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Publication date

1994

Published in

Vegetatio

[Link to publication](#)

Citation for published version (APA):

Tol, G. J., & Cleef, A. M. (1994). Above ground biomass structure of a *Chusquea tessellate* bamboo paramo, Chingaza National Park, Cordillera Oriental, Colombia. *Vegetatio*, 115, 29-39.

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Above-ground biomass structure of a *Chusquea tessellata* bamboo páramo, Chingaza National Park, Cordillera Oriental, Colombia

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Accepted 10 February 1994

Key words: Bunch-grass páramo, Leaf Area Index, Leaf distribution

Abstract

The present study was carried out in the bamboo (*Chusquea tessellata*) páramo of 'Parque Natural Nacional de Chingaza', Eastern Cordillera, Colombia from December 1987 to April 1988. Above-ground biomass structure of bamboo páramo was quantified in 16 plots. These data are compared with previous results on above-ground biomass structure of bunch-grass (*Calamagrostis* spp.) páramos.

The total (non-living and living) above-ground biomass of a *Chusquea tessellata* bamboo páramo was low (2,625 g DW· m⁻²) compared to bunch-grass páramo. Nevertheless, higher values of standing living biomass and litter are found in the bamboo páramo due to the leaf shed of the bamboo. The thick litter layer may inhibit germination and growth of nearby plants.

Maximum biomass is found near the ground surface. Cumulative LAI (ln transformed) and height in the bamboo vegetation are related parabolically for *Chusquea tessellata* and linearly for bunch-grass due to differences in leaf distribution. The mean bifacial LAI of living *Chusquea tessellata* leaves is 2.2 m²· m⁻², whereas it is 2.5 m²· m⁻² for all Poaceae.

Introduction

The páramo is present between the upper forest line (about 3,300–3,700 m alt.) and the nival belt (4,800–5,000 m alt.) of the Colombian Andes. Its vegetation is characterized by bunch-grasses (*Calamagrostis* spp.) and caulescent stem-rosettes (e.g. *Espeletia* spp., Asteraceae), accompanied by dwarf shrubs. In azonal wetter locations cushion-forming plants can be found (Bosman *et al.* 1993). Dwarf-bamboos (genus *Chusquea*; previously known as *Swallenochloa*; Clark 1989) are conspicuous in the vegetation of wetter zonal páramo (Cleef 1978, 1981).

The woody dwarf-bamboo species studied in the Chingaza study area is *Chusquea tessellata* Munro (Poaceae). *Chusquea* is one of the largest bamboo genera in the world with about 120 species, ranging from Mexico to Argentina, Chile and Uruguay, the Caribbean Islands and eastern coastal and southern Brazil (Soderstrom *et al.* 1988; Clark 1989). *Chusquea*

tessellata has the widest distribution of any species in the section *Swallenochloa*. In the Andes this species occurs from Venezuela to northwestern Bolivia. Altitudinally, it ranges from 2,800 to 4,300 m alt., the broadest and highest range for the section (McClure 1973; Clark 1989). The Costa Rican Talamanca bamboo páramos are dominated by another dwarf-bamboo species: *Chusquea subtessellata* Hitchcock.

In the Chingaza National Park (Eastern Cordillera, Colombia) Dierikx & Kaandorp (1986) mapped 21 páramo vegetation communities, nine of which included *Chusquea tessellata*. Recently Vargas & Rivera (in press) also reported on a *Chusquea tessellata* community from the Chingaza study area. Obviously, bamboo plays an important role in this páramo ecosystem. In the same park, close to 'Embalse de Chuza', about 60% of the area is covered with dwarf-bamboo vegetation and the mean above-ground standing biomass of *Chusquea tessellata* was determined at 1,419 g DW· m⁻² (Aristizabal & Castañeda 1983).

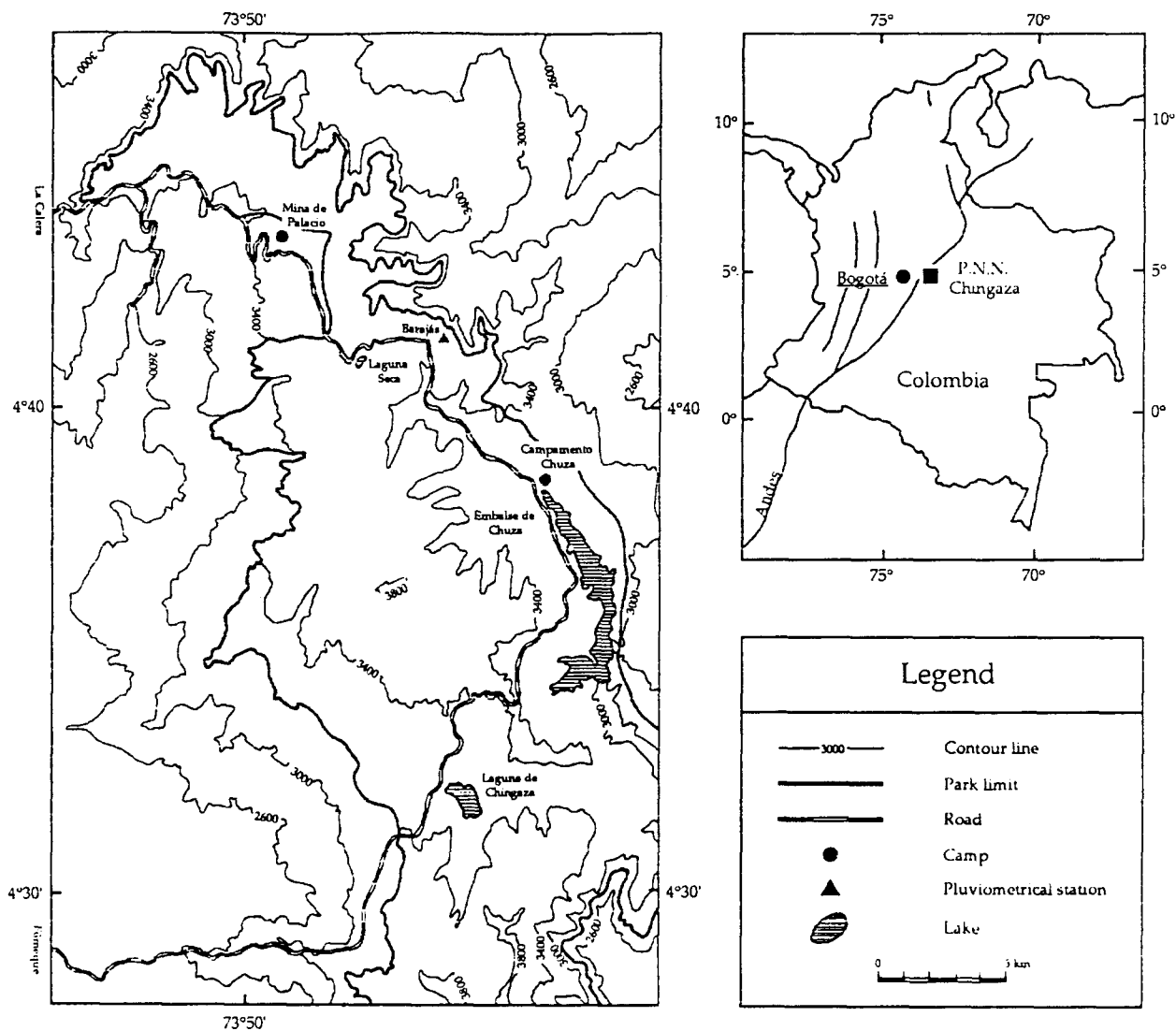


Fig. 1. Location of the study site (after maps 228, 229, 247 and 248 of IGAC, Santa Fé de Bogotá).

Most phytomass analyses in the tropics have been carried out in lowland forests and grasslands and only a few in highland ecosystems (Smith & Young 1987). In the framework of the Colombian-Dutch ECOANDES research programme (Van der Hammen *et al.* 1983, 1984, 1989 and in press), the present study was carried out as part of the in-depth studies of the high Andean páramo ecosystem. Inventory and mapping of the páramo vegetation (e.g. Cleef 1981; Cleef & Hooghiemstra 1984; Sturm & Rangel 1985; Franco-R. *et al.* 1986; Bekker & Cleef 1989; Salamanca *et al.* in press; Kloosterman *et al.*, in press) and páramo ecosystem studies (Lutz & Vader 1987; Beekman & Verweij

1987; Keizer 1989; Rossenaar & Hofstede 1992; Verweij & Beekman, in press; Hofstede *et al.*, in press) are needed for development of an ecologically sustainable management strategy for the páramo (Verweij & Budde 1992; Verweij & Kok 1992; Schmidt & Verweij 1992).

Thus far the bunch-grass páramo ecosystem has been most studied. Earlier Tol & Cleef (1992) reported on the nutrient status of a dwarf-bamboo páramo. This provides the first data on above-ground biomass structure of the same dwarf-bamboo páramo. The results are compared with those of previous studies in bunch-grass páramos, using the same biomass estimation methods,

at about the same altitude (3,620 m) on the opposite dry site of the Colombian Cordillera Oriental (Lutz & Vader 1987; Beekman & Verweij 1987) and elsewhere in the tropical Andes.

Methods

Site description

Fieldwork was carried out from December 1987 to April 1988 in the Chingaza National Park (Eastern Cordillera, Colombia), about 35 km E of Santa Fé de Bogotá at 4° 40' N and 73° 48' W (Fig. 1). This National Park covers 58,350 square kilometres. It is administered by the 'Instituto Nacional de los Recursos Naturales Renovables y del Ambiente' (INDERENA) and the 'Empresa de Acueducto y Alcantarillado de Bogotá' (EAAB). The Chingaza páramo is of importance as it forms the main natural drinking water source for Santa Fé de Bogotá. A number of small and large lakes of glacial origin are found in the study area. Below 4,000 m elevation these lakes are usually bordered by *Sphagnum* bogs. The study site was selected, using a 1:10,000 vegetation map (Dierikx & Kaandorp 1986), on a slope 2 km NW of the shallow lake 'Laguna Seca', at 3,650 m altitude; 9° (sd± 2.7) slope and ≈ 100° SE aspect. The criterion for the site selection was a homogeneous vegetation belonging to the *Calamagrostis bogotensis*-*Chusqueetum tessellatae* community (Franco-R. *et al.* 1986), consisting of dense bamboo clumps up to approximately 80 cm in height.

The EAAB-meteorological station Barajas, 5.4 km N of Laguna Seca (Fig. 1), is situated at the same altitude as the study site, and climate conditions are quite similar and representative for the study area (Fig. 2). The mean annual temperature is 6 °C while at night the temperature may drop below zero (−4 °C). The climate is relatively humid with about 1,850 mm annual precipitation and a distinct dry season from December to February. According to the Köppen system (Köppen & Geiger 1930), the climate can be classified as EH (>3,000 m).

The soils are poorly developed, usually showing hydromorphic characteristics, as a result of the humid climate, and lack podzolic features (Ingetec 1970; Sturm 1978). The soil can be classified as a histosol (soils having an organic horizon of 40 cm or more) according to the FAO/UNESCO soil classification system (FAO 1974).

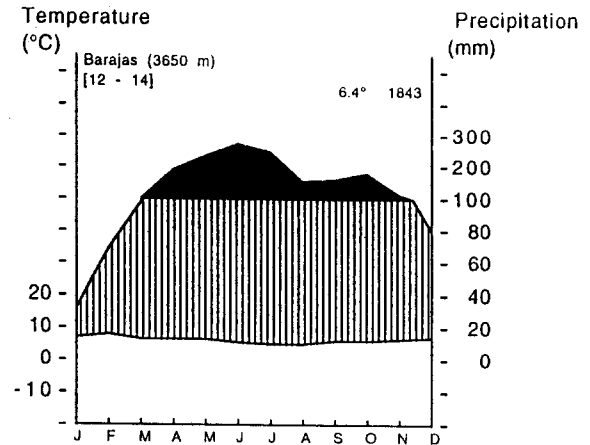


Fig. 2. Walter climate diagram for Barajas, 1974–1987 (4° 41' N and 73° 45' W topographic map 228 (edited by IGAC), data provided by EAAB).

Plot sampling

Biomass was estimated using a destructive sampling technique (Milner & Hughes 1968). Every month a number of bamboo clumps were randomly selected from dense bamboo vegetation. The clumps were sampled by clipping all standing vegetation from one square metre of clump surface. Litter and bryophytes were collected by hand. In December 1987 four clumps were sampled; monthly from January 1988 to April 1988, four, five and three clumps were sampled respectively. The material was separated into: *Chusquea tessellata* stems and leaves, grasses (*Calamagrostis effusa* and *C. bogotensis*), dwarf-shrubs, herbs, ground dwelling species (*Arcytophyllum muticum*, *Pernettya prostrata* and *Cardamine* sp.), bryophytes, litter and lichens.

No distinction was made between bunch-grasses and other tall grasses because the latter were just marginally present. Subsamples of all monocotyledons and dicotyledons were further separated in non-living and living material to estimate their non-living: living biomass ratio. Bamboo leaves, which abscised when gently pulled back just after clipping, were considered non-living. Plant material, consisting of 2/3 or more green material, was considered alive. All material was pre-dried in a greenhouse and subsequently oven-dried (105 °C, 24 h) and weighed in the Soil laboratory of the Instituto Geográfico 'Agustín Codazzi', Santa Fé de Bogotá.

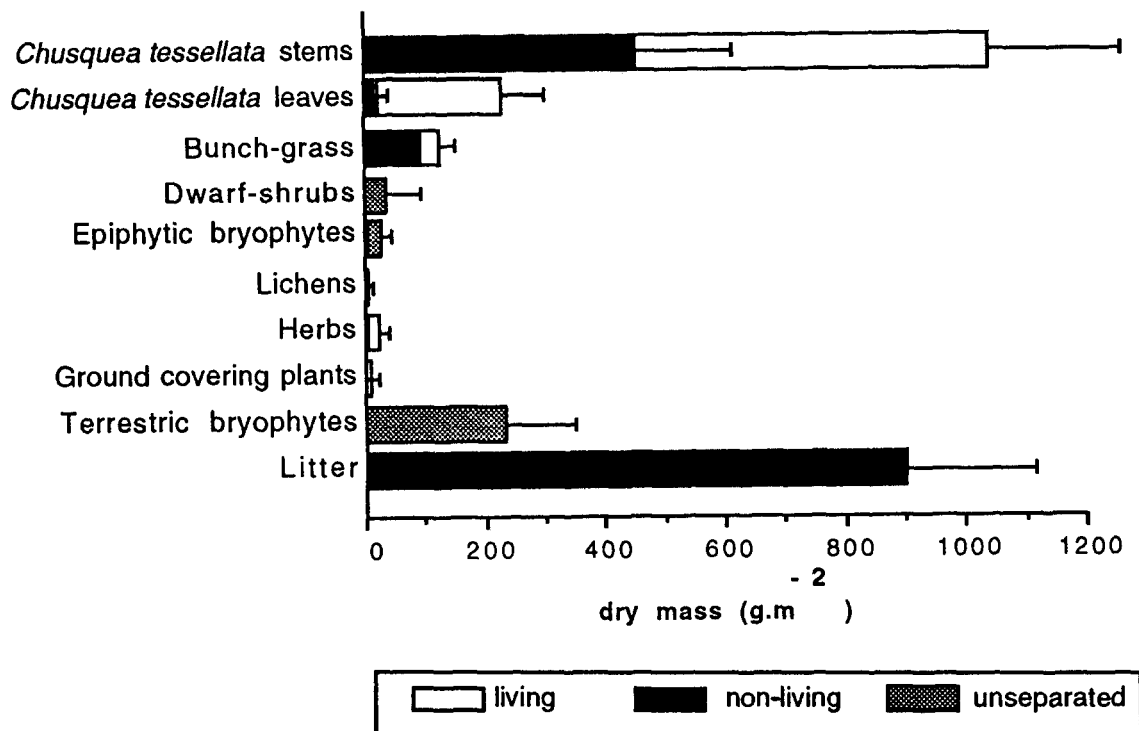


Fig. 3. Mean dry mass ($\text{g} \cdot \text{m}^{-2}$) of the different plant fractions ($n = 16$), lines indicate s.d.

Vertical structure

In February 1988 the vertical structure of the vegetation was determined within a 1 m^2 plot. The vegetation was harvested in 10 cm layers, according to ground surface. The yield was divided into different groups, dried and weighed as described above. In this paper aerial biomass is defined as above-ground biomass minus litter.

Leaf Area Index (LAI)

The LAI of *Chusquea tessellata* and *Calamagrostis effusa* (including *C. bogotensis*) was attained, using plants from the plot on which the vertical structure was determined. The area of all the bamboo leaves of one layer, was measured by copying the outline of the leaves onto paper with known area-weight relation. The area of the leaves was determined by cutting the leaf outlines from the paper and weighing them. In this manner the LAI could be calculated. It is assumed that the somewhat vertical *Chusquea tessellata* leaves are photosynthetically active on both sides, so the LAI includes bifacial leaf area.

For *Calamagrostis effusa* (incl. *C. bogotensis*) the relation mass-LAI of Lutz & Vader (1987) was used:
 $1 \text{ g } \textit{Calamagrostis effusa} \text{ living} = 98.425 \text{ cm}^2$
 $1 \text{ g } \textit{Calamagrostis effusa} \text{ non-living} = 109.349 \text{ cm}^2$
 It was recorded when bamboo leaves were infected with the fungus *Phyllachora chusqueae* P. Henn. & Lind. (det. Dr H. van der Aa, CBS, Baarn) and/or damaged and/or non-living. *Chusquea tessellata* leaves were graded on the degree of infection when more than two spots of fungi were detected on a leaf. Damaged leaves showed traces of insect herbivory.

Results

Above-ground biomass structure

The mean above-ground biomass of the 16 plots was $2,625 \text{ g DW} \cdot \text{m}^{-2}$ ($\text{sd} \pm 486$). Ground dwelling plants and herbs consisted mainly of living material. Seventy five percent of bunch-grass material was non-living (Fig. 3), while 78% of *Chusquea tessellata* was alive. During 4 months of monitoring some senescence could be detected (Fig. 4). The percentage of non-living

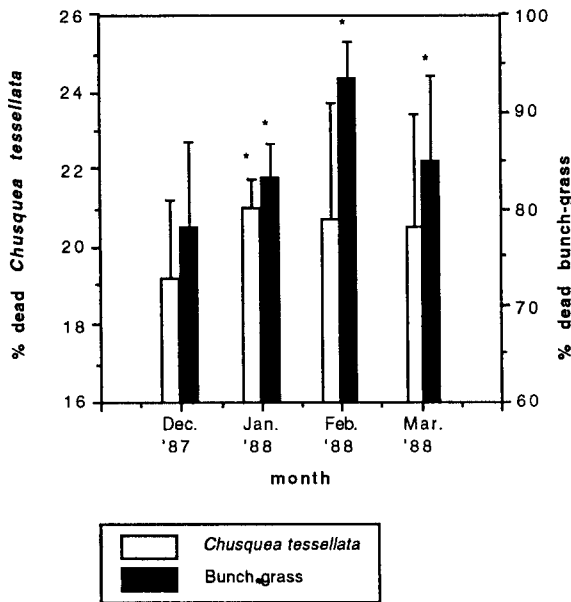


Fig. 4. Monthly (Dec. '87–April '88) percentage non-living material (mean \pm sd) from *Chusquea tessellata* ($n = 16$) and bunch grass ($n = 14$). (* $p > 0.1$).

Chusquea tessellata material reached its maximum in February. Bunch-grass showed peak percentages of non-living material in January.

Sixty percent ($854 \text{ g DW} \cdot \text{m}^{-2}$) of all aerial biomass of non-woody vascular plants was alive. The contribution of bamboo in biomass was related to the dominance of *Chusquea tessellata* in the vegetation cover. Seventy three percent of the aerial biomass consisted of *Chusquea tessellata*; bryophytes accounted for 15% and bunch-grasses for 7%. All other groups contributed marginally to the aerial biomass. Litter, consisting almost entirely of non-living *Chusquea tessellata* material, contributed up to 34% of the above-ground biomass (i.e., $900 \text{ g DW} \cdot \text{m}^{-2}$). The amount of bryophyte biomass correlated negatively with the amount of litter (Fig. 5).

Vertical structure

The páramo vegetation was dominated visually by *Chusquea tessellata* bamboo and to a lesser extent by *Calamagrostis effusa* (incl. *C. bogotensis*). Except for some dwarf shrubs, other plants did not exceed 10 cm in height (Fig. 8). The total dry mass per layer decreased with increasing height above ground. The ground surface was densely covered with litter and bryophytes. Litter was found in bamboo clumps to a

height of 30 cm. Epiphytic bryophytes were found to about 50 cm on the bamboo stems.

Most (57%) of the microphyllous *Chusquea tessellata* leaves in the bamboo clump, were found below 10 cm due to the numerous small *Chusquea tessellata* stems in the understorey. Above 10 cm the number of leaves decreased with height.

The percentage of undamaged leaves decreased with increasing leaf length (Fig. 6). The proportion of undamaged leaves of the longest leaf length class (111–120 mm) was exaggerated because of the small number of leaves in the sample ($n = 4$). The percentages of damaged and non-living leaves remained nearly constant, regardless of their length. Small leaves were seldom infected with fungus. Longer (i.e. older) leaves were more heavily infected with fungus.

LAI

The LAI of non-living bunch-grass leaves was always higher than that of living bunch-grass leaves (Fig. 7). The total area of living *Chusquea tessellata* leaves was greater than that of living and that of non-living bunch-grass, while the total area of non-living *Chusquea tessellata* leaves had a smaller LAI. For *Chusquea tessellata* cumulative LAI (ln transformed) and height are related parabolically. For *Calamagrostis effusa* (incl. *C. bogotensis*) they are related linearly as a consequence of the contrasting distribution of leaves in the bunch. The slopes for non-living and living LAI run parallel indicating a constant non-living:living ratio (Fig. 7).

The LAI of living *Chusquea tessellata* leaves was $1.13 \text{ (m}^2 \cdot \text{m}^{-2})$. The dry mass (105 g) of living leaves within the plot in which the vertical structure was determined was nearly half of the mean dry mass of all plots (206 g). Therefore, the LAI of this plot had to be multiplied by 1.96 to obtain a representative LAI value. This short cut was justified because biomass and LAI were strongly correlated ($r = 0.974$). The resultant mean LAI of *Chusquea tessellata* leaves was $2.2 \text{ m}^2 \cdot \text{m}^{-2}$ (sd ± 0.8). Similarly, the bunch-grass LAI (0.16) had to be multiplied by 1.80, resulting in a mean bunch-grass LAI of $0.29 \text{ m}^2 \cdot \text{m}^{-2}$ (sd ± 0.28). The mean LAI of the Poaceae in the Chingaza dwarf bamboo páramo was $2.5 \text{ m}^2 \cdot \text{m}^{-2}$ (sd ± 1.05).

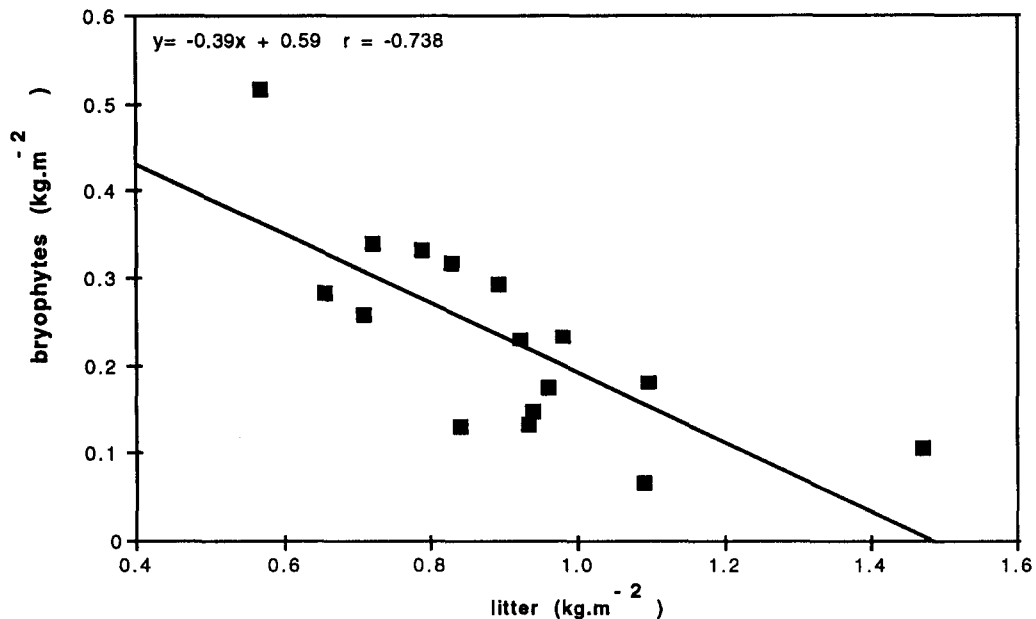


Fig. 5. Dry mass of bryophytes ($\text{kg DW}\cdot\text{m}^{-2}$) as a function of litter dry mass ($\text{kg DW}\cdot\text{m}^{-2}$) per plot ($n = 16$).

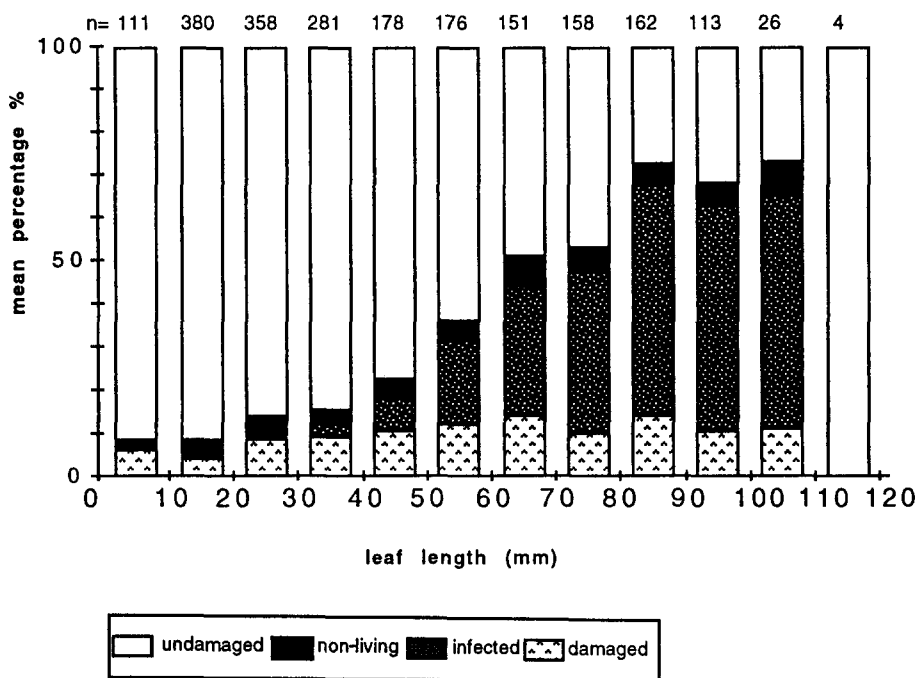


Fig. 6. Mean proportions of *Chusquea tessellata* leaves expressed as % of total on 1 m^2 arranged by leaf length classes (mm) ($n = 2,098$).

Discussion and conclusions

Studies of drier bunch-grass páramos indicate that the main part of the aerial biomass consists of *Espeletia* stem-rosettes (Lutz & Vader 1987; Beekman &

Verweij 1987; Verweij & Beekman, in press). Stem-rosettes of *Espeletia* are rare at our study site, although elsewhere in the area they are commonly associated with bamboos (Cleef 1981; Franco *et al.* 1986). In our plots the aerial biomass consisted principally of

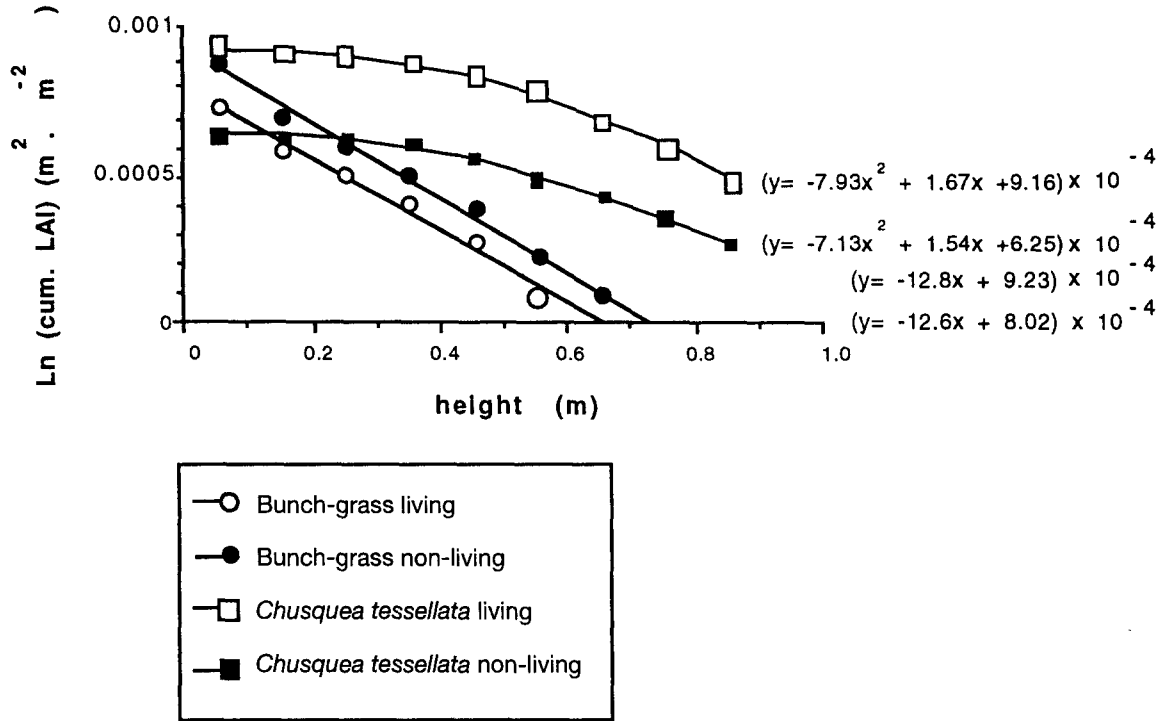


Fig. 7. Cumulative LAI (ln transformed) ($\text{m}^2 \cdot \text{m}^{-2}$) of non-living bunch-grass and *Chusquea tessellata* leaves as a function of the height (m).

Chusquea tessellata ($1,263 \text{ g DW} \cdot \text{m}^{-2}$; 73%). This is comparable to the biomass value of Aristizabal & Castañeda (1983) ($1,419 \text{ g DW} \cdot \text{m}^{-2}$). On average, the total above-ground biomass of the bamboo páramo type under study is lower than biomass values of other tropicalpine bunch-grasslands (Table 1). The biomass values extrapolated to 1 ha are assumed to be lower, taking account of the space between the clumps. However, this is also true for the bunch-grass páramo studies in the Colombian Andes, referred to in Table 1.

The bamboo plot studied can be classified as mesic and is therefore comparable with the bunch-grass páramo plots referred to before. In fact, other bamboo páramo vegetation types in the study area apparently contain much higher levels of above-ground biomass. Under favourable conditions *Chusquea tessellata* grows luxuriantly and forms dense groves. At these sites, soils are wet and peaty. Water and nutrients are readily collected from the surrounding slopes. Increased biomass values of *Chusquea tessellata* are found where total bases are higher (Tol & Cleef 1992). Apart from spatial variation, temporal variability is present in the bamboo páramo plots. At the end of the dry season senescence occurs, reducing the proportion

of living tissues. Consequently the amount of living material depends on when the samples are taken.

We suspect that below-ground biomass in the bamboo páramo is considerably greater than in the bunch-grass páramo, taking into account the impressive and dense rhizomes of the *Chusquea tessellata* stands (see also Soderstrom & Calderón 1978). However, the above: below-ground biomass ratio of *Chusquea tessellata* (1:0.4; G. J. Tol unpubl.) falls, in this low bamboo vegetation, in the range (1:0.4 to 1:1) found for species of non-seasonal cold environments, including high tropical mountains (Smith & Klinger 1985), and of ratios found for bunch-grass páramo (Lutz & Vader 1987 (1:0.5); Beekman & Verweij 1987 (1:0.3)).

Comparing bunch-grass páramo (Lutz & Vader 1987) with this bamboo páramo, the following points are of particular note (Fig. 8). Both páramo vegetation types are dominated by Poaceae of different growth forms. The dominant plants in the bunch-grass páramo is *Calamagrostis effusa* and in the bamboo páramo *Chusquea tessellata*. Total above-ground biomass of this bamboo páramo is lower than that of bunch-grass páramo, but living aerial biomass is higher. Sixty per cent of the aerial biomass of non-woody vascular plants is living in the bamboo páramo. Lower percentages

Table 1. Biomass figures ($\text{g DW} \cdot \text{m}^{-2}$) of tropical alpine grasslands.

Source	Country (Study area)	Latitude (degrees)	Altitude (m)	Vegetation type	Aerial biomass (a) ($\text{g} \cdot \text{m}^{-2}$)	Litter (b) ($\text{g} \cdot \text{m}^{-2}$)	Above-ground biomass (a+b) ($\text{g} \cdot \text{m}^{-2}$)
Cardozo & Schnetter (1976)	Colombia (Eastern Cordillera)	4°33' N 74°02' W	3,300-3,400	bunch-grass páramo			735-2,660
Lutz & Vader (1987)	Colombia (Eastern Cordillera)	4°35' N 74°04' W	3,620	bunch-grass páramo	2,476	615	3,091
Beekman & Verweij (1987)	Colombia (Eastern Cordillera)	4°35' N 74°04' W	3,620	bunch-grass páramo	3,052	334	3,386
Tol & Cleef (this study)	Colombia (Eastern Cordillera)	4°40' N 73°48' W	3,650	bamboo páramo	1,725	900	2,625
Hofstede & Witte (1993)	Colombia (Central Cordillera)	4°48' N 75°24' W	4,100	bunch-grass páramo	1,392	1,472	2,864
Smith & Klinger (1985)	Venezuela (Mérida Andes)	8°47' N 70°48' W	3,530-3,560	bunch-grass páramo	398-651*		
Ramsay (1992)	Ecuador (Eastern Cord.)	1°48' S 78°32' W	3,750 3,950	bunch-grass páramo	837 794		
Hnatiuk (1978)	New Guinea (Mt. Wilhelm)	5°47' S 145°01' E	3,400 3,510 4,350	tussock grassland	2,668 2,460 3,431*	329 369 122	2,997 2,829 3,553

* heavily grazed

of living aerial biomass occur in bunch-grass páramo (Lutz & Vader 1987 (24%); Beekman & Verweij 1987; Verweij & Beekman, in press (44%); Hofstede *et al.*, in press (33%)). Likewise, a lower value of total (living and non-living) Poaceae LAI (3.7) is found in the bamboo páramo compared with bunch-grass páramo (Lutz & Vader 1987 (12.8); Beekman & Verweij 1987 (4.7)). Living Poaceae LAI of the bamboo páramo (2.5) is similar or higher than that of tropicalpine bunch grasslands (Hnatiuk 1978 (1.6–2.4); Lutz & Vader 1987 (2.4); Beekman & Verweij 1987 (1.4); Hofstede *et al.*, in press (2.4)). The LAI value of the bamboo páramo falls in the range of unifacial, living LAI values for the central European Alps and the Venezuelan Andes, respectively, 0.4–1.3 and 0.05–1.2 (Vareschi 1953).

A main difference between the growth forms of bamboo and bunch-grass is that bunch-grass keeps most of its non-living leaves attached to the tussock, providing protection against strong solar radiation and freezing temperatures (Hnatiuk 1978). *Chusquea tes-*

sellata sheds senescent leaves, which become heavily infected with the fungus *Phyllachora chusqueae*. Apparently, this bamboo species must have other mechanisms and/or strategies against radiation and frost. In this connection it is interesting to note the characteristic 45° (upward) leaf inclination and the xeromorphic leaves of *Chusquea tessellata*.

A result of the leaf shedding is the higher amount of litter in the bamboo páramo ($900 \text{ g DW} \cdot \text{m}^{-2}$ (sd±211); Table 1). Bamboo leaves seem to have a slower turnover rate than bunch-grass leaves. Establishment of other plant species is more difficult on a thick layer of *Chusquea* litter and is thus strongly controlled by *Chusquea* litter fall (in agreement with Grime 1979). The bunch-grasses are co-dominant and can apparently withstand the co-occurrence of *Chusquea tessellata*, possibly by infiltration with stolons in the manner described by Coughenour (1985). Under extreme wet climatic or edaphic conditions *Calamagrostis* bunch-grass species are completely absent (Cleef 1981).

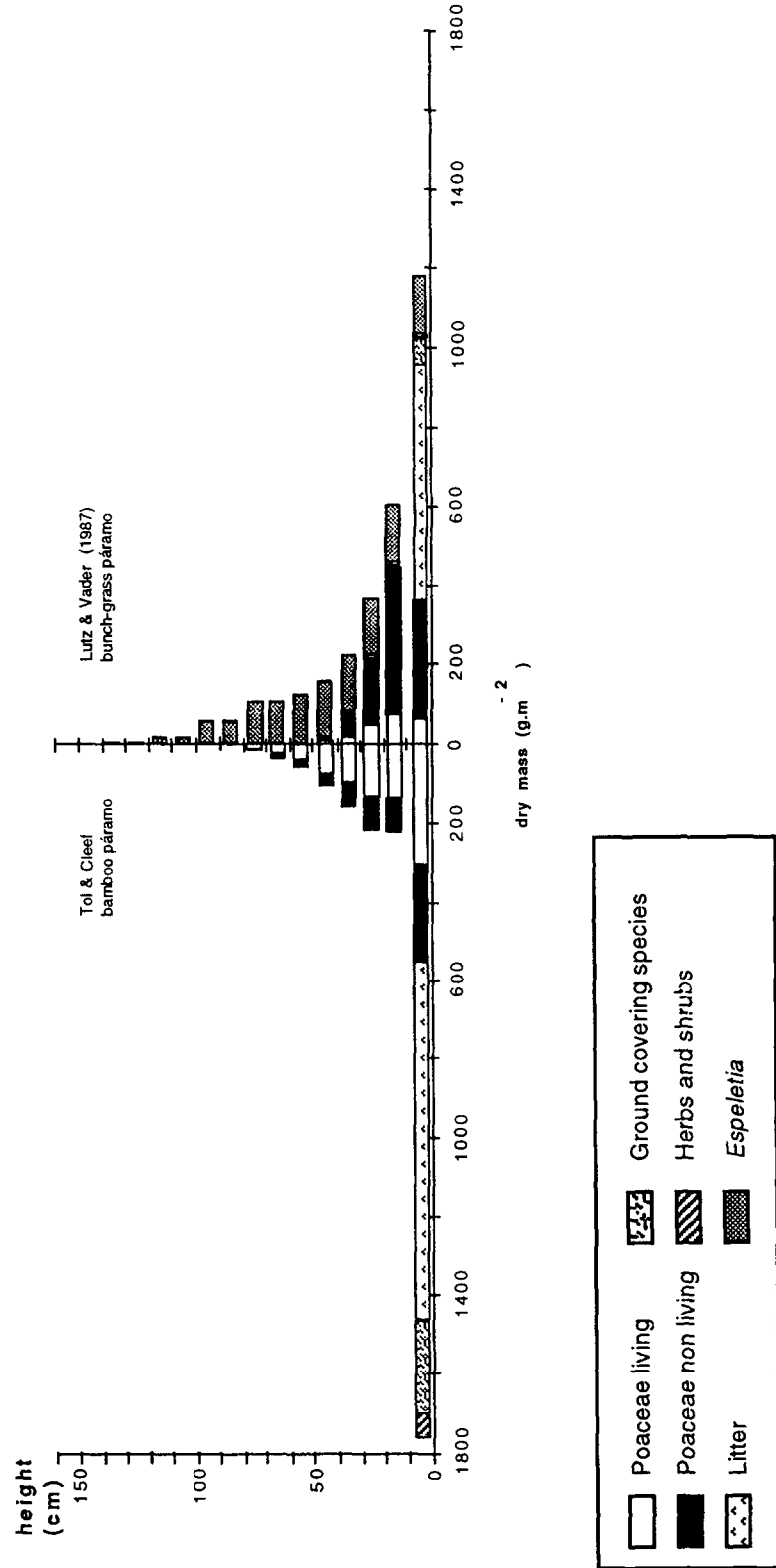


Fig. 8. Mean vertical distribution of biomass ($\text{g DW} \cdot \text{m}^{-2}$) per layer of 10 cm for the main compartments of the vegetation from a bamboo páramo (Tol & Cleef this study) and a bunch-grass páramo (Lutz & Vader 1987).

Acknowledgments

We would like to express our gratitude to the Arévalo family in Santa Fé de Bogotá who provided a home base during the first author's stay in Colombia. We thank the Instituto Geográfico 'Agustín Codazzi' for office and soil laboratory facilities. We are indebted to Dr. M. H. Ramirez-A. for logistical help. INDERENA kindly permitted fieldwork in the Chingaza National Park. The Waterworks of Santa Fé de Bogotá (EAAB) offered field accommodation in the Chingaza National Park. We remember the 'amistad' of the EAAB employees. Theo C. M. Brock, Yvonne Widmer, Robert G. M. Hofstede and two anonymous reviewers are thanked for comments on an earlier draft of this paper. Paul M. Ramsay kindly corrected the English text.

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