

# Recovery of Alpine Plants after a Severe Human Disturbance in the Andes of Central Chile

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## Abstract

Disturbance is likely to affect multiple life stages and may be most critical in seedling germination and establishment through indirectly affecting soil properties. Following disturbance, plants establish from seeds that either exist on the site or that disperse onto the site. Here, we examined the effects of a 1-year-old severe human disturbance (approx. 1 ha) on alpine vegetation recovery in the Andes of central Chile (33°S, 60°W) at 2800 m a.s.l. during two growing seasons (2006–2007). Particularly, we assessed the effects of soil properties and seed rain on post-disturbance seedling emergence using two sets of denuded slopes of different exposure (south and northwest, respectively) and two appropriate control areas. The disturbed area on the south-facing slope was drier than its respective control, while the opposite was observed on the disturbed area on the northwest-facing slope. The differences in soil water content between both slopes coincided with the results of seedling recruiting. The south-facing slope, with a more humid undisturbed area, showed a greater number of emerging seedlings than the disturbed slope. Conversely, on the northwest-facing slope, the main recruiting of seedlings was observed on the disturbed area, while the undisturbed area showed practically no emergence of new individuals. In addition, our results indicate that seedling recruitment occurred from a persistent seed bank constituted mostly by species with long-lived and deeply viable seeds, though in this particular study, we could not corroborate it empirically. Although long-term studies are desirable to make more definitive conclusions, our results provide the first step to understanding the capacity for vegetation recovery after a severe human disturbance in the Andes of central Chile, where seed banks and soil moisture seem to play a pivotal role.

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## Introduction

Disturbance plays an important role in structuring plant communities. The type of disturbance (referred to here as the removal of plant cover), including its size, severity, frequency, and timing, determines the characteristics of the seedling environment and, consequently, influences the kind of species that establish after a disturbance (Grubb, 1977; White, 1979; Bazzaz, 1983; Pickett et al., 1987; Sarmiento et al., 2003).

In alpine habitats, disturbances can be caused by geomorphological processes such as landslides, road building, or mining activities, as well as be a result of cryogenic soil movement (Johnson and Billings, 1962), small mammal burrowing and tunneling (Thorn, 1982), and recreational activities. In some cases, removal of superficial soil horizons also removes seed banks (Brown et al., 1978), while in the other cases, soils are well developed and highly organic, and usually contain large seed pools (Chambers, 1993).

After disturbance, plant establishment can occur either from pre-existing banks of propagules (e.g., persistent seed bank) or from seeds or other propagules that disperse onto the site (migrants) (MacMahon, 1980; Urbanska et al., 1999). Initial establishment after disturbance is often dominated by short-lived species that produce great amounts of seeds capable of forming highly persistent seed banks or disperse long distances (Grubb,

1977; Grime, 1979; Pickett and McDonnell, 1989). For example, on severely disturbed alpine herb-fields in which surface soil and buried seed pools have been removed, initial colonization is carried out by grasses with high dispersal capacity (Chambers et al., 1984; Chambers, 1993). In contrast, in undisturbed sites, long-lived species establish and develop more slowly, and typically produce low numbers of relatively large, short-lived seeds, dominating the aboveground vegetation (Chambers, 1993). Thus, seed availability is an important factor driving differences in seedling emergence between disturbed and undisturbed areas.

In addition, soil characteristics after disturbances have also been suggested as important in explaining differences in vegetation recovery (Jolls and Bock, 1983; Chambers and MacMahon, 1994; Forbis et al., 2004). For example, it has been shown that soil moisture and temperature (Vitousek, 1985) vary with disturbance. Increased light and higher soil temperature on disturbed sites provided a more favorable environment for seed germination of some alpine species of the genus *Carex* (Chambers, 1995; Amen and Bonde, 1964; Haggas et al., 1987). However, high soil temperatures may have negative effects on seedling survival through increasing soil drought (Bliss, 1971; Bell and Bliss, 1980; Forbis, 2003). Therefore, higher soil temperatures on disturbed sites may generate more favorable conditions for seed germination but not necessarily for seedling survival. These issues confirm the need to include various stages of a plant life cycle in

regeneration studies (Harper, 1977). Indeed, while some studies support that disturbed sites are better for the establishment and growth of seedlings than non-disturbed sites (Chambers et al., 1990), other studies fails to support it (e.g., Welling and Laine, 2000), indicating that further research is needed to draw some general conclusions about the role of disturbances on vegetation dynamics in alpine habitats.

The aims of this study were to examine vegetation dynamics after a severe human disturbance in the Andes of central Chile, assessing the importance of some soil properties and seed rain on post-disturbance seedling recruitment. Specifically, we asked: (1) Do disturbed sites differ in soil moisture and temperature compared to non-disturbed sites? (2) Following disturbance, does plant establishment occur from seeds that disperse onto the site through seed rain? (3) Do disturbed sites have greater seedling recruitment than non-disturbed sites? (4) Is seedling recruitment of short-lived species favored by disturbance? To answer these questions, the relationships among aboveground vegetation, seed rain, seedling emergence, and soil properties were examined on two sets of denuded slopes and two control areas in the Andes of central Chile.

## Methods

### STUDY SITE

The study was conducted in the central Chilean Andes (33°S, 60°W) at 2800 m a.s.l. in the surroundings of the La Parva Ski complex located ca. 50 km east of Santiago within the subandean scrub vegetation belt (2000–2800) above the *Kageneckia angustifolia* (Rosaceae) treeline located at 2200 m.

The climate in the study area is alpine with a Mediterranean influence, characterized by 5 to 8 months of snow-free growing season that typically extends from mid-October to mid-May (di Castri and Hajek, 1976). Mean total annual precipitation at 2500 m elevation is ca. 445 mm, falling predominately as snow between May and September (Santibáñez and Uribe, 1993), when snowmelt begins. In contrast, summers are dry, with occasional rainstorms (<20 mm). The snowpack varies between years, but most times it averages 1 to 2 m deep. Mean monthly air temperature during the growing season ranges from 7 °C in April to 12 °C in February at 2600 m (Cavieres and Arroyo, 1999).

We selected two slopes (approx. 45°) of different exposure but similar area (ca. 3000 m<sup>2</sup> each). One of these slopes was south facing, while the other was northwest facing. Each of the selected slopes suffered a severe human disturbance during the 2004–2005 growing season when a dam was built, and a bulldozer completely removed organic soil and vegetation cover. These severely disturbed slopes are not common in the area, but their frequency is increasing due to human activities. In addition, within 100 m of our study area, there were other types of disturbances such as sky runways and minor roads. Upon each slope, a disturbed area and a relatively intact, undisturbed area were chosen. Both slopes were ca. 20 m from the dam. Vegetation is dominated by the cushion plant *Laretia acaulis* (Apiaceae) in south-facing slopes and by *Nassauvia axillaris* and *Chuquiraga oppositifolia* (Asteraceae) in northwest-facing slopes. Although these species were the most abundant, small annuals of the genus *Chaetanthera* and some perennials such as *Hypochaeris clarionoides* and *Senecio polygaloides* were also present.

### SOIL PROPERTIES

During the 2006 and 2007 growing seasons, soil moisture, and temperature were determined for each area.

### Soil Moisture

Soil moisture was determined through the gravimetric method, analyzing 10 soil samples of 10 cm depth and approx. 300 cm<sup>3</sup> for each of the study areas. We chose this soil depth because it corresponds with the rooting zone of most of the species at the seedling stage. Soil samples were taken from January to May 2006 and from November 2006 to March 2007. Each sample was weighed, placed in a drying oven at 75 °C for 72 h and then reweighed. A different battery of soil samples were taken and sent to the Laboratory of Soil Analyses, University of Concepción, where a soil water retention curve was obtained using a psychrometric system. Gravimetric content for each sample were then converted to soil water potential through the following soil water retention curves obtained by the Laboratory of Soil Analyses:  $y = 0.3722x + 19.50$  and  $y = 0.5153x + 20.11$  for the disturbed and non-disturbed areas of the south-facing slope and  $y = 0.3845x + 17.81$  and  $y = 0.3804 + 18.42$  for the disturbed and non-disturbed areas of the northwest-facing slope. Finally, we used a Repeated Measures Analysis of Variance to assess differences in soil water potential through time between disturbed and non-disturbed areas.

### Soil Temperature

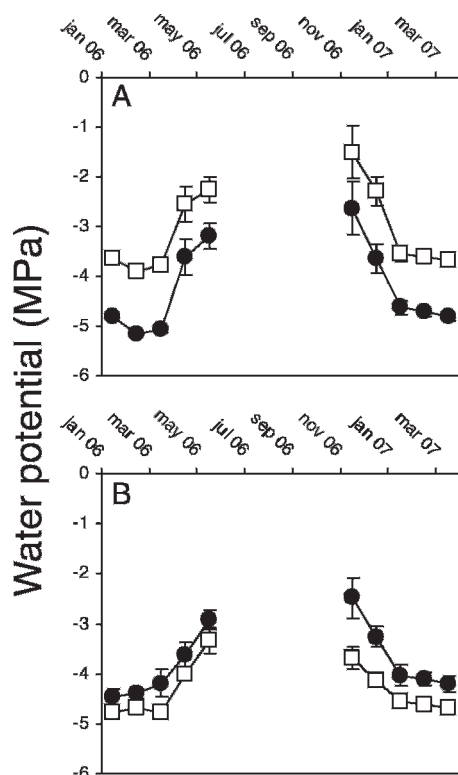
To asses differences in surface soil temperatures between disturbed and non-disturbed areas, soil temperatures were recorded during the entire growing season, starting on 23 December 2005 and ending on 21 March 2006 for the south-facing slope and 5 January 2007 to 31 March 2007 for the northwest-facing slope. At each slope, we used two four-channel mini-loggers (HOBO-H8; Onset Corp., Massachusetts, U.S.A.). One mini-logger was placed in the disturbed area while the other was placed in the control area. Temperature sensors were placed under bare soil between plants at 2 cm below soil surface and separated by at least 3 m from each other. We chose this soil depth to visualize the temperatures that emerging seedlings experienced in their first stages. Differences in soil temperatures between disturbed and undisturbed areas were assessed with paired sample *t*-tests.

### VEGETATION COVER

To determine vegetation cover, 15 quadrats (50 × 50 cm) per treatment separated by 5 m were placed on each disturbed and non-disturbed area. The minimum distance of quadrats from the disturbance edge was 20 m while the maximum was 40 m (these distances were also used for seed traps; see below). In each quadrat, we identified the species present and visually estimated the proportion of the quadrat area occupied by each species. These measurements were taken midway through the growing season (January 2006 and January 2007). Differences in vegetation cover between disturbed and non-disturbed areas were tested using two-way Analyses of Variance with site (disturbed and non-disturbed) and year (2006 and 2007) as factors. *A posteriori* Tukey's tests were used for comparisons among treatments.

### SEED RAIN

To quantify seed rain, 15 traps were randomly placed on each disturbed and non-disturbed area during the 2006 growing season. The traps were built using a plastic circle (10 cm diameter × 5 mm depth) buried into the ground. Above these plastic circles, a piece of paper was placed covered with tanglefoot (The Tangle Foot Company), an insoluble sticky paste efficient in trapping seeds which come in contact with it. This paper was replaced every 30



**FIGURE 1.** Water potential recorded through time in disturbed (black circles) and non-disturbed (white squares) areas of the south-facing slope (A) and the northwest-facing slope (B) in the surroundings of the La Parva Ski complex in the Andes of central Chile. Means are shown with 2 SE.

days during the 90 days of sampling between February and April, encompassing the full seed dispersal period. Recovered sticky papers were brought to the laboratory where the total number of seeds was counted with a binocular microscope, and a rate of number of seeds deposited per  $m^2$  per day was calculated. Seed identification was determined to the species level using a reference collection previously obtained in the field. Differences in seed rain between disturbed and non-disturbed sites were tested using Student *t*-tests prior to data transformation.

#### SEEDLING EMERGENCE AND SURVIVAL

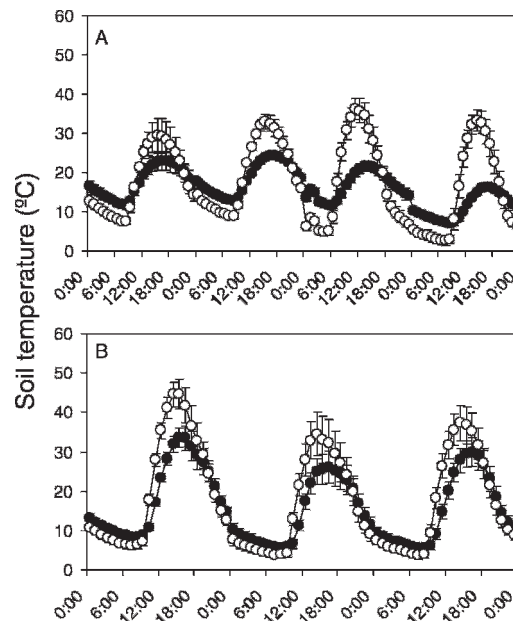
Seedling emergence and survival were monitored every two weeks for 112 days (1 November 2006–22 February 2007). In each area, we randomly placed eight quadrats ( $30 \times 22$  cm) subdivided into 12 cells ( $7.5 \times 7.5$  cm). Within each cell, we counted the number of seedlings. A newly emerged seedling from one that had been there from a previous census was determined by the presence of cotyledons and/or by the presence of the first pair of true leaves. A Repeated Measures Analysis of Variance was used to assess differences in seedling emergence (seedlings/ $m^2$ ) through time among disturbed and non-disturbed areas. Survival of seedlings of disturbed and non-disturbed areas was statistically compared with Log-Rank tests.

## Results

### SOIL PROPERTIES

#### Soil Moisture

In both slopes, disturbance had a significant effect on soil water potential (repeated measures ANOVA,  $F_{\text{south-facing}} =$



**FIGURE 2.** Daily cycles of average temperature in bare-ground disturbed (black circles) and non-disturbed (white circles) areas of south-facing slope (A) and northwest-facing slope (B) in the surroundings of the La Parva Ski complex in the Andes of central Chile during one entire growing season. Means are shown with 2 SE.

150.625,  $MS = 0.613$ ,  $P = 0.001$ ; and  $F_{\text{northwest-facing}} = 74.280$ ,  $MS = 0.134$ ,  $P < 0.001$ ). In the south-facing slope, water potential was lower at the disturbed area relative to the undisturbed area, while in the northwest-facing slope, the opposite was observed (Fig. 1). As expected, the south-facing slope had higher soil water potentials than the northwest-facing slope ( $-3.10 \pm 0.27$  MPa vs.  $-4.05 \pm 0.14$  MPa, respectively; mean  $\pm$  2 SE). Soil texture did not differ between disturbed and non-disturbed areas on either slope: ca. 70% of sand, lime (ca. 17%), and clay (ca. 13%).

#### Soil Temperature

For both slopes, surface soil temperature differed among disturbed and non-disturbed areas (paired *t*-tests,  $t = 9.359$ ,  $df = 2011$ ,  $P < 0.001$  and  $t = 15.244$ ,  $df = 2063$ ,  $P < 0.001$  for south-facing slope and northwest-facing slope, respectively). Soil temperature was similar between disturbed and non-disturbed areas during the night for both slopes, whereas soil temperatures of non-disturbed areas during the day were higher than those of disturbed areas (Fig. 2). In the south-facing slope, soil temperature in the undisturbed area ranged in average between 2.7 and 36.2 °C, and soil temperature of the disturbed area never exceeded 25 °C (Fig. 2a). For the northwest-facing slope, soil temperature of the non-disturbed area ranged in average between 3.85 and 44.6 °C, while soil temperature of the disturbed area reached a maximum of 33.6 °C (Fig. 2b). Thus, there was a wider variation of bare-ground temperature in undisturbed areas than in disturbed areas.

### VEGETATION COVER

We detected a significant effect of disturbance and year on vegetation cover in both slopes (ANOVA,  $F_{\text{disturbance}} = 31.984$ ,  $df = 1, 56$ ,  $P = 0.001$  and  $F_{\text{year}} = 5.318$ ,  $df = 1, 56$ ,  $P = 0.025$  for the south-facing slope and  $F_{\text{disturbance}} = 69.823$ ,  $df = 1, 56$ ,  $P = 0.001$  and  $F_{\text{year}} = 6.328$ ,  $df = 1, 56$ ,  $P = 0.015$  for the northwest-facing

TABLE 1

Percentage vegetation cover per species observed in disturbed and non-disturbed areas of two slopes of different exposure in the surroundings of the La Parva Ski complex in the Andes of central Chile during the 2006 and 2007 growing seasons. Means are shown with 2 SE. Means with different letters differ significantly (Student *t*-tests,  $P < 0.05$ ; and *a posteriori* Tukey HSD tests,  $P < 0.05$  for total cover).

Species	South-facing slope				Northwest-facing slope			
	2006		2007		2006		2007	
	Disturbed	Undisturbed	Disturbed	Undisturbed	Disturbed	Undisturbed	Disturbed	Undisturbed
<i>Acaena pinnatifida</i>			0.0 ± 0.0 <sup>a</sup>	1.2 ± 0.6 <sup>b</sup>				
<i>Adesmia</i> sp.	0.5 ± 0.4 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>	0.2 ± 0.2 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>	1.4 ± 0.6 <sup>b</sup>	0.5 ± 0.4 <sup>a</sup>	2.1 ± 1.3 <sup>a</sup>
<i>Berberis empetrifolia</i>					0.0 ± 0.0 <sup>a</sup>	3.0 ± 1.4 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	2.7 ± 1.7 <sup>b</sup>
<i>Chaetanthera euphrasioides</i>	0.0 ± 0.0 <sup>a</sup>	4.1 ± 1.3 <sup>b</sup>	12.8 ± 5.0 <sup>a</sup>	2.5 ± 0.9 <sup>b</sup>			2.1 ± 1.3 <sup>a</sup>	0.0 ± 0.0 <sup>b</sup>
<i>Chaetanthera pusilla</i>			0.8 ± 0.8 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>			2.3 ± 0.9 <sup>a</sup>	0.0 ± 0.0 <sup>b</sup>
<i>Chenopodium philippianum</i>			0.7 ± 0.7 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>				
<i>Chuiriraga oppositifolia</i>					0.0 ± 0.0 <sup>a</sup>	17.3 ± 4.6 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	16.0 ± 6.6 <sup>b</sup>
<i>Ephedra andina</i>					0.0 ± 0.0 <sup>a</sup>	0.3 ± 0.2 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	0.3 ± 0.3 <sup>a</sup>
<i>Erigeron andicola</i>	0.0 ± 0.0 <sup>a</sup>	1.3 ± 0.8 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	0.6 ± 0.4 <sup>a</sup>				
<i>Gramínea</i> sp. 1	0.0 ± 0.0 <sup>a</sup>	3.7 ± 1.7 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	6.6 ± 2.8 <sup>b</sup>				
<i>Gramínea</i> sp. 2					0.0 ± 0.0 <sup>a</sup>	3.9 ± 1.4 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	3.5 ± 1.0 <sup>b</sup>
<i>Haplopappus anthyloides</i>	0.0 ± 0.0 <sup>a</sup>	2.0 ± 1.2 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	2.3 ± 1.3 <sup>b</sup>				
<i>Hypochoeris clarionoides</i>	0.0 ± 0.0 <sup>a</sup>	3.3 ± 1.3 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	5.3 ± 2.2 <sup>b</sup>				
<i>Laretia acaulis</i>	0.0 ± 0.0 <sup>a</sup>	29.3 ± 7.1 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	27.5 ± 10.1 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	9.0 ± 3.7 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	6.3 ± 5.3 <sup>a</sup>
<i>Loasa caespitosa</i>	0.0 ± 0.0 <sup>a</sup>	1.3 ± 1.0 <sup>a</sup>						
<i>Nassauvia axillaris</i>					0.0 ± 0.0 <sup>a</sup>	18.2 ± 3.3 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	19.5 ± 5.4 <sup>b</sup>
<i>Nicotiana corymbosa</i>	2.2 ± 0.9 <sup>a</sup>	0.0 ± 0.0 <sup>b</sup>	12.7 ± 6.1 <sup>a</sup>	0.0 ± 0.0 <sup>b</sup>	0.8 ± 0.5 <sup>a</sup>	0.0 ± 0.0 <sup>b</sup>	16.5 ± 6.4 <sup>a</sup>	0.0 ± 0.0 <sup>b</sup>
<i>Oxalis squamata</i>	0.5 ± 0.4 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>	0.2 ± 0.2 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>	1.6 ± 0.6 <sup>a</sup>	0.0 ± 0.0 <sup>b</sup>	2.4 ± 1.2 <sup>a</sup>	0.0 ± 0.0 <sup>b</sup>
<i>Perezia carthamoides</i>	0.0 ± 0.0 <sup>a</sup>	1.3 ± 0.8 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	0.2 ± 0.2 <sup>a</sup>				
<i>Quinchamalium chilense</i>	0.0 ± 0.0 <sup>a</sup>	0.7 ± 0.5 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>	1.4 ± 1.0 <sup>a</sup>				
<i>Sanicula graveolens</i>	0.0 ± 0.0 <sup>a</sup>	0.7 ± 0.5 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>	0.5 ± 0.5 <sup>a</sup>				
<i>Senecio polygaloides</i>	0.0 ± 0.0 <sup>a</sup>	3.0 ± 2.2 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>	0.9 ± 0.8 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>	10.7 ± 2.4 <sup>b</sup>	0.0 ± 0.0 <sup>a</sup>	10.7 ± 3.9 <sup>b</sup>
<i>Taraxacum officinale</i>	0.0 ± 0.0 <sup>a</sup>	2.0 ± 1.1 <sup>b</sup>	0.6 ± 0.6 <sup>a</sup>	2.8 ± 2.8 <sup>a</sup>				
<i>Tristagma bivalve</i>	0.0 ± 0.0 <sup>a</sup>	0.7 ± 0.5 <sup>a</sup>	0.0 ± 0.0 <sup>a</sup>	0.3 ± 0.2 <sup>a</sup>				
<b>Total cover</b>	<b>3.2 ± 2.4<sup>a</sup></b>	<b>53.3 ± 15.4<sup>b</sup></b>	<b>28.0 ± 16.1<sup>a</sup></b>	<b>52.1 ± 15.1<sup>b</sup></b>	<b>2.4 ± 1.9<sup>a</sup></b>	<b>63.9 ± 8.3<sup>c</sup></b>	<b>23.9 ± 13.4<sup>b</sup></b>	<b>61.2 ± 12.9<sup>c</sup></b>

slope). Undisturbed areas for both slopes remained relatively stable and possessed greater percent cover than disturbed areas in which vegetation cover increased significantly during the second growing season (Table 1). In both disturbed areas and in both growing seasons, the annual herb *Nicotiana corymbosa* (Solana-ceae) was the most abundant species, where its abundance increased from 2.2% in 2006 to 12.7% in 2007 in the south-facing slope and from 0.8% in 2006 to 16.5% in 2007 in the northwest-facing slope (Table 1). In the south-facing slope, the annual species *Chaetanthera euphrasioides* (Compositae) also increased its cover significantly (Table 1). In contrast, in the non-disturbed area of the south-facing slope, the cushion plant *Laretia acaulis* (Apiaceae) was the most abundant species in both years (Table 1), while in the undisturbed area of the northwest-facing slope, the most abundant species were the shrubs *Nassauvia axillaris* and *Chuiriraga oppositifolia* and the perennial herb *Senecio polygaloides* (Table 1).

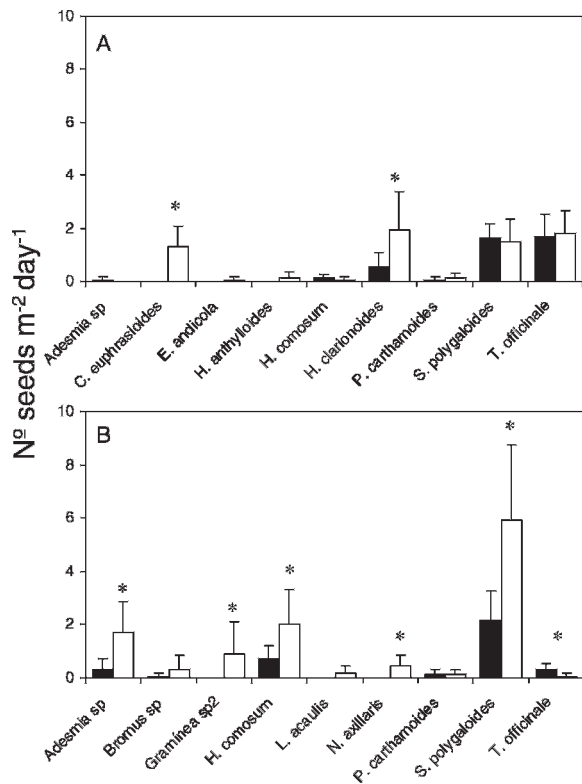
#### SEED RAIN

There were significant differences on seed rain between disturbed and non-disturbed areas on both slopes (Student *t*-tests,  $t = -2.040$ ,  $df = 28$ ,  $P = 0.05$  and  $t = -3.457$ ,  $df = 28$ ,  $P = 0.001$  for south and northwest-facing slopes, respectively), with non-disturbed areas receiving a greater number of seeds than the disturbed ones ( $6.89 \pm 2.91$  vs.  $4.10 \pm 1.35$  for the south-facing slope and  $11.67 \pm 3.62$  vs.  $3.69 \pm 1.34$  for the northwest-facing slope). However, in terms of species composition, disturbed and non-disturbed areas were very similar. For example, the most abundant seeds collected in disturbed and non-disturbed areas of the south-facing slope were from the asteraceous species *Hypo-*

*chaeris clarionoides*, *Senecio polygaloides*, and the exotic *Taraxacum officinale* (Fig. 3a). These species were also trapped in disturbed and non-disturbed areas of the northwest-facing slope, as well as the legume *Adesmia* sp. and the grass *Hordeum comosum* (Fig. 3b).

#### SEEDLING EMERGENCE AND SURVIVAL

Seedling emergence was almost one order of magnitude greater in the non-disturbed than in the disturbed area for the south-facing slope (repeated measures ANOVA,  $F_{\text{disturbance}} = 7.371$ ,  $df = 1, 14$ ,  $P = 0.017$  and  $F_{\text{time}} = 4.311$ ,  $df = 8, 112$ ,  $P = 0.001$ ). For the undisturbed area, the annual herb *Chaetanthera euphrasioides* was the most abundant species ( $791.3 \pm 55.3$  seedlings  $m^{-2}$ , mean  $\pm 2$  SE), accounting for ca. 83% of the seedling emergence (Fig. 4). In the disturbed area of this slope, *Nicotiana corymbosa* was the most abundant species, with  $185.2 \pm 34.5$  seedlings  $m^{-2}$  followed by *C. euphrasioides* with  $80.7 \pm 2.5$  seedlings  $m^{-2}$ . *Quinchamalium chilense* and other species were also found (Fig. 4). In contrast, in the northwest-facing slope (data not shown), seedling emergence was very low and never exceeded an average of 30 individuals  $m^{-2}$  (repeated measures ANOVA,  $F_{\text{disturbance}} = 0.337$ ,  $df = 1, 17$ ,  $P = 0.569$  and  $F_{\text{time}} = 4.101$ ,  $df = 8, 136$ ,  $P = 0.001$ ). As in the disturbed area of the south-facing slope, *N. corymbosa* was the most abundant species, with 55.9% of the total number of seedlings observed ( $31.4 \pm 20.3$  seedlings  $m^{-2}$ , mean  $\pm 2$  SE). Seedlings of the annual herb *C. euphrasioides* ( $10.6 \pm 6.1$  seedlings  $m^{-2}$ ) were also present. In contrast, for the undisturbed area of the northwest-facing slope, seedling emergence was limited to a very few individuals of *Nassauvia axillaris* ( $7.2 \pm 0.6$  seedlings  $m^{-2}$ ).



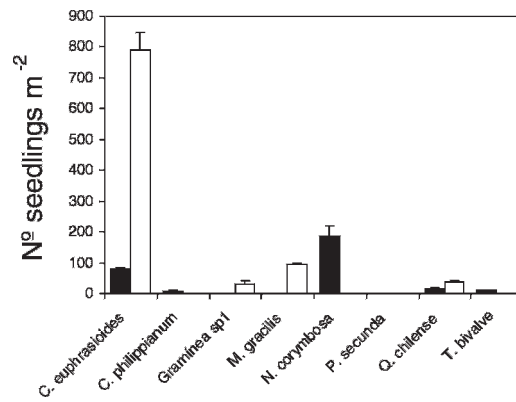
**FIGURE 3.** Number of seeds deposited per m<sup>2</sup> per day per species in seed traps located in disturbed (black bars) and non-disturbed (white bars) areas of south-facing slope (A) and northwest-facing slope (B) in the surroundings of the La Parva Ski complex in the Andes of central Chile during the 2006 growing season. Means are shown with 2 SE. Bars with asterisks differ significantly (Student *t*-tests, *P* < 0.05).

Survival in the disturbed area of the south-facing slope decreased for all species after the 56th day, with the exception of *Chenopodium philippianum*. Less than 20% of seedling survival was observed for *Quinchamalium chilense* and for the geophyte *Tristagma bivalve*. *Nicotiana corymbosa* showed 42% of seedling survival and almost 80% was measured in *Chaetanthera euphrasioides* (Fig. 5a). On the non-disturbed area, the graminea sample showed <5% of seedling survival after 60 days, while at the end of the monitoring period, *Q. chilense* and *C. euphrasioides* showed twice and 2/3 survival, respectively, compared to that measured on the disturbed area (Fig. 5b). Thus, *C. euphrasioides* had a higher survival in the disturbed area while *Q. chilense* had a higher survival in the non-disturbed area (Log-Rank tests,  $\chi^2 = 13.437$ , *df* = 1, *P* < 0.001 for *C. euphrasioides*, and  $\chi^2 = 117.992$ , *df* = 1, *P* < 0.001 for *Q. chilense*).

## Discussion

As has been shown for other alpine sites (e.g., McGraw and Vavrek, 1989; Chambers et al., 1990), we found that human disturbances on vegetated slopes of the high Andes of central Chile generated changes in some soil properties, with concomitant effects on vegetation recovery.

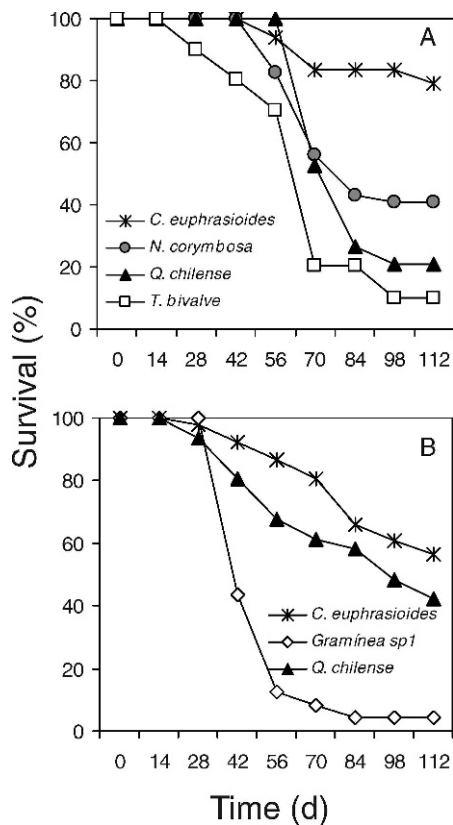
We found that one year after disturbance (i.e., during the first growing season of our study), vegetation cover observed in disturbed areas of both slopes did not exceed 3.2%. Particularly, we observed some scattered individuals of the perennial herbs *Adesmia* sp. and *Oxalis squamata* and some of the annual herb *Nicotiana corymbosa*. Vavrek et al. (1999) found that recolonization results from re-sprouted plants and/or from emergence from



**FIGURE 4.** Number of seedlings emerged per m<sup>2</sup> during the 2007 growing season in disturbed (black bars) and non-disturbed (white bars) areas of the south-facing slope in the surroundings of the La Parva Ski complex in the Andes of central Chile. Means are shown with 2 SE.

the deep seed bank, i.e., seeds present in the lowermost 10–20 cm depth layer of organic soil remaining after bulldozing. Hence, it seems likely that the presence of the perennial herbs mentioned above is the result of re-sprouting. During the second growing season, we found that vegetation cover in disturbed areas increased significantly in both slopes. This was mostly due to the presence of the annual species *Chaetanthera euphrasioides* and *N. corymbosa* and to a smaller degree, *Chaetanthera pusilla* and others (see Table 1). We did not detect seeds of *C. euphrasioides* and *C. pusilla* in seed traps (see Fig. 3). Thus the recolonization of these species in disturbed areas may be attributed to the existence of a persistent seed bank. Recently, Arroyo et al. (2006) showed that both *C. euphrasioides* and *C. pusilla* form persistent seed banks, where 53.0% and 10.7% of the seeds of *C. euphrasioides* remain viable after being buried for one and two years, respectively. *C. pusilla* showed similar percentages (53.3% and 18.0%) after yr 1 and yr 2, respectively (Arroyo et al., 2006). Several Alaskan tundra species have also shown a successful colonization after bulldozing for species with long-lived and deeply buried viable seeds (see Gartner et al., 1983; Vavrek et al., 1999). Although we are unaware of the capacity of the annual herbs *N. corymbosa* or *Chenopodium philippianum* to form a persistent seed bank, others have shown that the propensity to form persistent seed banks is negatively correlated with life history traits such as adult longevity (Venable and Brown, 1988; Rees, 1994). Therefore, if these two species follow the general trend, they are likely to have a persistent seed bank. Although non-disturbed areas received greater numbers of seeds, the species composition of the seed rain was similar between disturbed and undisturbed areas (see Fig. 3) indicating that, at least in terms of species composition, dispersal is very similar between both types of areas. However, for several species (e.g., *Hypochaeris clarionoides*, *Senecio polygaloides*, *Taraxacum officinale*, and *Hordeum comosum*) that reach the undisturbed area through the seed rain, seeds did not produce seedlings, suggesting that either they were unviable or that the microclimatic conditions generated after disturbances were not suitable for seed germination. Our results thus indicate that seedling recruitment after disturbance occurred mainly from a persistent seed bank constituted mostly by species with long-lived and deeply viable seeds.

The results obtained from this study reveal opposite trends for the south-facing and the northwest-facing slopes. For example, the disturbed area on the south-facing slope turned out to be drier than its respective control (non-disturbed) area. On the contrary, the disturbed area on the northwest-facing slope turned out to be



**FIGURE 5.** Percentage of seedling survival of different species emerged during the 2007 growing season in disturbed (A) and non-disturbed areas (B) of the south-facing slope in the surroundings of the La Parva Ski complex in the Andes of central Chile.

more humid than its respective control. These differences in soil water content between slopes coincide with the results of seedling recruitment. In the south-facing slope, where the undisturbed area was wet, the number of emerging seedlings was greater than on the disturbed area. On the other side, on the northwest-facing slope, the main recruitment of seedlings was observed on the disturbed area; meanwhile, on the undisturbed area, there was practically no emergence of new individuals. While the northwest-facing slope showed average soil temperatures that ranged between 3.9 and 44.6 °C, in the south-facing slope the highest temperatures never exceeded 36 °C. Thus, greater seedling emergence on the south-facing slope, especially in the non-disturbed area, can be explained by lower maximum soil temperatures and overall lower drought stress. Microsites with appropriate temperature and soil moisture conditions are crucial for survival of plants in the harsh alpine climate. For instance, Chambers et al. (1990) showed that in the alpine of the Rocky Mountains, microsites with good availability of water showed higher seedling recruitment in many species than microsites with less water (see also Bell and Bliss, 1980; Gold and Bliss, 1995). Similar results have been reported by Forbis (2003), who showed that seedling survival in several alpine species at Niwot Ridge, Colorado, was higher in meadows with good availability of water.

Another interesting result was observed for *Chenopodium philippianum*, *Nicotiana corymbosa*, *Phacelia secunda*, and *Tristagma bivalve*, which only recruited on the disturbed areas (see Fig. 4). This result suggests that these species have a high colonizing capacity, being able of significantly increasing their coverage between growing seasons (see Table 1), and that other disturbed surrounding areas, as adjacent paths where this annual herb is very abundant, could contribute to its expansion. The

observed difference in species identity of emerging seedlings between disturbed and undisturbed sites has been documented previously by Marchand and Roach (1980) and Chambers et al. (1984), who showed that life history and physiological traits of early colonizers often differ significantly from species that dominate relatively undisturbed sites. Brown et al. (2006) found that 9 out of 33 species recorded in a long-term study were exclusive to the disturbed sites, 5 of those being generally characteristic of open habitats of the Old Man Range.

An unexpected finding was the great amount of seedlings emerged per m<sup>2</sup> in the south-facing slope compared to the northwest-facing slope, especially in the non-disturbed area, where an average density of 957.8 seedlings m<sup>-2</sup> was monitored during 112 days, compared to 308.4 seedlings m<sup>-2</sup> at the disturbed area. King (1977) and Gross and Werner (1982) suggested that the establishment of seedlings in mature vegetation is rarely observed, presumably due to competition for resources or to the fact that many alpine species are highly clonal, and thus are expected to have low rates of seedling establishment (Angevine, 1983; Eriksson, 1989; Callaghan et al., 1992; Eriksson and Fröberg, 1996). However, Chambers et al. (1987), Schallag and Erschbamer (2000), and Forbis (2003) have also provided evidence of high seedling densities under natural undisturbed conditions in other alpine sites, indicating that the magnitude of this process is greater than previously thought.

Our results provide the first step in understanding the capacity for vegetation recovery after a severe human disturbance in the Andes of central Chile. However, a long-term study of plant successions after severe human disturbances such as bulldozing is recommended in order to better address long-term vegetation dynamics through time.

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