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Soil moisture and the distribution of giant Andean rosettes on talus slopes of a desert paramo

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ABSTRACT: The distribution of giant Andean rosettes and soil moisture content during the dry season were studied in blocky and sandy talus slopes of the high Venezuelan paramo between 4335 and 4400 m. Rosette plants were virtually restricted to blocky talus and to areas downslope from isolated boulders embedded in sandy talus. Plant roots always grew upslope and beneath stones. Water content at the soil surface was 10 to 20 times greater under blocky talus and beneath boulders than in contiguous, bare sandy talus. The soil surface in the latter was very dry (≤ 1 % water) when sampled both in 1987 and 1989. Soil moisture increased sharply with depth in all locations sampled, but always remained substantially higher below stones even at 20 cm depth. The amount of water available for plant growth above the permanent wilting point (PWP = –1500 kPa) was also significantly greater under stones and boulders. Soil texture was similar (sand to loamy sand) in both talus types. Organic matter content was slightly higher in blocky talus, but its effects on water retention at PWP were minor, and could not be used to explain the observed differences in field moisture. Soil profiles in sandy talus were of a Typic Cryorthent, while the blocky talus was underlain by a fragmental Entic Cryumbrept. Several dry-season records of soil temperature show that both the maxima and minima were somewhat lower under stones, but the differences with sandy talus were minor, and probably did not affect soil moisture. The higher water content found under stones and blocks could result from 3 processes. During precipitation, water readily flows over the impervious stone surfaces, and becomes concentrated in the sandy soil matrix found between and beneath stones. Afterwards, reduced water losses by evaporation occur due to the insulation provided by the superficial openwork layer of stones, which prevents capillary rise to the talus surface. In addition, falling temperatures at sunset could result in condensation in the hollow spaces between stones. Andean rosettes colonize blocky talus areas, and their roots grow under the stones, because soil there remains moist during the dry season, allowing plants to survive it more readily than in the desiccated bare sandy talus areas.

INTRODUCTION

Talus slopes form by the accumulation of loose rock debris of various sizes. They are common in alpine, arctic, and desert areas. Talus vegetation is usually sparse, especially on recent deposits. When present, plants are often associated with specific talus zones or substrate types. Several early studies found that plants commonly attain higher densities on talus covered by stones or large blocks (Cooper 1916, Harshberger 1929, Tansley 1939, Zotov 1940, Whitehouse 1951). Many ecological studies have also ascertained that vascular plants at high altitudes are frequently clustered about stones (Swan 1961, 1968, Hedberg 1964, Lauer & Klaus 1975, Pérez 1987a).

The association of vegetation with rocky talus substrates may result from different causes. An often adduced, but seldom investigated, reason is the greater *stability* of rock-accumulation areas (Leach 1930, Fisher 1952, McCune 1977, Lee & Hewitt 1982). Frequent slippage of a thin surficial talus layer in fine-debris areas can prevent seedling establishment and destroy plants already on the slope (Wardle 1972, Pérez 1985). Large blocks embedded in the slope are usually stable, thus areas sheltered by them become sites of preferential plant colonization. Another factor affecting plant distribution on talus is *soil moisture availability*. Talus-slope surfaces usually remain very dry, as most of the water either evaporates or rapidly percolates through the talus debris (McCune 1977). However, fine-grained material between and below stones can have a high moisture content (Cooper 1916, Touring Club Italiano 1958). This occurs because a cover of loose rocks, with large air spaces between,

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protects the soil beneath from evaporation by reducing the capillary movement of water to the surface (Harshberger 1929, Jenny 1930, Fisher 1952, Tranquillini 1964). Weaver (1919) experimentally determined that short-term water losses from talus covered by coarse gravel were 8 times lower than those from uncovered soil. Despite the apparent significance of soil moisture availability for plant distribution on taluses, no data on soil-water content under rocks seem to have been published. In deserts, preferential seedling growth next to 'nurse rocks' has been ascribed to favorable moisture conditions and protection against drought stress (Parker 1987). Evenari et al. (1975) also considered that moist soil pockets below stones in the Negev (S. Israel) could be the main water source for several species of desert shrubs during the dry season.

Alternatively, higher plant densities on rocky talus could be attributed to differences in *soil temperatures*. Walter & Medina (1969), trying to explain the distribution of small forests of the tree *Polylepis sericea* in the Venezuelan Andes, proposed an unsubstantiated hypothesis whereby blocky taluses could provide favorable (i.e. higher) substrate temperatures, and thus would be preferentially occupied by trees.

This report will focus on the association of a species of giant caulescent Andean rosette (*Coespeletia timotensis* Cuatr.) with areas of stone accumulation on talus slopes of the Páramo de Piedras Blancas (Venezuelan Andes). The ecological significance of the first factor cited above (i.e. greater stability of blocky talus) for these plants has already been established. Measurements of slope movement taken since 1980 on a large talus cone show that fine-debris areas shift downslope nearly 12 times faster (25.1 cm yr^{-1}) than blocky talus sections (2.2 cm yr^{-1}), which are densely covered by giant rosettes (Pérez 1985, 1986, 1988). Elsewhere in the paramo, Andean rosettes of many species also germinate and grow next to rocks apparently because these provide shelter against the intense disturbance by needle-ice growth that affects bare soil areas (Pérez 1987a). Several authors (Herrmann 1970, 1971, Cardozo & Schnetter 1976, Pérez 1987b) have indicated that soil moisture deficit may significantly affect the regional and local distribution of giant rosettes in the most arid paramos of the northern Andes. Based on a limited data set from Piedras Blancas, Pérez (1987a) showed that soil water content below isolated stones was much greater than in adjacent uncovered, level ground, thus suggesting that soil moisture variation could also help produce the observed contrasts in density of Andean rosettes over paramo talus slopes. No microclimatic data comparing talus substrates are available, although Azócar & Monasterio (1980) and Pérez (1989) studied the effects of a canopy cover of *Polylepis* trees and giant Andean rosettes, respectively, on air and soil temperatures of talus slopes in the paramo.

This study concentrated on the moisture content and temperature regimes of talus slopes in the Páramo de Piedras Blancas; its specific goals were to (1) investigate the spatial distribution of Andean rosettes in relation to areas of blocky and sandy talus; (2) compare the soil water content of these 2 contrasting talus types during the dry season; (3) analyze the profiles and some of the soil properties in these 2 talus zones; (4) examine their soil temperature fluctuations; (5) contrast the moisture content (also in the dry season) beneath isolated, talus-embedded blocks, and the adjacent fine, uncovered talus.

STUDY AREA

The Páramo de Piedras Blancas is in the Sierra de La Culata (NW Venezuelan Andes), at 8° 52′ N, 70° 54′ W, and above 3700 m (Fig. 1A, B). Piedras Blancas is a relatively arid paramo (*páramo desértico*), which receives about 800 mm annual precipitation. Nearby stations have a strongly unimodal regime: >100 mm fall monthly during the rainy season (from about May to August), while the drier months (December to March) have averages of <20 mm (Fig. 1C, D). The interannual variability of precipitation is greatest in the drier paramo areas; it amounts to ≤ 20 % in the highest stations, where yearly totals of <700 mm are often recorded (Andressen & Ponte 1973). Precipitation occurs mainly as rain, although snow and hail are frequent, especially during the rainy season; snow cover is discontinuous and thin (<4 cm), and usually melts within 24 h. Evaporation data are scant for the high Venezuelan Andes, but indicate an overall annual moisture deficit (greater evaporation than precipitation) above ca 4000 m. At Mucubají (3550 m) and El Aguila (4150 m), yearly evaporation is 833 and 846 mm, respectively. Evaporation is highest during the dry season, when values vary from 85 to 110 mm mo^{-1} (Baruch 1976) (Fig. 1C, D). Evaporation is also influenced by aspect, due to differential slope insolation: E- and SE-facing slopes are warmer and drier, as they receive about 15 % more radiation than W- and NW-facing aspects (Andressen & Ponte 1973). The opposing seasonal alternations of precipitation and evaporation (Fig 1C, D) result in a pronounced drought for 4 to 6 mo, during which soil moisture is very low (Pérez 1987b).

Due to its equatorial position and altitude, Piedras Blancas experiences marked daily temperature fluctuations. Air temperatures commonly reach minima of −5 to −11° C and maxima of 15 to 25 °C during the dry season. The diurnal amplitude is considerably

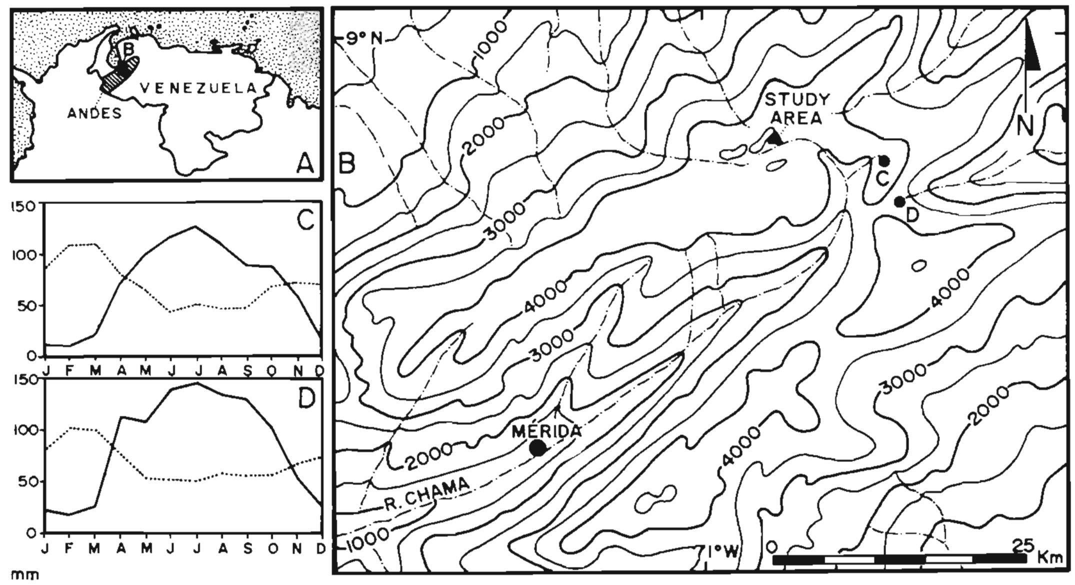

Fig. 1. (A) Location of the Venezuelan Andes.(B) Generalized map of the NW Venezuelan Andes; contour interval 500 m. Study area is shown by a dark triangle. (C) and (D) indicate nearby meteorological stations. (C) Climadiagram for El Aguila, 4150 m. (——) Precipitation, mm (1953 to 1974; annual mean: 820 mm). (·······) Evaporation, mm (1969 to 1974; annual mean: 846 mm). (D) Climadiagram for Mucubají, 3550 m. (——) Precipitation, mm (1966 to 1974; annual mean: 1017 mm). (·······) Evaporation, mm (1966 to 1974; annual mean: 833 mm). Adapted from Baruch (1976)

reduced during the rainy season, due to persistent cloud cover. About 325 to 350 daily freeze-thaw cycles occur per year in the area. This causes recurrent formation of needle ice, a type of ground frost (Pérez 1984, 1987a).

Soils have developed on igneous and metamorphic rocks, and belong mainly to the Entisol, Inceptisol, and Histosol orders. Small saturated areas on the floodplains along the larger creeks and next to glacial tarns have Typic or Terric Cryosaprists and Humic Cryaquents. Steep talus slopes are commonly occupied by Typic and Lithic Cryorthents, while more gentle slopes are associated with Lithic and Typic Cryochrepts (Pérez 1991). Paramo soils are usually shallow, have a low organic matter content, and a coarse texture with a large percentage of gravel and sand. Their fine fraction is mostly silt, with little clay (Pérez 1984, 1987a). The abundance of silt particles is mainly caused by the mechanical weathering of soil grains by repeated frost action.

Extensive talus slopes are found above ca 4100 m, below large rockwalls. This study examined a large, SE-facing talus cone. The slope has a length of over 400 m and extends from 4260 to 4450 m elevation. Slope angle in the active talus varies between 26 and 38.5°; the lower gradients are found at its basal section. The cone is flanked at the sides by 2 cliffs, which contribute debris to its surface. The talus fragments are made up of pegmatitic granite and amphibolitic schist. The slope surface presents a complex spatial arrangement of textural types, which, on the basis of mean particle size, have been previously classified into gravelly sand, small rocks, and large stones (Pérez 1986). This study examined only the finest (first) and coarsest (last) of these 3 talus textures. Due to gravity sorting, both the percentage of the slope occupied by large stones, and their average size, increase towards the base following a logarithmic function (Pérez 1986).

High paramo vegetation is characterized by several species of caulescent Andean rosettes (Asteraceae, Heliantheae, subtribe Espeletiinae), associated with many types of herbs and nanoshrubs (Vareschi 1970). Prominent among the rosettes is *Coespeletia timotensis*, the plant under study here. *C. timotensis* has a thick single monopodial stem ending in a dense crown of pubescent, evergreen leaves. The terminal, apical bud produces new leaves which eventually shrivel and dry but remain tightly attached to the stem as an insulating sheath (Cuatrecasas 1986). Like other Andean rosettes, *C. timotensis* develops continuously, yearround, but shows a marked seasonal periodicity, with growth rates during the dry season being only about 70% of those during the rainy season (Smith 1981, p. 23). This tall monocaulic rosette occurs in the Venezuelan Andes in dense woodlands above 4000 m, and as isolated individuals up to 4600 m (Pérez 1987b). In Piedras Blancas, *C. timotensis* rosettes attain a maximum height of 3.5 m (Fig. 2).

Fig. 2. Páramo de Piedras Blancas, 4335 m. View of the blocky, basal talus section, densely covered by rosettes of *Coespeletia timotensis*. The L transect crosses the picture at the bottom, the LM transect through the rosette cluster in the middleground center (see text for details). The person is 165 cm tall. Source rockwalls of amphibolitic schist are visible in the background. January 1990

METHODS

Field techniques. Percent ground cover by rosettes and other plants was determined along 5 point-intercept transects ranging in length from 36 to 106 m; sampling points were 50 cm apart. Transects were perpendicular to the slope direction and were evenly distributed from the talus apex to its base. They will henceforth be called upper (U), upper middle (UM), middle (M), lower middle (LM), and lower (L) transects. Rosette density was measured along four 4 m wide belt transects, extending 2 m above and 2 m below the U, UM, M, and LM belt transects. The substrate type associated with each rosette on these plots was noted. Plant density was obtained in the lower talus on a 400 m^2 (20 × 20 m) plot occupied by large blocks with some soil patches in the intervening spaces. In addition, rosette density was determined on three 100 m^2 (10 × 10 m) quadrats, each located on one of the talus textures mentioned above. Ten Andean rosettes, mainly of seedling size, were excavated in an area covered by large stones, and their roots examined in relation to adjacent rocks. Stones were carefully removed from the talus, and the soil matrix dug up by hand and with a small trowel. All roots from the smaller rosettes appeared to have been recovered; a few roots thinner than about 1 mm may have been overlooked in the largest, most deeply rooted individual. Specimens of the most common plant species were collected for later identification. Plant nomenclature follows Vareschi (1970).

Field moisture content was sampled during 2 dry seasons; a total of 170 samples (90 in 1987, 80 in 1989) were collected. On December 29, 1987, 60 paired surface-soil (0-5 cm depth) samples were taken; 30 from clast-covered talus and 30 from adjacent bare sandy areas in the upper talus (4360 to 4400 m). Subsoil samples (10-15 cm depth) were also collected in sandy areas. Paired samples were 1 to 2 m apart. The thickness of the surficial openwork layer of stones was measured at each blocky talus site. On December 31, 1989, 5 replicate paired profiles were sampled, 1 to 2 m apart, on the same 2 textures in the lower talus (4335 to 4370 m); samples were taken at 4 depths (0-5, 5-10, 10-15, and 15-20 cm). Two soil profiles were excavated and examined in contiguous bare gravelly sand and blocky talus areas. Profile soil samples were collected with a 125 cm^3 cylinder, which was pressed gently into the soil, so as not disturb its field bulk density.

On December 31, 1989, field soil moisture was investigated near and under 10 granitic blocks partly embedded in sand in the upper talus. Blocks were measured along 3 axes (*a* = longest, *b* = intermediate, *c* = shortest). Size (*a* axis) varied from 46 to 88 cm (mean: 63.9 ± 15.6 cm), and was limited by the ability of 2 people to move the boulders. Blocks were excavated and removed, and soil samples were taken from the area directly below the block center. Paired samples were gathered 1 to 2 m away, from the bare sandy talus. Samples were taken in both positions at 2 depths (0-5 and 10-15 cm). All moisture samples were kept in hermetically sealed containers until processed in the laboratory. Because Andean rosettes can greatly affect many soil properties including moisture content (Pérez 1987b, 1992), all samples were taken from non-vegetated areas.

Temperatures were continuously recorded with mechanical thermographs during three 7 d periods in

Table 1. Plant density and cover on the talus slope. Unless specified, data were gathered along belt and point-intercept transects parallel to slope contours

	Slope position				
	Upper	Upper middle	Middle	Lower middle	Lower
Transect length (m)	36	44.5	66.5	106	100
% Total plant cover	0	0	11.3	17.0	24.0
% Cover by *Coespeletia timotensis*	0	0	9.0	12.3	23.0
Density of *C. timotensis* (rosettes per 100 m^2)	0	0	8.3	10.4	56.8[a]

[a] Data from the 20 × 20 m plot

the dry seasons of 1981–82, 1987–88, and 1989–90. Thermographs were cross-calibrated prior to going to the field and briefly checked again before installation; the probable measurement error after empirical tests is ±0.5 °C (Pérez 1989). Air temperatures (+10 cm) were measured under a white shelter placed on sandy talus; air could circulate freely around this thermograph. Soil temperatures were taken in contiguous, non-vegetated sandy and blocky talus areas. Thermograph sensors were at 20 cm depth (10 cm openwork + 10 cm sandy matrix in blocky talus) in 1982 and 1987, and at 30 cm depth (15 cm + 15 cm in blocky talus) in 1989.

Analytical procedures. Soil moisture was measured gravimetrically by oven-drying the samples overnight (16 h) at 105 °C. Water content was calculated with the equation [(wet soil weight − dry soil weight)/dry soil weight] and expressed as a percentage of the dry soil weight. Soils were rubbed by hand and sieved to remove the gravel fraction (>2 mm); this is given as a percentage by weight. Organic matter content was assessed with the loss of weight on ignition at 375 °C. The mineral soil fraction was then sieved through a 9-mesh series (1.4, 1, 0.7, 0.5, 0.355, 0.25, 0.18, 0.125, 0.09 mm). The content of finer grains was determined with an ASTM 152H hydrometer using a Calgon solution as dispersing agent. Moisture content for the talus soils at the permanent wilting point (PWP = −1500 kPa) was estimated with a multiple linear regression which used the percentages of organic matter (X_1) and of fines (≤ 0.05 mm; X_2) as independent variables (cf. Nielsen & Shaw 1958). This regression was derived from 33 soil samples previously collected from the same talus slope (Pérez 1987b); the water content of these 33 samples at −30 and −1500 kPa was calculated with the pressure plate method (Richards 1965). The regression ($Y = 1.319X_1 + 0.069X_2 - 0.082$) was significant at $p < 0.001$, had a multiple correlation coefficient of 0.935, and could 'explain' about 87.5 % of the observed variation in moisture at PWP. Additional tests were performed for the soil profile samples. Soil colors were determined for dry samples with the Munsell charts. Soil pH was measured by electrode in a 2:1 water paste. Soil structure and consistence (dry and wet) were determined following the procedures in Soil Survey Staff (1975).

RESULTS

Plant distribution and characteristics of rosette roots

There was a clear gradient of increasing rosette density and cover down the slope. The uppermost talus was devoid of any vegetation. Cover by plants other than *Coespeletia timotensis* remained below 5 % everywhere. Rosette density rose abruptly at the talus base (Table 1, Fig. 2). This trend parallels the logarithmic increase in particle size, and in substrate stability, down the talus (Fig. 3). In fact, rosette density was not associated with slope position per se, but was instead a

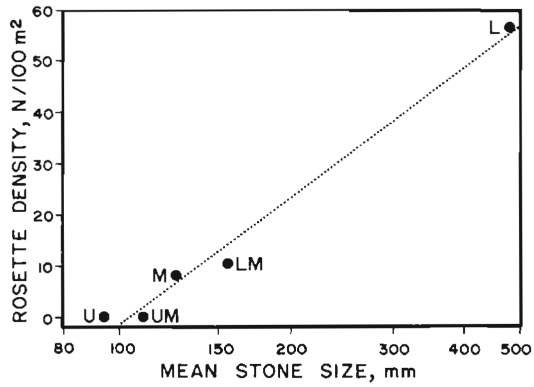

Fig. 3. Relationship between average stone size (length of longest axis in mm) on the talus surface and density of rosettes of *Coespeletia timotensis* (plants per 100 m^2) down the slope. Key for slope positions: U = upper, UM = upper middle; M = middle; LM = lower middle; L = lower. Regression slope is shown by dotted line: $Y = 83.543 \log_{10} X - 168.456$; $r^2 = 0.984$ ($p > 0.001$)

Table 2. *Coespeletia timotensis*. Density (plants per 100 m^2), stratified by talus textures, along the middle, lower middle, and lower transects; and number of rosettes (in parenthesis) growing at the edge of isolated blocks embedded in fine-debris talus

Surface type	Slope position (transects)		
	Middle	Lower middle	Lower
Gravelly sand	0	0	–
Small rocks	3.0	3.3	–
Large stones	16.7	9.8	56.8
Isolated blocks	(0)	(18)	–

function of the increasing proportion of the talus surface occupied by large rocks down the slope, which made up only 19.3 and 11.5 % of the U and UM transects, but covered 45.0, 53.1, and practically 100 % of the M, LM, and L transects, respectively (Pérez 1986).

Nearly all the rosettes were found on talus areas of accumulation of large stones or downslope from sizable single boulders firmly embedded in finer sandy material (Table 2, Fig. 4). This association of rosettes with coarser textures was also evident on the 100 m^2 quadrats: 26 plants were found on blocky talus, but only 9 on small rocks, and none on gravelly sand. The sand plot had only one cushion herb (*Arenaria musciformis* Pl. & Trian.), a grass (*Agrostis breviculmis* Hichc.), and 2 nanoshrubs (*Castilleja fissifolia* L. f., and *Hinterhubera imbricata* Cuatr.) which were growing at the downslope edge of small stones. These species were also present in the other 2 plots, which also contained *Helleria fragilis* Luces, *Gnaphalium* spp., *Senecio sclerosus* Cuatr., and *Senecio imbricatifolius* Sch. Bip.

The rosettes excavated were growing in an area completely covered by stones, where no fine material was exposed at the surface (Fig. 5). Stone size (*a* axis) varied from 8–10 to 30–35 cm (mean of ca 20 cm); most clasts were granitic. Plant height above the ground varied from 9 to 51 cm (mean = 20.8 cm). Maximum root length was 14 to 58 cm (mean = 24.4 cm), but rooting depth (measured normal to the slope surface) was only 6.5 to 33 cm (mean = 12.0 cm). Root growth patterns were clearly affected by the stones. All roots

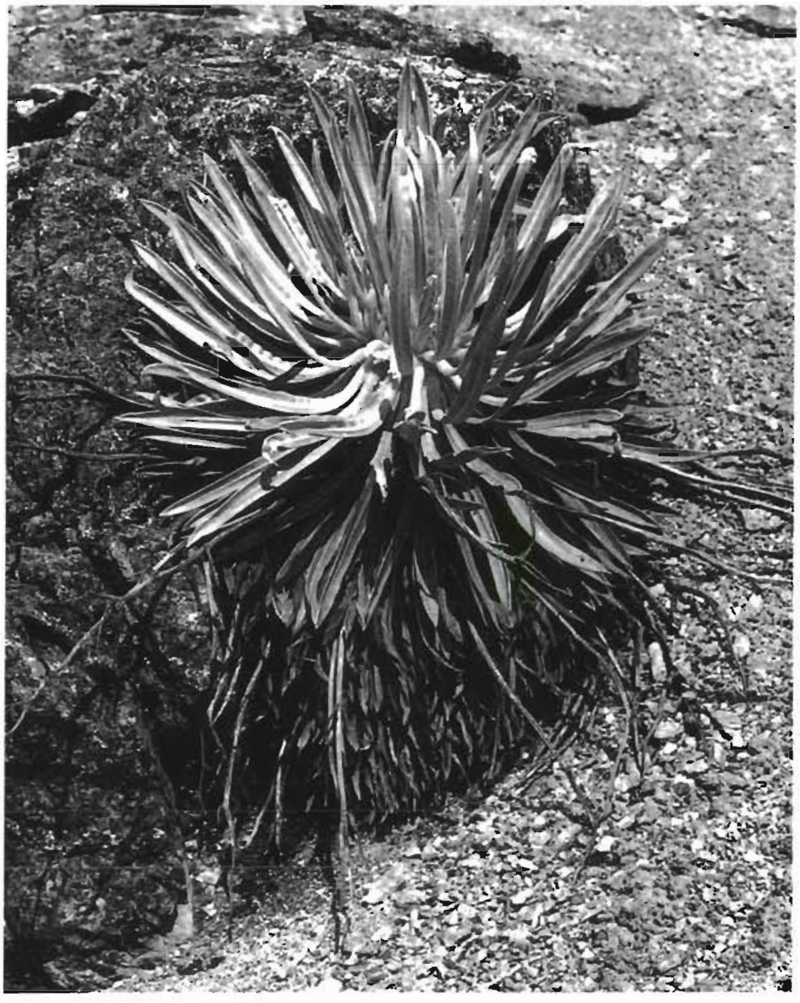

Fig. 4. *Coespeletia timotensis*. A 115 cm tall rosette rooted downslope from, and under, a large granitic boulder partly embedded in a steep, gravelly sand talus. Páramo de Piedras Blancas, 4540 m. December 1982

Fig. 5. *Coespeletia timotensis*. A 23 cm tall seedling rooted in a blocky talus area; the pocket knife is 8 cm long. Páramo de Piedras Blancas, 4345 m. December 1982

were asymmetrical: a thick (≤3.5 cm) taproot grew upslope under the nearest stone, and upon reaching the rock center or base, branched out into a dense fibrous mass of fine rootlets, which descended vertically or perpendicularly to the talus surface into the interstitial soil between clasts (Fig. 6). In a few cases, dense root mats clung tightly to the rock undersurface. Many paramo plants, as well as rosette seedlings on other types of substrates, also grow downslope from, and have roots beneath, stones (Pérez 1987a).

Field moisture content of talus areas

When sampled during mid-dry season in December 1987, soils in bare, sandy talus were considerably drier than those under adjacent rocks. Surface (0 to 5 cm) soils in the first location were completely dry and dusty, while those in the second were visibly moist and contained nearly 20 times as much water (Table 3A); the differences were given as highly significant ($p < 0.001$) by a Mann-Whitney *U*-statistic. Soil moisture increased substantially with depth in the bare sandy talus, but soils there between −5 and −10 cm were still considerably drier than *surface* soils beneath clasts, which had almost twice as much water. The depth of the surficial openwork layer of blocks varied from 8 to 25 cm. Mean moisture content was higher in sites with a thicker stone cover. Twelve sites with an openwork layer >15 cm had a field moisture of 16.42 ± 8.07 %, while 18 sites with a layer <15 cm thick had a water content of 9.42 ± 3.64 %. These differences were also significant ($p < 0.025$).

In 1989, moisture values of surface soils in the 2 localities were nearly identical to those found in 1987. Mean water content increased with depth in both talus types, but the rise in moisture was considerably steeper and more uniform in all the profiles of bare sandy zones (Fig. 7). Soils at 15 to 20 cm depth in these areas contained 7 times as much water, on the average, as the surface (0–5 cm) layer, but under stones, moisture increased only about 20 % within the same vertical distance (Table 3B). Notwithstanding these trends, surface soils below clasts were still appreciably more moist than the deepest layer sampled in sandy talus; the latter had about 65 % less water than the former. Differences in moisture were significant ($p < 0.01$) within all soil layers compared.

Soil properties and soil profiles

It is evident that soils below stones had a greater moisture content than those not protected by clasts. However, in order to establish that the presence of a stone cover is, indeed, responsible for the observed dif-

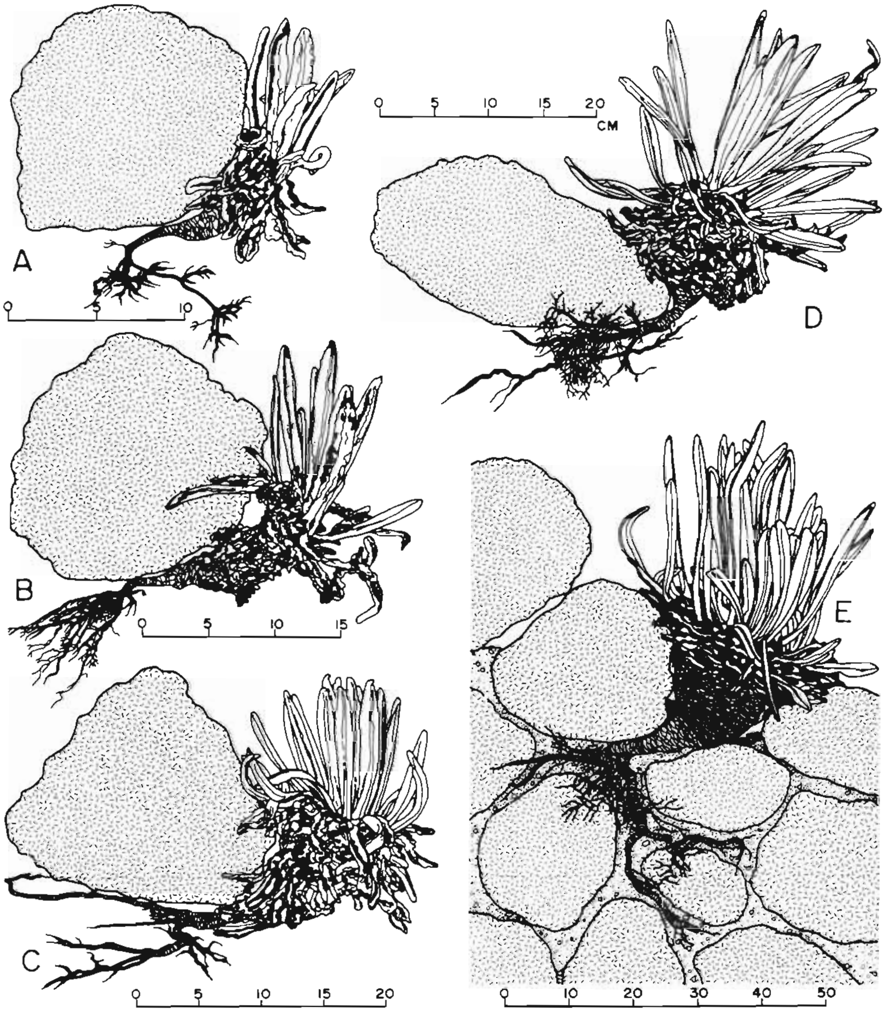

Fig. 6. *Coespeletia timotensis.* Cross-sections showing the relationship between the roots of seedlings (A to D) and adult rosettes (E) with granitic talus blocks. All plants were growing in areas similar to that shown in Fig. 5. Only one rock is shown for Plants (A) through (D), which were found in a similar situation to that of Rosette (E). Plant and stone sketches were drawn from photographs; all scales are in cm

ferences in soil water content, it is critical to examine some soil properties which affect water retention capacity, since moisture variation could be due to inherent differences in pedological characteristics. It is known that water storage in soils is mainly affected by texture and organic matter content (Pitty 1979). Ten pairs of samples were randomly selected from the upper-talus soils collected in 1987 and analyzed (Table 4). Gravel content was equally high (nearly 45 %) in both talus types. The soil fraction (< 2 mm) in the 2 talus areas had a very high content of sand (about 90 %), and both soils were classified as sands or loamy sands. The particle-size distributions showed little variability between talus types, and were simply indistinguishable (Fig. 8A, B). The average percentage of fines was similar in both talus areas, albeit a little lower under clasts (Table 4). Organic matter content was low, about 2 %, in the 2 localities. Soils below stones had a slightly higher content of organic material, but a comparison with sandy areas showed that the differences, like those of other soil properties, were not statistically significant.

The 5 paired profiles sampled in 1989 in the lower talus had similar soil characteristics (Table 5). Gravel content varied from about 34 to 44 %; it increased slightly with depth under stones, but had an irregular trend in adjacent sandy zones. The content of fine grains was low everywhere, between ca 9 and 14 %, but was somewhat higher below clasts. No statistically significant differences in texture could be detected within any of the 4 sampled soil layers. The particle-size distributions closely resembled those found 2 yr earlier in the upper talus (Fig. 8C, D). Overall soil texture showed little variability, although this was somewhat greater than in the previous population of samples; this is probably a function of the larger sample size in 1989. Organic matter content decreased gradually with depth under stones, but was significantly higher, in all 4 levels examined, than in bare sandy talus (Table 5).

Table 3. Moisture values for soils in blocky talus and adjacent gravelly sand areas: average field moisture content (± SD), and estimated percentage of available water above the permanent wilting point (PWP) (in parenthesis). Values given as a percentage of dry soil weight. (A) Dec 29, 1987, upper talus; sample size: 30. (B) Dec 31, 1989, lower talus; sample size: 5. Significance levels for comparisons between sampling positions are for a Mann-Whitney *U*-test

	Sampling depth (cm)	Sampling positions	
		Blocky talus	Gravelly sand
A	0–5	12.22 ± 6.69 (8.75)	0.62 ± 0.17^a (0)^a
	10–15	–	6.60 ± 2.24 (3.84)
B	0–5	12.14 ± 3.20 (6.99)	1.05 ± 1.14^b (0)^b
	5–10	14.18 ± 4.98 (9.47)	4.46 ± 1.39^b (2.33)^b
	10–15	14.65 ± 3.43 (10.30)	6.47 ± 0.95^b (4.21)^b
	15–20	14.79 ± 3.07 (10.63)	7.37 ± 0.72^b (4.75)^b

$^a p < 0.001$; $^b p < 0.01$

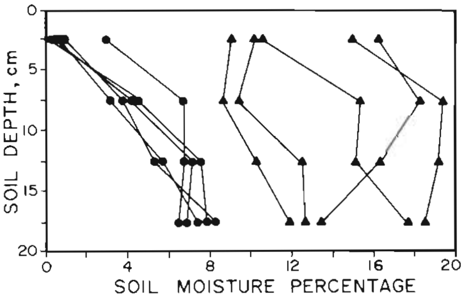

Fig. 7 Variation of field moisture content with depth as shown by 5 paired samples taken in adjacent areas of gravelly sand (●) and blocky talus (▲). Soil moisture expressed as a percentage by weight of dry soil. Values are shown at the mid-point of the sampled layer. Samples taken on Dec 31, 1989

Table 4. Some physical properties of soils in blocky talus and adjacent gravelly sand areas. Values are averages of 10 samples; standard deviation indicated. Samples collected in the upper talus in December 1987

Soil property	Sampling depth (cm)	Sampling position	
		Blocky talus	Gravelly sand
% Gravel by weight	0–5	42.69 ± 5.81	44.24 ± 2.93
	10–15	–	44.23 ± 3.26
% Fines (< 0.05 mm)	0–5	11.61 ± 4.18	13.41 ± 2.79
	10–15	–	12.35 ± 3.26
% Organic matter	0–5	2.09 ± 0.94	1.80 ± 0.36
	10–15	–	1.51 ± 0.38

The profiles indicate that the talus character is maintained with depth (Table 6). A striking, nearly ubiquitous feature of sandy talus areas was a 3 to 5 cm thick, loose AC upper horizon with crumb structure and high porosity. This is a *nubbin* layer (Washburn 1980) of small soil buds with irregular microtopography, generated by repeated needle-ice activity. The fine-grained talus was underlain by a sandy-skeletal, siliceous Typic Cryorthent with a simple AC/C profile and lithological discontinuities associated with sharp changes in particle-size distribution (Ronchetti 1962, Lee & Hewitt 1982). These indicate that the soil has evolved on the steep talus primarily by episodic, gravitational truncation and cumulization (Table 6A). The blocky talus had a 20 to 35 cm thick, openwork layer with large angular, mostly granitic clasts. This overlay a fragmental Entic Cryumbrept with a coarse sandy-skeletal siliceous matrix which occupied interstitial areas between stones (Table 6B). Blocks were found throughout the whole profile, but average stone size decreased with depth, as many small (ca 5 cm long) fragments were found below the openwork layer. This is due to the 'sieving effect' (Pérez 1986), whereby small particles arriving from upslope fall within the openings between large clasts at the surface, and gradually fill the voids. A comparison indicates that the profile in gravelly sand had lighter colors, higher pH values, and greater bulk densities, than that in the stone area. These differences seem to be due mainly to the greater organic matter content found in all horizons of the blocky talus profile.

Soil water available to plants

Moisture availability in soils can be calculated by subtracting the amount of water held at the permanent wilting point (PWP) from the water stored at field capacity (FC); these levels occur at −1500 and −30 kPa soil water tension, respectively (Foth 1990). Such measurements are likely to give a good estimate of the water actually available to Andean rosettes under field conditions, since the lowest leaf water potential values recorded for *Coespeletia timotensis* in Piedras Blancas during noon hours of the dry season are only slightly below −1500 kPa (Baruch 1976, p. 76).

The amount of water remaining in paramo soils at PWP was low in both zones, although it was slightly higher (3.47 to 5.15 %) in stone areas than in sandy talus (2.13 to 3.21 %) and in all surface horizons. These differences are probably related to the variation in organic matter content. The amount of water actually

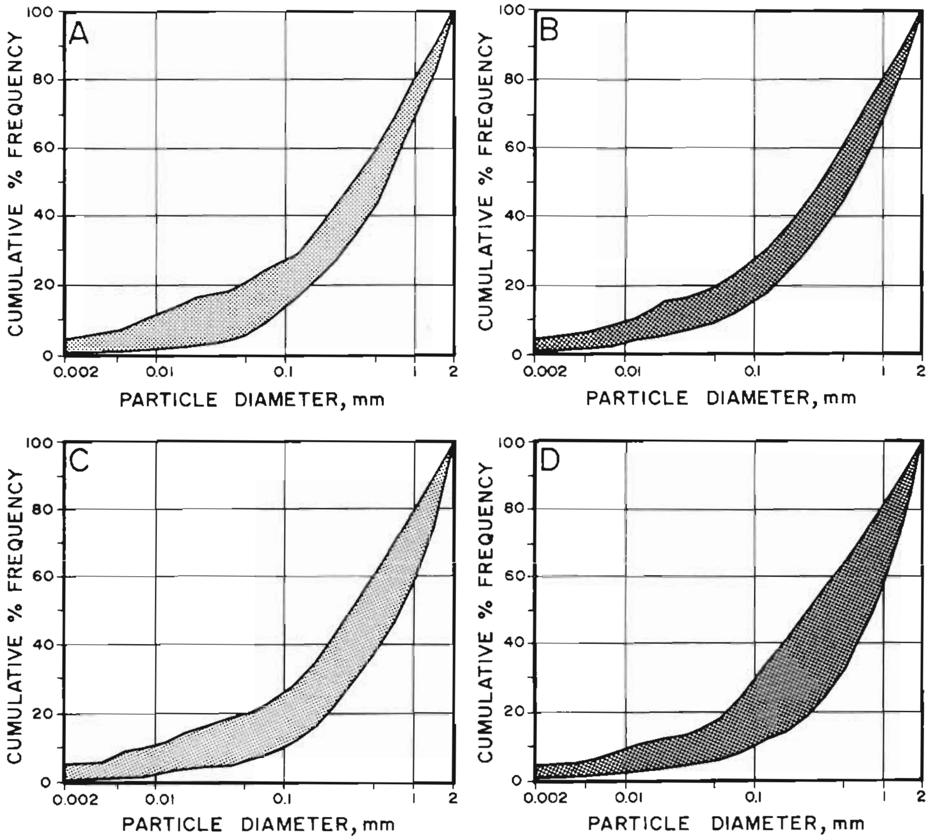

Fig. 8. Particle-size distributions for talus soils. (A) Blocky talus, (B) Paired samples from gravelly sand areas adjacent to (A). Each graphic envelope corresponds to 10 surficial (0–5 cm depth) samples, collected on Dec 29, 1987 in the upper talus (see Table 4). (C) Blocky talus; (D) Paired samples from gravelly sand areas adjacent to (C). Each graphic envelope corresponds to 20 samples, gathered from the upper 20 cm on Dec 31, 1989 in the lower talus (see Table 5)

available for plant growth in December 1987 and 1989 was estimated by subtracting the moisture content at PWP from the field moisture values; this calculation indicates several significant points (Table 3). Surface soils in sandy talus had absolutely no water available for plant growth, but surface soils under stones had a considerable store of usable moisture (ca 9 % in 1987, 7 % in 1989). *Available* moisture increased with depth in both slope areas, but remained substantially higher in blocky talus, which had 4 times more water at 5 to 10 cm depth, and more than twice as much between 10 and 20 cm depth (Table 3B). A series of *U*-tests indicated that all the differences between paired samples were statistically significant.

Table 5. Some physical properties of soils in blocky talus and adjacent gravelly sand areas. Values are averages of 5 samples; standard deviation indicated. Samples collected in the lower talus in December 1989. Significance levels of a comparison between sampling positions are for a Mann-Whitney *U*-test

Soil property	Sampling depth (cm)	Sampling position	
		Blocky talus	Gravelly sand
% Gravel by weight	0–5	37.55 ± 6.31	34.34 ± 7.08
	5–10	40.52 ± 5.92	43.02 ± 3.83
	10–15	41.79 ± 7.49	39.53 ± 3.59
	15–20	43.49 ± 7.32	36.23 ± 7.51
% Fines (< 0.05 mm)	0–5	13.28 ± 4.19	12.70 ± 3.64
	5–10	14.00 ± 4.38	9.26 ± 2.58
	10–15	12.92 ± 3.42	10.44 ± 2.25
	15–20	12.98 ± 2.16	10.62 ± 3.37
% Organic matter	0–5[a]	4.25 ± 2.75	1.65 ± 0.62
	5–10[a]	2.92 ± 1.02	1.25 ± 0.47
	10–15[a]	2.70 ± 0.97	1.16 ± 0.47
	15–20[b]	2.70 ± 0.95	1.46 ± 0.76

[a]$p < 0.01$; [b]$p < 0.05$

Field moisture content under talus blocks

Soil moisture below blocks was also higher than in adjacent uncovered areas. Differences in water content were greatest at the surface: soils under blocks had 10 times as much moisture as bare talus within the uppermost 5 cm, but only about 40 % more water between 10 and 15 cm depth. However, all the differences were significant (Table 7). Textural soil properties and organic matter content were practically the same in both sampling positions, and did not differ from those previously described for sandy areas (Tables 4 & 5); thus, estimated moisture at PWP was

Table 6. Soil profile descriptions. Soil terminology follows that of Soil Survey Staff (1975)

(A) Gravelly sand: Typic Cryorthent, sandy-skeletal siliceous, with a few (< 3%) small fragments of white pegmatitic granite. Slope angle 32°; altitude 4360 m. Plot devoid of vegetation

Horizon	Depth (cm)	Description
AC	0–5	Sand with 43.1 % gravel; soil fraction had 91.7 % sand and 8.3 % fines. Weak, medium crumb structure with loose dry consistence, generated by needle ice activity (nubbin layer); non-sticky, non-plastic wet consistence. Bulk density: 1.06 g cm^{-3} Dry color: 10YR 6.5/3, pale brown; pH: 5.0; 0.9 % organic matter. Abrupt wavy boundary to:
C1	5–35	Sand with 58.8 % gravel; soil fraction had 93.8 % sand and 6.2 % fines. Single grain, structureless; loose dry consistence; non-sticky, non-plastic wet consistence. Bulk density: 1.25 g cm^{-3} Dry color: 10YR 6.5/3, pale brown; pH: 5.5; 0.5 % organic matter. Diffuse wavy boundary to:
C2	35–80	Sand with 41.0 % gravel; soil fraction had 89.6 % sand and 10.4 % fines. Single grain, structureless; loose dry consistence; non-sticky, non-plastic wet consistence. Bulk density: 1.18 g cm^{-3}. Dry color: 10YR 7/3, very pale brown; pH: 5.3; 0.8 % organic matter. Gradual irregular boundary to:
IIC3	80–110+	Loamy sand with 63.2 % gravel; soil fraction had 83.2 % sand and 16.8 % fines. Weakly massive structureless; loose dry consistence; slightly sticky, slightly plastic wet consistence. Bulk density: 1.03 g cm^{-3} Dry color: 10YR 6/3, pale brown; pH: 5.2; 2.0 % organic matter.

(B) Blocky talus: Entic Cryumbrept; fragmental with a sandy-skeletal, siliceous matrix. Slope angle 31°; altitude 4355 m. Plot lacked any plant cover

Horizon	Depth (cm)	Description
-	25–0	Openwork layer of large, sharply angular clasts (most about 20 cm *a* axis, but up to 35–40 cm) of leucocratic, white to light gray, pegmatitic granite. A few (≤ 5 %) smaller melanocratic, dark-green fragments of amphibolitic schist with a silky sheen were also present.
A	0–5	Similar clasts to above, filled in by small (~5 cm) cobbles and a coarse matrix (53.4 % gravel; soil fraction: 86.8 % sand, 13.2 % fines); stones made up 50 to 70 % of total volume. Single grain, structureless; loose dry consistence; slightly sticky, slightly plastic wet consistence; moderately water-repellent. Bulk density: 0.88 g cm^{-3} Dry color: 10YR 4/2, dark grayish brown; pH: 4.6; 9.2 % organic matter. Abrupt wavy boundary to:
AC	5–23	Similar clasts and coarse matrix (38.7 % gravel; soil fraction: 85.4 % sand, 14.6 % fines). Single grain, structureless; loose dry consistence; non-sticky, non-plastic wet consistence, slightly water-repellent. Bulk density: 1.04 g cm^{-3} Dry color: 10YR 4.5/3, dark brown; pH: 4.65; 4.1 % organic matter Many rootlets of Andean rosettes present below 10 cm. Gradual irregular boundary to:
C	23–65+	Similar clasts and coarse matrix (43.7 % gravel; soil fraction: 84.6 % sand, 15.4 % fines). Single grain, structureless; loose dry consistence; non-sticky, slightly plastic wet consistence. Bulk density: 0.96 g cm^{-3}. Dry color: 10YR 5/3, brown; pH: 4.6; 3.5 % organic matter. A few fine rootlets of rosettes down to 40 cm depth.

similar in both sites. Subtracting the amount of water held at PWP from the field values indicated that available moisture was still greatest under the boulders; these differences were also significant. The bare sandy talus had no usable water at the surface, but some was still available for plants at depth; yet, deep soils below blocks had about 50 % more usable water. A comparison of Tables 3 & 7 indicates that moisture differences between blocks and bare sand were somewhat smaller than those reported for sandy and blocky talus.

Moisture content was examined in relation to block size. Linear regressions were run between water content under blocks and their 3 axial lengths. No association was found between boulder size and surface moisture, but water content at depth was directly dependent on block size. The best correlations were found with the *a* ($r = 0.635$) and the *c* axes ($r = 0.64$); however, a regression with block volume (defined as the product of $a \times b \times c$) gave better correspondence ($r = 0.66$, $p < 0.05$). Therefore, as block volume rises,

Table 7. Moisture values for soils beneath talus-embedded blocks and in adjacent bare areas: average field moisture content (± SD), and estimated percentage of available water above the permanent wilting point (PWP) (in parenthesis). Values given as a percentage of dry soil weight. Sampling date: Dec 31, 1989; sample size for each value = 10. Significance levels for comparisons between sampling positions are for a Mann-Whitney *U*-test

Sampling depth (cm)	Sampling positions Beneath blocks	 Bare sand
0–5	8.23 ± 1.38 (5.02)	0.81 ± 0.78^{a} (0)^{a}
10–15	9.93 ± 2.32 (7.36)	7.01 ± 1.24^{b} (4.80)^{c}

$^{a}p < 0.001$; $^{b}p < 0.0025$; $^{c}p < 0.01$

water content under the block increases at depth. This procedure, however, does not take into account the moisture level of the adjacent bare talus. An alternative approach was tried: a regression was run between boulder volume and the moisture *differences* (water content under blocks minus water content in adjacent bare areas) at 10–15 cm depth. Such correlation was highly significant ($p < 0.001$), and gave a higher coefficient ($r = 0.871$) (Fig. 9). This analysis indicates that as blocks increase in size, soils below them become substantially moister than the surrounding bare talus. The above regression accounts for 76 % (r^2) of the observed variability in water content.

Daily temperature cycles

The daily progression of air and soil temperatures on the talus had similar patterns during the 3 periods of record. Soil temperature fluctuations in 1987–88 were modest in both talus types; both maxima and minima were slightly lower below stones (*a* axis = 8 to 15 cm, mean of about 13 cm). Maxima there at –20 cm lie between 7.0 and 9.0 °C, while in bare sand varied from 7.8 to 9.4 °C. Freezing was not recorded in either talus type; minima under rocks were between 2.9 and 4.0 °C, and between 3.5 and 4.7 °C in sand (Fig 10A). The temperature records for 1982 and 1989–90 also show that blocky talus remained slightly cooler during the day and the night than bare sand.

In stone areas there was little interannual variability; rather, the most pronounced differences occurred between sunny and cloudy days. The diurnal amplitude was closely dependent on cloud cover: extreme temperature fluctuations took place under clear skies, while clouds decreased the daily range. The lowest minimum measured (January 28, 1982) was 2.5 °C; this was followed next morning by the highest maximum on record (10.8 °C) (Fig. 10B, left end of solid line). This happened during a prolonged period of exceptionally clear skies, when air temperatures climbed up to 23 °C. In contrast, 2 cold, cloudy days in January 1990 (Fig. 10B, right end of dashed line) produced a depressed curve, with little variation between the high (7.1 °C) and the low (5.4 °C). These last cycles are thought to be similar to those of the rainy season (see Pérez 1987c).

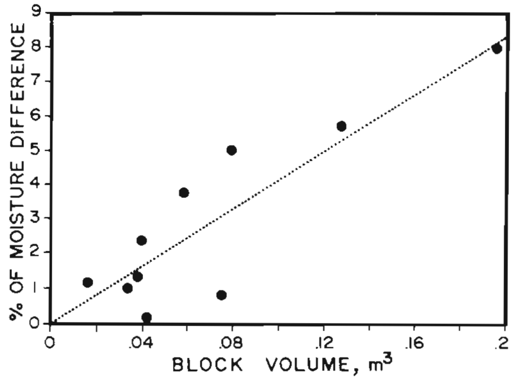

Fig. 9. Percentage of moisture difference (water content of soils under blocks minus water content of bare soils) between sandy soils from under isolated, talus-embedded blocks and from adjacent, uncovered talus areas. Block volume is the product of the 3 block axes ($a \times b \times c$). Moisture is expressed as a percentage by weight of dry soil. Samples taken on Dec 31, 1989. Dotted line shows regression slope: $Y = 41.981 \log_{10} X - 0.048$ ($p < 0.001$)

DISCUSSION AND CONCLUSIONS

Development of rosette roots was apparently influenced by the stones. Sharp bending of roots upslope is a common feature of talus plants, usually ascribed to surface instability (Weaver 1919, Fisher 1952, Kershaw & Gardner 1986). However, preferential upslope growth of roots in other rocky slopes has been attributed to moisture variability (Herwitz & Olsvig-Whittaker 1989). No data on the role of moisture in root growth in talus slopes is available, but Fisher (1952, p. 162) suggested that 'the great development of roots, as shown in their extended length, copious branching, and long root-hair zone, may be functionally related to the abundance of moisture found in the soil of the screes...' in New Zealand. In the Andean paramo, it appears that the asymmetrical and profuse root growth of giant rosettes beneath blocks is related both to the greater stability of stone areas (Pérez 1985, 1988) and to higher soil water content there.

A comparison of moisture variation with depth shows that the greatest differences in water content between

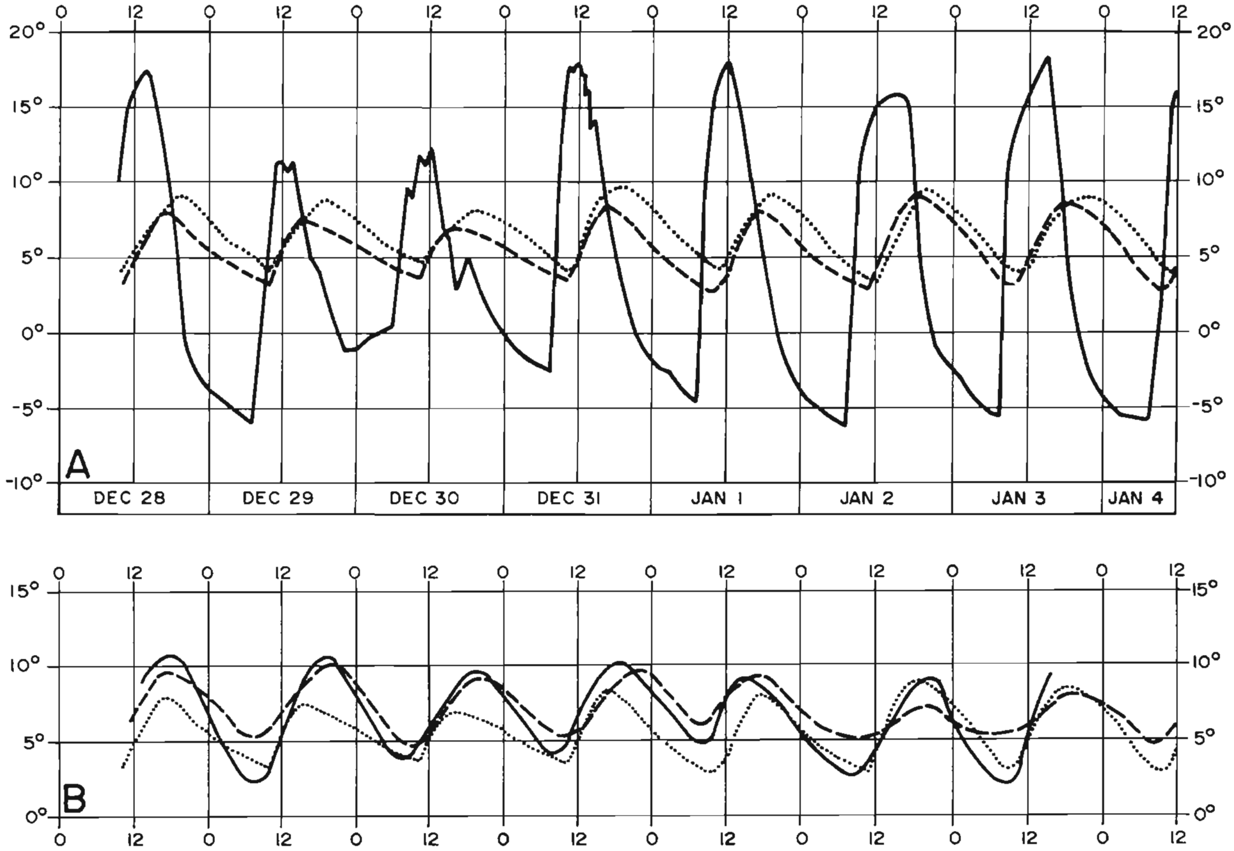

Fig. 10. Daily temperature fluctuations (°C) in talus slopes at Piedras Blancas. (A) 4350 m elevation; Dec 28, 1987 to Jan 4, 1988. (——) Air (+10 cm) temperature over sandy talus; (·······) soil temperature (-20 cm) in the same area; (– – –) soil temperature (-20 cm) in adjacent blocky talus. (B) Soil temperatures during the dry season in blocky talus areas at 4350 to 4365 m. (——) Jan 27 to Feb 2, 1982 (-20 cm); (·······) Dec 28, 1987 to Jan 4, 1988 (-20 cm); (– – –) Dec 29, 1989 to Jan 5, 1990 (-30 cm)

talus textures were found right at the soil surface. Because the upper soil layer in sandy talus remains physiologically dry (below the PWP) for several months, rosette seedlings with shallow, undeveloped roots would be particularly vulnerable to desiccation if they managed to germinate in open sandy areas, as they would find no available water there. Smith (1981) reported that Andean rosettes experience higher seedling mortality during the dry season, apparently due to desiccation. Thus, any edaphic features which increased moisture availability *near the ground surface* would multiply the chances of seedling germination and survival (Corey & Kemper 1968). The fact that some water was available at depth in sandy talus suggests that soil drought is an ecological problem primarily at the soil surface. That is, if a rosette seedling were, somehow, to become successfully established in open sand, it could then survive subsequent dry seasons by drawing moisture from deeper horizons, as its roots develop. In this view, soil drought would only affect plant establishment, and the beneficial role of rocks would mainly consist of extending favorable moisture levels, above the PWP, to the very talus surface, therefore allowing its colonization by rosettes.

The precise causes for the greater moisture under stones need to be determined. The analysis of soil properties demonstrated that this cannot be simply ascribed to pedological characteristics, since the slight variations of organic matter content could not effect sizable differences in soil waterstorage capacity. The impervious nature of stones on blocky talus areas would affect soil moisture content: as water runs off the rock surfaces, it infiltrates and becomes concentrated into the intervening interstices occupied by the sandy matrix (Cox 1933, Yair & Lavee 1974, 1976). A simple calculation shows that, since about 50 to 70 % of the volume in blocky talus was occupied by stones, water falling on these areas would be imbibed by the remaining 50 to 30 % of the soil matrix; thus the effective water delivery to it would be 2 to 3 times higher than in sandy talus. Another likely factor involved is the aforementioned ability of a rock cover to reduce water loss by evaporation at the ground surface. This is the basic premise in 'gravel mulching', an old technique utilized by farmers in arid areas all over the world to restrict soil water losses, which makes possible agriculture in marginal, dry environments (Lamb & Chapman 1943, Corey & Kemper 1968, Araña & López 1974). In addition, rapidly falling temperatures at sunset could result in condensation in the hollow spaces between stones (Coe 1969, Evenari et al. 1975). This would actually *increase* soil moisture within blocky talus.

Similar mechanisms would affect moisture under large boulders. However, some differences in the way water infiltrates the soil need to be investigated. Water falling on a block should cling to its surface and flow to the base of the stone in order to moisten the soil below, rather than percolating vertically at the periphery of the block. Future laboratory experiments will hopefully elucidate this point. Soil moisture was dependent on block size. This may have resulted from the greater surface area of bigger blocks, which would thus intercept and capture higher amounts of precipitation, and/or be an indication of the more effective insulation of soil below large blocks. The fact that blocky talus with thicker openwork layers was also associated with greater moisture levels suggests the second explanation may be more appropriate. Alternatively, water might also be preserved under blocks due to overburden pressure, which would compact the soil beneath; this could cause a reduction in average pore size and result in greater resistance to water loss.

Contrary to expectations, soil temperatures in blocky talus were slightly lower than in sandy areas. Lower maxima beneath stones (mean = 8.1° C, versus 8.9 °C in sand) probably resulted from shading of the soil matrix by the blocks, which would have restricted its absorption of solar radiation (Pérez 1989). The lower nightly minima under stones (mean = 3.4 °C, versus 4.1 °C in sandy areas) may have been caused by the downward circulation of cold air between the clasts (cf. Caine 1963). In any case, the temperature differences between talus types were always so slight (0.7 or 0.8 °C) and so close to the expected margin of measurement error (0.5 °C) that they are not considered to be significant factors in the observed rosette distributions. If anything, the lower maxima in stone areas might have contributed to lower evaporation rates, thus possibly helping to conserve water under clasts. The substantially greater variability of soil moisture measured in the 2 contrasting substrates indicates that this factor ought to be assigned a dominant role in establishing the observed spatial patterns of Andean rosettes on paramo talus slopes.

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