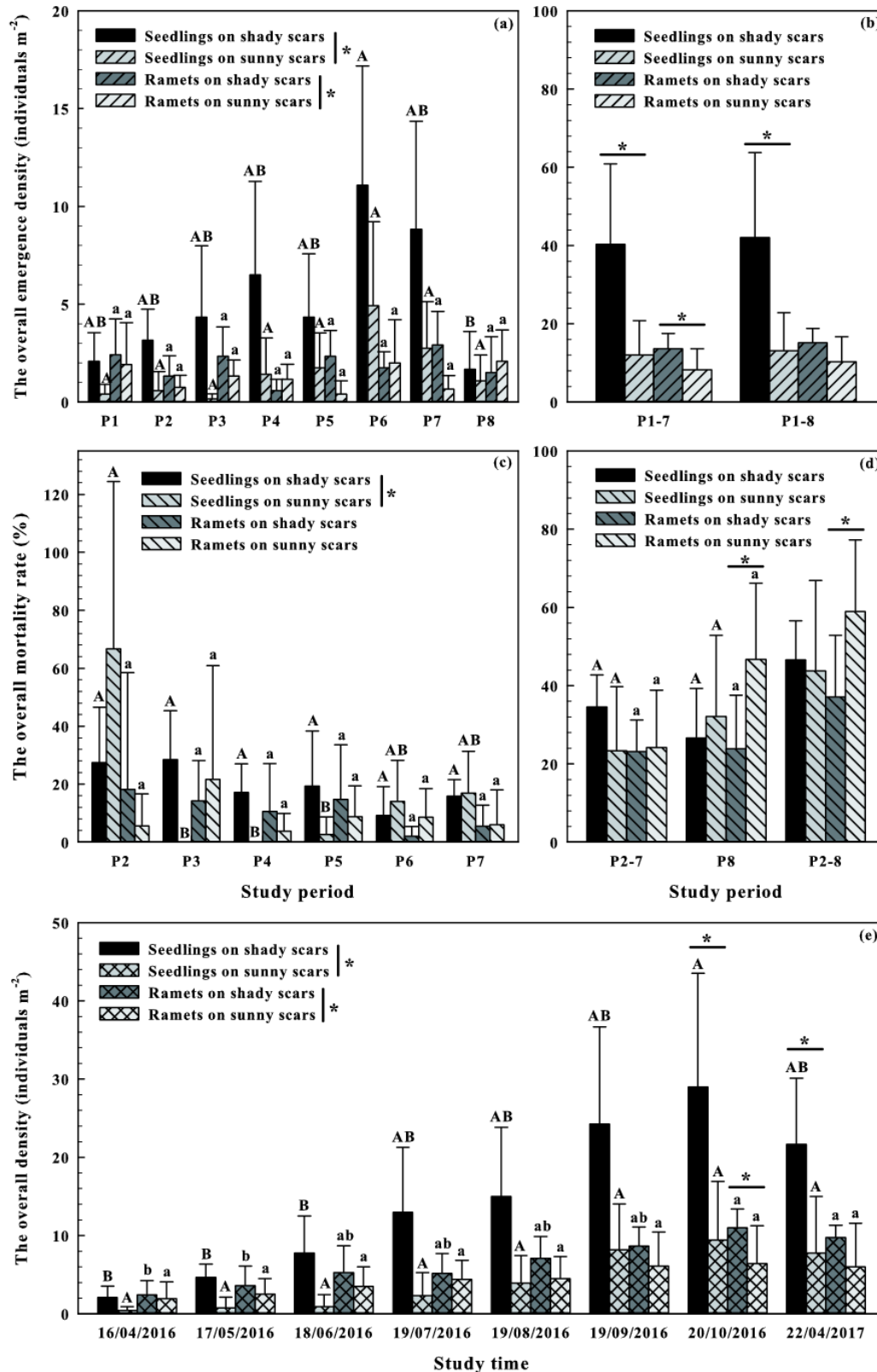


Figure 1.

The overall emergence densities, mortality rates and densities of seedlings and ramets on shady and sunny scars at different time scales. Uppercase (or lowercase) letters denote seedling (or ramet) recruitment dynamics at the 0.05 level. The signs * denote significant differences between shady and sunny scars or between seedlings and ramets at the 0.05 level.

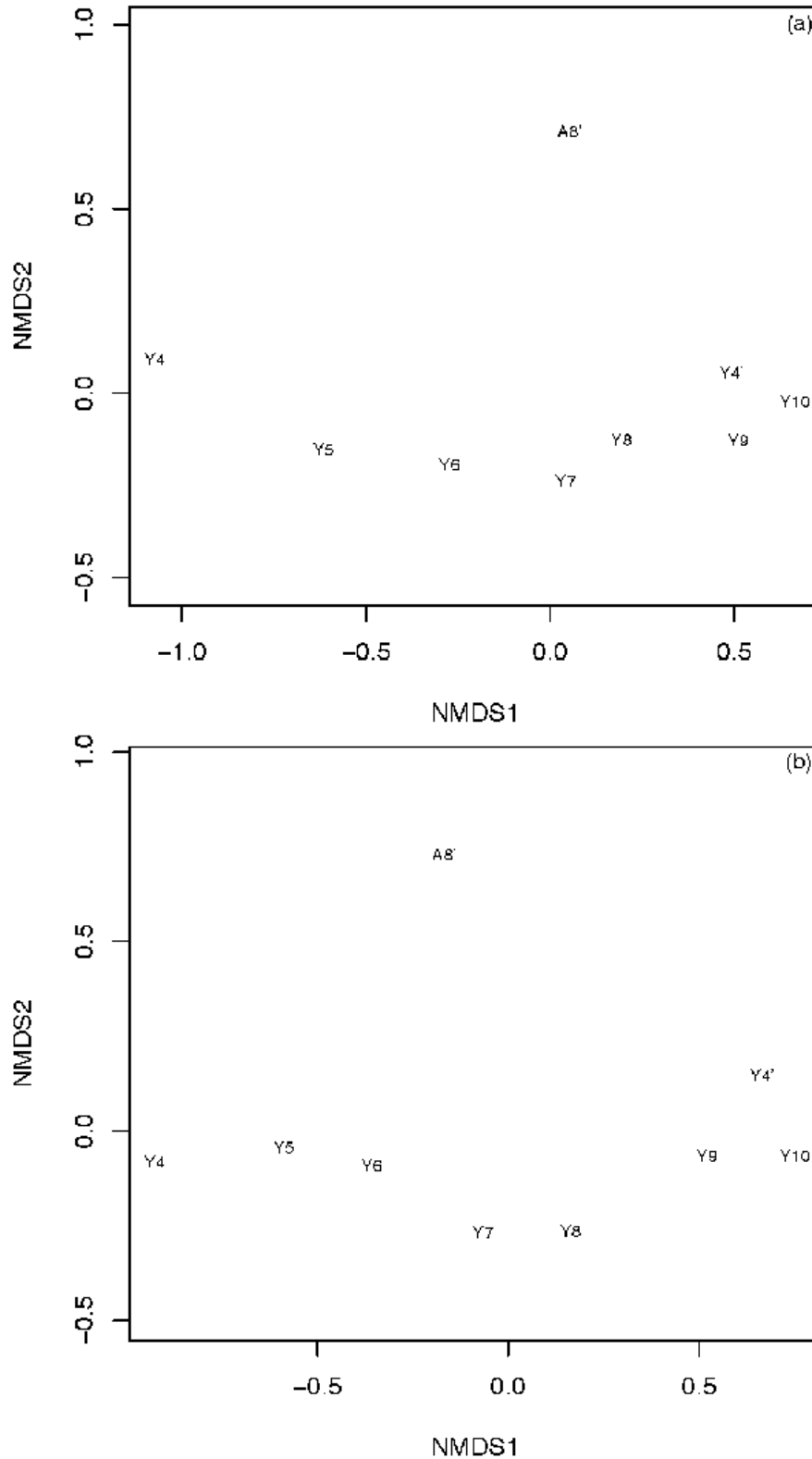


Figure 2. NMDS ordination based on species densities of the adult layers in mid-August 2017 and those of the young layers at T1–T8 on shady (a) and sunny (b) scars ($n = 6$; stress values = 0.0004 and < 0.0001 , respectively). Y4–Y10 and Y4' denote species composition of the young layers at T1–T7 and T8, respectively; A8' denotes species composition of the adult layers in mid-August 2017.