13 Functional Diversity of Wetland Vegetation in the High-Andean *Páramo*, Venezuela

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INTRODUCTION

Tropical and subtropical highland areas are characterized by a high diversity per unit area (Körner 1999), which is reflected not only in species numbers but also in the functional variability of the ecosystem (Walker et al. 1999). We analyzed functional variability and architectonic models to develop an ecological interpretation of taxonomic diversity in Andean wetlands.

Plant species are often grouped according to their morphological characteristics, e.g. for temperate regions, in terms of the height of growth meristems during the unfavorable season, as proposed by Raunkier (1934). This morphological grouping, however, is not directly applicable to the plant species in high tropical mountains. Here, the widest temperature oscillations occur daily instead of seasonally, growth is continuous throughout the year, and dormancy of the growth meristems occurs during a few hours at night, when temperatures go below 0°C (simulating the latency season that lasts several winter months in extratropical regions) (Sarmiento 1986; Rundell et al. 1994).

For this reason, Hedberg (1964) proposed a classification of the Afroalpine flora according to their different adaptive strategies into five groups: caulescent rosettes, acaulescent rosettes, tussock grasses, cushion and sclerophyllous shrubs, like some forbs and grasses that are commonly temperates. Hedberg's system has been accepted as being adequately representative of the common pattern in the cold intertropics to which the diverse plant communities of the Andean páramos belong (Hedberg and Hedberg 1979; Smith and Young 1987), from the humid páramo grasslands in Colombia (Hofstede 1995) to the dry páramos in Venezuela (Monasterio 1980a).

Tropical and subtropical highland areas are characterized by a high diversity per unit area (Körner 1999), which is not only reflected in the species numbers but also in the functional variability of the ecosystem (Walker et al. 1999). From this perspective, the different life-forms can be interpreted as architectonic models conditioned for a given function. For example, in the giant rosettes of the *Espeletia* genus, the marcescent leaves encasing the aerial stem prevents freezing during the night and allows the reestablishment of photosynthetic activities during the first hours of the day (Goldstein et al. 1984). Therefore, an analysis based on functional variability and architectonic models can be used for developing an ecological interpretation of taxonomic diversity.

Andean wetlands are located in the driest páramo of the Cordillera de Mérida, Venezuela. They occupy geomorphologic situations such as valley bottoms or microterraces, created by the deposition of fluvioglacial materials under the influence of continuous daily freeze–thaw cycles (Schubert 1979). These wetland environments are relatively more stable in terms of their temperature cycles, allowing the establishment of a grass vegetation (covering less than 10%

of land surface) made up of highly palatable forbs and grasses (80% vegetation cover), such as *Calamagrostis mulleri*, *Muehlenbergia ligularis*, *Carex albolutescens*, and *Agrostis breviculmis*, which, according to Ivlev's preference (Ramirez et al. 1996), have high protein content. In this sense, these environments are denominated as Andean grasslands. These wetland environments are dominated by Andean grasses (Molinillo 1992) with a high species richness and a high vegetation cover (80%). However, Andean wetlands occupy less than 10% of the land surface, whereas shrubland with caulescent rosettes of the *Espeletia* genus, sclerophylous shrubs, and cushions, all species with little palatable forage, dominate in the huge stretch of more than 90% of the land surface (Molinillo and Monasterio 1997a).

Andean grasses have high species richness, good stability, appropriate ground conservation and, together with other wetlands and marshes, form areas with high regional diversity (Molinillo and Monasterio 2002). However, the diversity in the Andean wetlands is seriously threatened by intensive grazing (Molinillo and Monasterio 1997a). Recently, the Andean páramos has been subjected to an accelerated process of degradation and transformation, characterized by farming intensification and continuing expansion of the agricultural frontier (Luteyn 1992; Hofstede 1995). The intensity and frequency with which the wetlands are visited by cattle are correlated with the agriculture activities (Pérez 2000). The increasing human intervention, frequently involving long fallow agriculture (Monasterio 1980b; De Robert and Monasterio 1993), led to higher stocking rates, grazing, and the formation of induced wetlands in which the dynamics are controlled by grazing patterns, especially during the dry season when the animals are gathered together in the Andean grasslands (Molinillo 2003).

During the fieldwork in 2002–2003, we observed that the cattle consumed the palatable forbs and grasses and trampled the vegetation in the Andean grasses. For this reason, the target of this study was to analyze the functional variability in species of the Andean wetlands by using ecological variables that are likely to be affected by grazing in the Andean páramos, such as the aboveground/belowground phytomass rate and growth meristem's protection. We compared the species sensitive to trampling in both intensively grazed and extensively grazed wetlands. This allows us to analyze the impact that extensive grazing has on life-forms that are critical for the conservation and sustainable use of the Andean wetland. In this work, we do not study the direct effect of grazing on the studied species, but some results can be interpreted as the effect of intensive grazing (0.2–0.4 UA/ha) on Andean grass (Molinillo 1992).

STUDY AREA

The study was undertaken in the wetland of Mifafí, in the Sierra La Culata of the Cordillera de Mérida, Venezuela. The area is a dry páramo in the cold intertropic, where the annual isotherm is 2.8°C, and the average yearly rainfall is 869.3 mm (Monasterio and Reyes 1980). The precipitation regime is unimodal, with a single maximum rainfall peak and a dry season from December to March. The Ciénaga de Mifafí is an Andean grassland (Molinillo and Monasterio 1997a) dominated by highly palatable forbs and grasses, acaulescent rosettes and cushions with little palatable forage, and on the side of wetland, caulescent rosettes of the *Espeletia* genus, which come from the rosette land, where the giant species *Espeletia timotensis* and *Espeletia spicata* (Monasterio 1980a) dominate.

The study was carried out for six species; three life-forms were analyzed: acaulescent rosettes, caulescent rosettes, and cushions. The acaulescent rosettes are studied in *Plantago rigida* and *Hypochoeris setosa*, the caulescent rosettes in *Espeletia batata* and *Espeletia semiglobulata*, and the cushions in *Aciachne pulvinata* and *Azorella julianii.* Forbs and grasses were not selected for this study because, although these life-forms are preferred by cattle, we were mainly interested in measuring the impact of trampling in Andean wetlands. The species were selected depending on the following criteria: annual or perennial, low consumption, little forage, and deficient protein content.

A key case study of grazed Andean wetland in the Cordillera de Mérida (Molinillo and Monasterio 2002) demonstrated that these six species are not palatable or consumed by cattle. Acaulescent rosettes strongly benefit from grazing. In a similar way, the cushion *Aciachne pulvinata* occupies open valley bottom areas where intensive grazing facilitates its establishment (Molinillo 1992). Caulescent rosettes of the *Espeletia* genus are not very palatable because they contain toxic secondary compounds in their young leaves. Nevertheless, they may be occasionally consumed by cattle to complete the diet. Finally, it is not well known if the cushion *Azorella julianii* is consumed.

A hydrological gradient associated with superficial drainage patterns within wetlands determines plant communities in terms of the dominant life-form structure. Humid areas are dominated by acaulescent rosettes, forbs, and grasses, and in the dry areas, caulescent rosettes of the *Espeletia* genus and cushions are common (Figure 13.1).

The study area is located in the National Park of Sierra La Culata. Despite the protected status of the study area, some activities such as the livestock grazing are not controlled by the park authorities mainly due to disagreement on management plans between the state and the local community. The problem of extensive grazing has not been solved yet (Molinillo and Monasterio 1997b; Monasterio and Molinillo 2003).

METHODS

Functional variability is analyzed for those variables that respond to the micro- and mesoclimatic thermal oscillations of the Andean páramos. These variables, which allow us to understand some functional characteristics in the wetland, are: architectonic model, aboveground/belowground phytomass (AP/BP) and necromass/total phytomass (N/TP) ratios, and growth meristem's protection (a distinctive characteristic of tropical regions).

To calculate phytomass ratios, aboveground and belowground biomass are calculated on adult, reproductive individuals. Biomass was determined using the cropping method: by harvesting and separating into leaves, flowers, stems, rhizomes or belowground stems, roots, and necromass. The phytomass ratios were calculated on a dry weight basis.

Growth meristem's thermal protection for the six species was analyzed through the temperature differences inside and outside the meristems in October, November, and December of 2002. Air temperature, soil surface temperature, and humidity were measured with a Lambrecht (°K) thermohygrometer. Leaf temperatures for each species were measured using copper-constant (36 caliber) thermocouples, at 2-h intervals during 3 days.

To analyze how plant architecture is related to ecosystem functioning in páramo wetlands, soil water-holding capacity was determined in stands mainly dominated by *P. rigida*, and used as a relatively simple model system. Soil sections (of 50 × 50 cm surface area) were extracted at different soil depths (0–4 cm, 4–10 cm, and 0–10 cm). These sections were then saturated with water for 48 h and weighed (saturated weight) and then dried and weighed again (dry weight). The difference between saturated and dry weights indicated the percentage of water saturation and the soil water-holding capacity per unit surface area for each soil depth.

RESULTS

The results of the phytomass ratios indicated that the AP/BP ratio was the variable showing the largest difference between species, with low values for *P. rigida*, *H. setosa*, and *A. julianii* and high values for *E. batata*, *A. pulvinata*, and *E. semiglobulata* (Table 13.1). Hence, two phytomass distribution patterns are evident, with species that assign a high proportion of total phytomass in aerial structures and species that accumulate a large proportion in belowground structures (Figure 13.2).

An indicator of the importance of phytomass storage in senescent organs in páramo flora is the necromass/leaf biomass ratio. The species with the highest ratios are *P. rigida* and *E. semiglobulata*; they are also the species with the more pronounced differences in AP/BP ratios (Figure 13.3). The high aerial phytomass proportion in rosette species is largely due to the leaf necromass attached to the aerial stem (Monasterio 1986), whereas in *P. rigida*, most of the necromass is attached to the belowground stem. Even so, both species share the low ratios

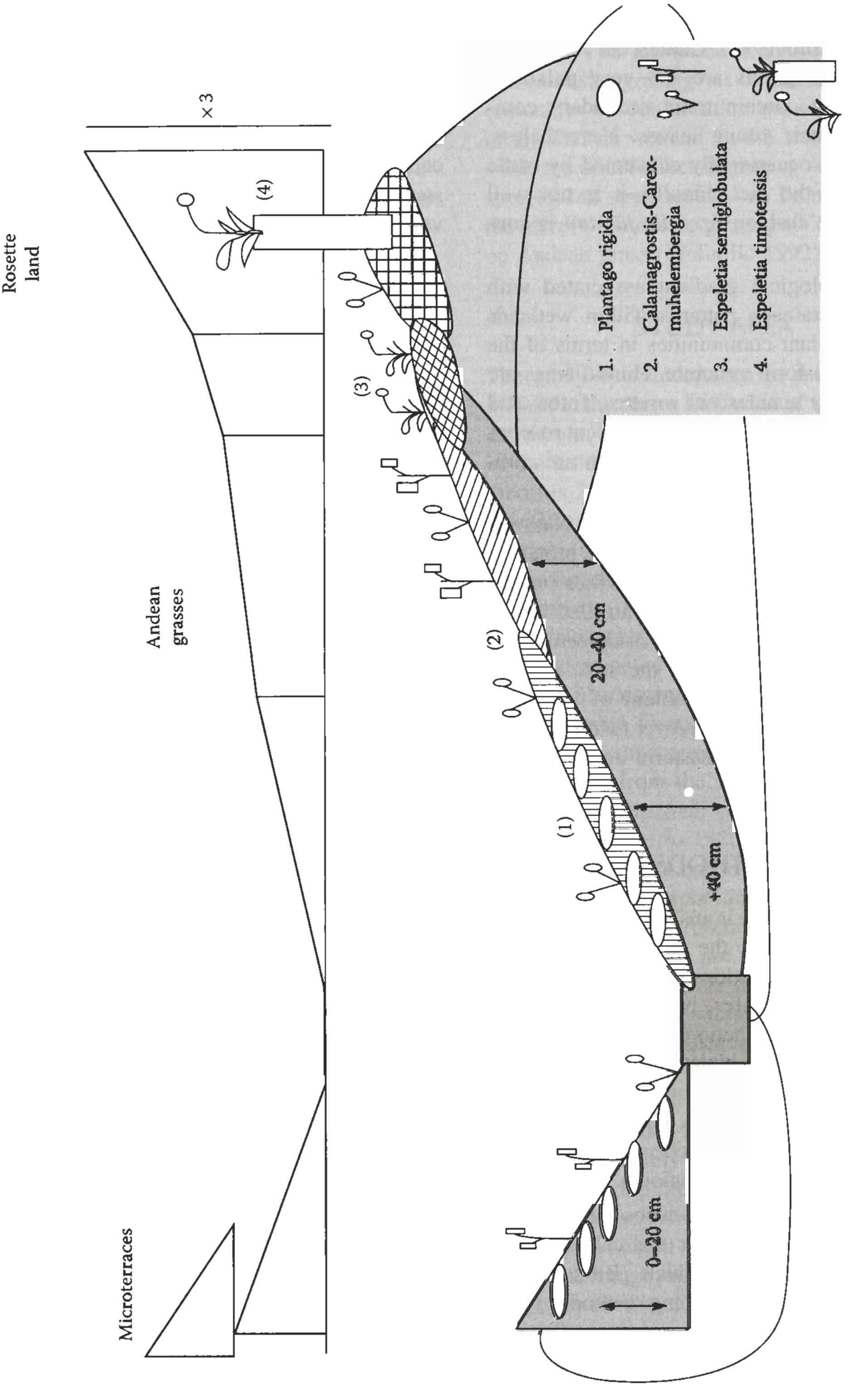

FIGURE 13.1 Horizontal spatial distribution of six species in the Ciénaga de Mifafí (4300 m), Cordillera de Mérida, Venezuela.

TABLE 13.1
Average phytomass ratios (± standard deviation) for species from Andean páramo wetlands

	Biomass Ratios					
Species	**AB/BB**	**ALB/TB**	**NAB/TB**	**ROB/TB**	**RB/TB**	**N/TP**
Plantago rigida	0.185 ± 0.074	0.130 ± 0.058	0.422 ± 0.084	0.424 ± 0.104	0.022 ± 0.028	0.704 ± 0.038
Hypochaeris setosa	0.457 ± 375	0.174 ± 0.108	0.546 ± 0.144	0.171 ± 0.108	0.108 ± 0.041	0.293 ± 0.164
Azorella julianii	0.200 ± 0.157	0.155 ± 0.101	0.537 ± 0.095	0.306 ± 0.141	0	0.281 ± 0.099
Espeletia batata	2.219 ± 1.906	0.458 ± 0.200	0.391 ± 0.203	0.032 ± 0.036	0.116 ± 0.065	0.425 ± 0.177
Espeletia semiglobulata	1484.03 ± 4405.49	0.293 ± 0.116	0.685 ± 0.125	0.021 ± 0.017	0	0.742 ± 0.092
Aciachne pulvinata	3.773 ± 1.704	0.759 ± 0.104	0	0.240 ± 0.104	0	0.528 ± 0.0857

Note: AB/BB = aboveground/belowground biomass; ALB/TB = assimilatory leaf biomass/total biomass; NAB/TB = nonassimilatory biomass (aerial and underground stems)/total biomass; ROB/TB = root biomass/total biomass; RB/TB = reproductive biomass/total biomass; N/TP = necromass/total phytomass.

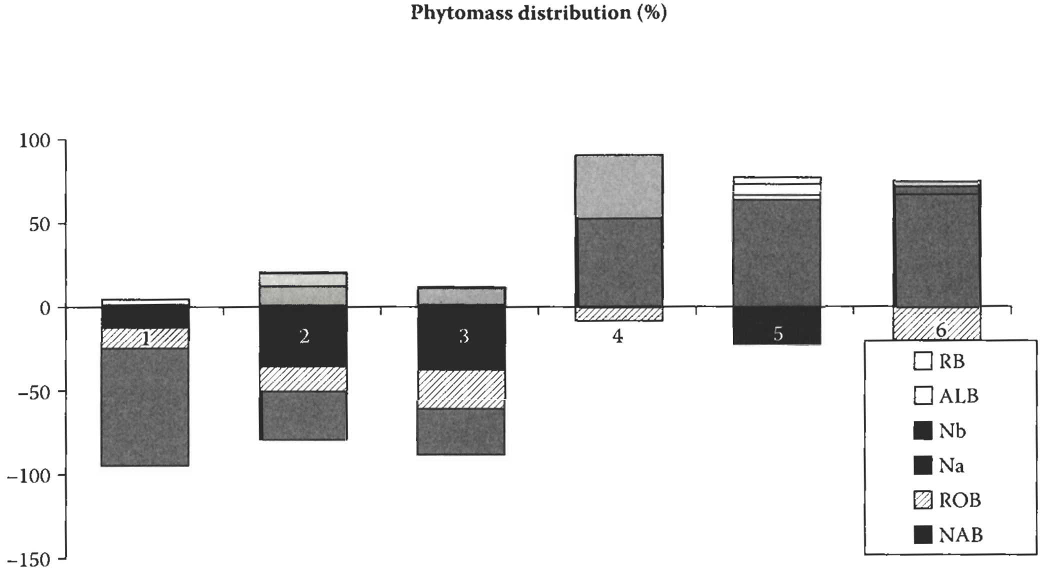

FIGURE 13.2 Vertical spatial distribution of phytomass in species of Andean wetlands. (1) *Plantago rigida*, (2) *Hipochoeris setosa*, (3) *Calandrinia acaulis*, (4) *Azorella julianii*, (5) *Espeletia batata*, (6) *Espeletia semiglobulata*, and (7) *Aciachne pulvinata*. NAB: nonassimilatory biomass, including aerial stems and rhizomes; ROB: root biomass, including primary and secondary roots; AN: aboveground leaf necromass; BN: belowground leaf necromass; LB: leaf biomass; and RB: reproductive biomass.

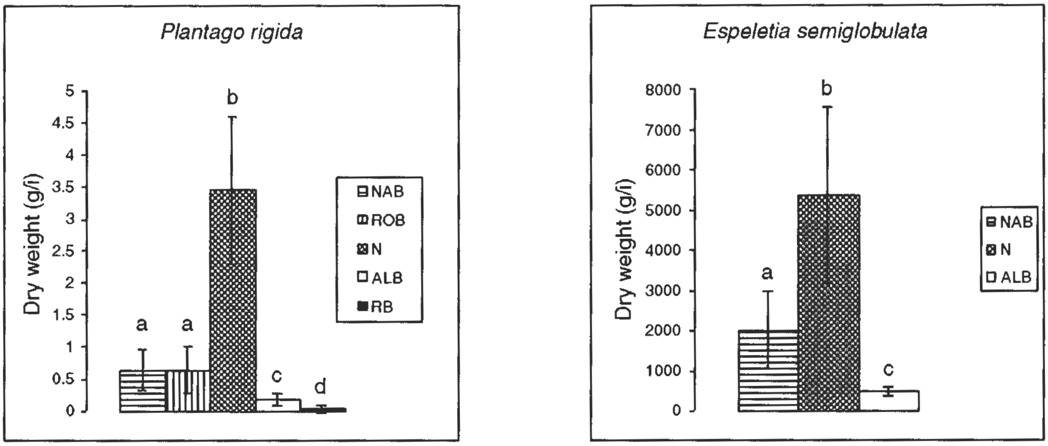

FIGURE 13.3 Average mass in different plant compartments for *P. rigida* and *E. semiglobulata* (± standard deviation). NAB: nonassimilatory biomass, in aerial stems or rhizomes; ROB: root biomass; N: leaf necromass; ALB: photosynthetic biomass; and RB: reproductive biomass. Different letters (a, b, c, d) indicate significant differences ($p = .05$).

of assimilatory leaf biomass to total phytomass, suggesting that they are slow-growing, long-lived species that store large amounts of phytomass during their life cycles.

In general terms, the six species accumulate a large proportion of phytomass as leaf necromass and show a low proportion of photosynthetic biomass. As a consequence, it suggests that extensive livestock grazing may enhance the vegetation cover in the Andean wetlands because it increases the trampling of species that have a large proportion of buried leaf necromass (such as *P. rigida*, *H. setosa*, and *A. julianii*), and it decreases the low proportion of leaves in long-lived species (such as the *Espeletia* genus) that are occasionally consumed by cattle (Molinillo 1992). The root biomass ratios reported here for all species are below those typically found in alpine ecosystems (Körner 1999). Within the species studied, the large proportions of root biomass are replaced by belowground stems in species such as *H. setosa* and *A. julianii*. Hence, the density of *H. setosa* increases in areas with intensive grazing.

The Mifafí wetland showed an annual isotherm of 4.7°C (±2.1°C) and pronounced daily temperature variations, with a maximum of 12.8°C (±2.4°C) and minimum of 0.7°C (±1.3°C) for the study period. All analyzed lifeforms protect their growth meristems from night frost, and this is reflected in the higher temperatures within meristems compared to external temperatures. Depending on the number of hours that meristems stay below 0°C, three adaptive strategies of wetland vegetation can be defined: species showing no freezing temperatures, such as *P. rigida* and *H. setosa*; species staying only a few hours under freezing temperatures, such as *E. semiglobulata* and *A. pulvinata*; and species with protected meristems, but which, nonetheless, spend several hours at subzero temperatures, such as *E. batata* and *A. julianii* (Table 13.2).

Moreover, the parabolic distribution of leaves (to protect growth meristems located in the center) in all species, except for *A. pulvinata* (in which more complex mechanisms are involved), contributes to the avoidance of leaf overheating during peak radiation hours (Monasterio and Sarmiento 1991). Continuous trampling by cattle can change the parabolic distribution of leaves, which protects the growth meristem from night frost, and this can explain the fast drop in temperature when the leaves of *Espeletia batata* were damaged by trampling.

Finally, the results of water saturation in vegetation stands dominated by *P. rigida* indicate that it is in the top 4 cm of the soil profile that the highest water-holding capacity is found (1640 l m^{-3}, Table 13.3). This coincides with the soil layer in which most of the leaf necromass from acaulescent rosettes are concentrated. The water capture is seriously threatened by intensive grazing and cattle trampling, which adversely affects hydrological functions in the Andean wetlands.

TABLE 13.2
Average maximum and minimum temperatures and number of hours registered with temperatures below 0°C for six species from Andean wetlands

	Vegetation Thermic Response					
Species	**Daily Maximum Temperature (°C)**		**Daily Minimum Temperature (°C)**		**Number of Hours Below 0°C**	
Plantago rigida	E	21 ± 6.6	E	0.2 ± 0.01	E	0
	I	18.7 ± 4.3	I	1.4 ± 0.4	I	0
Hypochoeris setosa	E	19.3 ± 6.7	E	1.7 ± 1.07	E	10
	I	15 ± 4.5	I	0.4 ± 1.4	I	0
Espeletia semiglobulata	E	17.9 ± 5.7	E	3 ± 2.05	E	10
	I	12.8 ± 3.1	I	0.3 ± 2.08	I	3
Espeletia batata	E	27.5 ± 6.3	E	4 ± 1.9	E	11
	I	30.8 ± 5.1	I	2.9 ± 1.2	I	7
Azorella julianii	E	26.1 ± 9.4	E	3.7 ± 2.5	E	12
	I	18.7 ± 7	I	1.3 ± 0.7	I	6
Aciachne pulvinata	E	34.5 ± 3.8	E	5.1 ± 1.9	E	11
	I	23.8 ± 4.5	I	0.4 ± 0.7	I	3

Note: E = external temperature; I = internal temperature.

TABLE 13.3
Water storage capacity in an Andean wetland dominated by *Plantago rigida*

Water Storage Capacity of an Andean Wetland					
Treatment	**N**	**Surface Area (cm²)**	**Saturated Weight (g)**	**Dry Weight (g)**	**Rainfall (mm)**
Total soil (0–10 cm depth)	4	171.4 ± 51.9	344.3 ± 53	127.7 ± 21.2	13,445 ± 4,474
Top soil layer (0–4 cm depth)	10	47.6 ± 6.6	137.6 ± 15.5	61.3 ± 9.1	16,455 ± 3,899
Lower soil layer (4–10 cm depth)	5	77.6 ± 9.90	207.6 ± 12.7	120.4 ± 11.3	11,414 ± 1,769

DISCUSSION

It is interesting to examine how the species that occupy the wettest environment in tropical highlands distribute their resources, and to analyze if these phytomass distribution patterns constitute "successful decisions" in terms of ecosystem functioning (Monasterio 1986). Moreover, the diversity of architectonic models studied in Andean páramo wetlands has important ecological implications, as it determines the vertical spatial distribution of energy incorporated into the ecosystem.

The results presented here show two different patterns of energy distribution. On the one hand, there are species that distribute large phytomass proportions to aerial structures (more than 30 cm aboveground), with AP/BP ratios above one. This model is common in species of tropical ecosystems (Smith and Klinger 1985). On the other hand, there are abundant species in wetland ecosystems with low aerial biomass and AP/BP ratios between 0.1 and 0.001. This last model of belowground accumulation is characteristic of species of alpine, arctic, and tundra ecosystems (Smith and Klinger 1985).

In alpine regions, where the low temperatures are the main limiting factor (Aber and Melillo 1991), the species show low photosynthesis and growth rates and slow litter decomposition. Life-forms dominant in Andean wetlands show morphological and ecophysiological adaptations to low temperatures and extreme daily temperature fluctuations (Goldstein et al 1984; Monasterio and Sarmiento 1991; Rada 1993). As a result of their adaptations to the extreme conditions of the páramo, the species show slow rates of plant growth (Rada 1993). In this sense, several authors agree that these ecosystems are fragile, showing slow rates of regeneration after disturbances such as grazing and fire (Luteyn 1992; Hofstede et al. 1995; Hofstede 2001).

The high leaf necromass proportions present in the studied species have been related to thermal insulation. In the case of giant rosettes, a cover of dead leaves isolates living tissues in aboveground stems, protecting them from nocturnal freezing and regulating their water balance (Goldstein and Meinzer 1983). This mechanism is also involved in thermal protection of leaf meristems (Smith 1974; Monasterio 1986). The stored necromass does not constitute an active energy reserve, but plays a critical role in nutrient translocation from dead leaves to active tissues (Garay et al. 1982) and might, in addition, contribute to water recharge in páramo wetland ecosystems. The same could be true of the acaulescent rosette *Plantago rigida* in our study, in which a large proportion of the leaf necromass encases the belowground stem, strongly increasing the water-holding capacity of the top few centimeters of the soil.

The effect of extensive grazing in the Andean páramos, in general, depends on the intensity, frequency, and sequence of cattle presence in the páramo grasslands (Molinillo and Monasterio 2002). A low animal intensity increases the species richness because the competitive exclusion decreases, and the fast-growing forbs are able to show explosive colonization. However, a high animal intensity decreases the diversity of species (Sarmiento et al. 2003). For example, the low frequency of grazing and fire in the west páramos decreased the tussock density and increased the fraction of forbs and grass species in the vegetation composition. However, a high animal intensity decreased the diversity of species (Sarmiento et al. 2003) and increased the fraction of less-palatable forbs (Hofstede 1995; Verweij 1995; Molinillo and Monasterio 2002).

There are some alternative management practices in the Venezuelan Andes, that emphasize the need to conserve páramo diversity (Sarmiento et al. 2003). Intensification of agriculture in some areas seems to be the best way to reduce the total area under cultivation, while maintaining production levels and improving biodiversity, given that representative natural areas are set aside for protection (Sarmiento et al. 2002). Another factor to be analyzed is the impact of grazing practice, which is likely to have a pronounced effect on the vegetation structure and diversity in Andean grasslands.

Even though the effect of extensive grazing within the wetland ecosystem is not analyzed here, the functional variability could certainly play a critical role in determining the water balance in these high-Andean páramo environments, in which the aboveground and belowground stems could act as water reservoirs, while standing leaf necromass could provide improved water capture by acting as a funnel. Therefore, the conservation of species and functional diversity for a sustainable use of the Andean wetlands necessarily implies appropriate cattle management strategies in the Venezuelan Andean region.

SUMMARY

Tropical mountain diversity is not only expressed as richness per unit area but also in terms of the functional variability of highland species. In the wetlands of the Andean páramo above 3800 m, a diverse array of plants coexist that can be grouped into acaulescent rosettes, caulescent rosettes, cushions, forbs, and grasses — the same life-forms defined by Hedberg (1964) for the Afroalpine belt. Each of these life-forms can be interpreted as an architectonic model in which phytomass distribution in aboveground and belowground structures (including senescent leaves) and thermal protection of growth meristems can provide key information on the functioning of the wetlands in the Andean páramo. The results of this study in the Venezuelan Andean wetlands show a variety of phytomass patterns, with species that accumulate phytomass in aboveground structures and species that do the same in belowground structures, particularly as buried leaf necromass. Phytomass accumulated as leaf necromass has different functions, such as protection of the growth meristems from low temperatures or water capture in the topsoil profile (e.g. an increase of water was found in wetlands dominated by the acaulescent rosette *Plantago rigida*, which has a high underground leaf necromass). Extensive grazing modifies the diversity and composition of species and, consequently, the relative abundance of the species that are not consumed by cattle (cows and horses) but are susceptible to damage by trampling. This has effects on the hydrological functioning of these ecosystems, which constitute the headwaters of important rivers draining into the Amazon catchment. Therefore, conservation of the biodiversity of the Andean wetlands necessarily implies appropriate cattle management strategies in the Venezuelan Andes.

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