

1 **The fate of seeds in the soil: a review of the influence of overland flow on seed removal and**  
2 **its consequences for the vegetation of arid and semiarid patchy ecosystems.**

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## 9 **Abstract**

10 Since seeds are the principle means by which plants move across the landscape, the final fate of  
11 seeds plays a fundamental role in the assemblage, functioning and dynamics of plant  
12 communities. Once seeds land on the soil surface after being dispersed from the parent plant,  
13 they can be moved horizontally by surface runoff. In arid and semiarid patchy ecosystems,  
14 where seeds are scattered into a very heterogeneous environment and intense rainfalls occur, the  
15 transport of seeds by runoff to new sites may be an opportunity for seeds to reach more  
16 favourable sites for seed germination and seedling survival. Although seed transport by runoff  
17 may be of vital importance for the recruitment of plants in these ecosystems, it has received  
18 little attention in the scientific literature, especially among soil scientists. The main goals of this  
19 review paper are (1) to offer an updated conceptual model of seed fate with a focus on seed  
20 destiny in and on the soil, (2) to review studies on seed fate in overland flow and the ecological  
21 implications seed transport by runoff has for the origin, spatial patterning and maintenance of  
22 patches in arid and semiarid patchy ecosystems, and finally (3) to point out directions for future  
23 research.

24 This review shows that seed fate in overland flow may result either in the export of seeds from  
25 the system (seed loss) or in the spatial redistribution of seeds within the system through short-  
26 distance seed movements (seed displacement). Seed transport by runoff depends on rainfall,  
27 slope and soil characteristics. Susceptibility of seed removal varies highly between species and  
28 is mainly related to seed traits, including seed size, seed shape, presence of appendages, and  
29 seed ability to secrete mucilage. Although initially considered as a risk of seed loss, seed  
30 removal by runoff has recently been described as an ecological driver that shapes plant  
31 composition from the first phases of the plant life, by favouring species with seeds able to resist  
32 erosion and by selecting for plant traits that prevent seed loss. Moreover, the interaction of seed  
33 transport by overland flow with the high seed trapping capacity of vegetated patches results in a  
34 “patch-to-patch” transport of seeds that plays a relevant role in vegetation establishment and  
35 patterning in arid and semiarid patchy ecosystems.

36 Overall, this review shows how the knowledge about seed fate in overland flow can be used to  
37 explain a number of important characteristics of whole plant communities. It also underlines  
38 important gaps of knowledge that should be filled in. Future lines of research are proposed in  
39 order to broaden our understanding of the origin, maintenance and dynamics of patchiness in  
40 arid and semiarid ecosystems and to improve restoration success of intensively eroded  
41 ecosystems. Among the most exciting challenges, empirical studies are needed to understand  
42 the relevance of short-distance seed displacements in the origin and maintenance of patchiness,  
43 addressing the feedbacks between structure and function and abiotic and biotic components, in  
44 order to validate existing models about the dynamics of arid and semiarid ecosystems and help  
45 to predict future changes under the scenarios of climate change.

46

47 **Key-words:** runoff, erosion, slope, seed movement, secondary dispersal, seed traits, mucilage,  
48 ecological driver, spatial pattern, abiotic, biotic, ecohydrology, ecogeomorphology, drylands

## 49 **1. Introduction**

50 The term “seed fate” has been used to describe what happens to seeds from the moment they are  
51 produced by mother plants until they become seedlings. In the 1970s and 1980s, seed dispersal  
52 was described as a simple and direct process of seed movement from the mother plant to the  
53 final microsite where the seed germinates or dies. Seed dispersal was accomplished by different  
54 biotic or abiotic agents (wind, animals, gravity) and its outcome was considered stochastic. The  
55 possibility of further seed dispersal after seeds reached their first landing surface was not taken  
56 into account (Vander Wall et al., 2002; Forget and Wenny, 2002). The lack of empirical studies  
57 on the ultimate stages of dispersal, due to the difficulty of measuring seed dispersal (Bullock et  
58 al., 2006), led to incomplete information about the pathways seeds might follow until they  
59 germinate (Vander Wall et al., 2002). However, in the early 1990s, the development of a variety  
60 of new techniques that permitted researchers to follow seeds in space and time (metal detectors,  
61 fluorescent dyes, genetic tools) provided evidence that seed dispersal was a far more dynamic  
62 and complex process than was previously portrayed (Forget and Milleron, 1991; Chambers and  
63 Mac Mahon, 1994; Böhning-Gaese et al., 1999). It became evident that seed fate involved  
64 multiple steps and agents and its outcome was non-hazardous. Thus, after the initial movement  
65 of seeds from the mother plant to the first landing site (“primary” dispersal), a second dispersal  
66 stage started to be considered consisting of any significant subsequent vertical or horizontal  
67 seed movement from this original site (“secondary” dispersal, Chambers and Mac Mahon, 1994;  
68 Böhning-Gaese et al., 1999). A variety of biotic and abiotic agents, including overland flow, are  
69 responsible for the secondary dispersal of seeds to new sites of the landscape.

70 Since successful regeneration by a plant depends upon its seeds being dispersed to safe sites  
71 where seeds can germinate and seedlings can establish (Harper, 1977; Schupp, 1995), secondary  
72 dispersal gives seeds new opportunities to reach favourable sites. This second chance may be of  
73 vital importance for seeds in hostile environments with extreme environmental regimes where  
74 most points of the landscape are unsuitable for seed germination, seed survival and seedling  
75 establishment. This is the case in arid and semiarid environments, also called “drylands”, which

76 cover over 40% of the Earth's surface (Reynolds et al., 2007). These water-limited landscapes  
77 frequently show a clear spatial pattern of vegetated patches interspersed within a bare soil  
78 matrix (Aguilar and Sala, 1999) which gives rise to a mosaic-like structure of sources and sinks  
79 of resources, the bare and vegetated patches respectively, with very different soil properties and  
80 variable interconnection (e.g. Schlesinger et al., 1990; Ludwig and Tongway, 1995; Bochet et  
81 al., 1999, 2000; Puigdefábregas, 2005). Vegetated patches have often been compared to  
82 "fertility islands" with a privileged micro-climate and improved soil properties (low solar  
83 radiation, low soil temperature, low evaporation rates, high concentration of resources, high  
84 fertility, high infiltration rates) within a matrix of poor and degraded bare ground (low fertility,  
85 high soil compaction, low water infiltration, high runoff volume, high wind and water erosion  
86 rates) (e.g. Schlesinger et al., 1990; Puigdefábregas and Sánchez, 1996; Cerdà, 1997; Bochet et  
87 al., 1998, 1999; Wilcox et al., 2003). Fertility islands may act as "nucleation" points facilitating  
88 the establishment of plant species that otherwise would be unable to establish (the process of  
89 "facilitation", Callaway, 2007). In this context, seeds dispersed from the parent plant are  
90 scattered into a heterogeneous environment which is notoriously patchy in terms of the quality  
91 of sites suitable for seed germination and for the subsequent survival of seedlings (Schupp,  
92 1995). Secondary dispersal may be therefore of vital importance for the recruitment stage of  
93 plants and have relevant ecological implications in the functioning of dryland ecosystems  
94 (Aguilar and Sala, 1997; Forget et al., 2002; Thompson et al., 2014).

95 Even so, secondary dispersal has generally received little attention in the scientific literature,  
96 much less than primary dispersal (Chambers and Mc Mahon, 1994). An online literature  
97 compilation of 697 papers on the fate of seeds in drylands published in the last 40 years  
98 provides evidence of this clear unbalance (see Fig. 1 and reference list in the Supplement).  
99 During this time period, only a small proportion of the annually published papers, less than one  
100 third, is related to secondary dispersal (Fig. 1). However, the evolution of the number of papers  
101 related to secondary seed dispersal in drylands shows a steady, even though fluctuating, increase  
102 from the mid-1990s until 2013 (Fig. 2), indicating that what happens to seeds once they have

103 reached a first landing surface is becoming an increasingly important issue among the scientific  
104 community. Figure 2 also shows that the attention given to the main agents of secondary  
105 dispersal during the same time period is clearly uneven. Secondary dispersal by overland flow  
106 started to be documented later than secondary dispersal by wind and animals, and the annual  
107 rate of publications about secondary dispersal by overland flow has been very low since then.  
108 Because seed fate issues lie at the interface between plant, animal and soil sciences and because  
109 studies on secondary seed dispersal have seldom been published in soil science related journals  
110 (Fig. 3), this paper seeks to bring readers, especially soil scientists, closer to understanding of  
111 the destiny of seeds in and on the soil. Understanding seed fate in the soil is not only a matter  
112 for the scientific community, but it is also crucial for the management of degraded ecosystems.  
113 Seeds are often one of the most important actors at the first stages of the restoration process,  
114 either through the influence of the soil seed bank which plays a fundamental role in the  
115 composition of the future vegetation (Peco et al., 1998), either through the use of seeding or  
116 hydroseeding revegetation techniques of disturbed areas (e.g. Tormo et al., 2007 for roadslopes;  
117 Fernández et al., 2012 for burnt areas; Porqueddu et al., 2013 for quarries).

118 The main goals of this paper are (1) to offer an updated conceptual model of seed fate with a  
119 special focus on seed destiny in and on the soil, (2) to review studies on secondary seed  
120 dispersal by runoff and the ecological implications this process has for the origin, spatial  
121 patterning and maintenance of patches in dryland ecosystems, and finally (3) to point out  
122 directions for future research. Our focus will be placed on drylands, because secondary dispersal  
123 has been recognized as a significant part of dispersal in environments with sparse vegetation  
124 (Nelson and Chew, 1977; Reichman, 1984; Chambers et al., 1991).

125

## 126 **2. Conceptual model of seed fates and movements in and on the soil**

127 Different models of seed fate have been proposed to describe the complex pathways populations  
128 of seeds might follow from seed production to seedling establishment. Since the early studies in  
129 the 1970s, models have progressively evolved and gained in complexity as new pathways of

130 seed movement and fate were found (Harper, 1977; Fenner, 1985; Chambers y Mc Mahon,  
131 1994; Baskin and Baskin, 1998; Vander Wall et al., 2002). On the basis of these previous  
132 models, Fig. 4 illustrates an updated conceptual model with a general description hereafter of  
133 the most likely alternative pathways a seed might follow from seed production to seedling  
134 establishment.

135 The model starts with the set of ripened seeds on the parent plant that have the potential to  
136 germinate (Fig. 4). Part of these seeds may be lost to death by means of pre-dispersal predation  
137 by animals or different types of disturbance affecting the parent plant (e.g. fire, water-logging).  
138 Seeds that escape predation, may be primarily dispersed via specific biotic or abiotic agents  
139 (animals, wind, rain, gravity) from the parent plant to a landing surface, the soil or any other  
140 type of surface (e.g. trunks, branches, litter, rocks). Once on the soil surface, seeds may  
141 experience different fates. First, they may germinate immediately if they have the chance to rest  
142 on a microsite with suitable conditions for germination and are non-dormant (i.e.  
143 physiologically active seeds). Second, seeds may be lost to death by post-dispersal predation  
144 (ants, rodents or birds) or decay due to pathogen attacks or senescence (Hulme, 1998). Third,  
145 seeds may rest at the initial point of deposition and remain on the soil surface for a short or long  
146 period, depending on the dormancy state of the seed and the occurrence of favourable  
147 conditions for germination. Seed dormancy has to be broken by the agents responsible for  
148 dormancy alleviation (time, temperature, moisture) before seeds can germinate in favourable  
149 environmental conditions (e.g. light, improved oxygen levels). Finally, seeds may be subjected  
150 to secondary dispersal processes and moved to new sites via horizontal and/or vertical seed  
151 movements.

152 Concerning vertical movements, seeds may be incorporated from the soil surface into the soil in  
153 either a non-dormant or a dormant state and form the soil seed bank (Thompson et al., 1993;  
154 Traba et al. 2004). Seeds entering into cracks at the soil surface, seed burial by small burrowing  
155 animals or by local accumulation of sediments may enhance vertical seed movements  
156 (Chambers and Mac Mahon, 1994; Chambers, 2000). Non-dormant seeds may germinate

157 immediately once they have entered the soil in the case of favourable environmental conditions  
158 for germination, and give rise to new seedlings if they are able to emerge above the soil surface.  
159 Dormant seeds may remain in the soil for long periods, waiting first for dormancy alleviation  
160 and then for the occurrence of favourable environmental conditions for germination. Seeds may  
161 also be moved vertically by animals in the opposite direction, from the soil seed bank to the soil  
162 surface, or be brought to the soil surface by a different kind of disturbances (e.g. runoff, wind).  
163 Seeds on or in the soil may also be moved horizontally to new locations by different biotic  
164 (animals) or abiotic (often wind, runoff and gravity) agents and experience there the same fates  
165 as the ones described for seeds landing for the first time on the soil surface after primary  
166 dispersal.  
167 The following sections will focus on seed movements caused by runoff and their implications  
168 for vegetation establishment and for the spatial organization and functioning of arid and  
169 semiarid patchy ecosystems.

170

### 171 **3. Seed removal by runoff: a review**

#### 172 ***3.1. Outcomes of seed removal by runoff: seed loss or seed redistribution?***

173 In drylands, rainfall is often concentrated into a small number of intense high erosive events that  
174 are responsible for more than 70% of the soil loss rates (Wainwright, 1996; Martínez-  
175 Casasnovas et al., 2005). Under these conditions, seeds in the seed bank or resting on the soil  
176 surface after primary dispersal are exposed to overland flow, especially in bare patches where  
177 high rates of runoff and sediment transport have been reported (Cerdà, 1997; Calvo-Cases et al.,  
178 2003; Boix-Fayos et al., 2005; Bochet et al., 2006).

179 The first evidence that runoff may act as a vector of seed transport were indirect and based on  
180 observations of seed dispersal strategies in runoff-prone areas (Friedman and Orshan, 1975;  
181 Friedman and Stein, 1980), comparisons of plant distribution with different dispersal  
182 mechanisms between slopes and wadis (Reichman, 1984), or descriptions of seed distribution  
183 patterns in different microhabitats (Ellner and Schmida, 1981), in desert ecosystems worldwide.



184 In the 1990s, it was argued that seed removal by runoff led to seed loss and might explain the  
185 lack or scarcity of vegetation on semiarid and arid hillslopes (Debusche and Lepart, 1992;  
186 Francis, 1991; Chambers and Mac Mahon, 1994). Although frequently invoked, this assumption  
187 was not empirically checked until the pioneering studies of García-Fayos and his collaborators  
188 about seed transport by runoff flow. Their studies aimed at quantifying rates of seed losses in  
189 order to determine whether seed removal by runoff could explain the lack of vegetation in  
190 highly eroded badland slopes of Southeast Spain (García-Fayos and Recatalà, 1992; García-  
191 Fayos et al., 1995; García-Fayos and Cerdà, 1997; Cerdà and García-Fayos, 1997, 2002; Table  
192 1). In these stressful environments characterized by extreme rates of erosion (Gallart et al.,  
193 2013), seed inputs into the soil seed bank due to seed fall were greater than the seed outputs due  
194 to removal by erosion (21% and 5.6-12.6% of the soil seed bank, respectively), thus resulting in  
195 a positive seed balance at the catchment scale (García-Fayos and Recatalá, 1992; García-Fayos  
196 et al., 1995). In the same badland area, seed losses were quantified in several experimental  
197 studies under simulated rainfall at 55 mm/h over 0.24 m<sup>2</sup> field plots with different slope angles  
198 and rainfall durations (Table 1). In all cases, average seed losses by runoff for the whole set of  
199 species were low (4%, 0.4 - 7.9% and <13% according to the experimental conditions of Cerdà  
200 and García-Fayos, 1997; García-Fayos and Cerdà, 1997 and García-Fayos et al., 1995,  
201 respectively) and seed loss rates of individual species did not exceed in any case 25% (García-  
202 Fayos and Cerdà, 1997). These results were in agreement with average seed losses obtained  
203 under natural conditions (García-Fayos et al., 1995) and also under laboratory conditions where  
204 only 11% of the seeds resting on an artificial surface were lost in average under simulated  
205 rainfall of similar intensity (Cerdà and García-Fayos, 2002, Table1). Moreover, the relationship  
206 between the rate of seed loss and the amount of runoff proved to be positive and exponential in  
207 these badland ecosystems (García-Fayos and Cerdà, 1997). According to all these results, it was  
208 concluded that seed loss by overland flow was not the key factor explaining the absence of  
209 vegetation on badland slopes as the probability of rainfall events of higher intensity and  
210 duration is low. Other possible alternative causes were suggested and further investigated, such

211 as scarce water availability for plants, high salinity, and the interaction of these latter factors  
212 with seed germination (García-Fayos et al., 2000; Bochet et al., 2009).

213 Recently, similar studies were carried out to test the same hypothesis in the Chinese Loess  
214 Plateau, i.e. the scarcity of vegetation as a consequence of seed removal by runoff (Jiao et al.,  
215 2011; Han et al., 2011; Wang et al., 2013; see Table 1). Similar results to that documented in the  
216 Spanish badland areas were obtained, since no seed losses were recorded in small bins filled  
217 with soils collected from the field at a similar rainfall intensity (50 mm/h) and different slope  
218 angles (Jiao et al., 2011; Han et al., 2011). However, the total amount of seeds lost by runoff  
219 was closely related to runoff volume and sediment yield and average seed losses reached 32.6  
220 and 66.0% values at rainfall intensities of 100 and 150 mm/h, respectively. Seed loss rates up to  
221 100% were described for some species in a similar laboratory experiment under 30 minute-  
222 simulated rainfall at 120 mm/h (Wang et al., 2013). However, because rainstorm intensities  
223 heavier than 50 mm/h are very occasional in the Chinese Loess Plateau, Jiao et al. (2011)  
224 concluded that seed losses by runoff could not explain the scarcity of vegetation in the Chinese  
225 Loess Plateau as it had been already pointed out for the semiarid badland slopes of Southeast  
226 Spain (García-Fayos and Recatalà, 1992; García-Fayos et al., 1995).

227 The generally low rates of seed losses described in these studies may be due, in part, to the  
228 burial of seeds into the soil after being trapped or at the time they get covered by local  
229 accumulations of sediments transported by overland flow (Chambers et al., 1991).

230 Moreover, caution is needed when it comes to interpreting these data in terms of seed losses for  
231 the ecosystem. Several authors have evidenced the limitations of extrapolating small-plot  
232 erosion measurements -and their associated processes- to larger areas, because different  
233 processes act at different scales (splash, interrill, rill and gully erosion) and thresholds and non-  
234 linear processes are involved at specific scales and at the connection between scales (Govers,  
235 1991; Cammeraat, 2002). Therefore, seed losses by overland flow measured at the plot scale in  
236 small areas (0.24 to 3 m<sup>2</sup>, Table 1) and over short distances relative to the interpatch spacing in  
237 patchy systems (< 2 m, Table 1) -as the ones reported in the aforementioned studies - could be

238 considered seed displacements or seed translocations to new sites at the hillslope scale. In this  
239 respect, another body of research suggested that seeds transported by overland flow are not lost  
240 but redistributed along the slopes through downslope seed movements from one location to  
241 another. Aerts et al. (2006) reported that 21 to 61% of the seeds of the species *Olea europea*  
242 were translocated to new sites under simulated rainfall within 3 x 3 m plots placed in restored  
243 forested areas in Ethiopia. Similarly, Jiao et al. (2011) and Han et al. (2011) described that 30-  
244 45, 46.9 and 20.4% of the seeds were moved from one site to another site inside a 1 m<sup>2</sup> and 2 m-  
245 long laboratory experimental bin at intensities of 50, 100 and 150mm/h, respectively, without  
246 being exported outside the bin. Using the same experimental setup, Wang et al. (2013)  
247 measured an average distance of 157.5 cm corresponding to seed redistribution by runoff within  
248 a 2 m-long bin which was longer than the length of the plots used by Cerdà and García-Fayos  
249 (1997) and García-Fayos and Cerdà (1997) to quantify seed loss rates. Thus, whether seeds are  
250 lost or redistributed may be a matter of scale and more studies quantifying seed transport by  
251 runoff are needed at larger scales, where processes other than sheet erosion may also take part in  
252 seed transport (e.g. rill and gully erosion). The only study that quantified seed transport by  
253 runoff at the slope and catchment scales in semiarid ecosystems gives evidences of both  
254 outcomes, seed loss and seed redistribution (García-Fayos and Recatalà, 1992). On the one  
255 hand, these authors observed an increasing seed density in the downslope direction from the top  
256 to the bottom part of the slope that supports, at least in part, the hypothesis of seed redistribution  
257 along the slope. On the other hand, the 6 to 20-fold difference in seed concentration at the  
258 outlets of catchments and in the regolith, demonstrates that seed losses out of the system also  
259 occur.

260

### 261 **3.2. Factors influencing seed removal by runoff**

#### 262 *3.2.1. External factors*

263

264 In some of the aforementioned studies, it was also claimed that several factors influence the  
265 severity of seed transport by runoff (Table 1). A strong relationship was found between the

266 magnitude of seed transport by runoff and rainfall and slope characteristics. Similar to what  
267 happens to soil particles (Govers, 1989; Parsons et al., 1993; de Vente and Poesen, 2005; Boix-  
268 Fayos et al., 2006), seed losses increased as slope angle (García-Fayos et al., 1995; Jiao et al.,  
269 2011; Han et al., 2011; but Cerdà and García-Fayos, 1997) and rain duration and intensity  
270 increased (García-Fayos et al., 1995; Jiao et al., 2011; Han et al., 2011), but it decreased with  
271 soil surface roughness (Reichman, 1984; Chambers, 2000; Aerts et al., 2006; Isselin-Nondedeu  
272 et al., 2006; Isselin-Nondedeu and Bédécarrats, 2007) and with total slope length (García-Fayos  
273 et al., 1995). Soil texture also influenced seed losses, since larger soil particles increased the  
274 amount of seeds trapped in the soil (Chambers et al., 1991; Traba et al., 2006). Results of these  
275 studies also suggested that seed characteristics could obscure the relationships between runoff  
276 and seed losses and were, therefore, further investigated (Friedman and Orshan, 1975; García-  
277 Fayos et al., 1995; Cerdà and García-Fayos, 1997; García-Fayos and Cerdà, 1997; Han et al.,  
278 2011).

279

### 280 3.2.2. *Seed characteristics*

281

282 A body of research aimed at understanding the relationships between seed morphology and seed  
283 removal by runoff (see Table 2) under the hypothesis that single seeds should behave in the  
284 same way as soil particles regarding erosion and overland flow (García-Fayos and Cerdà, 1997).  
285 Thus, because soil particle size and shape are considered good predictors of soil particle  
286 susceptibility to removal (Kirkby, 1980; Poesen and Savat, 1980; Parsons et al., 1991) and  
287 spherical soil particles are more susceptible to be removed by overland flow than plate-shaped  
288 ones (Winkelmolen, 1971), similar trends were expected for seeds. Models based on laboratory  
289 rainfall simulation experiments showed that seed size was the main factor explaining seed  
290 removal, whereas the shape became important only when the seed size exceeded a specific  
291 threshold value which depended on the experimental conditions (50 mg value in the  
292 experimental conditions of Cerdà and García-Fayos, 2002; García-Fayos et al., 2010). This rule  
293 was valid for spherical seeds, whereas for flat-shaped seeds heavier than 50 mg no seed removal

294 occurred from the threshold value onwards. The relevance of seed size and shape in the severity  
295 of seed removal by runoff were later corroborated under rainfall simulation conditions for  
296 species living in the Chinese Loess Plateau (Wang et al., 2013) and under field conditions in the  
297 French Alps (Isselin-Nondedeu and Bédécarrats, 2007; Isselin-Nondedeu et al., 2006). In  
298 general terms, likewise soil particles, small and rounded seeds proved to be more susceptible to  
299 removal by runoff. However, further investigations demonstrated that the influence of seed  
300 characteristics on seed removal was more complex as initially thought, because seed  
301 susceptibility to be removed by runoff could be affected by other properties, such as the  
302 presence of seed appendages (hairs, wings, awns) or the ability of seeds to secrete mucilage, a  
303 sticky gel that forms around the seed once the seed comes in contact with water and glues the  
304 seeds to the ground (García-Fayos, 2004; García-Fayos et al., 2010). The presence of  
305 appendages reduced seed susceptibility to be removed by overland flow as regards seeds of  
306 similar weight that did not have appendages (García-Fayos, 2004). Similarly, species with light  
307 seeds ( $\leq 0.7$  mg) able to secrete mucilage experienced 10% lower losses than the seeds with  
308 similar mass that did not secrete mucilage (García-Fayos, 2004; García-Fayos et al., 2010).

309 Although less studied, seed buoyancy is another seed trait that may also influence seed  
310 movement in surface water since buoyant seeds will be able to float and move with overland  
311 flow when water depth is higher than the seed size (Thompson et al., 2014).

312 Finally, some seed traits enhance the incorporation of seeds into the soil column and decrease  
313 therefore the seed susceptibility to be removed by overland flow (Chambers et al., 1991). Small  
314 seed size and a lack of appendages are relevant morphological attributes for seed incorporation  
315 into the soil (Chambers et al., 1991), even though specialized appendages such as hygroscopic  
316 awns can facilitate seed burial (Peart and Clifford, 1987). However, if seeds are buried too  
317 deeply, especially small seeds, they can fail to act as functional seeds for the ecosystem (Traba  
318 et al., 2004).

319

320 **4. Long-term and large-scale ecological implications of seed removal by runoff in arid**  
321 **and semiarid ecosystems**

322  
323 ***4.1. Seed removal by runoff: an ecological driver of vegetation***

324 *4.1.1. Seed removal by runoff shapes plant community composition (community level)*

325 Although average seed losses by runoff measured in dryland plant communities were generally  
326 low, specific seed losses rates varied strongly among species within a plant community (García-  
327 Fayos et al., 1995; Jiao et al., 2011; Wang et al., 2013) as a result of the interaction between the  
328 seed morphology and overland flow. Consequently, seed removal by runoff is expected to  
329 contribute to the final plant composition of eroded environments.  
330

331 Several recent studies aimed at exploring whether soil erosion, through its effects on seed  
332 removal by runoff, could explain the composition of plant community on eroded slopes in  
333 dryland ecosystems (Bochet et al., 2009; García-Fayos et al., 2010; García-Fayos et al., 2013;  
334 Wang et al., 2013; Engelbrecht et al., 2014). García-Fayos et al. (2010) found that the average  
335 susceptibility of seeds to be removed by runoff was lower for plant communities of species  
336 living on steep slopes than for plant communities developing in flat areas in a semiarid area of  
337 East Spain (but see Wang et al., 2013 for a similar study in the Chinese Loess Plateau).  
338 Moreover, the proportion of species possessing a trait able to improve seed resistance to  
339 removal by runoff (mucilage secretion or presence of hygroscopic awns), varied between plant  
340 communities, with a higher proportion of seeds displaying anchorage mechanisms on the eroded  
341 slopes when compared with the flat areas (Bochet et al., 2009; García-Fayos et al., 2013). This  
342 proportion was also correlated with soil properties associated with runoff generation (García-  
343 Fayos et al., 2013).

344 After analyzing the physical properties of seeds from species living in different deserts of the  
345 world, Thompson et al. (2014) observed that all the species analyzed, except one, produced  
346 seeds with lower densities than water, being therefore able to float and be transported by  
347 overland flow. However, these results should be corroborated with data from species living in

348 areas where overland flow is absent, before any conclusion can be stated about the role of  
349 erosion in this association.

350 Overall, these results provide evidence that erosion -through its selective pressure on seeds by  
351 overland flow and the interaction of this latter with seed morphology- filters plant species at the  
352 community level from the very first stages of the plant life. The role of erosion as an ecological  
353 driver that shapes the composition of plant communities had already been highlighted in  
354 previous studies in arid and semiarid environments (Guàrdia et al., 2000; Guerrero-Campo and  
355 Montserrat-Martí 2000, 2004; García-Fayos and Bochet, 2009; Bochet et al., 2009; Jiao et al.,  
356 2009). However, relatively little attention had been paid to the effect of erosion on seeds  
357 (mainly seed transport and germination) as compared to later stages of the plant life (seedlings  
358 and adult plants, de Luís et al., 2005; Tsuyuzaki and Haruki, 2008; Wang et al., 2012), even  
359 though seed stage is one of the most critical phases in vegetation development (García-Fayos  
360 and Cerdà, 1997).

361

362 *4.1.2. Seed removal by runoff selects for seed traits and for adaptative plant strategies*  
363 *(species level)*

364

365 As already mentioned and further explained in section 3.3, seed redistribution by runoff can  
366 provide seeds with a second chance to lie in a more favourable site for seed germination and  
367 seedling establishment in arid and semiarid patchy ecosystems. In some cases, however, seed  
368 removal by runoff can be responsible for the loss of seed germination opportunities when seeds  
369 of plants inhabiting eroded hillslopes are moved downhill to less favourable sites where seeds  
370 can get deeply buried or suffer from strong competition with other seedlings or pre-established  
371 plants in water- and nutrient-rich soils (Cantón et al., 2004). As a result, plants may have  
372 evolved strategies to escape from massive seed loss to unsafe sites (Engelbrecht, 2014). In this  
373 respect, the possible adaptative value of mucilage secretion under desert conditions as a  
374 mechanism preventing seed removal by runoff was initially proposed by Ellner and Shmida  
375 (1981) and recently explored by Engelbrecht et al. (2014). These authors analyzed at the species  
376 level whether mucilage secretion can be considered an adaptative response to soil erosion in

377 plant species inhabiting semiarid environments. More specifically, they related the amount of  
378 mucilage secretion by seeds to the severity of the two main sub-processes whereby water  
379 erosion acts on soil particles and presumably also on seeds (i.e. splash detachment and overland  
380 flow transport). The amount of mucilage secreted by seeds of the species *Fumana ericifolia* was  
381 directly proportional to their resistance to raindrop impact and was, moreover, positively related  
382 to the intensity of the erosive processes that the plants experienced in the field in semiarid  
383 Mediterranean shrublands. Furthermore, according to overland flow transport, all the seeds  
384 resisted the strength of runoff irrespective of the amount of mucilage they produced. However,  
385 the effect of mucilage secretion in the rate of seed removal by erosion was species-dependent  
386 and Engelbrecht et al. (2014) concluded that their results only partially supported the idea that  
387 seed anchorage mechanisms to the ground, such as mucilage secretion, can be considered an  
388 adaptation to the hazards that erosive conditions impose to plants that inhabits open dry habitats.

389

#### 390 ***4.2. Seed removal by runoff influences the origin, spatial pattern and maintenance of patches*** 391 ***in arid and semiarid ecosystems***

392 A few studies have investigated the long-term and large-scale ecological implications of seed  
393 removal by runoff in the structure and functioning of arid and semiarid ecosystems worldwide  
394 (e.g. Aguiar and Sala, 1997, 1999; Schurr et al., 2004; Puigdefábregas, 2005; Aerts et al., 2006;  
395 Saco et al., 2007; Venable et al., 2008; Emmerson et al., 2012; Thompson et al., 2014). Figure 5  
396 illustrates schematically these implications on the basis of the available literature described  
397 hereafter.

398 Various hypotheses have been put forward to explain the origin, spatial distribution and  
399 maintenance of patches in arid and semiarid ecosystems (e.g. Dunkerley et al., 1995; Pueyo et  
400 al., 2008; Kefi et al., 2008). Variations in slope angle and the presence of local accumulations of  
401 organic debris and sediments, depressions in the soil surface, rocks or ant mounds on nearly  
402 bare slopes have been reported as possible physical obstacles to overland flow that can enhance  
403 local germination of entrapped seeds and further establishment of seedlings (e.g. MacFadyen,



404 1950; Reichman, 1984; Aguiar and Sala, 1997; Chambers, 2000; Venable et al., 2008).  
405 Alternatively, seed anchorage mechanisms (mucilage and hygroscopic awns), can also be  
406 instruments whereby new patches of vegetation originate on eroded hillslopes (García-Fayos et  
407 al., 2013).

408 Whatever their origin, once a seedling establishes from a germinated seed, it interacts with  
409 overland flow intercepting the downslope movement of water, sediments and nutrients,  
410 improving locally the fertility and water availability below the plant canopy and favouring the  
411 growth of the plant and the patch (Cerdà, 1997; Bochet et al., 1999; Puigdefábregas, 2005). As a  
412 result, the system becomes heterogeneous in terms of the quality of sites suitable for seed  
413 germination, the subsequent survival of seedlings and the resources available for plant growth  
414 (Schupp, 1995). Spatial heterogeneity is promoted and maintained by complex interactions  
415 between patches and overland flow in a self-organizing process (Rietkerk et al., 2004).

416 These complex interactions give rise to two main spatial vegetation patterns that can be found  
417 worldwide: on the one hand, “spotted” patterns are represented by vegetation clusters that are  
418 irregular in shape and surrounded by bare soil (Aguiar and Sala, 1999) and, on the other hand,  
419 “banded” patterns form densely vegetated stripes parallel to the contour lines that alternate with  
420 almost bare soil stripes on very gentle slopes (Valentin et al., 1999). Nowadays, there is general  
421 agreement that surface runoff is a key control on the appearance of such vegetation patterns and  
422 that the dynamics of runoff areas is the main driver of the spatial organization of such  
423 patterned ecosystems (e.g. Valentin et al., 1999; Tongway and Ludwig, 2001). Recently,  
424 Moreno-de las Heras et al. (2011) recognized the importance of the directional downslope  
425 redistribution of surface runoff and sediments in the periodicity of the patch-size distribution in  
426 banded landscapes in Australia. More specifically, they argued that the co-existence of long-  
427 distance negative vegetation-water feedbacks (including downslope redistribution of runoff and  
428 plant competition for water) and short-distance positive feedbacks (local plant facilitation) are  
429 responsible for the regular patterns of the vegetation. Although seed dispersal and fate should  
430 play a crucial role in these feedback mechanisms (Kefi et al., 2008; Pueyo et al., 2008), the role

431 of surface runoff, as a vector of seed transport, in the functioning and maintenance of patchy  
432 ecosystems has been poorly documented.

433 The existing literature, based on empirical as well as theoretical studies, mainly supports the  
434 idea that a patch-to-patch transfer of seeds occurs that helps maintaining the patchy structure of  
435 the vegetation. The patch-to-patch transfer of seeds results from a combination of a “directed”  
436 dispersal of seeds through runoff to areas with favourable conditions (Howe and Smallwood,  
437 1982) and the high plant capacity to trap seeds. Aguiar and Sala (1997) provided strong  
438 empirical evidence that high seed transit due to secondary dispersal agents (mainly wind but  
439 also water) occurred in bare inter-patch areas in the Patagonian steppe of Argentina, at the same  
440 time as they reported high rates of seed trapping by the vegetation, whereas bare areas were  
441 unable to retain almost any seed. Similar results showing the patchy distribution of the seed  
442 bank and its concentration mainly in vegetated patches have been described in the Sonoran  
443 Desert of Arizona (Reichman, 1984) and in banded landscapes of Mexico and Niger  
444 (Mauchamp et al., 1993; Seghieri et al., 1997). Moreover, Aguiar and Sala (1997) observed that  
445 overlapping of high seed densities with the availability of safe sites gave rise to successful  
446 recruitment near the vegetated patches and helped maintaining or even reinforced the current  
447 spatial heterogeneity of the system. In banded landscapes, seeds trapped by the vegetation are  
448 present throughout the bands, but the better water availability at the upslope edge of bands, and  
449 the smaller runoff volume passing through to the downslope edge, leads to the colonization of  
450 the upslope edge by pioneer species and to the progressive death of plants at the downslope  
451 edge (Seguieri et al., 1997; Valentin et al., 1999). A possible outcome that has been inferred  
452 from these observations by many authors, that remains a controversial topic today, is that the  
453 vegetation patterning migrates progressively upslope (Thiéry et al. 1995; Montaña et al. 2001;  
454 Deblauwe et al. 2012). Nevertheless, the use of new technologies in the study of slow  
455 ecosystem dynamics (e.g. high resolution satellite images and airborne photographic surveys)  
456 provided recently unequivocal photographic evidence of marked upslope migration for different  
457 dryland areas exhibiting banded patterns worldwide (e.g. northeastern Chihuahan desert,

458 Somalian Haud and Mediterranean steppes of eastern Morocco, Deblauwe et al. 2012). In the  
459 same study, however, Deblauwe et al. (2012) stated that these dynamics which proved to be  
460 widely influenced by weather regimes cannot be considered as systematic because migration  
461 was undetectable at the available image resolution in other banded systems they investigated  
462 (e.g. central Australia, western New South Wales). The reasons causing some banded patterns to  
463 move fast and others to be static are still elusive. Deblauwe et al. (2012) provide a review of  
464 some possible mechanisms that may explain these differences, including seed translocation by  
465 overland flow. In a recent model, Saco et al. (2007) related the migrating or stationary condition  
466 of bands to the dispersal of seeds by overland flow. They found that the anisotropic  
467 redistribution of seeds by surface flow downslope might prevent the bands from traveling  
468 upstream, whereas isotropic seed dispersal mechanisms might be responsible for upslope band  
469 migration. However, empirical studies investigating seed fluxes are needed to validate this  
470 model and the possible migration-impeding role of seed redistribution. As regards banded  
471 patterns, the dynamics of spotted vegetation might be more complex, as the former usually act  
472 as closed hydrological systems and the latter highly depends on the connectivity of bare areas  
473 (Saco et al., 2007). Recent studies demonstrate that it is not only the extent to which vegetation  
474 patches prevail on a slope (Parsons et al., 1996; Wainwright et al., 2000; Bochet et al., 2000;  
475 Puigdefábregas, 2005), but mainly the connectivity of bare areas that influences hydrological  
476 processes such as runoff and sediment transport (Bautista et al., 2007; Puttock et al., 2013).  
477 Connectivity has the advantage as regards vegetation structure to provide an explanatory link  
478 between abiotic and biotic components to determine the hydrological and ecological function of  
479 the system (Turnbull et al., 2008, 2010). In their ecohydrological conceptual framework,  
480 Turnbull et al. (2008) hypothesized that structural connectivity -which determines the amount  
481 and extent of abiotic and biotic resource redistribution- is the key determinant of the  
482 connectivity of ecological and hydrological processes, and thus, of the functional connectivity  
483 which includes water, sediment and seed movement among the landscape. Thompson et al.  
484 (2014) recently developed a theoretical model of seed dispersal processes by runoff where

485 hydrological connectivity was considered as an influencing variable on seed movement by  
486 overland flow. The model supported the hypothesis of a patch-to-patch transmission of seeds  
487 under specific conditions of rainfall and connectivity between patches. According to the model,  
488 either long and intense storms heavy enough to trigger seed movement and to induce transport  
489 distances comparable to the inter-patch bare spacing or, repeated storms allowing repeated seed  
490 transport are required in combination with high topographical and hydrological connectivity to  
491 generate a patch-to-patch transport of seeds.

492 In the reviewed literature, however, a few empirical studies do not support the patch-to-patch  
493 hypothesis. These studies highlight the absence of seed movement from the bare inter-patch  
494 areas to the vegetation patches in combination with a low seed trapping capacity by the  
495 vegetation (Aerts et al. 2006) or with short dispersal distances relative to the pattern of spatial  
496 heterogeneity (Venable et al., 2008; Emmerson et al., 2010, 2012). The authors concluded that  
497 successful recruitment of the species used in these experiments could not rely on seed transport  
498 by runoff but depended on other mechanisms such as primary dispersal (Aerts et al., 2006) or  
499 the temporal delay of germination (Venable et al., 2008; Siewert and Tielborger, 2010).

500  
501 Overall, in arid and semiarid patchy ecosystems, seed fate in overland flow seems to be  
502 determined by the spatial organization of the vegetation and by the hydrological connectivity of  
503 bare patches that appear to influence the origin and maintenance of patches (Fig. 5). A range of  
504 abiotic as well as biotic processes contribute to the structure and functioning of these  
505 ecosystems, whereby seed establishment influences overland flow and, in turn, overland flow –  
506 through the directed transport of seeds between connected vegetated patches- influences  
507 vegetation establishment and patch dynamics (Moreno-de las Heras et al., 2011).

508

## 509 **5. Directions for future research**

510 This review shows that repeated seed transport by overland flow leads to either seed losses from  
511 the system or the redistribution of seeds within the system through short seed movements.  
512 Because seed losses by runoff were generally low in field conditions, we should be aware of the

513 risks of over-interpreting the role of seed losses by erosion in the structuring of plant  
514 communities (García-Fayos et al., 2010). Possible reasons explaining the low rates of seed  
515 losses reported in the literature should be further investigated behind seed burial into the soil  
516 through vertical movements (Chambers and Mac Mahon, 1994; Chambers, 2000) and the lack  
517 of data describing seed losses caused by erosion processes acting at larger spatial scales and  
518 responsible for the largest proportions of soil loss in these ecosystem (but see Espigares et al.,  
519 2011).

520 Conversely, seed removal in terms of seed displacements to short distances proved to play an  
521 important role in the vegetation composition and spatial patterning of arid and semiarid patchy  
522 ecosystems, through the interaction between vegetated patches, overland flow carrying the seeds  
523 downslope and seed traits. Thus, the directed short-distance displacement of seeds to suitable  
524 sites where seeds are preferentially trapped by the vegetated patches result in a “patch-to-patch  
525 transport” of seeds through well connected bare areas, that helps maintaining the patchiness of  
526 the system.

527 Since recent models have related the origin and maintenance of patchiness to the lack of long-  
528 distance dispersal syndromes for plants living in arid and semiarid ecosystems (Pueyo et al.,  
529 2008; Kefi et al., 2008), an exciting challenge for the future would be to link these models to  
530 field data of seed removal by runoff. The idea that dispersal is spatially limited in arid and  
531 semiarid ecosystems (Ellner and Schmid, 1981) and the idea that seeds are removed by runoff  
532 in such ecosystems may not be as contradictory as it has been shown that seed removal acts  
533 mainly through short seed displacements within the system. Therefore, more empirical studies  
534 are needed to understand the relevance of seeds moved by runoff in the broader context of long-  
535 distance negative feedbacks (spatial redistribution of surface runoff and plant competition for  
536 water) and short-distance positive feedbacks (local plant facilitation) that seem to control the  
537 functioning of these ecosystems (Pueyo et al., 2008; Kefi et al., 2008; Turnbull et al., 2008).

538 Arid and semiarid ecosystems are experiencing increasing pressures by human activities and  
539 climate change and future scenarios of climate change predict changes in vegetation (type, cover

540 and spatial distribution, Specht and Specht, 1995) and in rainfall distribution (higher intensive  
541 rainstorms, Nearing et al., 2004), leading both to more intense erosion events. In this context,  
542 we should be able to understand how these changes might influence seed movements in  
543 overland flow and their consequences for the composition, structure and functioning of these  
544 ecosystems. Under such scenarios, the complex feedbacks between the spatial distribution of the  
545 vegetation, runoff and erosion that influence the spatial redistribution of abiotic and biotic  
546 resources among the landscape may experience severe changes (Turnbull et al., 2008, 2011).  
547 For example, a reduced or altered distribution of the vegetation and an increased connectivity of  
548 bare runoff-generating areas would result in higher velocities and erosive forces of the flow and,  
549 consequently, a higher flow capacity to transport sediment, nutrients and also seeds. It is  
550 suggested that when the internal system stabilizing feedbacks are altered by exogenous forces,  
551 the resilience of the ecosystem (i.e. its capacity to absorb disturbance and reorganize) changes  
552 and the system becomes more sensitive to experience nonlinear functional dynamics and cross  
553 critical thresholds (Turnbull et al., 2008, 2011). Therefore, there is an urgent need for new  
554 experimental studies addressing the feedbacks between structure and function and abiotic and  
555 biotic components of systems that may help to predict future changes in semi-arid ecosystems  
556 under the scenarios of climate change.

557 Understanding the fate of seeds in overland flow is also a critical issue for the successful  
558 restoration of severely eroded slopes (such as road embankments, roadcuts, mine spoils, burnt  
559 areas). The advances in the knowledge of significant seed characteristics able to prevent seed  
560 removal by runoff and of the trapping efficiency of plants, litters and depressions in the soil  
561 surface and their consequences on successful plant recruitment, are of potential great benefit to  
562 practitioners and policy makers involved in roadslope restoration (Rey et al., 2005). The use of  
563 recently developed models combining overland flow dynamics with seed fate and erosion can  
564 also be of great benefit to design restoration projects of plant communities on eroded hillslopes  
565 (Thompson et al., 2014). However, a great effort should be made among the scientific

566 community to improve the ways to quickly and efficiently transfer this available knowledge to  
567 institutions devoted to restoration (Valladares and Gianoli, 2007).

568  
569 In conclusion, an interdisciplinary approach, involving scientists from different fields related to  
570 plant, soil, geomorphology, hydrology, ecological restoration and modelling should broaden our  
571 understanding of seed fate in overland flow and its ecogeomorphological consequences in  
572 vegetation structure and function to help fill the aforementioned gaps.

573

#### 574 **Acknowledgements**

575 I am indebted to Artemi Cerdà and the Executive Editors of *SOIL* for their kind invitation to  
576 prepare this review. I am also grateful to Patricio García-Fayos for his suggestions that helped  
577 improve the manuscript. I thank Richard Brazier as Topical Editor, and Begoña Peco, Artemi  
578 Cerdà and two other anonymous referees as reviewers for providing helpful comments to  
579 improve the manuscript.

580

581

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**Table 1.** Overview of experimental studies quantifying seed losses and seed movements by overland flow. Papers are listed chronologically.

Authors	Location	System	Rainfall characteristics	Scale	Measured variables	Studied factors	Main results
García-Fayos and Recatalà 1992	Alicante (Spain)	Semiarid Badlands	Natural rainfall 1 year (5 rainfall events)	Small catchments aprox.900 m <sup>2</sup>	Seed balance between seed inputs (primary dispersal) and seed outputs (erosion)		Positive seed balance  Evidences of seed losses outside the catchments: 6- to 20-fold more seeds in the sediment traps at the outlets of catchments than in the regolith  Evidences of seed redistribution on slopes: spatial gradient of seed density along the slope
García-Fayos et al. 1995	Alicante (Spain)	Semiarid Badlands	-Natural rainfall 2 years  -Simulated rainfall 55 mm/h, (40 and 110 min) and 45 mm/h, (40min)	Small catchments  0.24 m <sup>2</sup> field plots  3 m <sup>2</sup> field plots	Natural rainfall: Seed balance between seed inputs (primary dispersal) and seed outputs (erosion) as % of the soil seed bank  Simulated rainfall: % seed losses	Slope angle, length, rainfall duration	Natural rainfall -Positive seed balance -Annual seed losses: 5.6 – 12.6 %  Simulated rainfall: Seed losses: < 13 % under simulated rainfall Seed losses increased as slope angle and rain duration increased, and decreased as total transport length increased
García-Fayos and Cerdà 1997	Alicante (Spain)	Semiarid Badlands	Simulated rainfall 55 mm/h, 22 min	0.24 m <sup>2</sup> field plot (22-55° slope)	% seed losses	10 different species	Significant exponential relation between seed loss and runoff
	Valencia (Spain)	Abandoned fields	Simulated rainfall 55 mm/h, 22 min	0.24 m <sup>2</sup> field plot (2-4° slope)			Total seed loss < 10 % for all replicates Single species seed loss < 25 %
Cerdà and García-Fayos 1997	Alicante (Spain)	Semiarid Badlands	Simulated rainfall 55 mm/h, 40 min	0.24 m <sup>2</sup> field plot (2° pediment and 22-55° slopes)	% seed losses	Slope angle	Seed losses: 4 % on slopes in average 23 % in the pediment  Seed losses are negatively related to slope angle due to the strategy of seeds against erosion

Cerdà and García-Fayos 2002	Laboratory	-	Simulated rainfall 55 mm/h, 25 min	26 x 26 cm plot ( 11° slope) no soil	% seed losses	83 species	11 % average seed losses for all experiments
Aerts et al. 2006	Northern Ethiopia	Forest restoration areas	Natural rainfall one rainy season  Simulated rainfall 120 mm/h, 10 min	3x3 m <sup>2</sup> field plots (8-18° slope)	% seed displacement	Seeds of 1 species ( <i>Olea europea</i> )  Slope angle and roughness, Pioneer shrub species as vegetated patches	21-61 % seed movement  No significant influence of shrub species, slope angle and roughness on seed movement
Venable et al. 2008	Sonoran desert (Arizona)	Desert		Plots 10-30 m in diameter	Distance of seed displacement	Slope angle, pioneer shrub	Displacement distance < 1 m
Emmerson et al. 2010	Mid-east South- Australia	Chenopod shrubland with scattered trees	Natural rainfall 9 month-period		% of seed displacement Distance of seed displacement	Seeds of 1 local species ( <i>Erodiohyllum elderi</i> ) Grazing pressure (animal tracks : 0.3m wide and 0.2m deep), slope angle	After 9 months: Low proportion of seeds displaced out of tracks: <10 % Low distances of displacement out of tracks: 1.09 m Tracks increase the rate and distance of displacement Slope angle increased the proportion of seeds moved and the distance of seed displacement
Jiao et al. 2011	Loess Plateau China		Simulated rainfall 50/ 100/ 150 mm/h, 60 min	1 m <sup>2</sup> laboratory plots filled with soil from the field site (10/15/20/25° slope)	% seed losses % seed displacement Distance of seed displacement	16 different local species	Seed losses: 0 % at 50 mm/h rainfall intensity, 26-33 % at 100 mm/h rainfall intensity, 59-67 % at 150 mm/h rainfall intensity Average seed displacement distance: 6.2 cm maximum distance at 50 mm/h, 31.5 cm at 100 mm/h and 42.0 cm at 150 mm/h.
Han et al. 2011	Loess Plateau China		Simulated rainfall 50/ 100/ 150 mm/h, 60 min	1 m <sup>2</sup> laboratory plots filled with soil from the field site (10/15/20/25° slope)	% seed losses % seed displacement Distance of seed displacement	16 different local species  Rainfall intensity, Slope angle	Seed displacement (SD) and seed losses (SL): 0 % SD and 30-45 % SL at 50 mm/h rainfall intensity 46.9 % SD and 32.6 % SL at 100 mm/h 20.4 % SD and 66.0 % SL at 150 mm/h Significant influence of rainfall intensity on seed loss No influence of slope angle on seed loss at a same

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						rainfall intensity
Wang et al. 2013	Loess Plateau China	Simulated rainfall 120mm/h, 30 min	1m <sup>2</sup> laboratory plots filled with soil from the field site (20° slope)	Seed losses, Seed displacement ratio (seed displaced/ total seeds used)*100 Distance of seed displacement	60 plant species	Seed losses varied among species: 0 - 100% Seed displacement ratio: 3.3 to 100% Average seed displacement distances: 3.2 - 157.5cm

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## Figure captions

**Figure 1.** Temporal evolution of the total number of papers on seed fate and dispersal in drylands published between 1974 and 2013, along with the evolution of the relative number of papers focusing on secondary seed dispersal. Data were obtained from online key-word searches with Scopus database using the “All Document Type” option, date range from 1974-2013 and the following formulae in Topics: (a) (“*dispersal*” or “*seed fate*” and “*seed*”) and (*arid* or *semiarid* or *semi-arid* or *dryland* or “*patchy vegetation*” or “*patchy ecosystem*” or *patchiness* or *mosaic* or *desert*)” for seed fate studies in general; (b) (“*dispersal*” or “*seed fate*” and “*seed*”) and (*arid* or *semiarid* or *semi-arid* or *dryland* or “*patchy vegetation*” or “*patchy ecosystem*” or *patchiness* or *mosaic* or *desert*) and (“*secondary dispersal*” or “*secondary seed dispersal*” or “*seed removal*” or “*seed movement*” or “*secondary seed movement*” or “*secondary movement*” or “*secondary process*” or “*post dispersal*” or “*post-dispersal*” or “*seed bank*” or “*seedbank*”)” for secondary seed dispersal studies.

**Figure 2.** Temporal evolution of the total number of papers on secondary seed dispersal in drylands published between 1974 and 2013, along with the total number of papers for the same time period specifically addressing secondary dispersal by animals, wind and overland flow. Data were obtained from online key-word searches with Scopus database using the “All Document Type” option, date range from 1974 until 2013 and the following formulae in Topics: (“*dispersal*” or “*seed fate*” and “*seed*”) and (*arid* or *semiarid* or *semi-arid* or *dryland* or “*patchy vegetation*” or “*patchy ecosystem*” or *patchiness* or *mosaic* or *desert*) and (“*secondary dispersal*” or “*secondary seed dispersal*” or “*seed removal*” or “*seed movement*” or “*secondary seed movement*” or “*secondary movement*” or “*secondary process*” or “*post dispersal*” or “*post-dispersal*” or “*seed bank*” or “*seedbank*”)”, adding: (a) “and (*runoff* or *run-off* or *erosion* or “*water transport*” or “*overland flow*”)” for overland flow; (b) “and (*wind* or *eolian*)” for wind; (c) “and (“*animal\**” or *biotic* or *ants* or *birds* or *rodents*)” for animals.

**Figure 3.** Total number of papers on secondary dispersal in drylands published between 1974 and 2013 and classified by Journal Categories. The graph underlines the anecdotal number of papers (2) published in soil science related Journals (grey cone). Papers were assigned to a single main category even though in Scopus they could belong to several categories at a time. N=162. Papers were obtained from online key-word searches with Scopus using the “All Document type” option with the following formula: (“*dispersal*” or “*seed fate*” and “*seed*”) and (*arid* or *semiarid* or *semi-arid* or *dryland* or “*patchy vegetation*” or “*patchy ecosystem*” or *patchiness* or *mosaic* or *desert*) and (“*secondary dispersal*” or “*secondary seed dispersal*” or “*seed removal*” or “*seed movement*” or “*secondary seed movement*” or “*secondary movement*” or “*secondary process*” or “*post dispersal*” or “*post-dispersal*” or “*seed bank*” or “*seedbank*”)” in Topics for period 1974-2013. From the 165 retrieved papers plotted in Figure 2, three could not be classified as information about Journal Category was lacking in Scopus.

**Figure 4. Conceptual model of seed fate in and on the soil (grey area).** Rectangles represent seed states, dotted arrows indicate transitions between seed states and processes are written in italics. Grey arrows indicate seed movements and processes related to movement are in bold. After Schafer & Chilcote (1970), Fenner (1985), Chambers & Mac Mahon (1994), Van der Wall et al. (2002). The term “seed” used throughout the model and the text represents the diaspore or unit of dispersal (seed with surrounding dispersal structures).

**Figure 5.** Schematic figure of seed fate in overland flow at the (A) slope scale and (B) patch scale (patch-to-patch transmission of seeds). The figure represents how the spatial pattern of the vegetation influences seed distribution and seed fate and how, in turn, seed fate influences the origin and maintenance of patches in arid and semiarid patchy ecosystems.