Decomposition of cellulose in the superpáramo environment of Ecuador

Rozklad celulózy v prostředí ekvádorských superpáramo

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Decomposition activity of soil along a 400 m altitudinal gradient in the superpáramo of the Guagua Pichincha volcano, Ecuador, was studied employing the method of cellulose decomposition. Nylon-bags containing sheets of cellulose (filter-paper) were exposed in the field at the start of the dry season and were randomly collected at four monthly intervals. Sets of cellulose-bags were also placed in cushions of *Azorella pedunculata* at two different altitudes. The amount of decayed cellulose and the litter disappearance rates (LDR) were estimated. The decomposition of the cellulose generally decreased with altitude. However, at both ends of the gradient this trend was not evident due to the particular microenvironment of the respective sites. The effect of the dry season evidenced by decrease in the LDR was detected at the two lowest sites. The material decayed more slowly in the cushions than in the soil. The ecological significance of the cushion growth-form in terms of a nutrient supply is outlined.

Keywords: Tropical alpine environment, Andes, cellulose decomposition, altitudinal gradient, cushion plants

Introduction

Slopes of the highest mountains of the tropical South American Andes host vegetation called superpáramo. It stretches typically from 4100 m a. s. l., where the transition with the grass páramo is found, to the permanent snow-line at 4800 m (Luteyn 1992). In Ecuador, however, the lower limit of the superpáramo usually lies at 4200–4300 m (Ramsay 1992). The vegetation of the Ecuadorian superpáramo has been described elsewhere (e. g. Diels 1934, 1937, Acosta-Solís 1962,1984, Harling 1979, Jörgensen & Ulloa 1994). It can be distinguished into lower superpáramo characterized by sclerophyllous shrubs of *Loricaria* and *Chuquiraga*, and upper superpáramo where acaulescent rosette plants along with short-leaf grasses, prostrate shrubs and forbs, and cushion plants occur (Cleef 1981). The occurrence of cushion plants is remarkable in the Ecuadorian páramos and has been noted by many authors (e. g. Heilborn 1925, Benoist 1935). The upper superpáramo usually begins at an altitude of 4400–4500 m a. s. l. The climate of the superpáramo is generally cold and humid, and temperature and precipitation decrease with the altitude (Sarmiento 1986). The yearly average temperature at 3950 m (Cruz Loma, mountain range E of Rucu Pichincha) is around 6 °C (Ferdon 1950, cited in Cuatrecasas 1968), at 4800 m on the Cotopaxi volcano it is 0.8 °C (Jörgensen & Ulloa 1994). Rain or snow is frequent through the whole year and frequent clouds and fog contribute to the wet character of the upper parts of the mountains (Cuatrecasas 1968).

Nutrient release through plant litter decomposition is a very important factor in the páramo ecology (Hofstede 1995). However, only little attention has been paid to these processes in the tropical alpine environment. Decomposition processes in the high páramo are very slow. Hofstede (1995) studied disappearance rates of plant litter at three sites with various disturbance regimes. After one year of exposure about one third of litter decayed at the heavily disturbed site, while only ca 10% disappeared at the undisturbed one. Fire has been found to affect the litter decomposition in the grass páramo (Hofstede, in preparation). Janzen (1973) observed only a very limited litter breakdown in a shrubby subpáramo after fire. It was explained by low metabolic rates of decomposers due to the continuously low temperatures and also by the absence of larger decomposers in the tropical mountains. Hedberg (1964) suggested that earthworms might be less active in the afro-alpine environment than worms from the temperate latitudes. Dead leaves of the páramo cushion plants were observed to decay very slowly, thus forming a kind of peaty mass inside the cushion (Heilborn 1925, Benoist 1935, see also Espinosa 1932, Rauh 1988). Old leaves remaining on the stem of giant rosette plants of the genus *Espeletia* (*Asteraceae*) undergo minimized breakdown as well and form an efficient insulation layer for the trunk (Monasterio 1979, 1986, Smith 1979). The present study gives results of a brief investigation of the decomposition processes in the superpáramo environment of the Ecuadorian Andes.

Study site and the methods

The study was carried out on the E slope of Guagua Pichincha (4794 m a. s. l., coord. 0°10'S, 78°35'W) in the period July–November 1995. The mountain is an active volcano situated in the Western Cordillera of Ecuador. The lower superpáramo occurs at approximately 4350–4450 m and is dominated by the shrub *Chuquiraga jussieui* (*Asteraceae*) and the tussock grass *Calamagrostis intermedia*. Among shrubs and grasses numerous cushions of *Azorella pedunculata* (*Apiaceae*) occur. The cushions may reach a height of 80 cm and a cover of several square meters. The cushions on Pichincha are very hard and tough. Above an altitude of ca 4450 m the shrubs and tussock grasses disappear and the upper superpáramo vegetation occurs on typical sandy soils and screes. Massive rocky escarpments are found on the top of the mountain along the crater rim.

The method of cellulose decomposition (Tesařová 1987) was employed and the filter-paper was used as the organic material in the study. Small sheets of cellulose approximately 10 × 5 cm were placed in the bags made of nylon mesh (1 mm mesh size). The bags containing the cellulose were oven dried at 80 °C for two hours, weighed, marked with plastic tags, and exposed in the field. At monthly intervals the bags were taken back to the laboratory, where they were cleaned, dried, and weighed. A correction was made to eliminate the error due to the unremovable allochtonous inorganic matter attached to the cellulose according to Tesařová (1987). The cellulose remaining in the bags after the exposure was ignited in the oven at 500 °C (3 hours). The same procedure was followed with five clean cellulose sheets where the ash content was found to be 0.3±0.03 % of their original mass (mean ±S.D.). Based on this finding that the ash content of the used cellulose was negligible, the ash of the after exposure ignited cellulose was completely attributed to the inorganic material. The amount of the ash was then subtracted from the post exposure weight of the cellulose, and in this way corrected values were used to estimate the litter disappearance rate (LDR) according to Wiegert & Evans (1964):

$$LDR = \ln (W_0/W_1) \cdot (t_1-t_0)^{-1}$$

where W_0 = mass of the material at the time t_0, W_1 = mass of the material at the time t_1.

The disappearance of cellulose was studied along an altitudinal gradient in intervals of 100 m (from 4300 m to 4700 m). On July 11, sets of 20 bags were buried horizontally in the soil at a depth of 5 cm. At 4400 m and 4500 m two sets of cellulose-bags were also placed in cushions of *Azorella pedunculata*. The branches of the cushions were carefully pressed away using a knife so that the bags be placed inside. The bags were buried vertically to the maximum possible depth without damaging the plants; this was with their upper edge ca 5 cm below the cushion surface (Fig. 1). On four dates (August 11, September 23, October 22, November 27) five randomly chosen bags were taken for an analysis from each altitudinal level. Analysis of variance (statistical package STATGRAPHICS) was used to test for differences.

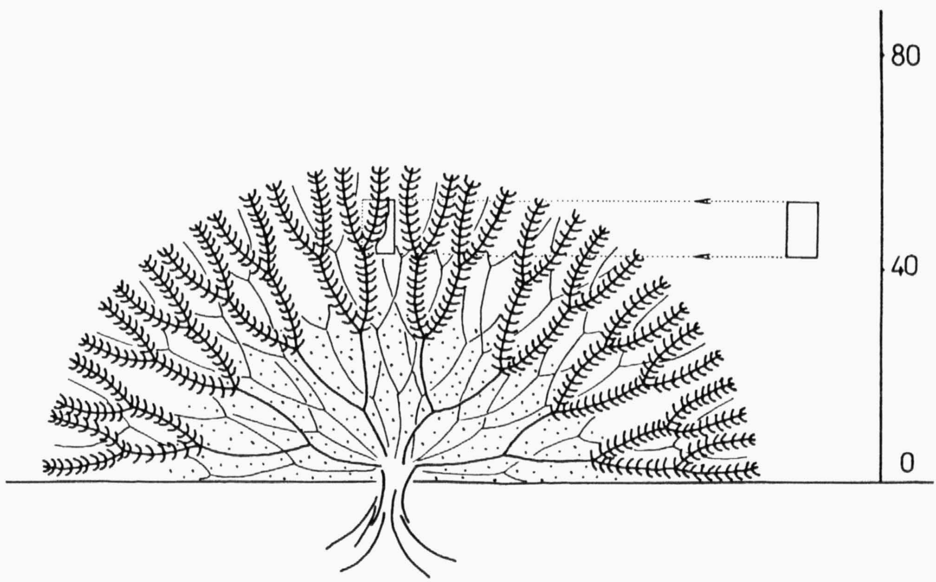

Fig. 1. – Simplified structure of the *Azorella* cushion and the location of the cellulose-bags inside, the soil layer indicated by dots.

Results

The allochtonous material attached to the cellulose affected the final weight of the material exposed in the soil by as much as 40–60 %, while for the material exposed in the cushions it was less than 1.5 %. Even after the correction had been made the variability of the data was very high, the coefficient of variation ranged from 9.4 % (at the first date at 4600 m) to

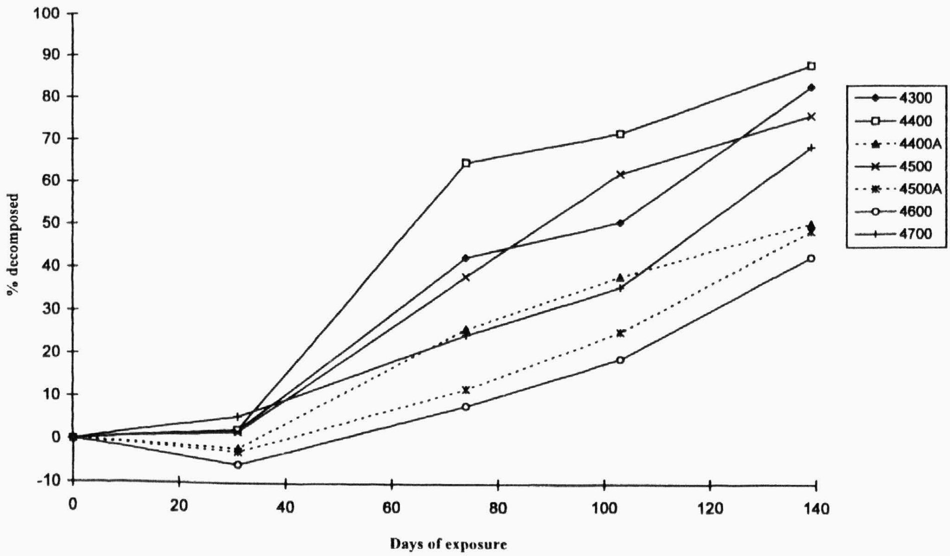

Fig. 2. – Decomposition of cellulose in the soil and in the cushions of *Azorella* (marked with A) along the altitudinal gradient in the superpáramo of Guagua Pichincha, the amount of decayed material in percentages of its original weight.

310.7% (at the first date at 4700 m). In the last sampling date in November at 4300 m tags of two bags were not found; therefore the calculated values of LDR and amount of disappeared cellulose are based on three data only.

It can be seen that the start of the decomposition was very slow; at 4600 m and in the cushions even negative values were observed (Table 1A, Fig. 2). The maximum average value of the LDR was detected at 4700 m and this was clearly due to the effect of one far outlying value. The greatest increase in the decomposition was detected in the second period, especially for the three lowest levels. At 4400 m the estimated LDR was 15.4 $mg \cdot g^{-1} \cdot day^{-1}$ and two thirds of the cellulose mass had been decayed by the second date. The minimum LDR value of 1.2 $mg \cdot g^{-1} \cdot day^{-1}$ was found at 4600 m (less than 9 % cellulose decomposed). In the third interval a marked drop in the LDR in the soil at 4300 m and 4400 m was observed, while at the other altitudes the decomposition accelerated. The LDR only slightly increased at 4700 m and also in the cushion from the lower site. At the end of the experiment (after 139 days of exposure) the most decayed material was found at 4400 m where almost 89 % had disappeared (LDR = 17.1 $mg \cdot g^{-1} \cdot day^{-1}$). At 4600 m, on the other hand, over 55 % of the cellulose remained (LDR = 5.3 $mg \cdot g^{-1} \cdot day^{-1}$). The two-way ANOVA for the LDR data proved significant differences for both tested factors, i.e. the altitude ($p < 0.001$, $F = 15.4$, d.f. = 4) and the exposure time ($p < 0.001$, $F = 28.6$, d.f. = 3). The interaction factor altitude*exposure was also significant ($p < 0.05$, $F = 2.0$, d.f. = 12). The multiple range test (Tukey's HSD, p = 95%) for the altitude factor revealed one group (altitudes 4300 m, 4500 m, and 4700 m) where differences could not be confirmed (Table 1A). This test done for the exposure time proved differences among the sampling dates with the exception for the second and the third period.

The decomposition activity (LDR) inside the *Azorella* cushions was much smaller than that in the soil near the plants. At both of the compared altitudes the respective differences were highly significant ($p<0.001$, $F=59.3$, d.f. = 1 and $p<0.001$, $F=67.4$, d.f. = 1 at 4400 m and 4500 m, respectively). The amount of the decayed material was about 2–3 times greater in the soil than in the cushion. By the last date, however, the differences tended to disappear. The ANOVA test for the exposure time was always significant at the level $p<0.001$ ($F=23.3$, d.f. = 3, and $F=36.0$, d.f. = 3), however, the multiple range test found overlaps in the last three dates. When the two cushions were compared, the decay of the cellulose ran faster in the one from the lower altitude ($p<0.05$, $F=6.0$, d.f. = 1). As in the previous case only a small difference was found at the end of the experiment (Table 1B). Though an overall significance was proved for the length of the exposure ($p<0.001$, $F=24.0$, d.f. = 3), overlaps were found also here in the last three dates.

Table 1. – The estimated litter disappearance rate LDR of cellulose [$mg \cdot g^{-1} \cdot day^{-1}$] along the altitudinal gradient on the Guagua Pichincha volcano (mean ± S.D.), n = 5. A: for the soil data, B: for the *Azorella* cushions. The last rows and column indicate the results of the multiple range comparisons (Tukey's HSD) and the letters indicate homogeneous groups.

Altitude	Days of exposure				Homogeneous groups
	31	74	103	139	
A:					
4300	0.8 ± 0.71	8.1 ± 3.13	7.2 ± 1.14	16.7 ± 7.63	a
4400	0.8 ± 1.01	15.4 ± 4.68	13.5 ± 4.24	17.1 ± 4.13	b
4500	0.7 ± 1.74	6.8 ± 1.22	10.2 ± 2.91	11.0 ± 2.08	a
4600	−1.8 ± 0.17	1.2 ± 0.61	2.3 ± 1.50	5.3 ± 4.57	c
4700	3.0 ± 9.44	4.4 ± 3.46	4.8 ± 2.66	9.4 ± 3.47	a
Homogeneous groups	a	b	b	c	
B:					
4400	−0.6 ± 0.79	4.4 ± 2.00	5.0 ± 2.04	5.6 ± 2.03	
4500	−0.9 ± 0.50	1.8 ± 0.69	3.1 ± 1.57	5.1 ± 1.45	
Homogeneous groups	a	b	b, c	c	

Discussion

Cellulose (filter-paper) rather than plant litter was employed in the study since the experiment could have been planned only for a short period. The process of breakdown of the plant litter lasts much longer (Tesařová 1993, Hofstede 1995) and in that case more time would have been needed for the experiment. The disappearance rates of the plant litter can not be inferred from this study, however, a relative comparison of the decomposition activity can be made.

The litter-bag method usually results in a great variability of the data and this was also the case of this study. When the bags are buried in the substratum, soil particles get stuck on the material which would tend to decrease the estimated decomposition rate. The correction made before the calculation of the LDR excluded this effect of the attached allochtonous material. The negative LDR values from the first sampling date thus suggest that the amount of the decayed cellulose was compensated by the soil microorganisms that colonize the material in the first phase of the decomposition (Jensen 1974). Loss of the fragmented cellulose from the bags (spillage) contribute significantly to the error in the estimation (Suffling & Smith 1974). The several extreme values that were found (e. g. one record at the first date at 4700 m) can most probably be explained by the spillage.

In general the decomposition, expressed as the LDR, decreased with the increasing altitude. This is mainly a consequence of the continuous decrease in temperature and precipitation and thus soil moisture, which are important factors controlling the decomposition processes (Witkamp 1963, Williams & Gray 1974, Jenkinson 1981). However, at both ends of the gradient a different trend was observed. The cellulose decayed faster at 4400 m than at 4300 m and the same was the case at 4700 m and at 4600 m. From the traces of fire it can be inferred that the grass páramo at 4300 m had been burned shortly before the experiment started, and the fire opened the vegetation cover there. In the shrubby superpáramo at 4400 m, however, no evidence of fire was observed. More pronounced microclimatic fluctuations were likely to occur at the burned site and probably affected negatively the LDR. It should be noted, however, that Hofstede (in preparation) found augmented decomposition following a fire in the grass páramo. The site at 4700 m was situated just below the rocky crater rim. Despite the higher altitude the vegetation there was better developed than at 4600 m, presumably due to the amelioration of the microenvironment. Plants profited from the water condensed from frequent fogs on rocks and boulders which improved the water regime of the soil around (P. Sklenář, personal observation, see also Pérez 1987a). The rocks sheltered the upper site from the wind, and the substrate around was also more stable. On the other hand, the site at 4600 m with poor vegetation was located on an open sandy/scree slope and was much more exposed to desiccation and solifluction. Consequently the observed decomposition activity of the soil was substantially lower.

The cellulose bags were exposed shortly after the dry season had started. The third period therefore fell at the very end of the dry spell, and the scarcity of precipitation was likely to cause the decrease in the LDR at the two lowest sites (see also van der Drift 1963). However, the fact that no effect of the drought was detected at the higher levels requires an explanation. Ecuadorian volcanoes, including Pichincha, form their particular weather conditions. The summit areas of the mountains where the superpáramo vegetation occurs are very often covered by clouds during both the wet and the dry season (see also Hedberg 1964, Körner et al. 1983), while at the same time the grass páramo only a few hundred meters below may be exposed to a sunshine. The greater number of days with clouds and fog may buffer the effect of the dry season at the highest elevations. At lower altitudes the drought can be more pronounced as may be inferred from the decomposition data. Cleef (1981) and van der Hammen & Cleef (1986) reported a condensation level at the lower superpáramo in Colombia which was considered most likely responsible for an increase in cover of mosses and lichens. The high abundance of bryophytes at the lower *Loricaria* superpáramo has also been observed at many Ecuadorian páramo areas. However, it was not that much conspicuous in the study area (P. Sklenář, personal observation).

It has been found that the decomposition activity was much smaller in the upper part of the *Azorella* cushion than it was in the surrounding soil. Although it was attempted to place the cellulose-bags as deep as possible, they probably did not reach the layer of the slowly developing soil inside the cushion and remained in the litter layer. It can be expected that the decomposition runs faster in the lower strata of the cushion since the soil just beneath the cushion plants has been shown to have greater microbial activity than the surrounding soil (Covarrubias & Contreras 1980, cited in Alliende & Hoffmann 1985, Schinner 1982).

The cellulose in the soil disappeared much faster in spite of the fact that cushions may be warmer than the soil (Ramsay 1992), and the following factors are suggested to explain this observation. Decomposers may have been less abundant in the cushions, or some of them even missing. Smith (1979) reported greater numbers of many groups of invertebrates (e. g. Annelida, Collembola, Thysanura) present among the decaying leaves attached to the stem of *Espeletia schultzii* than in the soil. In the examined upper layer of the *Azorella* cushions no such observation was made. Other possible reason may be the fact that unlike the soil which is exposed to temporary desiccation, the litter inside the cushions is permanently saturated by water (see below), and such conditions can be very unfavourable for the decomposition (Williams & Gray 1974).

The dense and very tough cushions are filled with dead organic material (leaves, stems, roots), and because of the humid and cold climate of the páramo it is permanently saturated with the rain water (Heilborn 1925, Benoist 1935, see also Espinosa 1932, Smith 1972, Laegaard 1992). The produced biomass remains almost completely within the slowly growing cushion and this growth-form of numerous páramo species can be understood as a kind of reservoir for the plant in terms of water and nutrients supply. Despite the slow litter decomposition and thus slow turnover the necessary amount of nutrients is available, and such a "semiclosed nutrient cycle" of plants growing in the unfavourable climate of the superpáramo must be advantageous. Its occurrence in the páramo and also in the arctic and alpine environments has been discussed by several authors (Svoboda 1977, 1986, Monasterio 1979, 1986, Smith 1979, Halloy 1983). The certainty of available water and nutrients can also be one of the possible explanations why numerous plant species frequently colonize the surface of the cushions. Such facultative epiphytes (Alliende & Hoffmann 1985) have been reported from the Ecuadorian páramo (Heilborn 1925, Diels 1934) as well as from other mountain areas (Griggs 1956, Alliende & Hoffmann 1985, Pérez 1987b, Rauh 1988, Pyšek & Liška 1991). For these plants the process of litter decomposition and release of nutrients inside the cushion is fundamental since their roots only rarely reach the soil beneath the cushion (Alliende & Hoffmann 1985, S. Laegaard, personal communication).

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Souhrn

Na 400 m dlouhém výškovém gradientu (4300–4700 m n. m.) v oblasti superpáramo ekvádorské sopky Guagua Pichincha byla po dobu 139 dní sledována rychlost dekompozice celulózy. Ve výškách 4400 m n. m. a 4500 m n. m. byla rychlost rozkladu studována také v horní vrstvě kompaktních polštářů druhu *Azorella pedunculata* (*Apiaceae*), který reprezentuje jednu z typických růstových forem ekvádorských páramo.

Rychlost rozkladu celulózy (filtrační papír) se obecně snižovala s rostoucí nadmořskou výškou, na obou koncích gradientu však došlo k opačnému trendu. Travinná vegetace ve 4300 m n. m. vypálená krátce před položením nylonových sáčků s celulózou do půdy byla zřejmě vystavena výraznějším mikroklimatickým fluktuacím než keřové páramo o 100 metrů výše a to se odrazilo na pomalejším rozkladu materiálu. Také ve 4700 m n. m. se celulóza rozkládala rychleji než ve 4600 m n. m. Horní stanoviště bylo chráněno před větrem skalními výchozy hrany kráteru a půda byla obohacována vodou kondenzovanou na okolní skále a kamenných blocích. To se projevilo příznivě na bohatším vegetačním pokryvu a na vyšší rozkladné aktivitě půdy.

Ve třetí části experimentu (září–říjen) se na poklesu rozkladné aktivity půdy ve dvou spodních výškových hladinách a částečně i uvnitř polštáře pravděpodobně projevil vliv vrcholícího období sucha. Skutečnost, že rozklad ve vyšších částech gradientu nebyl tímto ovlivněn, se vysvětluje mnohem častější přítomností mraků a mlhy ve vrcholových partiích nejvyšších ekvádorských hor (i v suchém období), které mohou alespoň částečně vyrovnávat deficit srážek.

Rozklad uvnitř polštářů druhu *Azorella pedunculata* probíhal výrazně pomaleji než v okolní půdě, statistický test byl vysoce průkazný. Jako možné vysvětlení se uvádí nižší četnost (případně i absence některých skupin) rozkladačů a permanentní vysoká vlhkost uvnitř polštářů. Dekompozice v polštáři z nižší nadmořské výšky probíhala rychleji, rozdíl zjištěný v závěru experimentu však byl jen minimální. Jednou z výhod, které znamená polštářová růstová forma pro rostliny, je skutečnost, že vyprodukovaný organický materiál se zadržuje uvnitř polštáře. Rozkladem opadu se postupně uvolňují živiny, jsou rostlině téměř beze ztrát k dispozici. Přestože rozklad uvnitř poštáře probíhá pomalu, postupná degradace odumřelých částí rostliny představuje jistý přísun živin. Ty jsou také stěžejní pro ty rostlinné druhy, které fakultativně osídlují povrch polštářů.

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