RESEARCH ARTICLE

Colonization of woodland species during restoration: seed or safe site limitation?

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A strategy of assisted natural regeneration uses selective restoration interventions to remove potential barriers to passive natural regeneration and succession toward target ecosystems. In woodland restoration, this may involve the planting of woodland clusters that serve as seed sources for further colonization and/or site amelioration to enhance colonization and growth of the target species. We tested the importance of seed and safe site limitations for the colonization of birch and willows in experimental treatments representing a matrix of revegetation (+/−) and planted birch and willow clusters (+/−) on an eroded area in South Iceland. The revegetation was initiated in the fall of 1999 and clusters of birch and willows planted in 2002. Density of birch and willow seedlings and their distribution among microsites was surveyed in 2005, 2006, 2010, and 2015. Willow seedlings were first noted in 2006 but birch seedlings in 2010. In 2015, seedling density in revegetated plots with planted clusters was over 20 times greater than that of revegetated plots without clusters, indicating a strong seed limitation. No seedlings were found in plots that had not been revegetated, showing very strong microsite limitation. However, revegetation increased the cover of biological soil crust and other microsites favorable for seedling establishment. The results demonstrate that both seed and safe site limit the colonization of birch and willows, key species in woodland restoration, and highlight the importance of identifying barriers to spontaneous succession before selecting restoration strategies.

Key words: biological soil crust, Iceland, large-scale restoration, microsite limitation, revegetation, seed limitation, seedling establishment

Implications for Practice

- Effective restoration strategies should be designed to overcome actual limits to the establishment of desired species; hence, assessment of site-specific limitations to seedling establishment should be used to select restoration interventions.
- Spontaneous colonization of woodland species on barren substrates can be both seed and microsite limited.
- Revegetation of unstable barren areas can overcome microsite limitation by improving soil stability and creating favorable microsites for seedling establishment.
- Planting of "woodland islets" that serve as seed sources and overcome seed limitation can be an efficient strategy for large-scale woodland restoration. This strategy will, however, only work if microsites suitable for seedling establishment of target species are available.

Introduction

Woodland restoration has traditionally relied on the contrasting approaches of passive natural regeneration and high-density planting or seeding of desired tree species (e.g. Shono et al. 2007; Benayas et al. 2008). Both approaches can lead to the restoration of functional and diverse ecosystems but they have several shortcomings: natural regeneration has an uncertain outcome and is often slow (Whisenant 1999; Benayas et al. 2008) while high-density tree plantings are costly in terms of labor and capital (Shono et al. 2007; Corbin & Holl 2012). High-density tree plantings may therefore be unfeasible in extensive landscape-scale restoration. A strategy of assisted natural regeneration combines both approaches by using selective restoration interventions to remove potential barriers to passive natural regeneration and spontaneous succession toward target ecosystems (Whisenant 1999; Shono et al. 2007; Chazdon 2008). In woodland restoration, this may involve the planting of woodland islets or clusters that serve as seed sources for further colonization (e.g. Robinson & Handel 2000; Aradottir & Eysteinsson 2005; Benayas et al. 2008; Corbin & Holl 2012), sometimes in combination with site amelioration to enhance growth and promote future colonization of the target species (Shono et al. 2007). Given that the abundance of most plant populations is limited by the availability of seed and microsites suitable for seedling establishment (e.g. Eriksson & Ehrlén 1992; Duncan et al. 2009; Garcia-Meza & Martorell

June 2018 *Restoration Ecology* Vol. 26, No. S2, pp. S73–S83

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2016), considerations of seed and microsite limitations are of key importance in the application of this strategy. Although several studies have assessed the effectiveness of woodland islets or applied nucleation (Zahawi & Augspurger 2006; Holl et al. 2011; Benayas et al. 2015; Corbin et al. 2016), we are not aware of any studies that have addressed the potential role of microsite limitation in the subsequent woodland establishment.

Growing awareness of extensive deforestation and land degradation has prompted a call for large-scale forest and woodland restoration in many parts of the world driven by a number of international and national policies (e.g. Suding et al. 2015; Chazdon et al. 2017; Mansourian et al. 2017). Iceland has experienced widespread ecosystem degradation and desertification since Norse settlement in the ninth century (Dugmore et al. 2009; Arnalds 2015), due to deforestation and intense utilization of its subarctic and boreal ecosystems interacting with volcanism and periods of cold climate (Amorosi et al. 1997; Gisladottir et al. 2010; Sigurmundsson et al. 2014). This has resulted in extensive degraded areas and deserts with poor soils, low biodiversity, limited ecosystem function, and unstable surfaces with active erosion (Arnalds 2015). Native birch woodlands, estimated to cover about one-fourth of Iceland at the time of settlement, were nearly decimated by the early twentieth century and now cover only 1,500 km^2 or about 1.5% of the country (Snorrason et al. 2016). Protection of the remaining native woodlands and restoration of woodland ecosystems on degraded landscapes are important conservation goals in Iceland (Aradottir & Eysteinsson 2005). The extent of the birch woodlands has been increasing slightly during the past few decades through natural regeneration brought about by changes in land use (Snorrason et al. 2016), but active restoration is also needed to reach the current restoration goals (Aradottir & Eysteinsson 2005).

A large-scale restoration project, Hekluskogar (Hekla woodlands), aiming at restoring 600 km^2 of native woodland and shrubland in the vicinity of the Hekla volcano, was initiated in South Iceland in 2006. Its goal was to increase resilience of local ecosystems to disturbance by tephra fall from eruptions of the Hekla volcano and reduce potential damage due to secondary dispersal of tephra by wind. A substantial proportion of the project's area is severely degraded and characterized with low (<33%, often <5%) vegetation cover and very active soil erosion (Aradottir 2007). Historical records indicate, however, that much of the area was covered with dense woodlands up until the seventeenth and eighteenth centuries (Sigurmundsson et al. 2014). Restoration approaches in the Hekla woodlands include both high-density planting and natural regeneration from remnant stands, but the main strategy is to plant woodland clusters that can serve as seed sources for further colonization, in combination with revegetation to stabilize the soil surface and reduce soil erosion where needed (Aradottir 2007). *Betula pubescens* (downy birch), the only native tree species that forms woodland in Iceland, plays a key role in the establishment of Hekluskogar. Native willows, especially *Salix lanata* (woolly willow) and *Salix phylicifolia* (tea-leaved willow), are also important; they form a shrub layer in the birch woodlands and can form a continuous shrub cover under various conditions, including

highland areas above the birch woodlands. An understanding of limitations to natural regeneration of native birch and willows in the Hekluskogar area and the efficiency of restoration interventions in overcoming these limitations is important for the design and implementation of woodland restoration of these and other severely degraded landscapes.

The objective of our study was to assess the importance of seed and safe site limitation for recruitment of key woodland species in a large-scale restoration experiment on an eroded area in South Iceland. We assessed seedling densities of birch and willows in restoration treatments representing a matrix of revegetation (+/−) and planted birch and willow clusters (+/−) to test the following hypotheses regarding natural recruitment of birch and willows on eroded areas: (1) colonization of native birch and willows on eroded areas is limited by the availability of both seed and microsites suitable for seedling establishment (safe sites); (2) revegetation of eroded areas can overcome the barrier of microsite limitation by increasing availability of safe sites; and (3) planting of birch and willow clusters (woodland islets) can overcome the barrier of seed limitation by providing local seed sources.

Methods

Site Description

The study was carried out at Geitasandur, a sandy desert in South Iceland (63°29′N, 20°13′W, elevation 80–85 m above sea level). The area was sparsely vegetated, most likely as a result of desertification in medieval times (Hjartarson 1995) and the soil surface was unstable due to frost action and wind erosion. The soils are classified as Vitric Andosol, have a sandy loam in the A and Bw horizons, 0.2% organic carbon content in the top 10 cm, low water retention, and a gravelly surface that is maintained by frost heave of gravel during winter (Arnalds et al. 2013). There is a coarse tephra layer at greater than 35-cm depth in the soil, overlying an impermeable hardpan that affected the hydrology of the soil (B. Orradottir 2007, unpublished data). Furthermore, the research area receives substantial aeolian deposition from the surrounding deserts during dust storms (Arnalds et al. 2013). The area has been protected from livestock grazing since the 1990s.

The nearest weather station Hella, 8 km to the west of the site, has July and January temperatures of 11 and −2°C, respectively, and 1,260-mm annual precipitation (Icelandic Meteorological Office; 1971–2000 averages), but dry periods during the summer can last over 3 weeks (Arnalds et al. 2013). Furthermore, average soil temperatures in summer can be several degrees above air temperatures due to the dark color of the basalt parent materials.

A large-scale reclamation experiment with 40 treatment plots, 100 × 100 m or 1 ha each, was established at Geitasandur in fall 1999, in a matrix of a sandy desert with about 5% vegetation cover (Aradottir et al. 2008). The experiment comprised of nine different revegetation and afforestation treatments plus untreated controls, replicated in a randomized block design (see Arnalds et al. 2013 for details). The current study included

Figure 1. An aerial photograph of one 1 ha plot; revegetated with planted birch and willow clusters (treatment 3). The four birch clusters show up clearly but the two willow clusters are outlined with a yellow line. Approximate locations of the three 96-m-long belt transects are indicated by the white lines. The inset shows an overview of the experimental site (Photo SCSI/ABÞ).

four of the experimental treatments: (1) untreated controls, eroded land; (2) revegetation with grasses and fertilization; (3) revegetation (as in 2) with planted clusters of downy birch and willows (woolly willow and tea-leaved willow); and (4) planted clusters with birch, willows, and native legumes, but without revegetation (Table S1, Supporting Information).

The initial seeding of grasses and fertilization were applied in late fall 1999, and the fertilization was repeated in 2001, 2003, 2005, 2008, and 2012. The seeded grasses were *Festuca rubra* (red fescue) and *Poa pratensis* (smooth meadow grass), using seeding rates of 8.7 and 17.3 kg/ha, respectively. The fertilized plots received 50 kg N/ha and 27 kg P_2O_5/ha each time. Each plot in treatments 3 and 4 had four birch clusters and two willow clusters (Figs. 1 & S1). The birch clusters were circa 6×30 m and had about eighty 1-year-old birch seedlings planted into three evenly spaced contour strips, 15–20 cm deep (Fig. 2A). The willow clusters were about 8×25 m, and had 80 willow cuttings, 40 of each species, planted into four evenly spaced contour strips (Fig. 2B). The clusters extended from approximately SW to NE to take advantage of wind dispersal by dry easterly and southeasterly winds (cf. Aradottir et al. 1997 for details).

The willow cuttings were collected from old reclamation areas, less than 5 km from the experimental site. The same mixture of willow clones was used in all plots, representing several clones of either species and both female and male clones. The birch and willow clusters were planted in late May 2002 and dead individuals were replaced in the following year. Approximately five individuals of the native legumes, *Vicia cracca* (tufted vetch), *Vicia sepium* (bush vetch), *Lathyrus japonicus* (sea pea), and meadow *Lathyrus pratensis* (vetchling), were also planted into each cluster of treatment 4 in 2002. Their survival was, however, poor and they had negligible effect on the overall vegetation cover (Aradottir et al. 2008). Thus, treatment 4 does

not contain the revegetated matrix, but can otherwise be considered comparable with treatment 3 (Fig. 2C).

The experimental area covered nearly 300 ha (Arnalds et al. 2013), but a part of it had especially unstable soil surface where wind erosion caused rapid sand deposition on the plots from the barren areas between the plots. This sand deposition overshadowed the effects of revegetation on vegetation cover and surface properties; hence, plots from this part of the area were excluded from the study (see Arnalds et al. 2013 for details). Our study thus included only three replicate 1-ha plots for each treatment measured, or 12 plots in all.

Measurements

The colonization of birch and willows seedlings was recorded in August–September 2005 and 2006, September–October 2010, and August–September 2015 along three 1-m-wide transects laid perpendicular across each plot, from SE to NW. Transects in plots with planted clusters (Fig. 1) crossed either a pair of birch clusters (two transects) or a pair of willow clusters (one transect). Otherwise, the location of transects was random. No measurements were done within 2 m of plot edges in order to minimize edge effects; hence, all transects were 96 m long.

All birch and willow seedlings with true leaves encountered on each transect were recorded, along with their size class (I: 1–2 leaves; II: 3–4 leaves; and III: >4 leaves). Height and crown dimensions (maximum diameter and diameter at 90° angle to maximum) were measured for plants in size class III. Microsite type—the characteristics of the immediate surroundings of each seedling (Table 1)—was reported for all plants of size classes I and II. The cover of each microsite type was assessed by 25 regularly distributed point measurements in each of 10 quadrats of 0.5×0.5 m randomly located on each transect; that is, 30 quadrats per plot.

Table 1. Description of the microsite types used to characterize safe sites for seedling establishment on Geitasandur, South Iceland.

Microsite Type	Description
Soil	Mineral soil
Sand	Loose sand, mostly <0.2 cm in diameter
Gravel	Gravel 0.2–2 cm in diameter
Pebbles	Rocks 2–5 cm in diameter
Rocks	Rocks >5 cm in diameter
Biocrust	Biological soil crust dominated with liverworts (especially *Anthelia* spp.)
Moss <1 cm	Bryophyte layer, <1 cm thick
Moss 1–2 cm	Bryophyte layer, 1–2 cm thick
Moss >2 cm	Bryophyte layer, >2 cm thick
Lichens	All lichens
Grasses	All grasses
Sedges and rushes	All sedges and rushes (mostly *Luzula* spp.)
Forbs	All forbs
Dwarf shrubs	All dwarf shrubs

Figure 2. (A) Planted birch cluster in revegetated plot (treatment 3). (B) Planted willow cluster in revegetated plot (treatment 3). (C) Planted willow cluster in plot without revegetation (treatment 4).

Data Analysis

The continuous data of seedling density, seedling size, and microsite cover were averaged over the three transects within each plot before calculating the mean and standard error for each treatment. Crown area of seedlings was calculated from the diameter measurements, assuming elliptical shape. As birch seedlings were only found in treatment 3 (revegetated with planted clusters), but willow seedlings were also found in treatment 2 (revegetated without planted clusters); seedling size was analyzed by two separate analysis: (1) a two-way analysis of variance (ANOVA) of the effects of block and species on height and crown area in treatment 3 and (2) a three-way ANOVA assessing the effects of block, treatment, and species on the crown area of woolly willow and tea-leaved willow. The crown area data were log-transformed to ensure the stability of variance and normal distribution of residuals and the results back-transformed before presentation. The effect of block, revegetation, and planted clusters on microsite cover was analyzed with a three-way, factorial ANOVA.

Due to high frequency of plots with no seedlings, it was not possible to compare seedling density among treatments by conventional parametric methods. Instead, we tested whether the seedling numbers per treatment deviated significantly from a random distribution, using a simple goodness-of-fit, chi-square analysis for each species and year.

Chi-square goodness-of-fit statistics was also used to determine if the observed number of birch and willow seedlings in each microsite type 2010 and 2015 showed a departure from a random occurrence among microsite types (cf. Elmarsdottir et al. 2003 for details). The analysis was carried out separately for species and for plots with and without planted clusters to account for the effect of seed source. The expected number of seedlings was calculated as the total number of seedlings in the relevant category multiplied by the proportional cover of each microsite type within that group. Where necessary, data for microsite types with low expected seedling numbers were combined for analysis to ensure that no more than 20% of microsite types had an expected number less than five. As the seedling data were based on transects within plots (cluster sampling), the analysis might fail to meet the assumption of independent distribution, which would increase type I error rates (Garson & Moser 1995). Thus, we used a 99% significance

Table 2. Seedling density (mean ± 1 SE) in the experimental plots on Geitasandur, South Iceland in 2005–2015.

		Untreated Plots		*Revegetated Plots*	
		birch	*willows*	*birch*	*willows*
	Year	*seedlings/m²*		*seedlings/m²*	
No planted clusters	2005	0	0	0	0
	2006	0	0	0	
	2010	0	0	0	0.034 ± 0.018
	2015	0	0	0	0.27 ± 0.13
Planted birch and willow clusters	2005	0	0	0	0
	2006	0	0	0	0.030 ± 0.019
	2010	0	0	0.013 ± 0.007	0.13 ± 0.05
	2015	0	0.002 ± 0.002	5.62 ± 0.14	3.23 ± 1.95

level and a conservative test statistic, that is, the deviation for each microsite type had to be equal to or greater than the critical chi-square value for the full analysis for each category at a significance level of $p \leq 0.01$.

The chi-square analysis was done in Excel, but SAS Enterprise Guide, version 6.1 (SAS Institute Inc., Cary NC, U.S.A.) was used for the factorial ANOVA.

Results

No seedlings were found on transects in the experimental plots in 2005, 26 seedlings in 2006, 152 seedlings in 2010, and 7,862 seedlings in 2015 (Table 2). All the seedlings recorded in 2006 and over 90% of the seedlings recorded in 2010 were willows, but in 2015, nearly two-thirds of the seedlings were birch. The seedling density was greatest in treatment 3, revegetated plots with planted clusters (Table 2). Only willow seedlings were found in treatment 2, revegetated plots without planted clusters; they were first found in 2010 and their density was more than an order of magnitude lower than in comparable plots with planted clusters in 2015. No seedlings were recorded in untreated plots (treatments 1 and 4), except for two willow seedlings that were found in untreated plots with planted clusters in 2015 (treatment 4). Chi-square analysis showed that distribution of seedlings among treatments deviated significantly from random for willows in all years and birch in 2015 ($p < 0.001$; $df = 3$ in all cases), but there were too few birch seedlings in 2010 for statistical testing.

Almost two-thirds of the birch seedlings recorded in 2015 were in size class II (3–4 leaves; Fig. 3). The proportion of seedlings in size class III was much higher in willows than birch, especially in treatment 2, revegetated plots without planted clusters (Fig. 3).

Birch seedlings were generally smaller than willow seedlings (Table 3), although the differences among the three species within treatment 3 were only significant for crown area ($p > 0.006$). Comparison of willow seedlings in treatments 2 and 3 showed that seedlings in treatment 2 were significantly taller ($p = 0.018$) and had significantly greater crown area ($p = 0.015$) than seedlings in treatment 3, but the effects of species on height or crown area and the interaction between
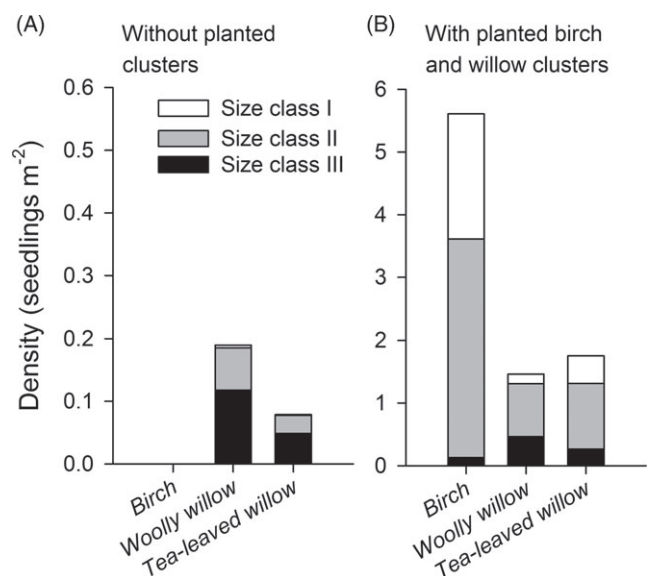
Figure 3. Average density of seedlings 2015 in size classes I–III in revegetated plots with and without planted birch and willow clusters. Note that the scale of the *y*-axis is an order of magnitude higher in the right graph.

treatment and species were always nonsignificant ($p > 0.05$). The effect of block was not significant ($p > 0.05$) in any of the analyses.

In 2015, barren microsites were more abundant in untreated than revegetated plots and this difference was significant for gravel, pebble, and rock microsites (Fig. 4; Table S2). Revegetation had a significant positive effect ($p < 0.05$) on the cover of all vegetated microsites except greater than 2-cm-thick moss; the most common microsites being dwarf shrubs, biocrust, mosses, and grasses. The presence of planted birch or willow clusters did not have a significant effect on the cover of any microsite, vegetated or barren. A slightly significant interaction between revegetation and planted clusters for the biocrust microsite ($p = 0.046$; see Table S1) reflects higher cover of biocrust in revegetated plots with clusters than without clusters (0.20 vs. 0.10, respectively) and lower cover in untreated plots with clusters than without them (0.00 vs. 0.03, respectively). Dwarf

Table 3. Height and crown area (mean ± 1 SE and maximum) of birch and willow seedlings in size class III in experimental plots on Geitasandur, South Iceland in 2015.

Treatment	Species	Height (cm)		Crown Area (cm^2)	
		mean	*max*	*mean*	*max*
Revegetated	*woolly willow*	5.5 ± 0.9	25	436 ± 1.6	4,420
	tea-leaved willow	8.1 ± 0.7	30	1,097 ± 1.1	7,857
Revegetated with planted birch and willow clusters	*birch*	2.9 ± 0.2	34	10 ± 1.1	240
	woolly willow	3.6 ± 0.4	32	128 ± 1.9	8,643
	tea-leaved willow	4.2 ± 1.4	30	187 ± 1.6	3,800

shrubs, biocrust, mosses, and grasses were the most common vegetated microsites in revegetated plots, but cover of mosses and biocrust was low in the untreated plots.

A goodness-of-fit analysis for distribution of seedlings in relation to microsite types showed that generally fewer seedlings were found in barren microsite types (soil, sand, gravel, pebbles, and rocks) than expected from random distribution and more seedlings were found in biocrust and thin mosses than expected from random distribution (Table 4). The distribution of seedlings found in treatments with planted clusters (treatments 3 and 4) in 2015 gave the most detailed information about the colonization potential of different microsites, because of the high number of seedlings recorded. For both birch and willows, the observed number of seedlings in biocrust and less than 1-cm-thick moss was over 270% of the expected number of seedlings in these microsite types, and the observed number of seedlings in the barren microsites was from 0 to 58% of the expected numbers. There were, however, some differences between species: more birch seedlings were found in grass microsites than expected from random distribution (180%), but the opposite applied to willow seedlings (38%). There were also significantly more birch seedlings in 1- to 2-cm-thick moss microsites than expected (363%), while the distribution of willow seedlings in 1- to 2-cm-thick moss microsites did not deviate significantly from random. Birch seedlings were negatively associated with forb microsites (3% of expected) while the relationship for willow seedlings was not significant. On the other hand, willow seedlings were positively associated with dwarf-shrub microsites (252% of expected), while the relationship for birch seedlings was not significant (Table 4).

Discussion

The absence of birch and willow seedling establishment in untreated plots (no revegetation) and very limited seedling establishment in treatments without planted clusters clearly demonstrates both microsite and seed limitation to population growth of birch and willows. This agrees with a number of studies from diverse habitats (e.g. Clark et al. 2007), including temperate heathland (Manning et al. 2005), temperate forest (Eriksson & Ehrlén 1992), tallgrass prairie (Long et al. 2014), and semiarid grassland (Fick et al. 2016; Garcia-Meza & Martorell 2016). In our study, restoration interventions consisting

of revegetation and planting clusters of birch and willows facilitated birch and willow colonization by overcoming these limitations.

Colonization in Different Microsites

Barren microsites (sand, soil, gravel, pebbles, and rocks) were unfavorable for birch and willow colonization. The barren microsites were dominant in untreated plots, which are characteristic of sandy eroded areas in Iceland. Positive association of seedlings with physical microsites, such as the presence of rocks or pebbles, has been reported in early succession (e.g. Elmarsdottir et al. 2003; Jones & del Moral 2005), but this did not apply in our study. Revegetation greatly increased the cover of vegetated microsites, including a number of microsite types that were favorable for seedling establishment. Biocrust and thin moss microsites (<1 cm) were favorable for both birch and willows, 1- to 2-cm-thick mosses were only favorable for birch, and thick mosses (>2 cm) were unfavorable for both. The species responded differently to other microsite types; grass microsites were favorable for birch and unfavorable for willows, whereas dwarf shrub microsites were only favorable for willows and forb microsites were unfavorable for birch.

The relatively low seedling densities in barren microsites and high seedling densities in biocrust and thin moss microsites agree with earlier colonization studies of birch (Aradóttir 1991), willows (Svavarsdóttir 2006; Muller et al. 2011), and several other species (Elmarsdottir et al. 2003; Karlsdóttir & Aradóttir 2006). According to Colesie et al. (2016), both the microsite types designated as "biocrust" and "moss" in our study can be designated as biological soil crust or biocrust; the first was dominated by liverworts, especially *Anthelia* spp., and the latter was dominated by bryophytes (Fig. 5). Biocrusts can facilitate seedling establishment by enhancing seed entrapment, germination, seedling survival, and growth, but the effects are both species specific and depend on the type of crust (Zhang et al. 2016). At our study site, the moss microsites were mostly limited to the revegetated plots where the cover of thicker moss microsites (≥1 cm) increased between 2010 and 2015. All seedlings reported in the thick moss (>2 cm) belonged to size class II, which implies that their colonization took place while the moss was thinner. This is also supported by a higher proportion of size class II birch seedlings relative to size class I in intermediate (1–2 cm) moss (82%) than in thin (<1 cm) moss (60%). These results suggest that facilitation of birch
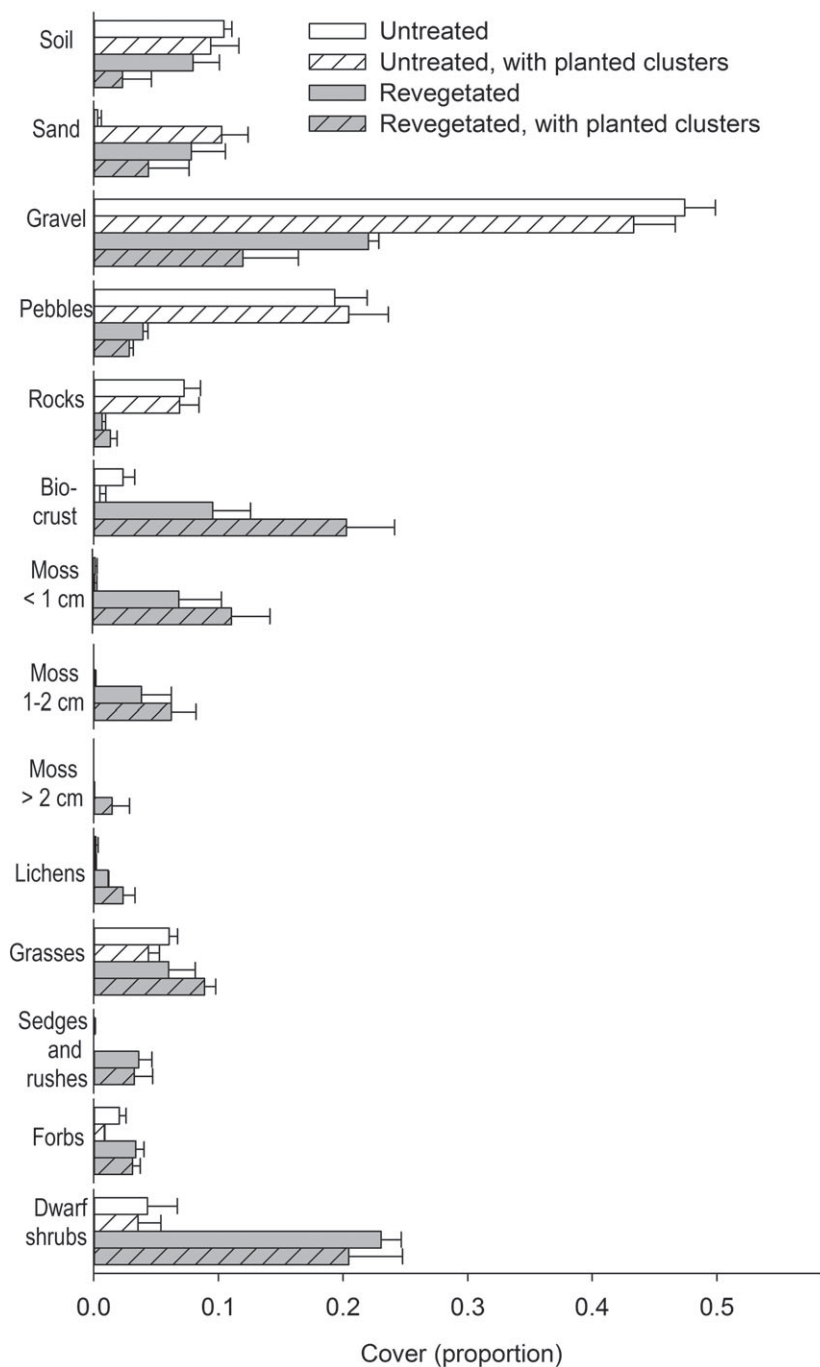
Figure 4. Cover (mean + 1 SE) of different microsite types in 2015 in plots that received different revegetation treatments ($n = 3$). The effect of revegetation treatment on microsite cover was significant ($p < 0.05$) for all microsites except soil, sand, thick moss (>2 cm thick), and grass, the effect of planted clusters was never significant, and the interaction between revegetation and clusters was only significant for the biocrust microsite (Table S2).

colonization by bryophyte biocrusts is limited to a relatively narrow "window of opportunity" while the bryophyte layer is still thin. The window may be even narrower for the willows, where only thin (>1 cm) moss microsites were favorable for colonization.

Grass microsites were favorable for birch colonization which was unexpected in light of earlier studies showing very low survival of birch seedlings in such microsites (Aradóttir 1991). Birch seeds have limited reserves and the seedlings can only survive for a few days under low light conditions (Grime & Jeffrey 1965) like those expected in a dense grass sward. The cover of grass microsites in our study was low and grasses did not form a continuous sward (see Gretarsdottir et al. 2004 for details). Thus, light conditions in grass microsites were

Table 4. Number of birch and willow seedlings in size classes I and II recorded in experimental plots at Geitasandur, South Iceland in 2010 and 2015, and results of chi-square goodness-of-fit analysis ($p \leq 0.01$) for occurrences of seedlings in microsite types. Microsite types with significantly more seedlings than expected from random distribution are indicated with "+" and microsite types with significantly fewer seedlings than expected from random distribution are indicated with "−"; microsite types where seedling number did not deviate significantly from random distribution are indicated with "ns"; empty cells indicate microsite types with low expected numbers of seedlings (generally <5); their data were combined in the "other" category.

Species	Plots Without Planted Clusters (Treatments 1 and 2)		Plots With Planted Birch and Willow Clusters (Treatments 3 and 4)		
	willows		*willows*		*birch*
Year	*2010*	*2015*	*2010*	*2015*	*2015*
No. seedlings	29	88	111	2,146	4,443
Microsite					
Soil		ns		−	−
Sand (<0.2 cm)	ns		−	−	ns
Gravel (0.2–2 cm)	ns	ns	−	−	−
Pebbles (2–5 cm)		ns	ns	−	−
Rocks (>5 cm)				−	−
Biocrust	+	ns	+	+	+
Mosses <1 cm		+		+	+
Mosses 1–2 cm				ns	+
Mosses >2 cm				ns	ns
Lichens				ns	ns
Grasses		ns	ns	−	+
Sedges and rushes				ns	ns
Forbs				ns	−
Dwarf shrubs		ns		+	ns
Other	ns	ns	ns		
df	3	7	5	13	13
χ^2	97	67	221	2,760	4,316

Figure 5. Birch colonization in thin moss microsite (bryophyte biocrust).

probably not impaired to the same degree as might be expected in a denser sward. This interaction does warrant further studies, as does the facilitation of willow establishment in dwarf shrub microsites and the inhibition of birch in forb microsites.

Colonization in Time and Space

Willow colonization was first observed in 2006, 4 years after the establishment of birch and willow clusters, but no birch seedlings were found at that time. Birch colonization had started by the next survey in 2010, but willows still encompassed over 90% of the recorded seedlings. In 2015, 13 years after the establishment of the clusters, the recorded density of birch in plots with clusters was 2-fold that of willow seedlings, while only willow seedlings were found in plots without clusters. These results demonstrate a strong seed limitation for both birch and willows, although it appeared to be stronger for the birch. The differences in the colonization patterns of birch and willows are probably a function of life history, seed dispersal mechanisms, and local abundance.

Both woolly and tea-leaved willows are prolific seed producers (Svavarsdóttir 2006). The willow plants in our study were established from fresh cuttings of both female and male plants, and we already observed some catkins on them within 2 years of the planting. This may explain how quickly willows started to colonize the plots with planted clusters. The birch seedlings observed in 2010 indicate that seed production started a few years earlier, which fits with onset of flowering and seed set in birch at the age of 5–10 years (Atkinson 1992). Increasing propagule pressure increases recruitment until microsite saturation is achieved (Long et al. 2014); thus, the high density of birch seedlings in 2015 implies a considerable local seed production in the preceding years. Density of birch seedlings in 2015 was twice that of willow seedlings, but as seedling density is generally highest near the clusters (A. L. Aradottir 2015, unpublished data), this may only reflect the fact that there were twice as many transects through birch as willow clusters.

The proportion of willow seedlings in size class II and especially in size class III was greater in plots without planted clusters than in plots with clusters. Willow plants in size class III were also both taller and had larger average crown area in the plots without clusters. This suggests episodic colonization caused by sporadic seed rain, either from the planted clusters or from the surrounding areas, as opposed to more steady colonization in plots with planted clusters.

Both the degree of disturbance of a restoration site and the degree of disturbance of its surrounding landscape affect its potential for recovery (Galatowitsch 2012). Our 300-ha study site was severely degraded at the beginning of the experiment (Arnalds et al. 2013) and had no local seed sources of birches and willows. Furthermore, the surrounding landscape matrix was highly modified with no remaining native birch stands within tens of kilometers from the study plots although some small planted birch stands were found 1–2 km away. The birch seed is a winged achene and birch has unimodal dispersal curves with log-linear decrease in seed rain with distance from the seed source (Matlack 1989; Sanz et al. 2011). Thus, primary dispersal is usually limited to a few meters or tens of meters depending on the source height and wind speed (Hughes & Fahey 1988; Sanz et al. 2011). Given the long distance to the nearest potential seed sources, we expect negligible background seed rain of birch. On the other hand, both willow species were found within a few 100 m of the experimental plots. The small willow seeds are attached to long plumes that can be lifted by even gentle breeze, allowing dispersal over long distances (Karrenberg et al. 2002). Thus, a low background seed rain of willows might be expected in the experimental plots, in addition to seed rain from the planted willows.

Implications for Large-Scale Restoration of Barren Areas

Our results show a stronger facilitation of woodland species colonization by planting potential seed sources in woodland islets than reported in earlier studies (Zahawi & Augspurger 2006; Holl et al. 2011; Benayas et al. 2015). Birch and willows are primarily wind dispersed and our results thus contrast with Corbin et al.'s (2016) suggestion that applying seed sources may be more important for tree species dispersed by animals than wind. Turnbull et al. (2000), however, propose that seed limitation may be strong in early successional habitats, which applies to our study site.

Our study clearly shows that planting seed sources only facilitated colonization where favorable microsites for seedling establishment were available. Planting of woodland clusters to overcome seed limitation is therefore a waste of resources in areas unfavorable for seedling establishment, unless they are accompanied with site amelioration to create safe sites. Our experimental site was a representative of extensive sandy deserts in Iceland that are the result of soil erosion (Arnalds 2015) and that are prevalent in the Hekluskogar area. They have very unstable surfaces due to intensive wind erosion, dust formation and cryoturbation, low nutrient content, and water holding capacity (Arnalds et al. 2013; Arnalds 2015). Lack of favorable microsites for seedling establishment in these eroded areas probably contributes to the long-term persistence of these degraded stages, comparable to mechanisms observed by Fick et al. (2016) in semiarid grasslands. Revegetation of such areas can stimulate succession toward heathland or birch shrubland if they manage to halt disturbances like erosion sand accretion, while adjacent untreated areas remain in the degraded stage (Gretarsdottir et al. 2004). The revegetation interventions helped to overcome physiochemical barriers to colonization, such as frost heaving, erosion, and limited nutrient availability and create favorable microsites for seedling establishment (Gretarsdottir et al. 2004). The ensuing succession, however, depends on the level of seed limitation and other potential biotic barriers.

Worldwide degradation of forests and woodlands has had serious consequences for biodiversity and ecosystem services, including soil protection and resilience following natural disasters (Foley et al. 2005). In Iceland, birch woodlands are more resilient than most other ecosystems toward tephra fall and secondary distribution of tephra, which are major components of volcanic impact and can cause extensive erosion (Arnalds 2013). The effects of tephra deposition generally extend over vast areas (Arnalds 2013) and restoration for resilience against tephra fall therefore calls for large-scale restoration. The present research is a part of a larger study aimed at improving current strategies used for restoring the resilience of ecosystems toward tephra fall and secondary distribution of tephra (Halldórsson et al. 2017). Our findings confirm the importance of selecting interventions that overcome barriers to spread of target woodland species, which in the case of Hekluskogar are revegetation where necessary to overcome microsite limitation and provide safe sites for seedling establishment, and planting of local seed sources where necessary to overcome seed limitation. Such site-specific selection of interventions is integral to efficient strategies needed for large-scale woodland restoration included in long-term natural disaster risk management in Iceland.

LITERATURE CITED

Amorosi T, Buckland P, Dugmore A, Ingimundarson JH, McGovern TH (1997) Raiding the landscape: human impact in the Scandinavian North Atlantic. Human Ecology 25:491–518

Aradóttir AL (1991) Population biology and stand development of birch (*Betula pubescens* Ehrh.) on disturbed sites in Iceland. PhD dissertation. Texas A&M University, College Station, Texas

Aradottir AL (2007) Restoration of birch and willow woodland on eroded areas. Pages 67–74. In: Halldorsson G, Oddsdottir ES, Eggertsson O (eds) Effects of afforestation on ecosystems, landscape and rural development. TemaNord 2007:508. Nordic Council of Ministers, Copenhagen, Denmark

Aradottir AL, Eysteinsson T (2005) Restoration of birch woodlands in Iceland. Pages 195–209. In: Stanturf JA, Madsen P (eds) Restoration of boreal and temperate forests. CRC Press, Boca Raton, Florida

Aradottir AL, Orradottir B, Arnalds O, Svavarsdottir K (2008) Ecological succession after reclamation treatments on an eroded area in Iceland. SER Europe Knowledge Base on Ecological Restoration. http://ser-koha.inbo.be/cgi-bin/koha/opac-detail.pl?biblionumber=897 (accessed 15 May 2017)

Aradottir AL, Robertson A, Moore E (1997) Circular statistical analysis of birch colonization and the directional growth response of birch and black cottonwood in south Iceland. Agricultural and Forest Meteorology 84:179–186

Arnalds O (2013) The influence of volcanic tephra (ash) on ecosystems. Advances in Agronomy 121:331–380

Arnalds O (2015) The soils of Iceland. Springer, Dordrecht, The Netherlands

Arnalds O, Orradottir B, Aradottir AL (2013) Carbon accumulation in Icelandic desert Andosols during early stages of restoration. Geoderma 193:172–179

Atkinson MD (1992) Biological flora of the British Isles. *Betula pendula* Roth (*B. verrucosa* Ehrh.) and *B. pubescens* Ehrh. Journal of Ecology 80:837–870

Benayas JMR, Bullock JM, Newton AC (2008) Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Frontiers in Ecology and the Environment 6:329–336

Benayas JMR, Martinez-Baroja L, Perez-Camacho L, Villar-Salvador P, Holl KD (2015) Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland. New Forests 46:841–853

Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320:1458–1460

Chazdon RL, Brancalion PHS, Lamb D, Laestadius L, Calmon M, Kumar C (2017) A policy-driven knowledge agenda for global forest and landscape restoration. Conservation Letters 10:125–132

Clark CJ, Poulsen JR, Levey DJ, Osenberg CW (2007) Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. American Naturalist 170:128–142

Colesie C, Felde VJMNL, Büdel B (2016) Composition and macrostructure of biological soil crusts. Pages 159–172. In: Weber B, Büdel B, Belnap J (eds) Biological soil crusts: an organizing principle in drylands. Springer International Publishing AG, Cham, Switzerland

Corbin JD, Holl KD (2012) Applied nucleation as a forest restoration strategy. Forest Ecology and Management 265:37–46

Corbin JD, Robinson GR, Hafkemeyer LM, Handel SN (2016) A long-term evaluation of applied nucleation as a strategy to facilitate forest restoration. Ecological Applications 26:104–114

Dugmore AJ, Gísladóttir G, Simpson IA, Newton A (2009) Conceptual models of 1,200 years of Icelandic soil erosion reconstructed using tephrochronology. Journal of the North Atlantic 2:1–18

Duncan RP, Diez JM, Sullivan JJ, Wangen S, Miller AL (2009) Safe sites, seed supply, and the recruitment function in plant populations. Ecology 90:2129–2138

Elmarsdottir A, Aradottir AL, Trlica MJ (2003) Microsite availability and establishment of native species on degraded and reclaimed sites. Journal of Applied Ecology 40:815–823

Eriksson O, Ehrlén J (1992) Seed and microsite limitation of recruitment in plant populations. Oecologia 91:360–364

Fick SE, Decker C, Duniway MC, Miller ME (2016) Small-scale barriers mitigate desertification processes and enhance plant recruitment in a degraded semiarid grassland. Ecosphere 7:e01354

Foley JA, Defries R, Asner GP, Barford C, Bonan G, Carpenter SR, et al. (2005) Global consequences of land use. Science 309:570–574

Galatowitsch SM (2012) Ecological restoration. Sinauer Associates, Inc., Sunderland, Massachusetts

Garcia-Meza D, Martorell C (2016) A trade off in the absolute magnitudes of seed and microsite limitations and their effects on population regulation. Oikos 125:308–314

Garson GI, Moser EB (1995) Aggregation and the Pearson chi-square statistic for homogeneous proportions and distributions in ecology. Ecology 76:2258–2269

Gisladottir G, Erlendsson E, Lal R, Bigham J (2010) Erosional effects on terrestrial resources over the last millennium in Reykjanes, southwest Iceland. Quaternary Research 73:20–32

Gretarsdottir J, Aradottir AL, Vandvik V, Heegaard E, Birks HJB (2004) Long-term effects of reclamation treatments on plant succession in Iceland. Restoration Ecology 12:268–278

Grime JP, Jeffrey DW (1965) Seedling establishment in vertical gradients of sunlight. Journal of Ecology 53:621–642

Halldórsson G, Ágústsdóttir AM, Aradóttir ÁL, Arnalds Ó, Hagen D, Óskarsson H, Mortensen LE, Pagneux E, Pilli-Sihvola K, Raulund-Rasmussen K, Svavarsdóttir K, Tolvanen A (2017) Ecosystem restoration for mitigation of the impacts of natural hazards. Technical Report TemaNord 2017:546. Nordic Council of Ministers, Copenhagen, Denmark. https://doi.org/10.6027/TN2017-546

Hjartarson A (1995) Á Hekluslóðum. Ferdafelag Íslands, Reykjavik, Iceland

Holl KD, Zahawi RA, Cole RJ, Ostertag R, Cordell S (2011) Planting seedlings in tree islands versus plantations as a large-scale tropical forest restoration strategy. Restoration Ecology 19:470–479

Hughes JW, Fahey TJ (1988) Seed dispersal and colonization in a disturbed northern hardwood forest. Bulletin of the Torrey Botanical Club 115:89–99

Jones CC, del Moral R (2005) Effects of microsite conditions on seedling establishment on the foreland of Coleman Glacier, Washington. Journal of Vegetation Science 16:293–300

Karlsdóttir L, Aradóttir ÁL (2006) Propagation of *Dryas octopetala* L. and *Alchemilla alpina* L. by direct seeding and planting of stem cuttings. Icelandic Agricultural Sciences 19:25–32

Karrenberg S, Edwards PJ, Kollmann J (2002) The life history of Salicaceae living in the active zone of floodplains. Freshwater Biology 47:733–748

Long Q, Foster BL, Kindscher K (2014) Seed and microsite limitations mediate stochastic recruitment in a low-diversity prairie restoration. Plant Ecology 215:1287–1298

Manning P, Putwain PD, Webb NR (2005) Formulating a general statistical model for *Betula* spp. invasion of lowland heath ecosystems. Journal of Applied Ecology 42:1031–1041

Mansourian S, Stanturf JA, Derkyi MAA, Engel VL (2017) Forest landscape restoration: increasing the positive impacts of forest restoration or simply the area under tree cover? Restoration Ecology 25:178–183

Matlack GR (1989) Secondary dispersal of seed across snow in *Betula lenta*, a gap-colonizing tree species. Journal of Ecology 77:853–869

Muller E, Cooper EJ, Alsos IG (2011) Germinability of arctic plants is high in perceived optimal conditions but low in the field. Botany-Botanique 89:337–348

Robinson GR, Handel SN (2000) Directing spatial patterns of recruitment during an experimental urban woodland reclamation. Ecological Applications 10:174–188

Sanz R, Pulido F, Camarero JJ (2011) Boreal trees in the Mediterranean: recruitment of downy birch (*Betula alba*) at its southern range limit. Annals of Forest Science 68:793–802

Shono K, Cadaweng EA, Durst PB (2007) Application of assisted natural regeneration to restore degraded tropical forestlands. Restoration Ecology 15:620–626

Sigurmundsson FS, Gisladottir G, Oskarsson H (2014) Decline of birch woodland cover in Þjórsardalur Iceland from 1587 to 1938. Human Ecology 42:577–590

Snorrason A, Traustason B, Kjartansson BÞ, Heiðarsson L, Ísleifsson R, Eggertsson Ó (2016) Náttúrulegt birki á Íslandi—Ný úttekt á útbreiðslu þess og ástandi [the natural birch woodland in Icelands—a new assessment of distribution and state]. Náttúrufræðingurinn 86:97–111

Suding K, Higgs E, Palmer M, Callicott JB, Anderson CB, Baker M, et al. (2015) Committing to ecological restoration. Science 348:638–640

Svavarsdóttir K (ed) (2006) Innlendar víðitegundir: líffræði og notkunar-möguleikar í landgræðslu. Landgræðsla ríkisins, Gunnarsholt, Iceland

Turnbull LA, Crawley MJ, Rees M (2000) Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225–238

Whisenant SG (1999) Repairing damaged wildlands. A process oriented, landscape-scale approach. Cambridge University Press, Cambridge, United Kingdom

Zahawi RA, Augspurger CK (2006) Tropical forest restoration: tree islands as recruitment foci in degraded lands of Honduras. Ecological Applications 16:464–478

Zhang Y, Aradottir AL, Serpe M, Boeken B (2016) Interactions of biological soil crusts with vascular plants. Pages 385–406. In: Weber B, Büdel B, Belnap J (eds) Biological soil crusts: an organizing principle in drylands. Springer International Publishing AG, Cham, Switzerland

Supporting Information

The following information may be found in the online version of this article:

Table S1. The treatments included in the study were established on sparsely vegetated eroded land.
Table S2. Results of factorial ANOVAs (F-values) comparing cover of microsites among treatments with and without revegetation (R) and planted birch and willow clusters (C) in 2015.
Figure S1. Overview of a part of the experimental area.
Figure S2. Control plot without revegetation or planted clusters.