Road Slope Revegetation in Semiarid Mediterranean Environments. Part I: Seed Dispersal and Spontaneous Colonization

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Abstract

The importance of neighboring vegetation as a seed reservoir for spontaneous colonization of adjacent road slopes was analyzed in a semiarid region of east Spain. Two independent methodological approaches were used to examine the relative contribution of seed from neighboring vegetation and the efficiency of different seed dispersal strategies in plant colonization. We first used a randomization test to compare floristic similarity between road slopes, neighboring flora, and local flora (the regional species pool found in the same climate and soil conditions as the road slopes). Second, we compared seed dispersal mechanisms of road slope vegetation with those of the surrounding area using frequency analysis. Species composition of road slopes was more similar to that of the flora of adjacent surrounding areas than expected by chance. Anemochorous (wind-dispersed) plants were over-represented in road slopes 8 years after road slopes were built. We concluded that seed dispersal from neighboring vegetation is an important factor in the vegetative colonization of road slopes. However, this initial species pool was also strongly shaped by the harsh environmental conditions of roadcuts and southern aspect. These results have important implications in road slope restoration because they suggest that naturally vegetated areas should be maintained adjacent to road slopes to enhance seed immigration from species adapted to local site conditions, which will accelerate the successional process. The application of this single reclamation strategy and mixed strategies that combine the use of natural colonization and soil amendment for road slope restoration in Mediterranean environmental conditions is discussed.

Key words: dispersion, environmental limitations, floristic composition, neighboring vegetation, randomization test, restoration, soil erosion.

Introduction

Understanding the mechanisms behind the establishment of plant communities is a significant area of research in plant ecology. Although at a regional scale species composition is primarily determined by environmental conditions, on a local scale plant assemblages are largely determined by dispersal processes (Ozinga et al. 2005). In the last decade, many studies have provided evidence that seed dispersal contributes significantly to plant colonization in different types of environments. A broad suite of descriptive studies have focused on comparisons of the floristic composition of different pools of species (local vs. regional) and on the hypothesis that the availability of diaspores and probability of their arrival at a specific site are inversely related to the distance of the diaspore source (Willson 1993). Butaye et al. (2002) pointed out that 91% of the species occurring in newly colonized forest patches in a fragmented agricultural landscape in Central Belgium were contained in the neighboring older forests within a radius of 1,000 m. In a mixed deciduous forest in Belgium, Verheyen and Hermy (2001) attributed a decline in the frequency and abundance of species with increasing distance from the colonization source to the dispersal limitation. Dzwonko (1993) obtained similar results in a fragmented agricultural landscape of southern Poland; he argued that nearby old-growth forests provided the main source of diaspores to newly colonized woodlands and that the species composition and richness of newly colonized areas were determined by their distance from old-growth forests. Moreover, in these woodlands, seed dispersal strategy greatly affected which seeds reached isolated woods; hovering and flying anemochores (wind-dispersed seeds) and endozoochores (dispersed by animals by ingestion) were the best colonizers, whereas heavy anemochores, myrmecochores (ant-dispersed seeds), and barochores (gravity-dispersed seeds) were much less successful (Dzwonko & Loster 1992).

Another suite of studies that involved experimentally adding seeds to either existing populations (seed augmentation) or unoccupied sites (seed introduction) also permitted assessment of the importance of seed availability and dispersal to the species diversity and abundance of plant communities (Primack & Miao 1992; Ehrlen & Ericksson 1996; Zobel et al. 2000; Tofts & Silvertown 2002; Foster & Tilman 2003). In all these studies, addition of missing diaspores increased the species density and

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richness, providing evidence that presence of diaspores alone is a major contributor to the number and abundance of species in communities in a wide range of environments.

Recent studies in disturbed environments have revealed that plant colonization is often limited by the availability of immigrant propagules and by the considerable distance of appropriate seed source to target areas. These results have been found in a broad range of study areas including volcano slopes (del Moral & Wood 1993), abandoned lignite-mining areas (Kirmer & Mahn 2001), and basalt quarries (Novák & Prach 2003). Novák and Prach (2003) pointed out that to date very few quantitative studies have focused on the role of the neighboring vegetation in the colonization of disturbed sites. This is all the more surprising because severely disturbed environments with unvegetated areas represent an ideal opportunity for understanding the process of colonization in competition-free microsites.

Road slopes are one type of disturbed area that offer this opportunity and are abundant around the world. Many floristic surveys of roadside vegetation within various climatic regimes and gradients have been published, revealing the importance of rainfall, temperature, altitude, and soil fertility in determining roadside floristic composition (Frenkel 1970; Holzapfel & Schmidt 1990; Heindl & Ullmann 1991; Ullmann et al. 1995; Godefroid & Tanghe 2000). However, very little is known about the importance of seed dispersal from neighboring vegetation in the colonization of road slopes (Alborch et al. 2003). Bochet and García-Fayos (2004) found that slope angle, slope type (roadfill vs. roadcut), and slope aspect (north vs. south) are the primary determinants of vegetation development and floristic composition of road slopes under semiarid conditions. These authors also showed that duration of available water for plants and soil fertility are the key factors explaining differences in vegetation when slope angle is lower than 45°. They assumed that seed dispersal processes from adjacent areas were similar in all types and aspects of road slopes and that differing slope conditions are the primary forces shaping the pool of species that established. Our research tests the assumption that seed dispersal processes are controlled by similar factors in all types and aspects of road slopes and therefore differential species immigration is not controlling these differences.

We hypothesize that most seeds arriving at a site have dispersed from the nearest areas, and consequently, the vegetative composition of road slopes is more similar to that of surrounding areas than to that of the local flora (the pool of plant species of the regional flora living in the same climate and soil conditions as the area where the road slopes were built), regardless of the type and aspect of the road slope. Because service roads and wire fences surrounding a road slope may act as barriers to plant migration and animal movement, we expect that species with long-distance dispersal mechanisms that are independent of animals may be most successful in reaching a road slope. Consequently, we hypothesize that wind-dispersed species will be over-represented on road slopes relative to the flora of the surrounding areas. To test these hypotheses, we compared floristic composition and seed dispersal strategies of vegetation on 36 road slopes differing in slope type and aspect to those of both surrounding areas and the local flora.

The resulting information may be applicable to restoration ecology because it has been argued repeatedly that spontaneous processes such as colonization and succession are a suitable tool for restoration of various disturbed sites (Novák & Prach 2003). Moreover, Matesanz et al. (2006) encouraged future research focused on understanding the establishment of autochthonous species and identifying environmental conditions under which commonly used and expensive hydroseeding with commercial species could be avoided.

Methods

Study Area

The study area is situated in the region of "La Plana de Utiel-Requena" of the Valencian Community, Spain (lat 39°29′N, long 1°06′W). Road slopes selected as study sites are located between 267 km and 307 km of the east–west A-3 divided highway that links Madrid with Valencia. Road slopes were 6–8 years old at the time of vegetation survey. Soils are derived from calcareous marls and clays of tertiary origin (García 1996). The climate is semiarid, with 418 mm of precipitation and a mean temperature of 14.2°C at the Requena meteorological station (Pérez 1994). Intra- and interannual variations of rainfall are important, with the most abundant and erosive rainfalls falling in May and October. Frost events may occur in winter, and summer drought usually lasts for 1–3 months. A broader description of the study site and road building conditions can be found in Bochet and García-Fayos (2004).

The existing vegetation adjacent to the road slopes has suffered the impact of human activities for centuries. Vineyards, almond, and olive groves cover a large proportion of the area adjacent to these road slopes, but shrublands and open forests still remain in small patches between the cultivated fields. The dominant tree species is *Pinus halepensis* (Pinaceae); the most abundant shrubs are *Rosmarinus officinalis* and *Thymus vulgaris* (Lamiaceae), *Genista scorpius* (Fabaceae), and *Quercus coccifera* (Fagaceae); and the most prevalent grasses are *Brachypodium retusum*, *Koeleria vallesiana*, *Stipa offneri*, and *Helictotrichon filifolium* (Poaceae). Soil, climate, and vegetation are similar among study sites, with comparable ratios of cultivated areas to shrubland patches in the vicinity of all road slopes.

Road Slope Selection

Thirty-six road slopes were selected, all greater than 5 m long (top to bottom of the slope) and 20 m wide and with less than 5% cover of rock outcrops. Slope angles ranged between 25 and 45°. The road slopes encompassed different slope types and aspects; we sampled nine north- and 11 south-facing roadcuts and seven north- and nine south-facing roadfills. Roadcuts result from the excavation of high areas, and roadfills are built by accumulating and compacting unconsolidated materials from adjacent areas.

The slopes were hydroseeded with a standard mixture of commercial species just after the road was built, with no addition of topsoil. Only two of the hydroseeded species (*Medicago sativa* and *Onobrychis viciifolia*) remained 8 years after road building.

Floristic Composition

In order to capture the species with different phenologies, floristic composition was sampled once in early spring and once in early summer on the road slopes (RS) and in adjacent surrounding areas (ASF) between 2000 and 2002. Hydroseeded species present on road slopes were not included in the floristic lists. The complete list of species present in the 36 adjacent surrounding floras was defined as "local flora" (LF) of the study area.

Floristic composition (presence/absence data) of a road slope was determined by two people walking the slope parallel to the road, one in the upper part and the other in the lower part of the slope, recording all species found in their respective fields of vision. One-meter wide belts along the upper and lower borders of the slopes were not sampled to avoid possible interferences with the surrounding flora. Although the total area sampled was different for every road slope, we did not find any relation between the size of the sampled areas and the percentage of common species between the road slope and the surrounding area ($r = 0.044$, $p = 0.799$, $n = 36$). The area sampled in the surrounding flora was proportional to the area sampled in the road slope. Surrounding flora was sampled in a semicircle with a radius of 150 m (Fig. 1). The list of species present in the adjacent surrounding flora was compiled using the same survey method as the road slopes.

Dispersal Categories

All species were classified into two main dispersal categories: anemochorous and other dispersal strategies. These two main categories were used because anemochorous species have a higher probability of reaching a slope from the surrounding area than do species in the other dispersal categories (barochores, autochores [self-dispersed], ballistics [free-fall dispersal], and myrmecochores). Additionally, even though zoochorous (animal-dispersed) species have the potential to be dispersed farther than anemochorous species, the absence of vegetation with suitable perches for birds on road slopes and the presence of wire fencing preventing animals from accessing the slopes can considerably decrease the probability of finding zoochorous species on road slopes.

Species were assigned to dispersal categories based on information from available databases (Molinier & Müller 1938; van der Pijl 1972; Hensen 1999). In the few cases in which species dispersal mechanism was not included in the databases, morphology of the seed and comparison with close taxa of a known dispersal category were used to assign a dispersal strategy (Higgins et al. 2003).

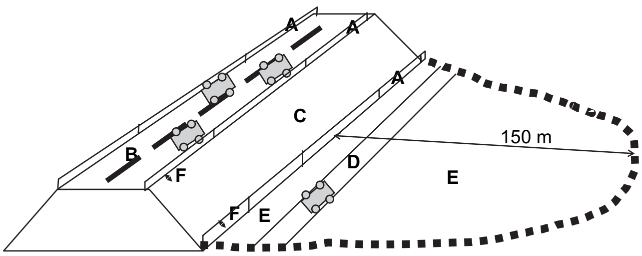

Figure 1. Sampling design for road slopes and surrounding vegetation. A, wire fencing; B, road; C, road slope; D, service road; E, surrounding vegetation; F, one-meter wide unsampled vegetation belts.

Statistical Analyses

A randomization test was performed to determine the extent to which floristic composition of the road slope (RS) was determined by seed dispersal from species of the adjacent surrounding flora (ASF). The null hypothesis was that if seed dispersal from the surrounding vegetation did not play an important role in road slope colonization, then similarity between species in the existing road slope flora and adjacent surrounding area should not be higher than similarity with a random set of species of the local flora (LF). The methodology and programming procedure were based on Butaye et al. (2002), although they were slightly modified to accommodate the objectives and requirements of our study (Fig. 2).

First, the number of species matches between each road slope flora (RS_i) and its adjacent surrounding flora (ASF_i) was calculated and expressed as the percentage of the species present in the road slope (observed value, $CS_{RS_i - ASF_i}$).

Second, subgroups (SG) with the same number of species as that of each surrounding flora to each road slope (ASF_i) were randomly selected from the local flora (LF). Third, the number of species matches between each road slope (RS_i) and the randomly assigned subgroup (SG) was calculated and expressed as the percentage of the species present in the road slope ($CS_{SG - RS_i}$). The randomization model was run 5,000 times for each road slope to generate a null reference distribution. When the observed value ($CS_{RS_i - ASF_i}$) was greater than the 99.9 percentile value obtained from the random distribution generated under the null hypothesis, it was considered to be significantly different ($p < 0.001$) from that expected at random (Fortin & Jacquez 2000).

The difference (D) between the observed value and the 99.9 percentile value of the random distribution was used to test for differences in the size of the effect of dispersal between road slope types and aspects. A generalized

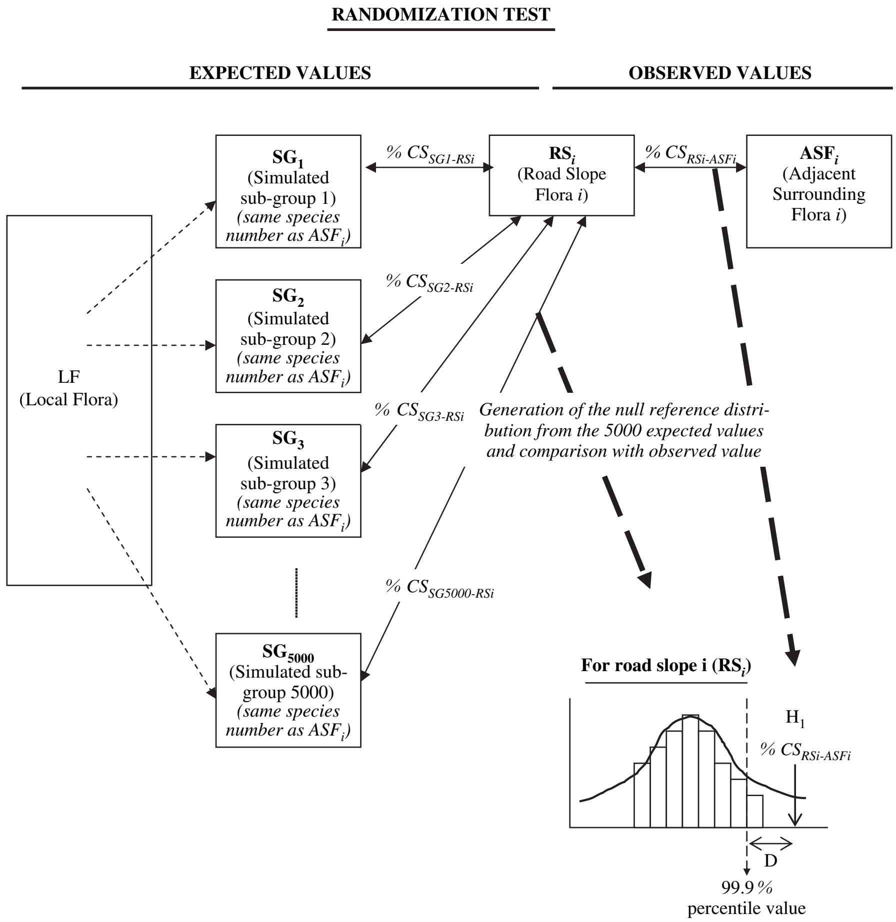

Figure 2. Schematic diagram of the randomization procedure to test whether the floristic composition of the road slope was determined by the species composition of the adjacent surrounding flora (detailed explanation in Materials and Methods section). $CS_{RS_i - ASF_i}$ (observed value): number of species matches between each road slope flora (RS_i) and its adjacent surrounding flora (ASF_i), expressed as the percentage of the species present in the road slope. $CS_{SG - RS_i}$: number of matches in floristic composition between each road slope (RS_i) and the randomly assigned subgroup (SG), expressed as the percentage of the species present in the road slope. The randomization model was run 5,000 times for each road slope to generate a null reference distribution. D = observed value − 99.9 percentile value.

linear model analysis was performed with slope type and aspect as factors after checking variable D for normality and homoscedascidity.

A chi-square goodness-of-fit test was used to measure how far the distribution of the frequencies of dispersal categories in the road slopes deviated from the distribution in the corresponding surrounding flora. The number of species falling into each dispersal category was recorded for each road slope (=observed frequency) and for the corresponding surrounding area. The expected frequency was calculated for each dispersal category by multiplying the number of species in the road slope by the proportion of each dispersal category obtained in the surrounding flora.

Data from the 36 replicates were also tested for heterogeneity using chi-square analysis (Zar 1996). After the homogeneity of the distribution of dispersal categories for each group of road slopes was confirmed, it was assumed that all replicates from one type and aspect of road slope came from the same population or from populations having the same class ratios, and therefore frequencies of the replicates were pooled. Pooling was achieved by totaling all the observed frequencies of one slope type, totaling all the expected frequencies, and then performing a chi-square test on these totals. Because the number of categories tested was equal to 2, the Yates correction for continuity (χ^2_c) was applied (Zar 1996).

Results

A total of 310 vascular species were recorded in the road slopes and surrounding flora. One hundred and seventy-seven species were common to road slopes and surrounding areas, 119 species were specific to surrounding areas, and 14 were recorded only on road slopes. Percentages of species overlap by aspect and slope type between the road slopes and their adjacent surrounding floras are provided in Table 1.

Randomization Test

Species composition of road slopes resembled that of the adjacent surrounding flora more than expected by chance; road slopes were therefore not a random sample of the local flora of the study area. In each of the 36 road slopes, the percentage of shared species was significantly higher than expected by chance (99.9 percentile value, $p < 0.001$; Table 1). Moreover, no significant differences existed in D values between the slope types and the aspects ($F_{[1,32]} = 2.128$, $p = 0.154$ for type; $F_{[1,32]} = 0.016$, $p = 0.900$ for aspect; and $F_{[1,32]} = 0.000$, $p = 0.987$ for their interaction), indicating that the contribution of seed dispersal to plant colonization was not affected by either the type or the aspect of the slopes (Table 1).

Dispersal Categories in Road Slopes and Adjacent Surrounding Areas

Because chi-square analyses, performed both including and excluding the two replicates that showed expected

Table 1. Results of the randomization test for the influence of the floristic composition of the surrounding flora on species composition of RS.

ID	*Slope Type*	*RS*	*ASF*	*CS (%)*	*D*
1	Rf N	38	99	86.84	31.58
2	Rf N	62	89	59.68	17.74
3	Rf N	21	116	95.24	23.81
4	Rf N	54	117	72.22	16.66
5	Rf N	54	97	83.33	35.18
6	Rf N	45	103	86.67	33.33
7	Rf N	30	120	86.67	23.34
				$\overline{X} \pm SD = 81.52 \pm 11.81$	
8	Rf S	73	102	53.42	5.47
9	Rf S	48	90	68.75	20.83
10	Rf S	45	87	84.44	37.77
11	Rf S	37	122	81.08	18.92
12	Rf S	54	156	90.74	18.52
13	Rf S	46	106	80.43	26.09
14	Rf S	56	105	82.14	30.35
15	Rf S	46	105	78.26	28.26
16	Rf S	28	105	71.43	10.72
				$\overline{X} \pm SD = 76.74 \pm 10.93$	
17	Rc N	29	121	79.31	17.24
18	Rc N	32	105	78.13	18.75
19	Rc N	26	120	88.46	19.23
20	Rc N	55	113	76.36	21.81
21	Rc N	35	83	77.14	28.57
22	Rc N	45	110	88.22	32.66
23	Rc N	8	82	87.50	12.50
24	Rc N	21	96	76.19	14.29
25	Rc N	30	129	93.33	26.66
				$\overline{X} \pm SD = 82.74 \pm 6.57$	
26	Rc S	40	117	95.00	35.00
27	Rc S	40	105	70.00	15.00
28	Rc S	47	116	83.33	25.88
29	Rc S	56	117	85.71	30.35
30	Rc S	17	109	82.35	11.76
31	Rc S	13	95	76.92	7.69
32	Rc S	24	124	100.00	33.33
33	Rc S	26	92	73.08	19.23
34	Rc S	47	118	82.98	23.41
35	Rc S	40	95	80.00	27.50
36	Rc S	37	114	94.59	35.13
				$\overline{X} \pm SD = 84.00 \pm 9.37$	

ID, road slope identification. Slope type: Rf, roadfill; Rc, roadcut; N, north-facing; S, south-facing. RS, number of species recorded in the road slope. ASF, number of species recorded in the adjacent surrounding flora. CS, common species between the RS and ASF expressed as a percentage of the species present in the road slope. $D = (CS - 99.9$ percentile value of the null reference distribution).

frequencies less than 5, produced similar results, we present results for the whole set of 36 road slopes.

The test of heterogeneity performed with the whole set of 36 replicates revealed that replicates were homogeneous ($\chi^2 = 34.210$, $df = 35$, $p > 0.05$), indicating that no interaction existed between slope type and aspect and that segregation of dispersal categories in road slopes was similar for all slope types and aspects. Replicates were also homogeneous when analyzed separately for each slope type and aspect ($\chi^2 = 5.64$, $df = 6$, for north roadfills; $\chi^2 = 4.99$, $df = 8$, for south roadfills; $\chi^2 = 12.48$, $df = 8$, for north roadcuts; and $\chi^2 = 9.23$, $df = 10$, for south roadcuts; $p > 0.05$ in all cases). Pooled observed frequencies of anemochorous species were in all cases significantly higher than the corresponding pooled expected frequencies in the surrounding areas, whereas the opposite trend was observed for the "other" dispersal category (Table 2). These results indicated that the proportion of anemochores was significantly higher in the road slopes than expected under the null hypothesis, whereas the combined proportion of barochores, autochores, zoochores, ballistics, and myrmecochores were significantly lower than expected regardless of the slope type and aspect. The average percentages of anemochores in the road slopes and surrounding vegetation were, respectively, 45.2 ± 5.3 and 33.2 ± 3.7% for north-facing roadfills, 39.7 ± 6.1 and 31.7 ± 2.3% for south-facing roadfills, 43.0 ± 10.7 and 34.1 ± 3.4% for north-facing roadcuts, and 37.3 ± 8.1 and 31.5 ± 3.0 for south-facing roadcuts.

Discussion

In road-fragmented landscapes, where spontaneous colonization relies almost entirely on vegetation in close proximity to the slopes, seed dispersal from surrounding areas is a major contributor to plant colonization and a major factor determining species composition on road slopes, regardless of slope type and aspect. Ninety percent of species found on road slopes after an 8-year colonization period originated primarily from the immediate vicinity, whereas a small proportion of species occurring on road slopes (10%) were not recorded in the surrounding flora. The latter group might be absent from the surrounding species list due to survey methodological limitations. Alternatively, these species might have been introduced by human dispersal mechanisms via machinery during road building (Schmidt 1989) or might have migrated along the road slopes (Tikka et al. 2001). However, according to van Dorp et al. (1997), migration rates of species along narrow and unproductive linear landscape elements, such as road slopes, should be low. The percentage of species able to disperse from the surrounding flora adjacent to road slopes (i.e., 60%, mainly ruderal) was similar to that obtained by Tikka et al. (2000) for road and railway edges within natural grasslands but much higher than that reported by Butaye et al. (2002) for forest species of an agricultural landscape.

Wind-dispersed species were over-represented in the flora of the road slopes, as predicted. Anemochores, as well as long-distance dispersed zoochorous species, have been identified as quick colonizers of new sites in a wide range of habitats (Hardt & Forman 1989; Dzwonko 1993; Burke & Grime 1996; Campbell et al. 2003). However, along roadways, zoochorous species are unlikely to be quick colonizers because the environmental conditions and security requirements of motorway environments (e.g., absence of trees and perching places for birds; presence of wire fencings, service roads, and traffic noise) make road slopes inhospitable for breeding birds and other kind of animals (Cuperus et al. 1996; Verdú & García-Fayos 1996). After an 8-year colonization period, short-distance dispersed species, such as barochores, autochores, and ballistics, had fewer opportunities to reach the slopes from adjacent surrounding areas. van Dorp et al. (1997) and Kirkman et al. (2004) indicated that species with short-range seed dispersal are unlikely to recolonize restored ecosystems and are therefore particularly vulnerable to habitat fragmentation. However, the probability of short-distance seed dispersal species colonizing slopes should increase with time.

Despite the relatively high and consistent immigration rates of species from the surrounding areas to the road

Table 2. Results of the chi-square analysis comparing the distribution of dispersal mechanisms of species on road slopes and in adjacent surrounding vegetation.

	Dispersal Category					
	Anemochorous		*Other*			
Slope Type	*Observed*	*Expected*	*Observed*	*Expected*	χ^2	p
All road slopes	571.00	460.22	834.00	944.78	39.30	<0.05
Rf N	136.00	103.20	168.00	200.80	15.31	<0.05
Rf S	167.00	136.63	266.00	296.37	9.54	<0.05
Rc N	122.00	97.18	159.00	183.82	9.31	<0.05
Rc S	146.00	123.22	241.00	263.78	5.91	<0.05

The observed and expected values correspond to the pooled frequencies of a specific group of road slopes (see Materials and Methods section). Rf, roadfill; Rc, roadcut; N, north-facing; S, south-facing; χ^2, chi-square value; p, significance level.

slopes in this study and the similarity in the number of species per square meter regardless of type and aspect recorded by Bochet and García-Fayos (2004) in the same slopes, these areas have relatively low vegetative cover. Cover values were 78 and 44% on north and south roadfills and 10 and 5% on north and south roadcuts, respectively. If hydroseeded species were not included, these values would be even lower because these species make up over 50% of the vegetative cover on all road slopes. This seems to indicate that, once a seed has reached the slope, other ecological filters control the next steps of the colonization process.

One potential limiting factor to vegetative establishment on steep slopes could be the removal of seeds or uprooting of plants by severe run-off (Cerdà et al. 2002). Bochet and García-Fayos (2004) observed that roadcuts suffered higher rates of soil erosion than did roadfills. However, this is unlikely to be important in the arid conditions of this study area. Cerdà and García-Fayos (1997) demonstrated that seed losses by run-off were lower than 10% on semiarid badland slopes and could not fully explain the lack of vegetation (García-Fayos et al. 1995). In addition, Alborch et al. (2003) did not find any significant differences in soil seed densities between roadcuts and roadfills in the studied road slopes, thus supporting the conclusion that neither seed dispersal nor seed losses by run-off and soil erosion could explain the differences in vegetation development and composition in road slopes.

Tormo et al. (2006) showed by experimental sowing on road slopes of the same study area that the soil conditions of road slopes were the most limiting factor to plant colonization after seed had reached the slope. This result is consistent with low soil fertility found on the study road slopes (Bochet & García-Fayos 2004); total nitrogen (0.072 ± 0.003%) and organic matter contents (1.1 ± 0.3%) of road slopes were up to three and six times lower, respectively, than in the surrounding areas.

The importance of soil conditions to vegetative establishment is further supported by gradients in vegetative cover seen on different aspects and types of road slopes. Vegetative cover decreases in a gradient from north roadfill to south roadfill to north roadcut and to south roadcut slopes suggest that ecological constraints increase in the same order. Bochet and García-Fayos (2004) attributed differences in plant colonization success on both types of slope to the better general soil conditions of roadfills with respect to roadcuts. Among the soil properties studied, they found differences in total nitrogen (0.074 ± 0.003 and <0.070 ± 0%, respectively), soil organic matter (1.3 ± 0.2 and 0.8 ± 0%, respectively), available phosphorus (2.5 ± 1.5 and 0.5 ± 0.1 mg P_2O_5/100 g soil, respectively), and soil moisture content at wilting point (0.136 ± 0.008 and 0.170 ± 0.004 cm^3 water/cm^3 soil, respectively, for roadfills and roadcuts), indicating higher water-holding capacity in roadfills than in roadcuts. However, the largest differences observed between the different types of slopes were the hydrological properties of the soil, specifically the number of days of water availability for plants. There were less than 15 days of water available for plants in roadcuts, regardless of aspect, and in south-facing roadfills; however, north-facing roadfills and surrounding areas of road slopes continued to have water available for more than 7 months (Bochet & García-Fayos 2004). Differences in water availability during seedling establishment explained the very low success of plant colonization and the differential ability of plant species to establish in badland slopes of climatically similar areas (García-Fayos et al. 2000). We hypothesize, therefore, that duration of water availability for plants during establishment is a limiting factor for seed establishment on road slopes. In order to confirm this hypothesis, further studies on seed germination ecology of colonizing species are needed in water-stressed conditions.

Our results have relevant implications for the restoration of road slopes. They suggest that in road slope areas where abiotic conditions are favorable and the probability of high-erosive rainfalls is low, reclamation strategies might rely completely on spontaneous processes (colonization and natural succession) such as is used in other types of disturbed environments (Khater et al. 2003; Novák & Prach 2003). This can be achieved by maintaining natural vegetation belts (a minimum of 20 m wide) along the edges of the slopes that act as seed reservoirs. The probability of seed arrival to these slopes increases with the proportion of anemochorous plants in those vegetation belts.

However, in sites in which abiotic conditions are adverse, such as our semiarid road slopes, the arrival of seeds is not a guarantee of successful establishment, high vegetative cover or erosion control (Tormo et al. 2006). In such areas, a mixed reclamation strategy based on the combination of spontaneous processes (dispersal from neighboring vegetation) and soil amendment is needed to ensure colonization and accelerate spontaneous succession. Depending on the degree of soil degradation, soil could be amended either by applying fertilizers without additional seeding (Elmarsdottir et al. 2003) or by adding topsoil usually rich in organic matter and local seeds (Tormo et al. 2007, this issue).

In conclusion, even in semiarid environments, reclamation methods using the dispersal, germination, establishment, and expansion capacities of native species adapted to the local environmental conditions provide promising alternatives to hydroseeding with commercial, but nonlocally adapted, species. Currently such alternatives to hydroseeding are rarely considered to revegetate road slopes in semiarid environments, despite their important advantages. These alternative reclamation strategies are inexpensive, use native colonizers well adapted to the local environmental conditions, and produce resultant vegetation that normally reaches a higher diversity and natural value than that found in hydroseeded areas (Prach 2003).

Implications for Practice

- Spontaneous colonization from adjacent vegetated areas is a suitable tool for road slope restoration.
- Natural vegetation should be preserved along the edge of road slopes to serve as a seed reservoir for spontaneous colonization; this vegetated area should be a minimum of 20 m wide.
- The higher the proportion of anemochorous plants in the adjacent surrounding vegetation, the higher the probability of successful seed dispersal to road slopes.
- The success of spontaneous colonization in road slope restoration will depend, however, on the local site conditions: if the abiotic conditions are favorable and the probability of high-erosive rainfalls is low, successful reclamation strategies could rely completely on spontaneous processes (colonization and further succession) and if the abiotic conditions are unfavorable, as in semiarid regions, the successful establishment of seeds is not guaranteed to produce high vegetative cover and erosion control. In this case, a mixed reclamation strategy is preferable, relying on the spontaneous processes of seed dispersal from adjacent vegetated areas and improvement of soil conditions, either by fertilizer application without any additional seeding or by addition of topsoil (Tormo et al. 2007, this issue).

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