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Distribution of grasses along an altitudinal gradient in a Venezuelan paramo

Distribución de gramíneas a lo largo de un gradiente altitudinal en un páramo de Venezuela

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ABSTRACT

In Venezuelan paramos grasses, after Asteraceae, are the second family in numerical importance. We studied their distribution in an altitudinal gradient located in Venezuela, Sierra de La Culata, between 2,500 and 4,200 m of altitude. Twenty one 32 m parallel line transects every 50 m were placed along the gradient, perpendicular to the main slope. Each line was divided into contiguous 50 x 50 cm sampling units. Grass species occurrence inside each sample unit was considered to determine their frequency in each line or altitude. The peak and altitudinal amplitude was determined through the weighted averaging method. A total of 47 grass species were found along the gradient. *Agrostis* was the best-represented genus in the gradient. Considering the distribution ranges, we assume that there are different biotic and abiotic processes determining the distribution patterns. The species occurring at the highest altitudes were temperate elements, while those in the lowest areas were tropical and subtropical elements. Seven species in the gradient are endemic to the Venezuelan paramos. Grass distribution patterns in the paramo may be related to phytogeographical origin. In order to better understand the plant altitudinal distribution pattern is necessary to consider the plant responses to low temperatures, high incoming radiation, water stress and slope aspect.

Key words: altitudinal patterns, phytogeography, Poaceae, South American Andes, tropical high mountain.

RESUMEN

En los páramos de Venezuela las gramíneas son la segunda familia numéricamente más importante, después de las Asteraceae. Nosotros estudiamos su distribución en un gradiente altitudinal ubicado en Venezuela, Sierra de La Culata, entre 2.500 y 4.200 m de altitud. Para esto colocamos 21 transectas de 32 m de longitud a lo largo del gradiente, ubicados de manera perpendicular a la pendiente, cada 50 m en altitud. Cada transecta estaba dividida en unidades de muestreo contiguas de 50 x 50 cm. Para estimar la frecuencia de las especies en cada transecta o altitud, consideramos la ocurrencia de las mismas dentro de cada una de las unidades de muestreo. Determinamos el óptimo y la amplitud altitudinal a través del método de los promedios ponderados. Encontramos un total de 47 especies de gramíneas distribuidas a lo largo del gradiente. *Agrostis* fue el género mejor representado. Teniendo en cuenta los intervalos de distribución, podemos asumir que hay diferentes procesos que determinan la distribución de las especies, pudiendo estos ser de origen biótico y abiótico. Las especies que ocurren a mayores altitudes correspondieron a elementos templados, mientras que aquellos que ocurren en áreas de menor altitud fueron elementos tropicales y subtropicales. Siete de las especies del gradiente son endémicas a los páramos de Venezuela. Los patrones de distribución de las gramíneas en el páramo, parecen estar relacionados con el origen fitogeográfico. Para entender mejor los determinantes de los patrones de distribución altitudinal es necesario considerar las relaciones existentes entre las respuestas de las especies a las bajas temperaturas, radiación, estrés hídrico y exposición.

Palabras clave: patrones altitudinales, fitogeografía, Poaceae, Andes suramericanos, alta montaña tropical.

INTRODUCTION

The distribution of a species is the result of physiological adaptation to biotic and environmental conditions, and to evolutionary events (Clayton 1981, Ricardi et al. 1997, Sklenáȓ & Jørgensen 1999, Sklenáȓ & Ramsay 2001). Gates (1980) considers temperature and humidity as the main determinants of distribution patterns in grasslands. In the particular case of South America Andean Mountains, species distribution has been influenced greatly by both tectonic and climatic dynamics (van der Hammen 1988).

The highlands in Venezuela are represented by paramo, a Neotropical ecosystem between the timberline and the snowline (Smith 1994, Luteyn 1999), with particular features such as: low ambient temperatures, higher daily temperature oscillations than seasonal ones, and a high frequency of night frost throughout the year (Cuatrecasas 1968, Monasterio 1980a, Baruch 1982, Sarmiento 1986).

Rosettes and grasses are the main growth forms in the Venezuelan paramos (Hedberg & Hedberg 1979, Fariñas & Monasterio 1980, Monasterio 1980a, 1980b). Rosettes have been well studied. For instances: radiation and distribution (Cuatrecasas 1986, Monasterio & Sarmiento 1991), population dynamics (Estrada & Monasterio 1988), and adaption to cold environments (Meinzer & Goldstein 1985, Rada et al. 1985, Monasterio 1986, Rada et al. 1987, Meinzer et al. 1994). But grasses, the second family in numerical importance after the Asteraceae (Luteyn et al. 1992, Briceño & De Robert 1996, Ricardi et al. 1997) have received less attention.

The common occurrence of grasses under cold environmental conditions has been reported (Teeri & Stowe 1976, Clayton & Renvoize 1986, Schwarz & Redmann 1987, Sage & Sage 2002). Clayton (1981) highlights the properties of some taxonomic groups in the Poaceae (Aveneae, Poeae and Stipeae) to adapt to cold conditions, either in high mountains or in temperate zones. Relationships between the distribution patterns in some subfamilies and tribes of the Poaceae and the environmental variables that determine such patterns have been established (Hartley 1958a, 1958b, 1961, 1973, Hartley & Slater 1960). Low temperature resistance mechanisms for the Poaceae in the paramo evidence the adaptation of some species in the family to these environmental conditions (Márquez 2002).

Researchers have related the distribution of plant species, including grasses, in the paramo, with temperature (Baruch 1984, Ricardi et al. 1987, Fariñas & Monasterio 1998, Luteyn 1999, Sklenáø & Jørgensen 1999), and biogeographic aspects (van der Hammen & Cleef 1986, Monasterio & Sarmiento 1991, Ricardi et al. 1997). In all these studies, the authors consider the altitudinal distribution of plants based on the presence of the species and not their frequency.

At present, paramos are under increasing antropic pressures. In this sense, Grytnes (2003) points out the importance in understanding altitudinal species patterns for the management of species diversity. The aim of this study is to understand the altitudinal distribution of paramo grasses.

MATERIAL AND METHODS

Study area

The paramo has 2,000 m of altitudinal extension (Monasterio 1980a). We studied a 1,700 m altitudinal transect, located in Sierra de La Culata, Mérida, Venezuela (8º51’04" N, 70º43’10" W and 8º51’09" N, 70º49’25" W). We selected an east-facing slope characterized by a unimodal precipitation pattern. Both precipitation and temperature decrease as altitude increases (Fig. 1). The number of days with frost increases with altitude and during the dry season (Monasterio & Reyes 1980).

The highest zone in the gradient shows a high and open rosette paramo vegetation defined as desert paramo by Monasterio (1979, 1980a). At this altitude, the vegetation cover is spatially patched and is mainly composed by woody and herbs perennial species, predominantly tall rosettes and cushions (Monasterio 1980a). Grasses have low frequencies and occupy the lowest stratum, often represented by cushion forms. The middle part of the gradient (around 3,500 m of altitude) has three strata, the lowest and middle ones are occupied by grasses (covering 40 and 80 %, respectively) and herbs (Fariñas & Monasterio 1980). Rosettes and shrubs occupy the highest stratum. Finally, in the lowest zone of the gradient, the vegetation is a mixture of rosettes, grasses, herbs and shrubs (Monasterio & Reyes 1980), all of them forming a continuous vegetation cover and occupying all strata.

In general terms, soils in the paramo are relatively young and have been under the effect of glaciations (Schubert 1976, 1981, Hooghiemstra 1989). Moreover, soils are often acidic and poorly developed with a low content of inorganic nutrients (Baruch 1979, 1982), high content of organic carbon and total nitrogen, and low water holding capacity (Fariñas 1975).

Grass distribution sampling

Grass distribution was studied along a gradient between 2,500 and 4,200 m of altitude including the following locations: El Baho, Las Tapias, Paso Real Hotel, Los Plantíos, Pico El Gavilán, and Pico El Águila (Fig. 2).

Twenty-one lines of 32 m in length were placed along the gradient, arranged perpendicular to the main slope, and located every 50 m of altitude (sampling was not possible at some altitudes due to difficult access or antropic disturbed conditions). Each line was divided into contiguous 50 x 50 cm sampling units. Grass species occurrence inside each sample unit was considered to determine their frequency in each line or altitude. Finally, the peak and altitudinal amplitude was determined through the weighted averaging method (Ellenberg 1979, ter Braak & Barendregt 1986) using the following equations, for the optimum:

$$\hat{VI}_{ik} = \frac{\sum_{j=1}^{m} Ae_{ij} VA_{kj}}{\sum_{j=1}^{m} Ae_{ij}}$$

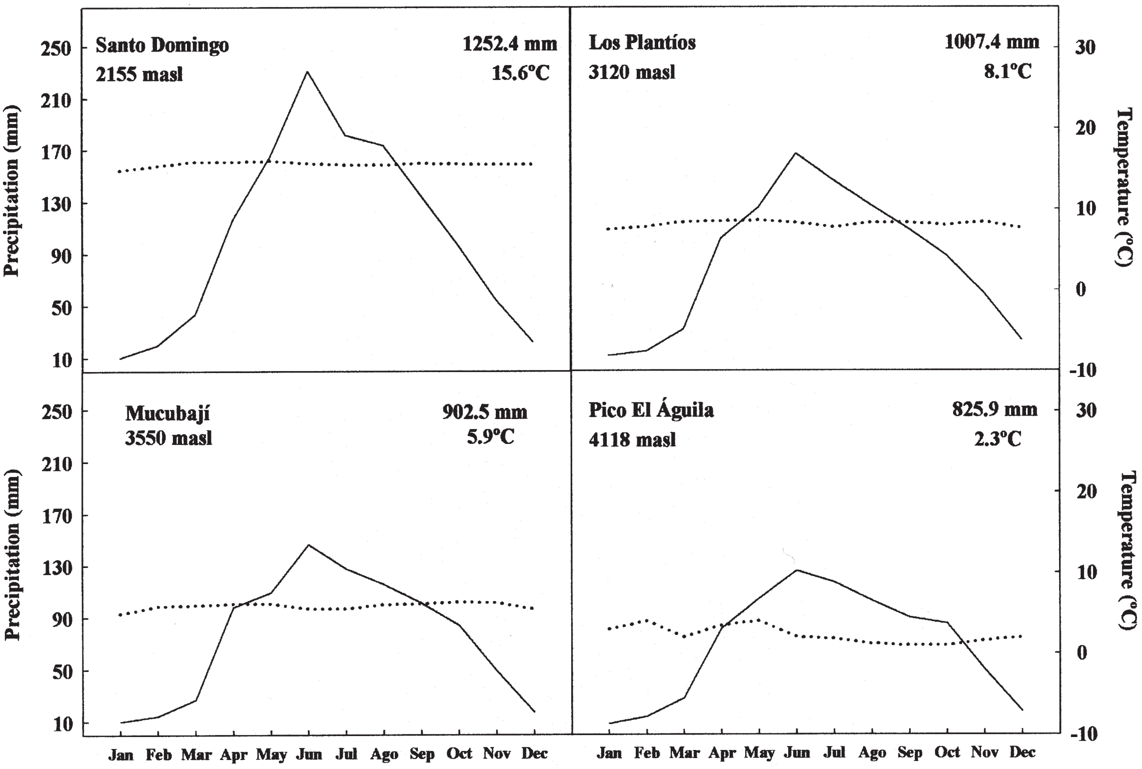

Fig. 1: Mean precipitation and temperature (1960-1995) at different altitudes. There is a decrease in both environmental variables as altitude increases (Ministerio del Ambiente y Recursos Naturales Renovables, Dirección de Hidrología y Meteorología).

Promedios de precipitación y temperatura (1960-1995) a diferentes altitudes. Se aprecia una disminución de ambas variables ambientales a medida que la altitud se incrementa (Ministerio del Ambiente y Recursos Naturales Renovables, Dirección de Hidrología y Meteorología).

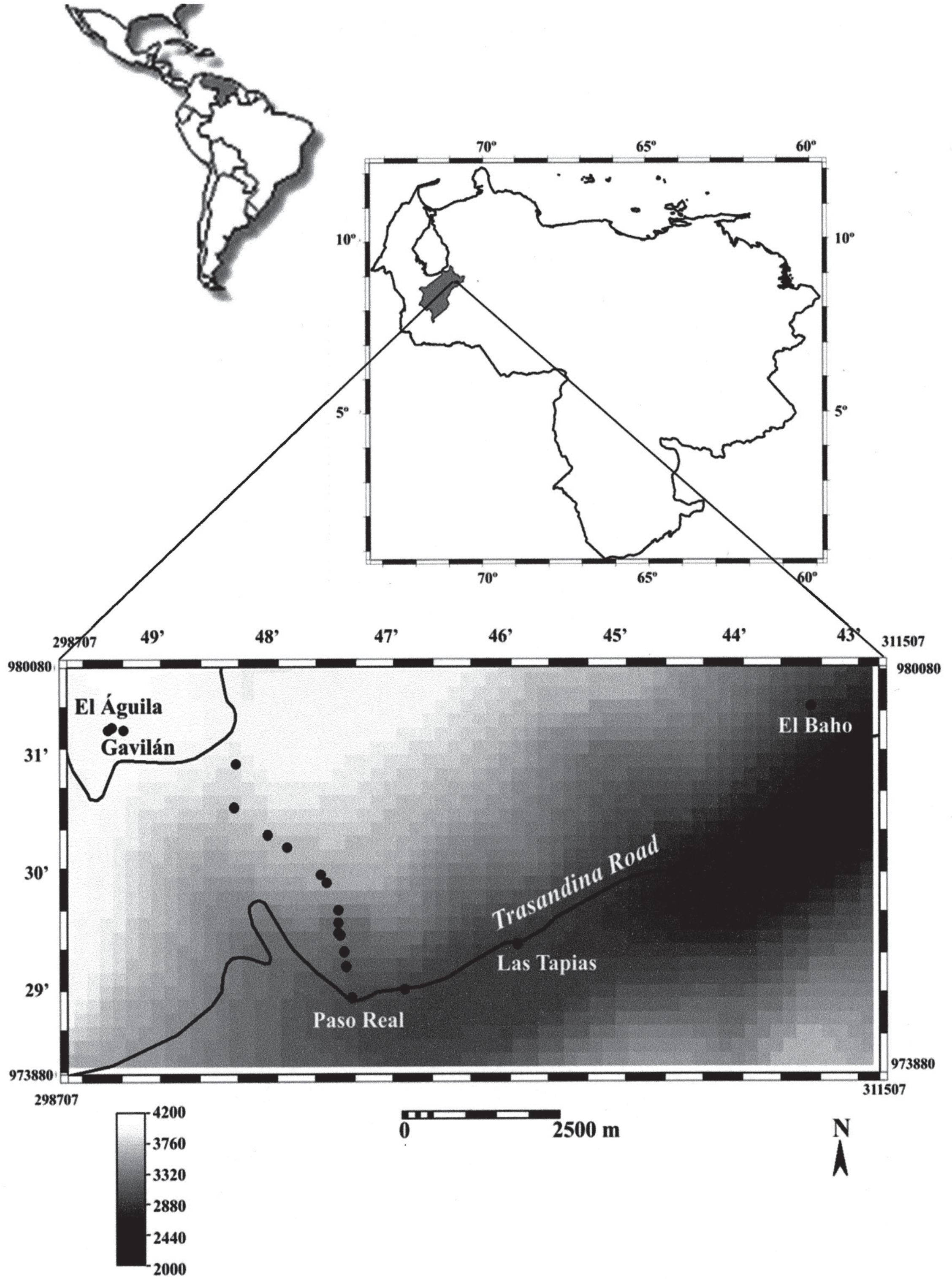

Fig. 2: Spatial location of the study area (UTM coordinates at corners correspond to 19N Zone). The filled circles indicate the studied locations in the altitudinal gradient.

Ubicación especial del área de estudio (las coordenadas UTM localizadas en las esquinas corresponden a la Zona 19N). Los círculos negros indican los puntos de muestreo en el gradiente.

$\hat{V}I_{ik}$ is the weighted averaging of species *i* for factor *k* (altitude). Ae_{ij} is species *i* abundance at place *j*. VA_{kj} is environmental variable *k* at place *j*, and *m* is the number of sample units. On the other hand, altitudinal amplitude was calculated as follows:

$$t_{ik} = \sqrt{\frac{\sum_{i=1}^{m} Ae_{ij}\left(VA_{kj} - \hat{V}I_{ik}\right)^2}{\sum_{i=1}^{m} Ae_{ij}}}$$

where t_{ik} is species *i* amplitude to factor *k*, Ae_{ij} is species *i* abundance at place *j*, VA_{kj} is environmental variable *k* at place *j*, $\hat{V}I_{ik}$ is the weighted averaging for species *i* to factor *k* and *m* is the number of observed lines.

Samples were taken in August 2001, during the rainy season to guarantee flowering of as many grass species as possible. Individuals were taken to the lab, pressed and dried for later botanical determinations according to Hitchcock (1927), Luces (1953), Rosengurtt et al. (1970), Pohl (1980), Tovar (1993), Briceño & Morillo (1994), and Davidse et al. (1994). The Clayton & Renvoize (1986) tribal division was applied. Bouchers were placed in the Herbarium MER of the Facultad de Ciencias Forestales y Ambientales, Universidad de Los Andes.

RESULTS

Forty seven species were found along the gradient (Fig. 3). Some species were located just at one altitude (indicated as a black circle in Fig. 4), as well as species with wide and restricted distributions. Species located at one altitude were common at the extremes of the gradient, whereas wide distributions were found in the middle of the gradient. Some species support the hypothesis that unimodal distribution and symmetry is not common showing truncated distributions (Fig. 4). The following species: *Sporobolus indicus, Vulpia bromoides, Axonopus fissifolius, Trisetum kochianum, T. pringlei, Muhlenbergia venezuelae, Nassella mexicana, Trisetum deyeuxoides, Poa petrosa, Agrostis basalis* and *A. breviculmis* show a narrow distribution in the gradient. The opposite is true for *Pennisetum clandestinum, Aegopogon cenchroides, Trisetum irazuense, Paspalum pilgerianum, Poa annua, Nassella linearifolia, Agrostis tolucensis, Calamagrostis pittieri, Agrostis trichoides* and *Aciachne acicularis.*

Taking into account the complete gradient, there was a substitution of species forming a continuum along the altitudinal gradient (Fig. 4). *Agrostis* was the richest genus in the gradient with six species, followed by *Festuca* and *Trisetum* with five species each. *Agrostis basalis, Agrostis breviculmis, Bromus catharticus* and *Calamagrostis heterophylla* were found exclusively above 4,000 m of altitude. Other species were restricted to the middle and lower zones of the gradient. *Calamagrostis pisinna, Cortaderia hapalotricha, Festuca pinetorum,* and *Paspalum pygmaeum* were only collected outside of the sampling units.

The species found belong to 10 tribes (Table 1): Arundineae (two species), Aveneae (16 species), Bromeae (two species), Cynodonteae (one species), Eragrostideae (three species), Meliceae (one species), Paniceae (six species), Poeae (11 species), Stipeae (four species), and Triticeae (one species). Poeae and Aveneae are the most important tribes in terms of number of species, which include wide temperate elements (van der Hammen & Cleef 1986). Eragrostideae is the only tribe with a tropical origin (Clayton & Renvoize 1986), distributed between 2,445 and 3,675 m of altitud with a mixture of species belonging to endemic *(Muhlenbergia venezuelana)*, holartic *(M. ligularis)*, and wide tropical elements (van der Hammen & Cleef 1986). The Cynodonteae, Meliceae, and Paniceae tribes had tropical and subtropical origins (Gould & Shaw 1983, Clayton & Renvoize 1986, van der Hammen & Cleef 1986), with a similar distribution to that of Eragrostideae, between 2,470 and 3,550 m of altitude. On the other hand, Arundineae, with austral-antarctic *(Cortaderia hapalotricha)* and wide temperate *(Danthonia secundiflora)* elements (van der Hammen & Cleef 1986), Bromeae and Poeae tribes, with wide temperate elements (Gould & Shaw 1983, Clayton & Renvoize 1986, van der Hammen & Cleef 1986), were distributed between 2,470 and 3,980 m of altitude. Aveneae, Stipeae, and Triticeae showed wide temperate elements, typically from high altitudes (Clayton & Renvoize 1986, van der Hammen & Cleef

1986), and were distributed between 2,470 and 4,180 m of altitude. These last tribe groups reached the highest elevations in the gradient.

Aciachne is the only genus endemic to the Andean region including Central and South America, while there are seven species endemic to Venezuelan paramos (14.9 %): *Agrostis basalis, A. jahni, A. meridensis, Muhlenbergia venezuelae, Festuca elviae, F. fragilis,* and *Poa petrosa,* four of them found above 3,800 m of altitude (Fig. 4). There are eight introduced species, representing 17 % of the total: *Polypogon monspeliensis,* from Eurasia, *Trisetum spicatum, Lolium perenne,* and *Poa annua,* natives from Europe, *Panicum trichoides,* from Africa and Asia, *Pennisetum clandestinum,* native of tropical Africa, and *Vulpia bromoides* and *V. myuros*, natives of Eurasia and North Africa. Thirty-eight species found in the gradient were native of America (Table 1).

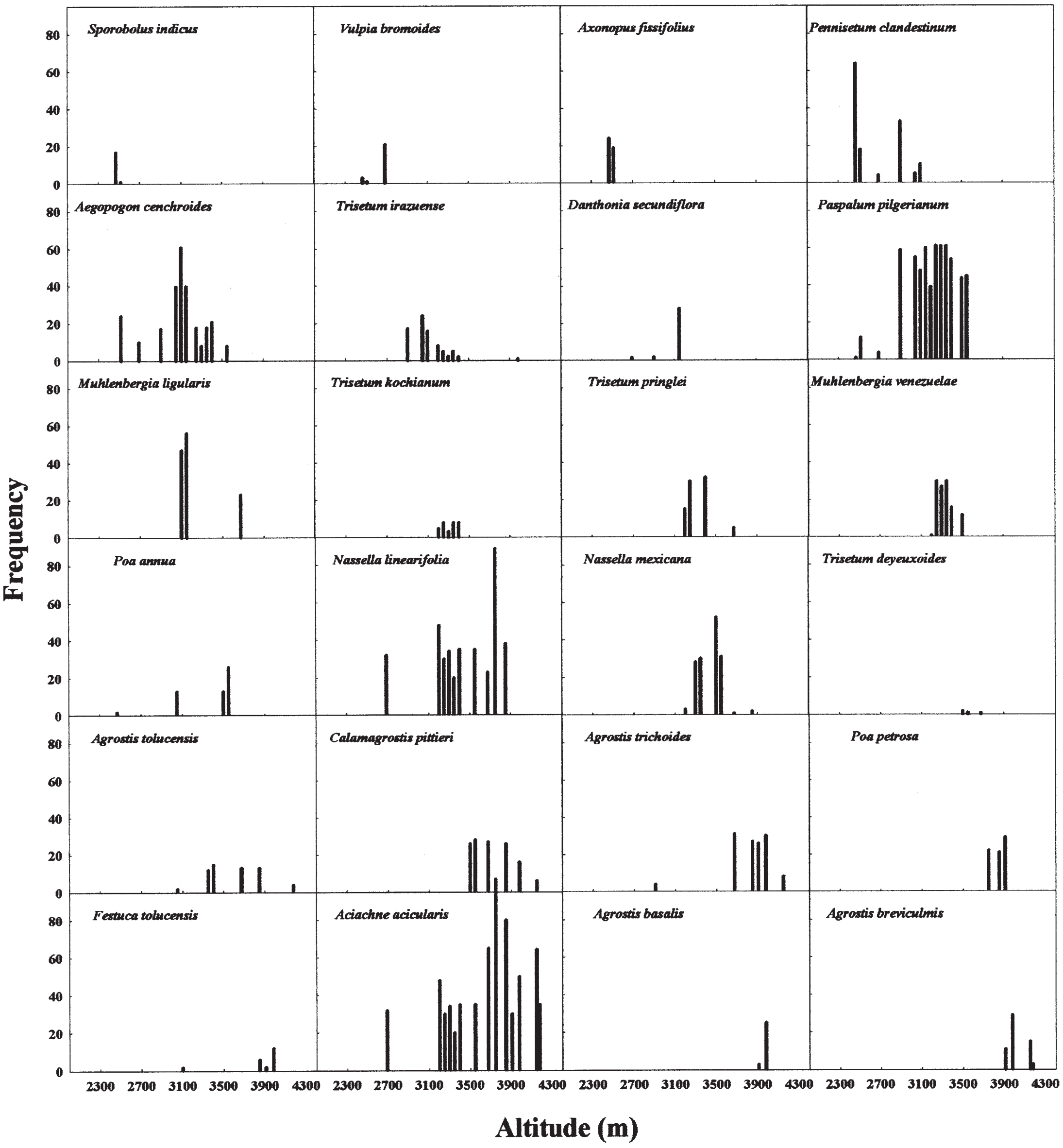

Fig. 3: Species frequency at each altitude. Species found at more than one altitude were considered. Note the distributions pattern, which may or not be symmetrical.

Frecuencia de las especies a cada altitud. Se consideraron aquellas especies localizadas en más de una altitud. Nótese la forma de las distribuciones, las cuales pueden ser simétricas o no.

TABLE 1

Species found in the studied gradient. Tribes with their phytogeographical element, species observed distribution range and altitudinal optimum calculated through the weighted averaging method: [a]from Clayton & Renvoize (1986); [b]according van der Hammen & Cleef (1986); [c]from Hitchcock (1927), Luces (1953), Rosengurtt et al. (1970), Pohl (1980), Tovar (1993), Briceño & Morillo (1994), Davidse et al. (1994), and Luteyn (1999); [d]from Gould & Shaw (1983); [e]species found outside the sample units

Especies encontradas en el gradiente estudiado. Se muestran las tribus con su elemento fitogeográfico, así como los intervalos y óptimos de distribución de las especies, calculados a través del método de los promedios ponderados: [a]Clayton & Renvoize (1986); [b]van der Hammen & Cleef (1986); [c]según Hitchcock (1927), Luces (1953), Rosengurtt et al. (1970), Pohl (1980), Tovar (1993), Briceño & Morillo (1994), Davidse et al. (1994) y Luteyn (1999); [d]Gould & Shaw (1983); [e]especies encontradas fuera de las unidades de muestreo

Tribe[a]	Phytogeographic element[b]	Species	Altitudinal		Present geographical distribution[c]
			Range (m)	Optimum (m)	
Arundineae	Neotropical	*Cortaderia hapalotricha* Pilg.[e]	-	-	CR to BO
	Wide temperate	*Danthonia secundiflora* J. Presl.	2,690-3,150	3,106	CO EC PE BR AR
Aveneae	Endemic	*Agrostis basalis* Luces	3,910-3,980	3,973	VE
		Agrostis jahni Luces	3,100	3,100	VE
		Agrostis meridensis Luces	3,910	3,910	VE
	Wide temperate	*Agrostis breviculmis* Hitchc	3,910-4,180	4,021	CO EC PE BO CH
		Agrostis tolucensis Kunth	3,050-4,180	3,593	ME to CH
		Agrostis trichodes (Kunth) Roem. & Schult.	2,905-4,150	3,839	CO EC PE
		Calamagrostis heterophylla (Wedd.) Pilg.	4,150	4,150	EC PE BO
		Calamagrostis pisinna Swallen[e]	-	-	CO
		Calamagrostis pittieri Hackel	3,500-4,150	3,707	CR CO
		Polypogon elongatus Kunth	2,470	2,470	ME to AR BO
		Polypogon monspeliensis (L.) Desf	2,470	2,470	Native from Eurasia
		Trisetum deyeuxoides (Kunth) Kunth	3,500-3,675	3,556	ME to EC
		Trisetum irazuense (Kuntze) A. Hitchc.	2,905-3,980	3,102	ME to EC
		Trisetum kochianum Hern.	3,200-3,400	3,309	ME GU CR
		Trisetum pringlei (Scribner ex Beal) A. Hitchc.	3,200-3,675	3,325	S of ME CR PA
		Trisetum spicatum (L.) K. Richter	2,905	2,905	Native from Europe
Bromeae	Wide temperate	*Bromus catharticus* Vahl	3,980	3,980	S of USA to CH AR
		Bromus lanatus Kunth	2,905	2,905	CO EC PE BO CH
Cynodonteae	Tropical and subtropical[d]	*Aegopogon cenchroides* Humb. & Bompl. ex Willd	2,515-3,550	3,099	USA ME Antillas Mesoamerica to BO BR
Eragrostideae	Endemic	*Muhlenbergia venezuelae* Luces	3,200-3,500	3,334	VE
	Holartic	*Muhlenbergia ligularis* (Hackel) Hitchcock	3,100-3,675	3,227	GUA CO to BO AR
	Wide tropical	*Sporobulus indicus* (L.) R. Br.	2,445-2,511	2,478	USA Antillas
Meliceae	Tropical and subtropical[d]	*Triniochloa stipoides* (Kunth) A. Hitchc.	3,150	3,150	ME to BO N of BR
Paniceae	Neotropical	*Axonopus fissifolius* (Raddi) Kuhlm	2,470-2,515	2,534	Native from American tropics and subtropics
		Paspalum pilgerianum Chase	2,470-3550	3,225	CO EC PE
	Tropical and subtropical[d]	*Panicum trichoides* Swartz	2,615	2,615	Africa and Asia
		Pennisetum clandestinum Hochst. ex Chiov	2,470-3,100	2,672	Native from tropical Africa
	Wide tropical	*Paspalum inconstans* Chase	2,615	2615	CO EC PE BO
		Paspalum pygmaeum Hackel[e]	-	-	PE BO
Poeae	Endemic	*Festuca elviae* Briceño	3,100	3,100	VE
		Festuca fragilis (Luces) Briceño	3,910	3,910	VE
		Poa petrosa Swallen	3,750-3,910	3,842	VE
	Wide temperate	*Festuca pinetorum* Swallen[e]	-	-	ME
		Festuca tolucensis Kunth	3,100-3,980	3,858	ME to CR CO
		Festuca ulochaeta Steudel	3,550	3,550	EC PE BO BR AR
		Poa annua L.	2,470-3,550	2,690	Native from Europe
		Poa aequatorensis Hackel[e]	-	-	EC PE
		Lolium perenne L.	2,905	2,905	Native from Europe
		Vulpia bromoides (L.) Gray	2,470-2,515	2,506	Eurasia and N Africa
		Vulpia myuros (L.) Gmelin[e]	-	-	Eurasia and N Africa
Stipeae	Neotropical	*Aciachne acicularis* Lægaard	3,675-4,180	3,966	CR to CO
	Wide temperate	*Nassella linearifolia* (Fourn.) R. Pohl	2,690-3,850	3,426	S of ME Mesoamerica CO BO
		Nassella mexicana (A. Hitchc.) R. Pohl	3,200-3,850	3,442	ME to BO
		Nassella mucronata (Kunth) R. Pohl	2,905	2,905	ME to AR BO
Triticeae	Wide temperate	*Brachypodium mexicanum* (Roem. & Schult.) Link	2,690	2,690	ME to BO

AR = Argentina; BO = Bolivia; BR = Brasil; CH = Chile; CO = Colombia; CR = Costa Rica; EC = Ecuador; GUA = Guatemala; GU = Guyana; ME = México; PA = Panamá; PE = Perú; VE = Venezuela

DISCUSSION

Some authors have argued that grasses are an important element of paramo vegetation (Monasterio 1980a, Fariñas & Monasterio 1980, 1998, Baruch 1984, Luteyn et al. 1992, Ricardi et al. 1997). Our results support these observations, since grasses were found at all studied altitudes. Simpson & Todzia (1990) suggest that their success, as in the Asteraceae, must be due to dispersion mechanisms, often facilitated by wind action (Jacobs 1999) and animal transportation. However, the occurrence of grasses become patchily distributed as altitude increases, an observation that contrasts with the more continuum pattern observed at lower elevations, and that seems associated to climatic constraints (Sklenáȓ & Ramsay 2001). Palynological information obtained in Colombia suggests that the Poaceae have been an important element of paramo vegetation since the Pleistocene (Salgado-Labouriau 1978, van der Hammen & Cleef 1986, van der Hammen 1988, Behling et al. 1998, Marchant et al. 2001). However, there is no accurate information on the grass genera that occupied

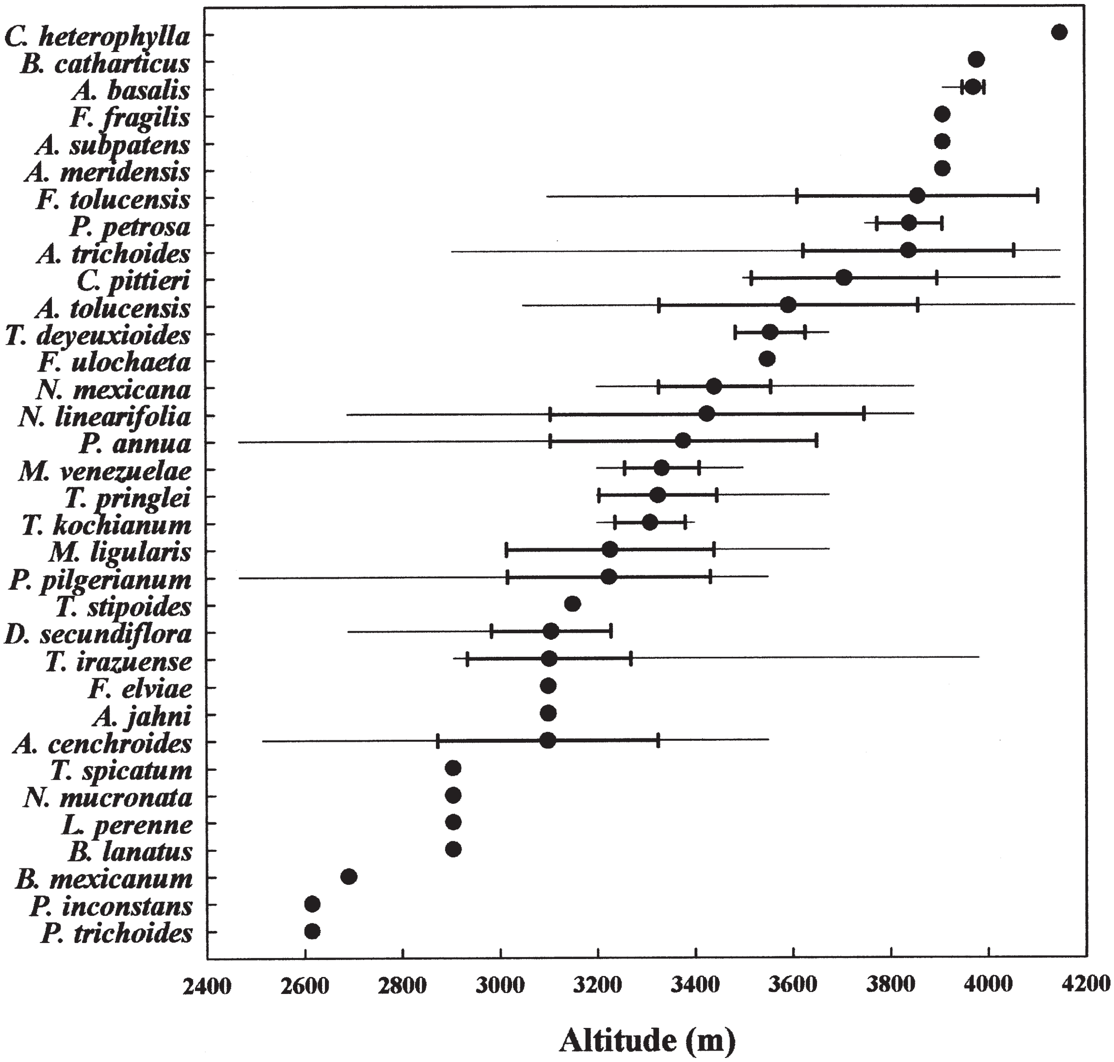

Fig.4: Species distribution in the altitudinal gradient. Species altitudinal optimum occurrence (•), the calculated amplitude (⊢⊣),observed altitudinal limits (—).

Distribución de las especies en el gradiente altitudinal. óptimo altitudinal de las especies (•), amplitud calculada (⊢⊣) y límites altitudinales observados (—).

the paramos. It is not well understood what determines the amplitude of different species in the paramo. Körner (1992) proposed a mixture of processes defining the spatial pattern: at lower elevations prevail biotic processes, such as competition by light, water, nutrients and space, and at higher elevations prevail abiotic processes all of them conditioned by severe environmental conditions, such as freezing temperatures and water stress.

Some species mentioned in this study have been reported by other authors working in other paramos: Ricardi et al. (1987) found *Agrostis breviculmis, A. meridensis, A. tolucensis, Bromus pitensis* (syn. *B. lanatus* Kunth), *Calamagrostis mulleri* (syn. *C. heterophylla* (Wedd.) Pilg.), *Festuca tolucensis, Muhlenbergia ligularis, Poa annua, P. petrosa, Nassella mexicana, Trisetum irazuense,* and *T. spicatum* in the Piedras Blancas paramo, at 4,200 m of altitude. This paramo is both drier and higher compared to our study site, suggesting that these species can resist more extreme conditions than those found in our study area. All these species belong to the Pooideae subfamily, which according to Clayton (1981) represents a new venture for the grasses due to their adaptation to cold climates. On the other hand, probably most grass species in the paramo arose recently because most of them (35 species out of 47.74 %) are native to America, which could be an evidence of active speciation processes. Endemism in grass species along the gradient is high (14.9 %) with respect to genera of vascular plants reviewed by van der Hammen & Cleef (1986) in the eastern Colombian cordillera, representing only 7.3 %. These values could be interpreted as an evidence for active speciation in the Poaceae of the Northern Andes, since some genera such as *Agrostis, Festuca* and *Poa* with temperate origin are occurring in the gradient with endemic species *(Agrostis jahni, A. meridensis, Festuca elviae, F. fragilis* and *Poa petrosa).* Sklenáȓ & Jørgensen (1999) found *Agrostis breviculmis, Bromus catharticus,* and *Trisetum spicatum* in the paramos of Ecuador. They also calculated the average and altitudinal amplitude, but they did not consider the pattern of species frequency along the gradient, only their extreme occurrence. Moreover, Baruch (1984) considered *Calamagrostis mulleri* and *C. pittieri* as high elevation species, and *Agrostis trichoides, Paspalum* sp., and *Aegopogon cenchroides* as low paramo species. Similarly, Cabido et al. (1997) working in Córdoba, Argentina, found *Agrostis breviculmis, A. tolucensis,* and *Muhlenbergia ligularis* at the highest extreme of their gradient (2,100 m of altitude). In this case, it is important to consider the altitudinal differences with respect to our gradient due to latitudinal differences. The distribution of *Poa* was studied with a botanical approach at a global scale by Hartley (1961), and in the Venezuelan páramos by Briceño (1987). Hartley (1961) indicates that high frequencies in *Poa* species in both high latitudes and altitudes, suggest that temperature is closely related to distribution, and an adaptation to cold and temperate climates (Clayton 1981, Clayton & Renvoize 1986). Márquez (2002) found that the main adaptation of grasses to cold environments is related to frost tolerance.

Aveneae, Poeae, Stipeae, and Triticeae are frequently found at high altitudes in the Andean region, as well as in temperate regions (Hartley 1973, Gould & Shaw 1983, van der Hammen & Cleef 1986). Their temperate origin probably facilitated the colonization of the tropical high mountain. Burkart (1975) emphasizes the boreal influence on paramo grasses due to the migration bridge represented by the Andean mountain range. The consequence of this high degree of migration is a low endemism in the Andean mountains with respect to Africa (Luteyn et al. 1992, Sklenáȓ & Ramsay 2001). In our case, the only endemic genus is *Aciachne* (Burkart 1975, Luteyn et al. 1992). On the other hand, the genus *Bromus* and *Brachypodium* are relatively scarce at high altitudes and latitudes (Hartley 1973). However, *Bromus* has relatively high frequencies in the paramo. *Festuca* is a genus with a long evolutionary history and it is believed that it has adapted easily to recent climatic conditions (Hartley 1973). *Poa* is the most interesting case in the Poaceae because it is a cosmopolitan genus, with temperate characters but present in tropical high mountains (Hartley 1973).

This study suggests that there is an important grass occurrence in the paramo with a temperate origin (49 %), as was mentioned by van der Hammen & Cleef (1986) for paramo genera in the eastern Colombian cordillera and

Ricardi et al. (1997) for Piedras Blancas in Venezuela. Therefore, the phytogeographic origin seems to determine, to a great extent, grass distribution in our transect. However, for a better understanding of the distribution pattern determinants it is necessary to study grass adaptative mechanisms to paramo climatic conditions (low temperatures, high incoming radiation, water stress).

Since Poaceae are highly sensitive to temperature and humidity changes (Berry & Björkman 1980, Ehleringer & Monson 1993), and to variations in environmental CO_2 (Körner & Diemer 1994, Street-Perrott et al. 1997) the study of their distribution patterns could be a powerful tool, which may help to understand aspects related with local climatic conditions, adaptations to environmental and vegetation responses to climatic changes. In this sense, if we consider the inverse of species amplitude as a measure of sensibility, those located in the extremes have to be specially taken into account for future research (*Panicum trichoides, Paspalum inconstans, Brachypodium mexicanum, Bromus lanatus, L. perenne, N. mucronata, T. spicatum,* at the lowest altitude, and *A. meridensis, A. subpatens, F. fragilis, A. basalis, C. heterophylla,* at the highest altitude). Studying grass distribution changes in time could be employed as a diagnostic method in studies of global change, as it would allow recording possible variations in altitudinal ranges in response to changes in environmental conditions.

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