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Vegetation as an Ecological Indicator of Surface Instability in Rock Glaciers

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Abstract

We studied relationships between vegetation, substrate texture, and surface movement velocity in two active rock glaciers in the Central Alps (northern Italy). We also compared the vegetation on the two active rock glaciers with that of adjacent stable areas and with that of an inactive rock glacier. The vegetation patterns on the two active rock glaciers differed sharply from those on the stable areas nearby and on the inactive rock glacier with respect to both total plant cover and floristic composition. Surface movement on the two active rock glaciers ranged from 0–5 to 35–40 cm yr^{-1} and was largely independent of slope inclination. The most unstable sites were almost free of mosses and lichens and were characterized by vascular species tolerating surface instability in virtue of varying morphological adaptations. However, the distributional pattern of vascular species could not be directly related to surface instability but depended on a combination of substrate texture and movement intensity.

Introduction

Surface instability is a major factor influencing the morphodynamic evolution of the landscape in the alpine environment. Geomorphological features such as soil creep, debris flow, and solifluction lobes, as well as several periglacial landforms, originate as a consequence of surface instability. Surface instability is also responsible for the origin of larger-scale landforms such as landslides and, especially, rock glaciers.

Rock glaciers are widespread in the alpine environment, where they can be regarded as reliable indicators of permafrost (French, 1976; Haeberli, 1985; Cheng and Dramis, 1992; Guglielmin et al., 1994). Rock glaciers are usually classified into two main categories based on the presence or absence of surface movement: active or inactive (Barsch, 1996). Surface movement in active rock glaciers can be due to several processes, such as permafrost creep, changes in hydrology, and solifluction, which often vary greatly from point to point, thus resulting in highly heterogeneous patterns of movement intensity (Haeberli, 1985; White, 1987; Whalley et al., 1995; Kääb et al., 1997). There is evidence that the complex microrelief that can often be observed on the surface of active rock glaciers reflects varying movement intensity within the rock glacier body (Johnson, 1992). Both surface morphology and disturbance brought about by surface instability have been found to exert important effects on vegetation patterns in rock glaciers and surrounding areas (Carbiener, 1966; Gerdol and Smiraglia, 1990; Cannone and Burga, 2001).

Traditional studies addressing relationships between vegetation and surface instability in the alpine environment have been carried out on scree slopes and moraines (see Schröter, 1926, and references therein). In both habitats, plant cover and patterns of surface movement are controlled primarily by slope angle and gravity. More recently, relationships between vegetation patterns and surface instability in arctic and alpine regions have been the object of studies focusing, e.g., on community typology (Valachovic et al., 1997), growing strategies and adaptations to mechanical disturbance (Somson, 1984), root mechanical properties (Jonasson and Callaghan, 1992), and vegetation dynamics (Svoboda and Henry, 1987; Jumpponen et al., 1998). Most of the studies cited here are based on qualitative assessment of surface stability at the sites where vegetation was sampled. To our knowledge, there are no papers presenting studies of the relationship of plant distributional patterns to quantitative measurements of surface movement in arctic-alpine habitats.

In this paper we aimed at quantitatively analyzing relationships between vegetation patterns and surface instability in an alpine area. We selected two active rock glaciers as suitable habitats to carry out investigations since: (1) quantitative data on surface movement were available as a result of a 10-yr field study, and (2) the distributional pattern of surface movement intensity in rock glaciers is known to be independent of slope angle. Since our objective was to analyze the effect of surface movement per se on vegetation patterns, we did not address the mechanisms responsible for surface movement in the two rock glaciers.

Materials and Methods

DESCRIPTION OF THE STUDY AREAS

The main part of our study was carried out in two active rock glaciers (Pisella and La Foppa 1) in the central sector of the southern Alps, Upper Valtellina, Sondrio Province, northern Italy (Fig. 1). This region is rich in periglacial landforms (Guglielmin and Smiraglia, 1997) and has micaschist and gneiss as the most common parent rocks.

Pisella is situated at 2850–2970 m a.s.l. on a south-exposed slope (Resnati and Smiraglia, 1990). La Foppa 1 is situated at 2650–2770 m a.s.l., on a north-exposed slope (Guglielmin et al., 1994). The habitat in the two areas is similar despite the contrast in aspect. Both lie in the alpine vegetation belt, well above the upper limit of arolla pine (*Pinus cembra*) forests, which is generally situated at 2200 m a.s.l. The alpine vegetation consists mainly of alpine *Carex curvula* grasslands and snowbed communities of *Salix herbacea*.

For comparision, we sampled vegetation on an inactive rock glacier. Since there are no cases of inactive rock glaciers within the alpine vegetation belt in this region, we chose an inactive rock glacier, Lago Blu, at 2300–2450 a.s.l. as a reference site. Lago Blu is situated in the krummholz subalpine vegetation belt, close to La Foppa cirque. It was classified as an inactive rock glacier by Guglielmin and Smiraglia (1997).

FIELDWORK

Surface Movement

Data on surface movement velocity were drawn from measurements by Smiraglia (1989) in a 300 × 180–m area for Pisella and from

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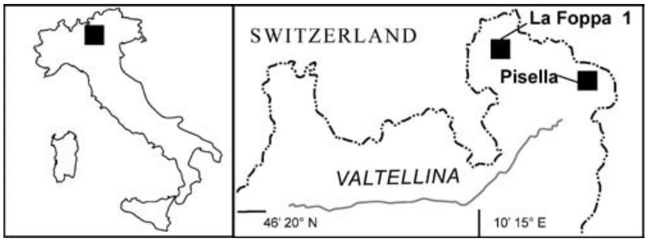

FIGURE 1. Map indicating the geographical location of the two active rock glaciers.

measurement by Guglielmin (unpubl.) in a 250 × 150–m area for La Foppa 1. Details on the method are described in Smiraglia (1989). In brief, surface movement has been measured at a number of points using a theodolite located in a fixed position, usually a rock lying outside the rock glacier. The measurements have been repeated at a 10-yr interval, and movement velocity, expressed as cm yr^{-1}, has been mapped.

From the maps, we draw data on surface movement velocity for each quadrat where we sampled vegetation, as described in the following sections.

Vegetation and Habitat

A 25 × 25–m grid was set up on both mapped areas, and a 2 × 2–m quadrat was laid down at each intersection point in the two grids. There were a total of 89 sampling quadrats at Pisella and 62 sampling quadrats at La Foppa 1. Total vegetation cover and the cover of each vascular species was estimated visually within every quadrat. Species nomenclature is in accordance with Pignatti (1982). Cover estimates were also given for cryptogams. The latter were not identified as species but grouped into three broad categories: mosses (including a few liverworts), epilithic lichens, and ground lichens.

At each quadrat, velocity of surface movement was drawn from the maps (see earlier description). In addition, slope angle was measured with a compass, and substrate texture was determined in a 50 × 50–cm subquadrat by visual estimation of percentage cover of the following textural categories:

- blocks: Ø > 25 cm;
- pebbles: 5 cm < Ø < 25 cm;
- gravel: 0.5 cm < Ø < 5 cm;
- fine material Ø < 0.5 cm.

For comparison, we also sampled vegetation in several stable areas close to each of the two active rock glaciers (Pisella and La Foppa 1) and near the inactive rock glacier (Lago Blu) as well. In those areas vegetation was recorded, as described earlier, at a number of haphazardously chosen 2 × 2–m quadrats. Movement was assumed to be absent in those areas; hence environmental variables were not measured.

DATA ELABORATION

The matrices of vascular species (or cryptogam group) cover and environmental variables in the two active rock glaciers served as the basis for a multivariate analysis of the data by canonical correspondence analysis (CCA). The data were square-root transformed prior to analysis. The environmental variables showing reciprocal dependency (inflation factor > 20) were eliminated from the analysis.

The analysis was carried out separately for the two rock glaciers, Pisella and La Foppa 1, downweighting the rare species. A Monte Carlo permutation test was performed in order to assess the significance of differences between the patterns obtained from the ordination and random ones. All computations were performed using the CANOCO Software, Version 4 (Ter Braak and Šmilauer, 1998).

Results

Compared with the two active rock glaciers, the vegetation of the inactive rock glacier was much denser (mean total cover: 68% at Lago Blu versus 21% at Pisella and 11% at La Foppa 1) and richer in species (40 vascular species recorded at Lago Blu versus 19 and 13 at Pisella and La Foppa 1, respectively). Floristically, Lago Blu differed dramatically from the two active rock glaciers, especially regarding the presence of dwarf shrubs (*Empetrum hermaphroditum*, *Juniperus nana*, *Loiseleuria procumbens*, *Rhododendron ferrugineum*, *Vaccinium myrtillus*, and *Vaccinium vitis idaea*) typical of subalpine heathlands as well as graminoid species (*Avenula versicolor*, *Carex curvula*, *Festuca halleri*, and *Juncus trifidus*) typical of alpine grasslands. Both groups were completely absent at both Pisella and La Foppa 1 (Table 1). The vegetation of the inactive rock glacier did not show any apparent difference from that in the adjacent stable areas (data not shown). It is, hence, reasonable to hypothesize that surface instability does not represent a limiting factor for plant establishment at Lago Blu.

In contrast, the vegetation of the two active rock glaciers differed sharply from both that in the nearby stable areas and that in the inactive rock glacier. The vegetation of both Pisella and La Foppa 1 was essentially formed of pioneer species, such as *Cardamine resedifolia*, *Cerastium uniflorum*, *Geum reptans*, *Leucanthemopsis alpina*, *Poa alpina*, *Ranunculus glacialis*, and *Saxifraga bryoides* (Table 1), mostly occurring on scree slopes. The stable areas close to the Pisella rock glacier were mainly covered by snowbed species, such as *Salix herbacea* (dominant), *Alchemilla pentaphyllea*, *Arenaria biflora*, *Cerastium cerastioides*, *Gnaphalium supinum*, *Luzula spicata*, and *Soldanella pusilla*. The vegetation in the stable areas close to La Foppa 1 comprised typical species of alpine grasslands, such as *Carex curvula* (dominant), *Gentiana punctata*, *Leontodon helveticus*, *Ligusticum mutellina*, and *Senecio incanus*, and, to a lesser extent, snowbed species (*Cerastium cerastioides*, *Salix herbacea*, and *Soldanella pusilla*: Table 1). We can therefore assume that surface movement influences the capability of the single species of colonizing and developing unstable areas on active rock glaciers.

The habitat conditions varied greatly within both Pisella and La Foppa 1 (Table 2). Slope angle was similar in the two rock glaciers, the highest values being recorded on the steepest parts of small mounds characterizing the surface microrelief at the two areas. Substrate texture was in general coarse, with blocks representing the most abundant textural category, especially at Pisella (Table 2). Fine material was rather scarce and generally restricted to small pockets among pebbles and blocks. Surface movement ranged between 0–5 cm yr^{-1} and 35–40 cm yr^{-1}. Sites with high movement were more frequent at La Foppa 1 (Table 2).

The correlation coefficients among environmental variables showed remarkably different patterns between the two areas (Table 3). Slope inclination was unrelated to both substrate texture and movement at Pisella but negatively correlated with blocks at La Foppa 1. Blocks were overall negatively correlated with one or more of the other textural categories, but this pattern was sharper at La Foppa 1 (Table 3). Movement intensity showed overall poor or no correlations with substrate texture and slope. Indeed, movement was slightly negatively correlated with fine material only at Pisella (Table 3).

Total plant cover ranged between 0 and 70–85% and was generally higher at Pisella (Table 2). In both areas total plant cover was significantly higher at the sites where substrate texture was finer. At Pisella, total plant cover was significantly lower at unstable sites, where substrate texture was coarser. Conversely, total plant cover was

TABLE 1

Mean covers and frequencies of vascular species, mosses, ground lichens, and epilithic lichens in the two active rock glaciers, Pisella and La Foppa 1 (figures in boldface)[a]

	Pisella				La Foppa 1					
	Rock glacier		Adjacent stable areas		Rock glacier		Adjacent stable areas		Lago Blu	
	Cov. %	Freq. %	Cov. %	Freq. %	Cov. %	Freq. %	Cov. %	Freq. %	Cov. %	Freq. %
Agrostis aplina									0.01	0.1
Alchemilla pentaphyllea			2.1	21.3						
Androsace alpina	**0.03**	**4.5**								
Arenaria biflora			2.4	47.2						
Avenula versicolor									2.6	55.8
Campanula barbata									0.4	10.1
Cardamine resedifolia	**0.19**	**16.8**	1.3	8.5	**0.16**	**4.8**				
Carex curvula							70.5	93.5	14.8	59.4
Cerastium cerastioides			4.1	74.7			0.1	6.3		
Cerastium uniflorum	**6.64**	**34.8**			**0.37**	**3.2**				
Cirsium spinosissimum									0.7	11.1
Deschampsia caespitosa									0.3	2.9
Doronicum clusii					**0.08**	**1.6**			0.4	7.1
Empetrum hermaphroditum									1.5	18.5
Eritrichium nanum	**0.07**	**2.2**								
Festuca halleri									0.8	5.4
Gentiana bavarica	**0.14**	**10.1**	0.1	4.5						
Gentiana punctata							0.1	0.6		
Geum reptans	**1.66**	**30.3**			**3.12**	**35.5**				
Gnaphalium supinum	**0.04**	**2.2**	16.8	82.3					1.0	6.1
Homogyne alpina									0.4	3.5
Juncus trifidus									5.5	42.7
Juniperus nana									18.1	51.1
Leontodon helveticus			0.1	3.6			3.8	73.2	2.6	39.7
Leucanthemopsis alpina	**1.34**	**20.2**	6.6	85.8	**3.29**	**40.3**	5.1	88.3	0.8	22.4
Ligusticum mutellina							3.5	15.7	1.5	9.8
Linaria aplina	**0.06**	**4.5**			**0.01**	**3.2**				
Loiseleuria procumbens									15.9	48.8
Luzula alpino–pilosa									2.9	12.2
Luzula lutea									1.9	8.1
Luzula spicata			0.1	2.3					0.01	0.1
Luzula sudetica									0.3	3.3
Minuartia sedoides	**0.44**	**1.1**							0.1	2.3
Oreochloa disticha									1.2	17.5
Oxyria digyna	**0.00**	**2.2**			**0.01**	**1.6**				
Phyteuma hemisphaericum									0.7	12.1
Poa alpina	**0.90**	**31.5**	6.1	81.3	**1.73**	**48.4**	6.2	53.8	0.3	9.4
Polygonum viviparum									2.3	29.8
Potentilla aurea									0.01	0.1
Primula daonensis									0.4	5.4
Ranunculus glacialis	**0.06**	**5.6**			**0.16**	**1.6**				
Rhododendron ferrugineum									4.8	42.4
Salix herbacea			80.2	95.4			5.2	32.6	0.3	3.5
Salix waldsteiniana									5.6	27.4
Saxifraga aspera									0.7	3.4
Saxifraga bryoides	**7.77**	**38.2**			**1.29**	**22.6**			0.3	5.2
Saxifraga moschata	**0.01**	**1.1**			**0.23**	**8.1**				
Saxifraga seguieri	**0.08**	**4.5**								
Sedum alpestre	**0.08**	**6.7**			**0.16**	**6.4**			0.01	0.1
Senecio incanus	**0.05**	**6.7**			**0.08**	**1.6**	1.7	44.8	0.8	27.9
Soldanella pusilla			0.1	32.5			0.1	2.7	0.3	6.8
Taraxacum alpinum	**0.01**	**6.7**	0.1	21.8						
Vaccinium myrtillus									4.8	34.2
Vaccinium uliginosum									0.8	10.7
Vaccinium vitis–idaea									4.4	24.9
Veronica alpina	**0.91**	**20.2**	2.9	65.2	**0.16**	**4.8**	0.1	8.5	0.3	6.3

TABLE 1

(Cont.)

	Pisella				La Foppa 1				Lago Blu	
	Rock glacier		Adjacent stable areas		Rock glacier		Adjacent stable areas			
	Cov. %	Freq. %	Cov. %	Freq. %	Cov. %	Freq. %	Cov. %	Freq. %	Cov. %	Freq. %
Mosses	**0.60**	**21.3**			**0.75**	**25.8**	4.5	38.5	0.01	0.1
Ground lichens	**0.60**	**6.7**			**0.13**	**4.8**	8.5	55.9	10.3	52.8
Epilithic lichens					**0.17**	**11.3**			0.4	2.7

[a] Also shown are mean covers and frequency of vascular species and cryptogam groups in stable areas adjacent to both active rock glaciers and in an inactive rock glacier (Lago Blu).

unrelated to surface movement at La Foppa 1 (Table 3). No epilithic lichens were found at Pisella, presumably because the higher movement recorded on coarse-textured substrates prevented the establishment of epilithic lichens on boulders. In contrast, epilithic lichens, besides mosses and ground lichens, did occur at La Foppa 1, although with a rather modest frequency and cover (Table 1). Twelve of the vascular species were common to both areas. However, the dominance patterns differed between the two rock glaciers, with *Cerastium uniflorum* and *Saxifraga bryoides* representing the dominant species at Pisella and *Geum reptans* and *Leucanthemopsis alpina* the dominant species at La Foppa 1. *Poa alpina* was frequent at both areas, especially La Foppa 1, but always with low cover (Table 1).

The first two CCA axes accounted for >70% of the variance in the total species/environment relations, although the eigenvalues associated with those axes were rather low (Fig. 2). However, both CCA ordinations were highly significant ($P < 0.005$) based on the Monte Carlo permutations tests. In the Pisella ordination, the movement vector was opposite to that of fine material (Fig. 2a), whereas in the La Foppa 1 ordination the movement vector was fairly close to the fine-material vector (Fig. 2b), as expected based on the differing correlation patterns between these environmental variables in the two areas (Table 2). The slope vector formed wide angles with the movement vector in the La Foppa 1 ordination but not in the Pisella ordination (Fig. 2). In the Pisella ordination, *Geum reptans* and *Saxifraga bryoides* had positive values when their centroids were projected onto the movement vector, thus indicating a positive association with soil instability, which was in turn associated with coarser substrate and slope (Fig. 2a). At Pisella, *Cardamine resedifolia* and *Cerastium uniflorum* also showed a slight positive association with movement. Conversely, the centroids of several species lay in the positive half of the movement vector in the La Foppa 1 ordination: *Cerastium uniflorum*, *Geum reptans*, *Oxyria digyna*, *Ranunculus glacialis*, *Sedum alpestre*, and, to a lesser extent, *Cardamine resedifolia*, *Doronicum clusii*, and *Veronica alpina*. Mosses, ground lichens, and epilithic lichens always had negative associations with the movement vector, especially epilithic lichens in the La Foppa 1 ordination (Fig. 2).

TABLE 2

Means and ranges of environmental variables in the two active rock glaciers (Pisella, n = 89, and La Foppa 1, n = 62)

	Pisella	La Foppa 1
Slope angle (°)	25.2 (5–50)	24.1 (5–55)
Blocks (%)	74.0 (5–100)	51.7 (5–100)
Pebbles (%)	8.5 (0–45)	32.2 (0–85)
Gravel (%)	8.5 (0–50)	11.0 (0–50)
Fine material (%)	8.8 (0–40)	5.0 (0–25)
Movement (cm yr^{-1})	12.8 (0–40)	19.7 (5–35)

Discussion

Total plant cover in the two active rock glaciers investigated was overall modest, with total plant cover <20% in most of the sampling sites. The vegetation consisted mainly of vascular species characteristic of scree slopes and moraines (class *Thlaspietea rotundifolii*, order *Androsacetalia vandellii*, according to the Braun-Blanquet syntaxonomy: Grabherr and Mucina, 1993) but also included vascular species typical of alpine grasslands (class *Caricetea curvulae*) and snowbeds (class *Salicetea herbaceae*) as well as mosses and lichens. The first result of our study is that low vegetation cover and high frequency of pioneer species can, in general, be regarded as indicators of active rock glaciers.

In contrast, the vegetation of the stable areas adjacent to the active rock glaciers was denser (mean total plant cover always >70%, up to 100% in certain areas) and richer in species typical of alpine grasslands. The inactive rock glacier also was characterized by a well-developed vegetation forming a continuous carpet over most of the area. Regrettably, the vegetation at Lago Blu is not fully comparable with that at Pisella and La Foppa 1 owing to the lower elevation of Lago Blu. The latter certainly is responsible for the presence at Lago Blu of dwarf-shrub species, which are almost totally lacking at high-elevation sites in the alpine vegetation belt. Nonetheless, some graminoids and herbs typical of alpine grasslands and snowbeds (especially *Carex curvula*, *Leontodon helveticus*, *Ligusticum mutellina*, and *Salix herbacea*) occurred both at Lago Blu and at the stable areas close adjacent to Pisella and La Foppa 1. Interestingly, the vegetation at Lago Blu is very similar to that recorded at an inactive rock glacier in the subalpine vegetation belt in the northern Apennines (Tomaselli and Agostini, 1990).

The main aim of our study was to relate vegetation patterns to small-scale variations in surface movement intensity. In fact, we found both floristic composition and surface movement intensity to vary remarkably within both of the rock glaciers investigated. We could separate the effects of substrate movement from those related to slope inclination and texture. Unstable areas in alpine regions are, in general, hostile to plant growth. The capability for plants to colonize newly formed debris, such as recently deglaciated moraines and scree slopes, is principally controlled by seed dispersal (Ryvgarden, 1971) and the availability of safe sites suitable for seed germination and seedling establishment (Jumpponen et al., 1999; Niederfriniger Schlag and Erschbamer, 2000). Conversely, the ability of plant species to persist in such a harsh environment depends on various morphological, ecophysiological, or life-history characteristics. The latter qualities allow plants to cope with factors that may limit plant growth in alpine habitats, e.g., low soil resource, broad fluctuations in air and soil temperatures, rapid drying of surface soils, and mechanical disturbance brought about by surface substrate instability (Chapin, 1993).

The most unstable sites in both of our study areas were free from cryptogamic vegetation. In alpine habitats, epilithic lichens usually are confined to rock faces and stable blocks because they are unable to

TABLE 3

Pearson's correlation coefficients among environmental variables, also including total plant cover, at Pisella (n = 89) and La Foppa 1 (n = 62) rock glaciers[a]

	Pisella					
	Slope angle	Blocks	Pebbles	Gravel	Fine mat.	Movement
Slope angle	1.00					
Blocks	−0.13	1.00				
Pebbles	0.04	**−0.91****	1.00			
Gravel	0.16	0.16	**0.75****	1.00		
Fine material	0.12	0.12	**0.80****	0.84	1.00	
Movement	−0.03	−0.03	−0.21	**−0.23***	**−0.32***	1.00
Plant cover	0.01	0.01	**0.78****	**0.71****	**0.77****	**−0.34****
	La Foppa 1					
	Slope angle	Blocks	Pebbles	Gravel	Fine mat.	Movement
Slope angle	1.00					
Blocks	**−0.31***	1.00				
Pebbles	0.06	**−0.68****	1.00			
Gravel	**0.43****	**−0.71****	−0.01	1.00		
Fine material	0.23	**−0.63****	−0.06	**0.80****	1.00	
Movement	0.13	−0.06	−0.11	0.11	0.29	1.00
Plant cover	0.21	**−0.64****	0.07	**0.80****	**0.66****	0.07

[a] Significant values are in boldface (* $P < 0.05$; ** $P < 0.01$).

colonize mobile stones and blocks. Ground lichens and mosses usually thrive in pockets of fine earth where the surface has reached sufficient stability. Both are mechanically destroyed or jacked up from the substrate as a result of burial or soil displacement (Ellenberg, 1988). In contrast, we found two vascular species to tolerate surface movement intensity as high as 35 cm yr^{-1}. *Geum reptans* and, to a lesser extent, *Cerastium uniflorum* tolerated high movement intensity independent of substrate texture. Both are typical components of the scree and moraine vegetation in the Alps (Grabherr and Mucina, 1993), being well adapted to withstand mechanical disturbance through elongation and regeneration. *Geum reptans* is a clonal species that can spread laterally up to 2 m by means of long subaerial stolons creeping on the debris (Stöcklin and Bäumler, 1996). On the other hand, *Cerastium uniflorum* creeps over the scree and has lower regeneration ability compared with *Geum reptans* (Somson, 1984). *Saxifraga bryoides* tolerated high movement intensity, especially on coarse debris. *Saxifraga bryoides* also is a clonal species, whose genets can reach 50 cm owing to lateral elongation of rhizomes that usually root in deeper layers, where the substrate is richer in fine material and more stable.

All of the other species tolerating surface movement did so on fine-grained debris only, with the partial exception of *Cardamine resedifolia*. The most representative species in this group certainly are *Oxyria digyna* and *Ranunculus glacialis*. Both possess long, thin roots giving rise to a clump of leaves. The leaves, especially those of *Ranunculus glacialis*, may hold up the debris, thus playing a role in creating stabler patches within debris slopes (Schröter, 1926). However, coarse-grained, unstable debris is likely to cause mechanical damage to the weak root system of those species, which are hence almost exclusive to fine-grained substrate on scree slopes and moraines (Oberdorfer, 1994). *Doronicum clusii* has a peculiar growth form, with a big but fragile rhizome usually situated at a considerable depth where it rarely undergoes mechanical damage. Aboveground stems are newly formed every year, even if the previous-year stems have been more or less severely damaged. Other species tolerating moderate surface movement on fine-grained substrates, such as *Linaria alpina*, *Sedum alpestre*, and *Veronica alpina*, do not possess any apparent morphological adaptation to cope with surface instability. All of them have a clumped growth form and have poor, if any, regeneration ability. *Linaria alpina* creeps over the scree, whereas *Sedum alpestre* and *Veronica alpina* are short-lived plants, rooting at a modest depth in small pockets of fine-grained debris. Those species probably rely upon an avoidance strategy rather than representing true stress-tolerant species. Indeed, they are mostly settled at relatively stable sites even within a generally unstable habitat such as alpine debris slopes. In addition, although their vegetative organs are unable to tolerate mechanical disturbance, these species have high rates of sexual reproduction, with most individuals dying shortly after fruiting (Stöcklin and Bäumler, 1996).

We found all of the other vascular species recorded at our sampling sites to tolerate only low, if any, surface movement intensity (see Fig. 2). Some of them were perennial species characterizing snowbeds (*Eritrichium nanum*, *Gentiana bavarica*, and *Taraxacum alpinum*) or alpine grasslands (*Poa alpina* and *Senecio incanus*), usually on stable substrate. All of these species lack any adaptation to mechanical disturbance for possessing a clumped growth form, with no or very modest lateral elongation. Only *Poa alpina* is fairly common in pioneer habitats, especially on moraines, where it holds up the debris thanks to a high tillering rate (Somson, 1984).

In conclusion, the vegetation patterns we recorded in the two active rock glaciers sharply differed from both the adjacent stable areas and from an inactive rock glacier, probably because of the stressful conditions associated with substrate movement. Highly unstable sites in active rock glaciers were easily recognized by the absence of mosses and lichens. In contrast, the distributional pattern of vascular species could not be directly related to surface instability but depended on a combination of environmental factors, mainly substrate texture and movement intensity, with slope angle playing a minor role in this respect. Further research is needed to shed light on the ecological adaptation of alpine species to different combinations of movement, substrate texture, and slope.

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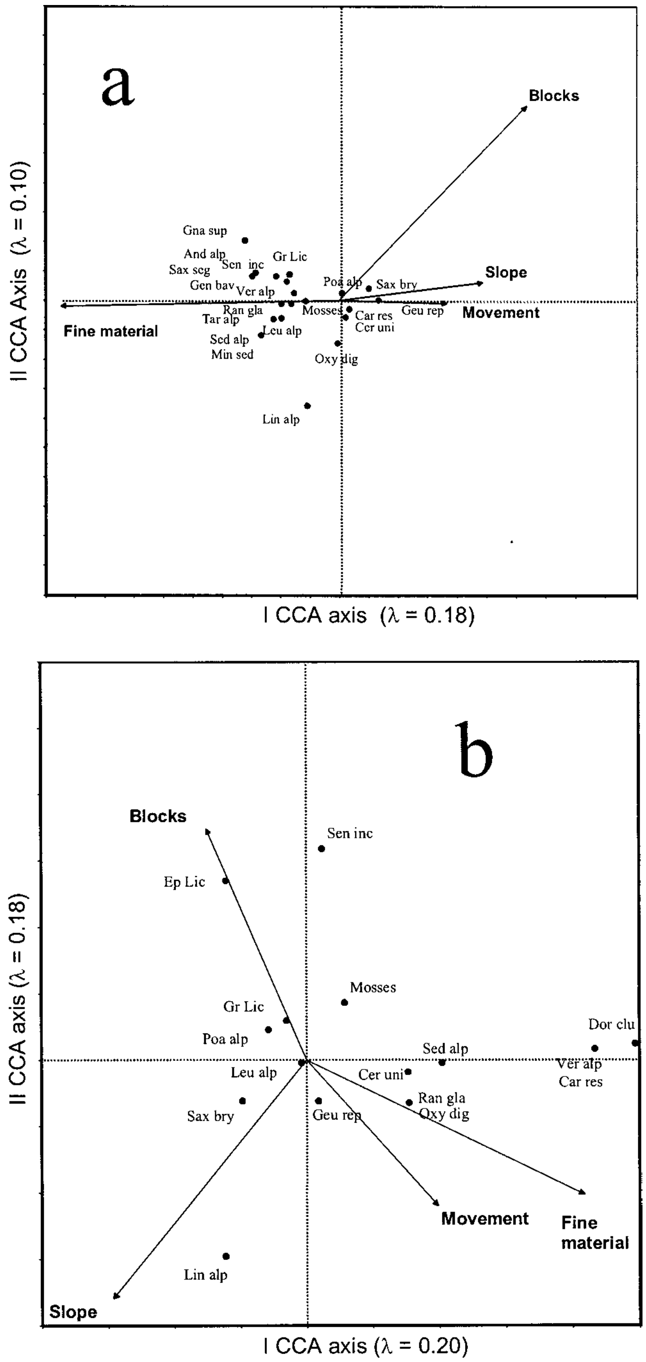

FIGURE 2. Biplot ordinations of species (including cryptogam groups) and environmental variables on the first two CCA axes for Pisella (a) and La Foppa 1 (b). Axes eigenvalues are in brackets. Species abbreviations: Androsace alpina (And alp), Cardamine resedifolia (Car res), Cerastium uniflorum (Cer uni), Gentiana bavarica (Gen bav), Geum reptans (Geu rep), Gnaphalium supinum (Gna sup), Leucanthemopsis alpina (Leu alp), Linaria alpina (Lin alp), Minuartia sedoides (Min sed), Oxyria digyna (Oxy dig), Poa alpina (Poa alp), Ranunculus glacialis (Ran gla), Saxifraga bryoides (Sax bry), Saxifraga seguieri (Sax seg), Sedum alpestre (Sed alp), Senecio incanus (Sen inc), Taraxacum alpinum (Tar alp), Veronica alpina (Ver alp), *Mosses, ground lichens* (Gr Lic)*, epilithic lichens* (Ep Lic).

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