

Research Article

Carbon and Water in Upper Montane Soils and Their Influences on Vegetation in Southern Brazil

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Considering the many environmental functions of the upper montane soils, the aims of this study were (1) to verify if the soils of upper montane forests and grasslands of Caratua Peak (1850 m a.s.l.) have similar characteristics to those found in other highlands in southern and southeastern Brazil; (2) to reinforce the geomorphological and pedological factors that impose the establishment of each type of vegetation in these highlands; and (3) to estimate potential soil carbon stocks and potential soil water retention. Follic and haplic histosols were found in the grasslands, and dystrophic regosols were found in the forests. The soils were dystrophic, extremely acidic, and saturated with Al and total organic carbon. In contrast to the grasslands, the upper montane forests were prevalent in valleys and subjected to morphogenetic processes resulting in soils that contained thicker mineral horizons. The grasslands occupied ridges and divergent convex ramps, and the pedogenetic processes in these regions promoted thicker histic horizons. The potential water retention capacities were high and strongly related to the high porosities of histic horizons associated with the gleyic horizons. In particular, the carbon stocks were two- to three-fold higher than those found in soil ecosystems from the same latitude but lower altitude.

1. Introduction

Soil organic matter, which accumulates to a depth of 1 meter, weighs approximately 1500×10^{15} g (Pg = petagrams) and constitutes the majority of continental organic carbon [1, 2]. Considering the soil surrounding native vegetation, Brazil stocks 5% of the global carbon reservoir [1], indicating that a single country can significantly influence global carbon fluxes [3]. According to published studies [4–7], stock levels of below ground carbon increase concomitantly with higher altitudes. In southern Brazil, carbon stock levels of isolated soils can be two to three-fold greater in high altitudes compared to low altitudes from the same latitude [7].

Since the upper montane soil horizons include histic and humic horizons, they play an important role in the immobilization of carbon and regulation of hydric fluxes [8–10]. The vast accumulation of organic matter in these environments originates from a lack of decomposition by microbes

owing to unfavorable conditions, such as low temperature, high humidity, low respiration, lack of available nutrients, and high exchangeable Al concentrations [9–11]. Moreover, the organic matter is highly humified and forms relatively stable organometallic complexes, predominantly with Al and Fe that serve as poor substrates for decomposition by microorganisms [9, 11–13].

The humic substances contribute to the sustainability of these ecosystems by increasing their nutrient contents and increasing their capacity for cation exchange and water retention. In turn, the ecosystem recycles carbon matter through above- and below-ground litterfall of developing vegetation [9, 10]. During rainy periods, the upper montane soils minimize erosion by becoming waterlogged and draining slowly; thus, regulating the hydric fluxes to the headwaters of the river basins [10, 14, 15]. In dryer periods, upper montane soils collect water from horizontal precipitation (water present in clouds) that commonly occurs in upper montane forests

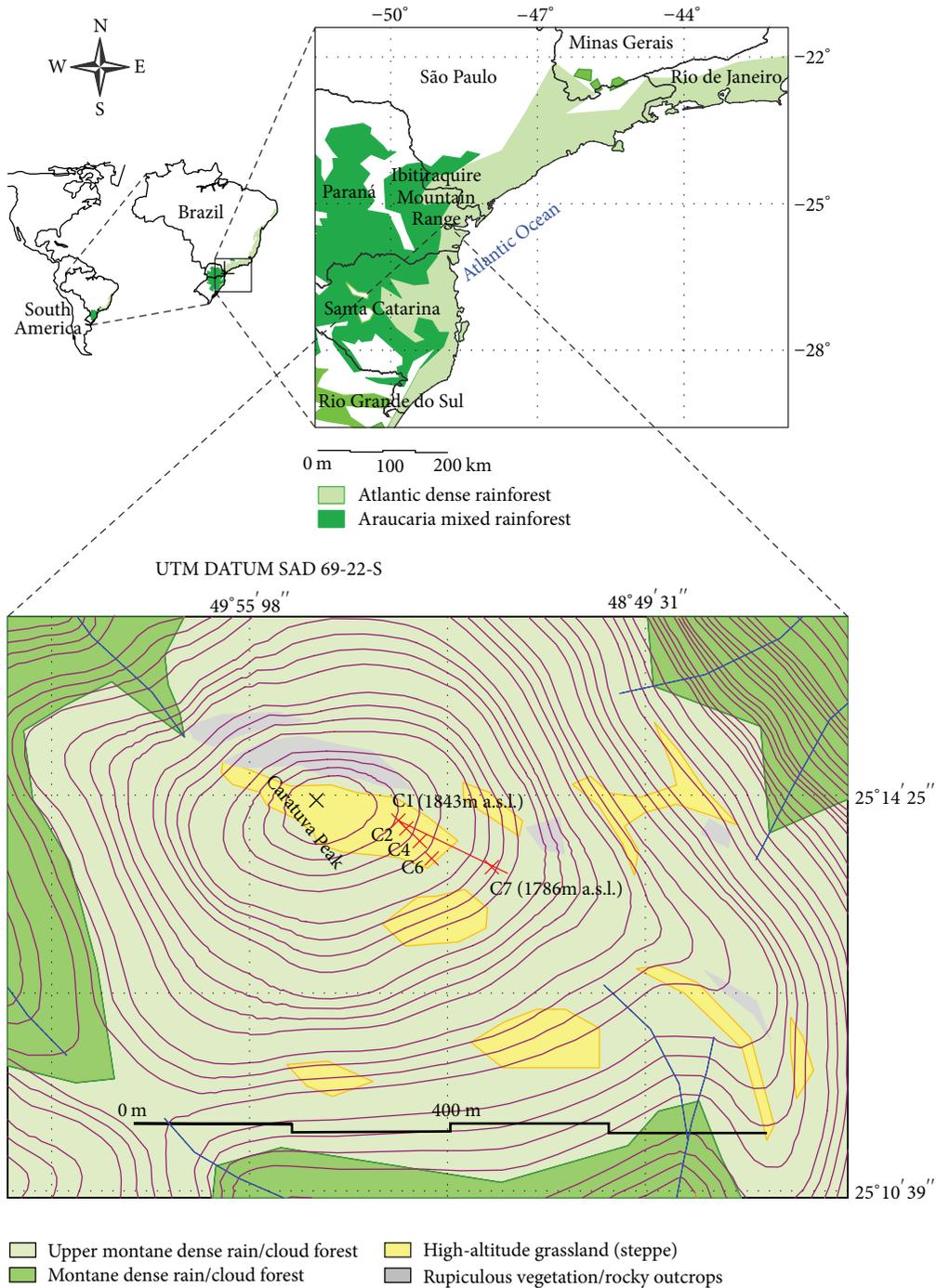


FIGURE 1: Sampling sequence in the Caratua Peak, in the Ibitiquere Mountain Range, southern Brazil.

[14, 15]. This water can be retained by vegetation and soil or forwarded to the headwaters immediately downstream, thereby avoiding major losses.

Soil from the mountaintop regions of many upper montane environments has been developing for a few thousand years (some of them starting from the middle and late Holocene period). In this period, significant climate change promoted the invasion of forests on grasslands. Since then,

these two types of vegetation have coexisted in a restricted landscape and are controlled by geomorphological features [7] forming the unique environment endemic to upper montane regions today.

Estimates of soil carbon stocks at regional, national, and global scales are important for the understanding of changes in carbon flux [16, 17]. To improve our capacity for providing, promoting, and executing actions that mitigate

the consequences of the global climate change related to the greenhouse gases, we need to acknowledge the importance of carbon stocks in different soil types and study the factors that influence their distribution [3, 16, 18]. Considering that a significant amount of organic matter is stocked in the surface of soil (up to 30 cm deep), there is a great risk of carbon dioxide liberation to the atmosphere when vegetation is burned, cut, or converted to support agriculture or livestock [17]. The loss of natural and soil ecosystems can have a significant economic impact [14]. Thus, the need to understand soil organic matter dynamics in different areas in the world is great [19].

Upper montane soils are still understudied [3, 6, 9, 20, 21], and their importance is not yet fully appreciated [10]. In southern Brazil, some studies have characterized soils in upper montane rain/cloud forests [7, 22–28], but information about high altitude grassland soils is scarce [7, 27, 28]. According to previous studies conducted in the state of Paraná, southern Brazil, soils from grasslands and forests of upper montane ecosystems are undeveloped, extremely acidic, highly concentrated with carbon and have low base saturation and high exchangeable Al saturation. These observations are consistent with those reported in other upper montane regions of southeastern Brazil, which include different lithologies and vegetation types [9, 10, 29] and upper montane cloud forests of Aparados da Serra Geral, in the state of Santa Catarina, also in southern Brazil [26]. Another important environmental function described for these soils is their high capacity for water retention (in some cases more than 500 L m²), which results from high total porosities of their histic and gleyic horizons [7].

Considering that studies about upper montane soils are very scarce, the aims of this study were (1) to verify if the soils of upper montane forests and grasslands of Caratua Peak (1850 m a.s.l.) have similar characteristics to those found in other highlands of the mountain ranges in southern and southeastern Brazil, which vary in altitude; (2) to reinforce the geomorphological and pedological factors that impose the establishment of each type of vegetation in these highlands; and (3) to estimate potential soil carbon stocks and potential soil water retention.

2. Material and Methods

2.1. Study Area. The study area is located in Caratua Peak (transect between 1840 and 1770 m a.s.l.). This is the second highest mountain of southern Brazil, located in the Ibitiraquire Mountain Range, a subrange of Serra do Mar (Sea Mountain Range) with coordinates 25°14'S and 48°49'W (Figure 1). The Caratua Peak is within the Paraná Peak State Park, that spans parts of the municipalities of Antonina, Morretes, and Campina Grande do Sul.

Like most of the mountains in the sea mountain range of Paraná, their upper portions are formed by alkali granites embedded in high-grade metamorphic terrains with contacts clearly failing in keeping with their late to posttectonic origin [30]. According to Mineropar, intrusive, igneous rocks from Ibitiraquire Mountain Range (Graciosa granite) originated

nearly 550 million years ago in the late pre-Cambrian to Cambrian period. It was cut by faults in the NE-SW axis by the Brasiliano (or Pan African) cycle (events of the end of the late Proterozoic) and the Ponta Grossa Arch, a major structure in the NW-SE basin of the Paraná River [31].

The upper parts of Ibitiraquire Mountain Range are covered with natural vegetation such as dense rain/cloud forests and grasslands (steppes). In the studied slope, the high-altitude grasslands are located near the summit, which lacks stony and rocky elements and is dominated by hydric divergence. The upper montane cloud forests occupy the crests downslope of the upper montane region and associated valleys with strong, undulating, and mountainous reliefs dominated by hydric convergence (Figure 2).

The Atlantic rainforest covers the greatest extension of Ibitiraquire Mountain Range, reaching the upper montane formation, with the highest part of the slopes reaching higher than 1830 m a.s.l. The majority of these forests are well preserved due to their isolation and difficult accessibility, despite some sites having been damaged by fires, such as other slopes of Caratua Peak in 2007. In some slopes, located in the west, on the occidental side of the sea mountain range (at about 1300 m a.s.l.), there is an ecotonal zone between the Atlantic rainforest (Montane dense rainforest) and the Montane Araucaria forest. The high-altitude grasslands appear in the uppermost parts of the mountains, beginning from 1750 m a.s.l. in Caratua Peak and from 1350 m a.s.l. in some other mountains. They are in excellent condition with no signs of human interference with the exception of mountain trails.

The sampling points were in a topographical sequence beginning near the sharp ridge of Caratua Peak (1850 m a.s.l.) covered by high-altitude grasslands and dominated by *Chusquea pinifolia* (Nees) Ness (Poaceae; caratua) with about 0.5 m height on histosols (according to World Reference Base for Soil Resources: FAO-WRB) in divergent, convex ramps. After an abrupt alteration in slope, the landscape changes to concave, converging ramps, with colluvionar stability that provide a Cg (gleyic) layer and a grassland/shrubland physiognomy to histosols (2.2 m height), which are also dominated by the caratua. After another abrupt break of the slope (1790 m a.s.l.), the studied ramp gives rise to the upper montane cloud forest situated on mineral soils with a histic layer (Figures 1 and 2).

As previously commented, in the studied high-altitude grasslands, *C. pinifolia* is the dominant species, comprising at least 25% of the vegetation. In a survey of this physiognomy covering many mountains of the Ibitiraquire Mountain Range, 85 vascular plant species were found [32, 33]. Additionally, *Croton mullerianus* L. R. Lima (Euphorbiaceae), *Rhynchospora exaltata* Kunth (Cyperaceae), *Lagenocarpus triquetrus* (Boeck.) Kuntze (Cyperaceae), and *Machaerina austrobrasiliensis* M. T. Strong are among the most important species. Tree species with extensive influence on the structure of the neighboring upper montane forests, of about 5 m in height, include *Myrsine altomontana* M.F. Freitas and Kin.-Gouv. (Myrsinaceae), *Handroanthus catarinensis* A. Gentry (Bignoniaceae), and *Symplocos corymboclados* Brand (Symplocaceae). These species also occur on the

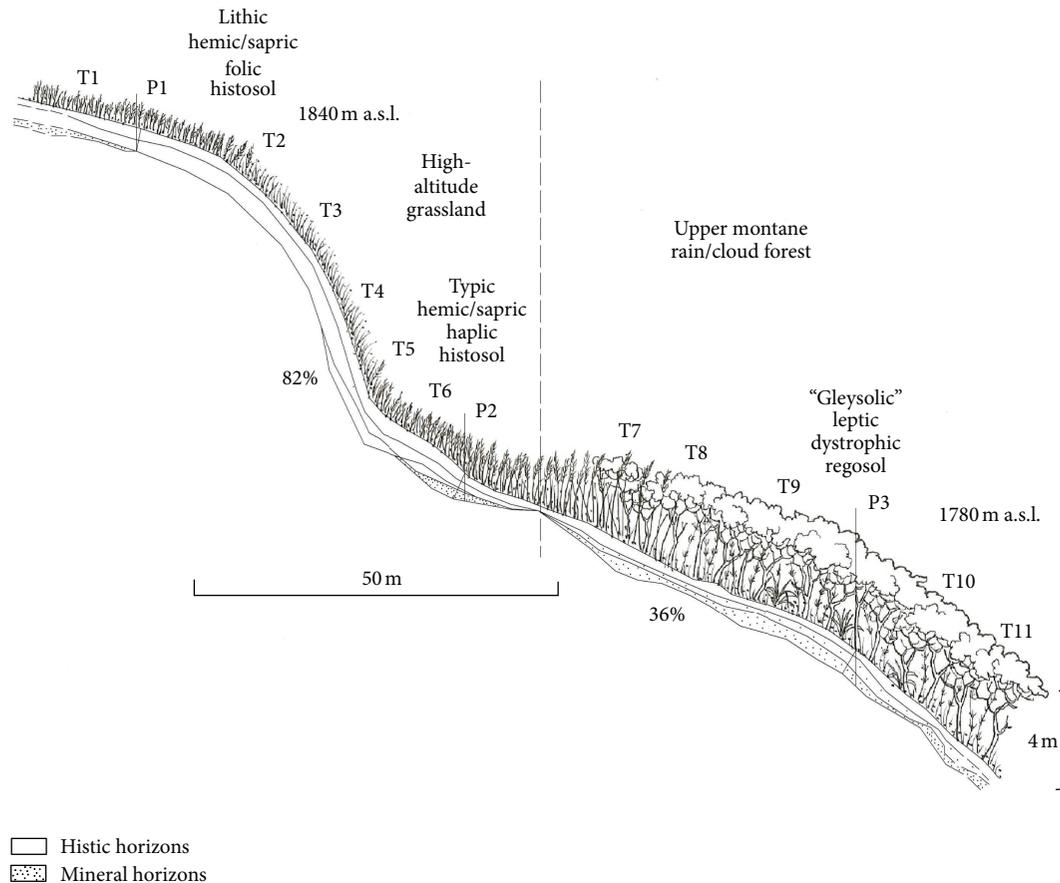


FIGURE 2: Toposequence indicating the sampling points (auger = T and profiles = P) in the Caratuva Peak, of the Ibitiraquire Mountain Range in southern Brazil.

grasslands, although sparsely, with low coverage, and in a shrub form, approximately 0.5 m in height, on the mountaintop grasslands with an average of 2.2 m height in the grasslands immediately downslope of the convergent ramps with higher colluvion stability.

The change in vegetation from grassland to forest is abrupt, with a small ecotonal area with a shrubland physiognomy containing species of both formations in a range of 2 to 10 meters. According to [34, 35], *Ilex microdontia* Reisseck (Aquifoliaceae), *Siphoneugena reitzii* D. Legrand (Myrtaceae), *Myrceugenia seriatoramosa* (Kiaersk) D. Legrand and Kausel, and *Drimys angustifolia* Miers. (Winteraceae) contribute by 57.5% of the phytosociological importance ($PAP \geq 10$ cm) of the sample sites in the Ibitiraquire Mountain Range, including the Caratuva Peak. The estimated basal area was $40.3 \text{ m}^2 \text{ ha}^{-1}$, and the tree density was 4600 ind ha^{-1} .

The climate of upper portions of the sea mountain range of Paraná is classified as Cfb (subtropical), according to the Köppen classification system. It is predominantly wet, and the average temperature of the coldest month is between -3°C and 18°C , while the average temperature of the warmest month is below 22°C [22]. Roderjan and Grodski [36] observed an absolute minimum temperature of -5°C , an average annual temperature of 13.4°C , and an absolute maximum temperature of 30°C at 1385 m a.s.l. in

an upper montane forest at Anhangava Peak, approximately 24 km southwest of the Caratuva Peak. Based on the mean temperature variation of 0.56°C at each 100 m elevation, a mean temperature of 10.8°C can be estimated for the ridge of the Caratuva Peak. The precipitation in the sea mountain range is well distributed throughout the year and varies greatly depending on the local topography. Measurements in the coastal region exceed 2000 mm per year, and on the slopes of the mountains these values can reach 3500 mm [37].

2.2. Sample Collection and Data Analysis. The cores were carried out along a transect (toposequence), spanning high altitude grasslands and upper montane forests (Figures 1 and 2). After the soil survey, three profiles were analyzed, in which two of them represented the histosols of the grasslands and the regosols of the forests. Complementary superficial (0–20 cm) and subsuperficial (20–40 cm) samples were collected with a hand auger. In these profiles, morphological descriptions and definition of the diagnostic horizons and samplings were done following Santos et al. [38], in order to classify the soils according to the Brazilian Soil Classification System [39]. The Von Post scale [39] was used to classify the stage of decomposition of organic matter in the field.

Physicochemical analyses were based on air-dried soil, and granulometric analysis was carried out according to

the densitometer method [40]. Due to the limitation of the laboratorial procedure for histic material, only the clay fractions for the majority of the samples were obtained. The chemical and physicohydraulic analyses were performed according to published reports [40]. The potential water retention capacities were estimated by the volumetric humidity and calculated by the subtraction of the aeration porosity from the total porosity [41]. Data were reported by units of L m^{-2} and $\text{m}^3 \text{ha}^{-1}$ according to the thicknesses of the horizons.

The total organic carbon (TOC) analyzed by dry weight method was done in Stable Isotope Laboratory of the Center for Nuclear Energy in Agriculture, Brazil (Table 1). Soil carbon stocks (kg C m^{-2}) were calculated according to Batjes [1] and Yimer et al. [17]. First, the TOC (g kg^{-1}) of each horizon was multiplied by the soil density (kg m^{-3}) and by its thickness (in m). The density of coarse particles ($\geq 2 \text{ mm}$), generally subtracted from the soil density to use only the fraction $\leq 2 \text{ mm}$ [13, 19] was a variable not necessary due to its negligible values. Data were reported by units of Mg C ha^{-1} . The stocks of C of all points of the transect were based on their thicknesses and on the correspondent concentrations and densities of the nearest profiles.

The Ibitiraquire Mountain Range has an estimated 790 ha of high-altitude grasslands [44]. The soil C stocks were estimated for these ecosystems as an approach to predict their magnitude. The soil C stocks for the upper montane ecosystems, including both the grasslands and forests of Sea Mountain Range in Paraná were estimated based on the areas calculated by PRÓ-ATLÂNTICA [45]. However, we emphasize that in this study only the potential soil C stocks were estimated. Further estimations on scales of greater detail and consideration of additional types of soils present in other portions of the mountains are needed.

To compare chemical properties among the main horizons of 0 to 20 cm and 20 to 40 cm and the soil C stocks of the studied grasslands and forests, Kruskal Wallis tests ($P < 0,05$) were performed. Spearman correlation coefficients (R_s) were calculated to verify the behavior of the chemical parameters along profile depths.

3. Results and Discussion

3.1. High-Altitude Grassland Soils in Caratuva Peak. A predominance of histosols in the high-altitude grasslands in Caratuva Peak was observed. The histic horizons (mainly "O", humid colors 10YR 3/3 and N2/) presented with high concentrations of TOC (400 g kg^{-1}). Profile 1 (nearer to the ridge) was classified as "lithic hemic/sapric folic histosol" and profile 2 (about 100 m downslope) as "typic/hemic sapric haplic histosol". The first profile was comprised of seasonal hydromorphic soil (O and O2/H horizons) and its location in a divergent convex slope, was more drained than profile 2 (Table 1 and Figure 3(a)). In the haplic histosol (less drained than the upslope folic histosols), three subhorizons were identified including two histic (O and H) and one mineral (Cg). The mineral subhorizon was not considered to be a terric histosol because it had a medium texture and was found to be less than 30 cm thick in the 1 m depth of soil surveyed.

This reducing environment was influenced by its position within a divergent concave slope (near the end of the ramp) combined with the low saturated permeability of the deepest mineral horizons, which delay the run off of the system (Table 3). Both soils had a prevalence of hemic herbaceous materials in topsoil.

The characteristics of these extremely acidic soils are similar to those found in other high-altitude grasslands of the Sea Mountain Range in southern Brazil [7, 27, 28] and those studied in soils associated with rocky outcrops in Mantiqueira Mountain Range in southeastern Brazil [9, 10, 46, 47]. The Al, $m\%$ (aluminum saturation) and cation exchange capacity (CEC) of the histic horizons increased with depth ($R_s = 1$; $P < 0,01$; Tables 1 and 2). This was due to the mineral fraction (mainly clay) in the system. The bases of the histic horizons ($S = \text{sum of bases}$) were probably drained in relation to depth of values of three- to sixfold lower than on the surface (Tables 1 and 2). The P concentrations were considered to be in the low to medium range [48], and the base saturation (BS%), very low in topsoil, decreased proportionally with depth ($R_s = -1$; $P < 0,01$; Tables 1 and 2).

3.2. Upper Montane Rain/Cloud Forest in Caratuva Peak. In the third part of the toposequence downslope, the soil was classified as "gleysolic leptic dystrophic regosol" (Tables 1 and 2; Figure 3(c)). The histic horizon (10YR 2/1) was less than 40 cm thick and had high TOC (421 g kg^{-1} , Table 3). Below, two mineral horizons were observed, Big (10YR 5/2) and C (10YR 5/4), both with "mottles" in color (10YR 5/7). Due to the geomorphic position, the soils observed were "shallow" according to EMBRAPA (2006). The Big horizon signified the action of hydric fluxes. The "concave convergent" slope in "strong undulated" relief permitted the formation of mineral horizons through the combined action of morphogenetic (colluvium) and pedogenetic processes. These extremely acidic soils also presented with low base saturation, consistent with those found in other upper montane soils [7, 22–28].

As compared to the study by Scheer et al. [7], which was conducted in a mountain range 41 km south of our study site, the organic horizons of the upper montane soils in Caratuva Peak contained higher exchangeable base P concentrations, CEC, and potential acidity than the mineral horizons (Tables 1 and 2). CEC and acidity were due to the H^+ ions from the carboxylic and phenolic groups of the organic matter [9, 11]. The base of the desaturated Big horizon presented with high Al saturation (alitic character), suggesting that it was part of the forest cycle between the histic horizon and the litter. According to the literature, regosols have yet to be found and described in upper montane environments in southern Brazil.

3.3. Common Characteristics of Upper Montane Soils. The low fertility rates observed in vegetation of upper montane landscapes are related to the loss of nutrients caused by leaching from high rainfall amounts (horizontal precipitation, [15, 49]), in addition to generally low nutrient concentrations afforded by parental material [10]. According to these authors,

TABLE 1: Soil properties of the upper montane ecosystems in Caratua, southern Brazil.

Horizon	Depth. cm	Color	pH CaCl ₂	Al ³⁺	H ⁺ + Al ³⁺	Ca ²⁺	Mg ²⁺	K ⁺	S	CEC	P mg dm ⁻³	BS %	<i>m</i> %	Ca/Mg	*Factor cmol _c dm ⁻³ to cmol _c kg ⁻¹
Profile 1: grassland: lithic hemic/sapric folic histosol															
O1	0–20	10YR 3/3	3.3	1.4	22.5	1.5	1.3	0.6	3.4	25.9	13.0	13	29	1.2	2.6
O2	20–30	N2/	2.9	13.1	57.0	0.5	0.2	0.1	0.8	57.8	3.8	1	94	2.5	2.0
Profile 2: grassland: typic hemic/sapric haplic histosol															
O1	0–20	10YR 3/3	3.1	1.8	29.3	0.7	0.8	0.5	2.0	31.3	13.9	6	48	0.9	2.6
O2	22–49		3.0	3.6	45.5	0.2	0.2	0.1	0.5	46.0	9.2	1	87	1.0	2.6
H1	49–55		2.9	15.2	53.0	0.2	0.1	0.02	0.3	53.3	3.8	1	98	2.0	2.0
Cg	55–70		3.4	7.4	19.0	0.2	0.1	0.05	0.4	19.4	3.2	2	95	2.0	1.0
Profile 3: forest: “gleysolic” leptic dystrophic regosol															
O	0–15	10YR 2/1	2.6	3.1	41.6	0.4	0.6	0.3	1.3	42.9	16.6	3	70	0.7	2.7
Big	15–28	10YR 5/2	3.4	2.7	9.7	0.1	0.1	0.05	0.3	10.0	2.2	3	92	1.0	1.0
C	28–57	10YR 5/4 (mottles) 10YR 5/7	3.9	2.1	8.4	0.2	0.1	0.04	0.3	8.7	1.2	4	86	2.0	1.0

*Transforming factor from cmol_c dm⁻³ to cmol_c kg⁻¹ calculated based on the inverse of the density of the prepared sample for the analysis of each horizon.

TABLE 2: Chemical properties of the soil horizons of the upper montane ecosystems in Caratua Peak ($n = 2-6$). Values in parentheses represent the standard errors.

Horizon	Depth (average) cm	pH CaCl ₂	Al ³⁺	H ⁺ +Al ³⁺	Ca ²⁺	Mg ²⁺	K ⁺	S	CEC	P mg dm ⁻³	BS %	<i>m</i> %	Ca/Mg	*Factor cmol _c dm ⁻³ to cmol _c kg ⁻¹	
Grassland: histosols															
O1 $n = 6$	0–20	3.2a (0.1)	1.5b (0.1)	27.7b (2.4)	0.9a (0.2)	0.9a (0.1)	0.47a (0.0)	2.3a (0.3)	26.6b (1.7)	15.6a (1.5)	8.0a (1.2)	40.2a (4.4)	1.0a (0.2)	2.6	
O2 $n = 6$	20–40	3.1a (0.0)	7.1a (1.7)	46.8a (2.1)	0.3b (0.1)	0.2b (0.0)	0.1b (0.0)	0.6b (0.1)	47.4a (2.2)	7.7b (1.6)	1.2b (0.2)	90.2b (2.0)	1.2a (0.3)	2.6	
O3/H $n = 3$	40–55	3.1a (0.1)	9.9a (2.7)	43.5ab (6.1)	0.17b (0.03)	0.17b (0.07)	0.07b (0.04)	0.4b (0.1)	43.9ab (6.2)	6.03b (1.24)	1.0b (0.0)	95.7b (1.4)	1.2a (0.4)	2.7	
Cg $n = 2$	55–70	3.5	7.25	19.70	0.15	0.10	0.05	0.30	20.00	4.45	1.50	96.00	1.50	1.0	
Forest: regosols and gleysols															
O1 $n = 5$	0–20	2.9b (0.2)	2.3a (0.3)	35.9a (2.5)	0.7a (0.3)	1.0a (0.2)	0.46a (0.0)	2.1a (0.5)	38.0a (2.5)	26.0a (2.9)	5.4a (1.2)	53.6b (6.9)	0.6a (0.2)	2.7	
CgI/Big $n = 5$	20–40	3.4a (0.2)	3.7a (0.5)	13.6b (1.6)	0.1b (0.0)	0.1b (0.0)	0.05b (0.0)	0.3b (0.0)	13.9b (1.6)	2.4b (0.2)	2.2b (0.4)	92.8a (0.9)	1.2a (0.2)	1.0	
C $n = 2$	40–60	3.8	3.2	11.3	0.2	0.1	0.05	0.4	11.6	1.5	3.0	89.0	2.0	1.0	

*Transforming factor from cmol_c dm⁻³ to cmol_c kg⁻¹ calculated based on the inverse of the density of the prepared sample for the analysis of each horizon. Averages followed by the same letter in vertical correspond the medians that do not differ statistically by the Kruskal-Wallis test ($P < 0.05$).

acidity favors the dissolution of kaolinite and aluminosilicates, while the Al saturates the exchange complex. Therefore, nutrient cycling is essential because it leads to higher amounts of nutrients in superficial organic horizons [10] through their retention in high-density roots [9, 11], which increase the efficiency of hydrosoluble absorption [7]. Although the upper montane soils contained high Al saturation, considerable amounts of this element complexed with organic matter.

Therefore, its concentration was controlled in the soil solution, and toxicity to plants was avoided [9, 11, 13, 50, 51].

The genesis occurred in seasonal hydromorfisms of these soils was controlled by the elevated altitudes, facilitating cloud formation, lower temperatures, higher storage of organic matter by the low mineralization rate [24], and high rainfall amounts. The accumulation of organic matter surpassed the decomposition rate, because despite the existence

TABLE 3: Physicohydraulic properties of soil in profiles in Caratuva Peak ($n = 2$).

Horizon	Thickness cm	Clay/silt/ sand** g kg ⁻¹	Porosity (%)			Available water (%)	Saturated permeability cm h ⁻¹	TOC %	Soil density kg m ⁻²	C stock kg m ⁻²	Potential water retention capacity L m ⁻²
			Total	Macro	Aeration						
Profile 1: grassland: lithic hemic/sapric folic histosol											
O1	20	175	98.4	35.1	37.5	5.8	319.5	41.9	0.117	9.80	121.8
O2/H	10	200	95.8	12.1	12.8	5.2	0.3	40.9	0.238	9.73	83.0
Total	—	—	—	—	—	—	—	—	—	19.54	204.8
Average plus standard errors extrapolating to all sampling points ($n = 3$)										(26.1 ± 3.3)	(338.2 ± 8.5)
Profile 2: grassland: typic hemic/sapric haplic histosol											
O1	22	100	99.9	34.4	35.3	7.4	158.2	42.3	0.108	10.05	142.1
O2	27	125	98.3	12.6	13.5	5.7	36.2	37.9	0.133	13.61	229.0
H	6	125	87.3	9.6	10.2	7.3	3	20.8	0.302	3.77	46.3
Cg	15	125	62.8*	9.2*	9.3*	5.3*	7.2*	1.37*	1.089*	2.24	80.3
Total	—	—	—	—	—	—	—	—	—	29.67	497.6
Average plus standard errors extrapolating to all sampling points ($n = 3$)										(46.3 ± 2.7)	(565.6 ± 7.7)
Profile 3: forest: "gleysolic" leptic dystrophic regosol											
O	15	138	99.2	34.8	36.4	6.6	238.9	42.1	0.113	7.10	94.1
Big	13	125	62.8	9.2	9.3	5.3	7.2	1.37	1.089	1.94	69.6
C	29	125	62.8*	9.2*	9.3*	5.3*	7.2*	1.37*	1.089*	4.33	155.2
Total	—	—	—	—	—	—	—	—	—	13.37	318.8
Average plus standard errors extrapolating to all sampling points ($n = 5$)										(15.9 ± 2.5)	(398.8 ± 8.9)

* Values estimated based on horizons with similar characteristics.

** Limited estimates for granulometric analysis due to the high organic matter concentrations.

of concurrent biological transformation, humified organic carbon was highly preserved [23].

3.4. What Can Explain the Occurrence of Forest or Grasslands in Upper Montane Environments? According to studies carried out in high-altitude grasslands of southern Brazil, the histosols and histic entisols are the most common soils [7]. Both soils contained histic horizons without mineral horizons or without their presence at 40 cm depth. Histic horizons between 20 to 40 cm deep that lacked mineral horizons (also known as a histosol, according to the Brazilian Classification, EMBRAPA [39]), seem to suppress the establishment of trees taller than 1 m [7]. Together, the depth of histic horizons (in some cases > 50 cm), their low global densities, the high density of roots from typic grassland species, and the exposure of mountaintops to strong winds constitute conditions that are refractory to the growth and establishment of large trees that could promote the advancement of upper montane forests over grasslands as suggested previously [7] and reinforced by our data. However, lithic folic histosols (histic horizons between 20 and 35 cm deep) and histic litholic entisols (histic horizons < 20 cm) were identified by Roderjan [22] and Rocha [24] in upper montane cloud forests. Despite being stunted (low stature, high density, and low basal area), these forests were classified as dwarf forests.

Future climate changes affecting rainfall levels may result in the disappearance of grasslands through considerable loss

of area to forests or erosion of histic horizons caused by oxidation [7]. Other areas must be investigated to know whether the forests have already reached the maximum limit of expansion on the high-altitude grasslands of the Sea Mountain Range [7]. Studies of soils associated with high-altitude rocky complexes in southeastern Brazil [10] revealed that some peatlands (histosols) can dry sufficiently by a drainage system, leading to a forest growth but maintaining the large stocks of carbon. In addition to climate change, the fragility of upper montane ecosystems is challenged by the impact of human activity at nearby hiking trails and camping sites. The mountain range of Caratuva Peak (Paraná Peak State Park) attracts many visitors, and, in dryer periods, the environment has a high susceptibility to anthropic fires and a high risk of loss of these ecosystems [7].

The chemical composition of histic horizons below the depth of 20 cm depth at high-altitude grasslands was remarkably different from mineral horizons found at the same depth in soils of upper montane forests (Tables 1 and 2). Previously, other soils with relatively low densities and high basal areas were observed in upper montane rain/cloud forests in southern Brazil including cambisols [22, 24], argisols [24], and gleysols [7, 24] in valleys and peaks with higher colluvium. Upper montane forests in (typic humic and typic dystrophic) entisols were studied by Roderjan [22], Portes [25], and Vashchenko et al. [28]. The mineral horizons (A humic and C) of these soils as well as Big and C of regosols observed in Caratuva Peak seemed to promote higher mechanical

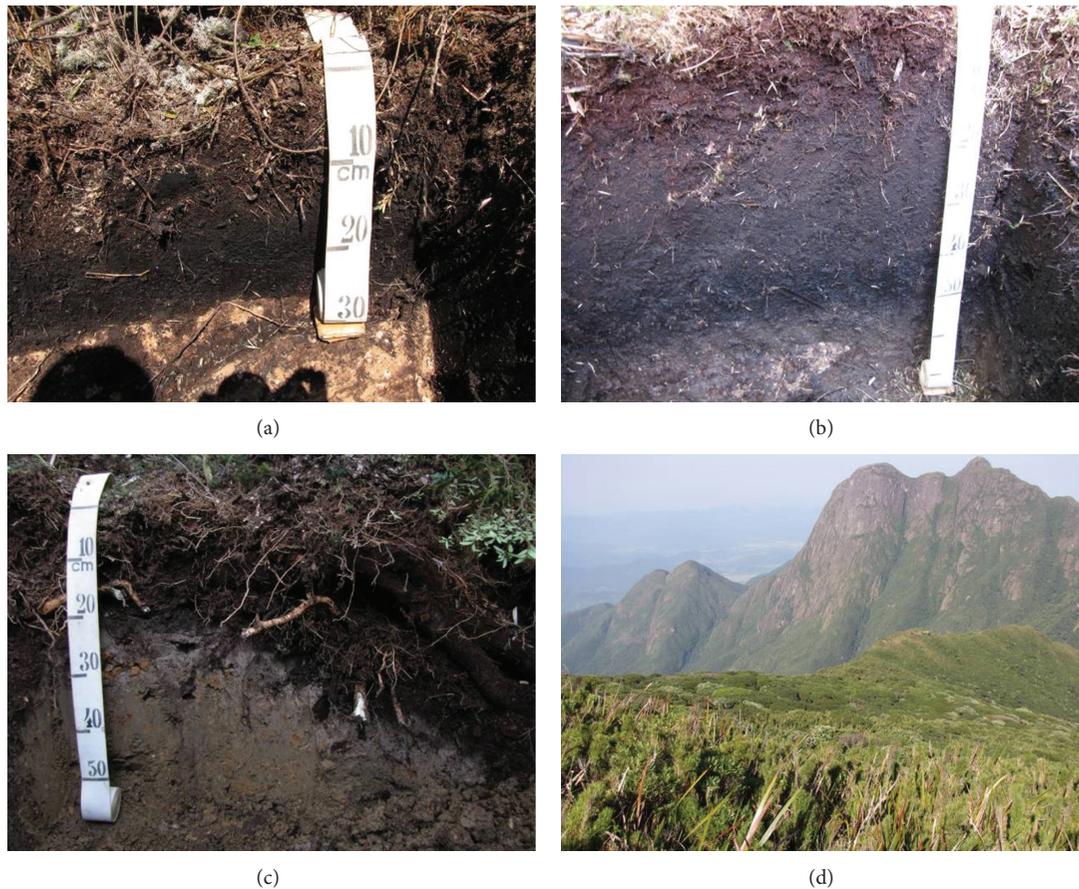


FIGURE 3: (a) Profile 1: histosol in high-altitude grassland near the ridge of Caratuva Peak. (b) Profile 2: histosol in high-altitude grassland nearer to the grassland-forest ecotone. (c) Profile 3: regosol in upper montane rain/cloud forest. (d) Toposequence in Caratuva Peak (foreground). At the bottom, Paraná Peak, southern Brazil.

aggregation and sustainability of trees, common in high-altitude grasslands [7, 28], compared to histic horizons of histic litholic entisols observed by Portes [25]. Therefore, in these environments, geomorphic features and climate control the soils, which regulate the occurrence of forest or grassland vegetation.

3.5. Carbon Stocks in Upper Montane Soils of Caratuva Peak.

The soil carbon stocks in the high-altitude grasslands ranged from 195.4 to $512.5 \text{ Mg C ha}^{-1}$ (mean \pm standard error: $260.7 \pm 32.7 \text{ Mg C ha}^{-1}$ for the lithic histosols near the ridge and $462.7 \pm 26.8 \text{ Mg C ha}^{-1}$ for the typic histosols downslope). The soil carbon storage estimated for the upper montane cloud/rain forest on regosols and gleysols varied from 93.9 to $220.6 \text{ Mg C ha}^{-1}$ ($158.6 \pm 24.9 \text{ Mg C ha}^{-1}$). The storage was statistically higher in grassland than in forest (U test; $P < 0.05$; Table 3).

Based on soil data from Serra da Igreja [7], the potential C stocks estimated for the soils of high-altitude grasslands and the upper montane dense cloud/rain forest in the state of Paraná, southern Brazil, were $0.54 \times 10^6 \text{ Mg C}$ and $1.25 \times 10^6 \text{ Mg C}$, respectively. These values, particularly grassland stocks, were in line with the observations presented in this

study. Specifically, we found that potential C stocks from high-altitude grasslands and Upper montane dense rainforest in the state of Paraná based on Caratuva Peak soil data and PRO ATLÂNTICA vegetation cover data [45] contained $0.59 \times 10^6 \text{ Mg C}$ and $0.91 \times 10^6 \text{ Mg C}$, respectively. This indicates that although these upper montane environments are separated by about 500 m a.s.l. (Caratuva Peak stretches between 1790 and 1840 m s.n.m. and Igreja Mountain Range between 1325 and 1335 m s.n.m.), similar chemical characteristics, physical characteristics, and levels of carbon stocks were observed.

The small differences could be caused by many factors including geomorphic position (slope types, declivity, etc.), temperature differences, rainfall levels, variable decomposition rates, and primary productivity. Larger and more detailed samplings are needed to identify the main factors. Thus, the presence of histic horizons rather than altitude consideration could be a better parameter to help determine sites of preservation (in discussion for the current Brazilian Forest Code), as the same type of upper montane vegetation is commonly found below 1800 m a.s.l. in southern Brazil.

Because the Ibitiraquire Mountain Range was estimated to have 790 ha of high-altitude grasslands [44], the soil C stocks for these ecosystems range from $0.138 \times 10^6 \text{ Mg C}$ to

TABLE 4: Soil carbon stocks in different forest and grassland ecosystems.

Location	Coord. (Aprox.)	Altitude (m a.s.l.)	Soil/lithology	Vegetation	Temp, annual average (°C)	Rainfall (mm)	Carbon stock (Mg ha ⁻¹ ± SE)	Author
Sehstedt, Germany	51°17'N; 10°39'E	280	Vertisols, limestone	Managed grassland	8.0	550	86 ± 1.7	Don et al. [13]
Kaltenborn, Germany	50°47'N; 10°14'E	335	Quartzipsammments, sandstone	Managed grassland	8.0	650	48 ± 1.3	Don et al. [13]
Bale, Ethiopia Mountains	6°45'N; 39°45'E	2390–2800	Andosols, volcanic rocks	Afromontane forest	12.1	985	326 ± 2.2	Yimer et al. [17]
		2800–3250	Andosols, volcanic rocks	Afromontane forest	9.2 a 12.1	985	364 ± 2.2	Yimer et al. [17]
Pyrenees Mountains, France and Spain	42°50'N; 0°40'S	1845–2900	Granites, slates, and limestones	Subalpine shrub phytognomy	9.2	985	460 ± 2.2	Yimer et al. [17]
Diverse	—	—	1 m	Alpine and subalpine grasslands	–0.7 a 5	1416 a 1904	153 ± 0.9	Garcia-Pausas et al. [19]
Diverse	—	—	1 m	Tropical forest	—	—	186 ± 104**	Jobbágy and Jackson [2]
	—	—	1 m	Tropical grassland and Savanna	—	—	132 ± 87**	Jobbágy and Jackson [2]
Amazon region, Brazil	—	—	Mineral soils (lato. agri. cambi. gleysols, etc.)	Forests	—	—	98	Batjes and Dijkshoorn [16]
	—	—	Quartzipsammments		—	—	40	Batjes and Dijkshoorn [16]
	—	—	Histosols		—	—	724	Batjes and Dijkshoorn [16]
Juruema, Amazon, Brazil	10°28'S; 58°28'W	260	Xingu complex, agri, and latosols	Dense rainforest	24	2200	60 ± 10.3	Novaes Filho et al. [18]
Amazon region, Brazil	—	—	—	Dense rainforest	—	—	103	Britez et al. [42]
Many studies in South and Southeastern Brazil	—	—	—	Grassland	—	—	79	Britez et al. [42]
	—	—	—	Mixed rainforest	—	—	71	Britez et al. [42]
	—	—	—	Dense rainforest	20.9	—	61	Britez et al. [42]
	—	—	—	Seasonal semideciduous forest	—	—	37	Britez et al. [42]
Cachoeira reserve, Antonina, southern Brazil	29°19'S; 48°42'W	20	Haplic cambisols	Herbaceous pasture	20.9	2400	98.5 ± 15.4**	Balbinot [43]
				Early successional dense rainforest			118.5 ± 14.1**	Balbinot [43]
				Medium successional dense rainforest			113.7 ± 17.8**	Balbinot [43]
				late successional submontane dense rainforest			100.7 ± 18.1**	Balbinot [43]
Igreja Mountain, Paraná range, southern Brazil	25°36'S; 48°51'W	1335	Histosols, granite	High-altitude grassland	13.4	>2000	102.0 ± 19.1	Balbinot [43]
		1325	Gleysols, granite	Upper montane dense rain/cloud forest	13.4	>2000	314 ± 17.2	Scheer et al. [7]
Ibitiraqure Mountain, Paraná range, southern Brazil	25°14'S; 48°49'W	1830	Lythic histosols, granite	High-altitude grassland	10.7	>2000	260 ± 32.7	This study*
		1810	Typic histosols, granite	High-altitude grassland	10.7	>2000	462.3 ± 26.8	This study*
		1790	Regosols and gleysols, granite	Upper montane dense rain/cloud forest	10.7	>2000	158 ± 24.9	This study*

0.361×10^6 Mg C. Additionally, the studies at the Sea Mountain Range of southern Brazil revealed that the soil carbon stocks by unit area in high-altitude grasslands are higher than the stocks of the upper montane forests. Moreover, both stocks are considerably higher when compared to soils of other ecosystems (Table 4). Therefore, to obtain precise estimates, more surveys are needed.

Differences in C stocks from various mountain aspects, topographic/geomorphic positions, and parent materials are very common in the same mountain [17, 19]. Although the C concentrations are 30-fold lower in mineral horizons than histic horizons of upper montane rain forests, they comprise almost half (46%) of the carbon soil stocks. This is explained by the 10-fold greater density of mineral horizons compared to histic horizons (Table 3). However, the mineral horizons of the observed histosols in grasslands contribute between 0 and 8% of total soil carbon due to their small thickness and to lower densities.

3.6. Upper Montane Soil Carbon Stocks and the Carbon Storage in Above-Ground Forest Biomass. The mean values of soil carbon stocks of high-altitude grasslands and upper montane forests of the Igreja Mountain Range were 314.7 and 217.2 Mg C ha⁻¹, respectively, according to Scheer et al. [7], and the corresponding estimates for Caratuva Peak were 361.4 ± 48.9 and 158.6 ± 24.9 Mg C ha⁻¹. These estimates were higher than the highest estimates for the above-ground biomass of submontane rainforests (about 200 Mg C ha⁻¹, mean near 120 Mg C ha⁻¹), which represents the highest above-ground productivity among the Atlantic Forests [52, 53].

Based on many forest structure surveys of the Atlantic Forest in the state of Paraná [42], carbon stocks in above-ground biomass are estimated at 26 Mg C ha⁻¹ (early secondary successional stage) and 153 Mg C ha⁻¹ (mature forest). As stated previously, such information highlights the great importance of upper montane soil carbon stocks. Namely, the high-altitude grassland soils have the capacity to stock more than twice the above-ground biomass of the lower montane Atlantic rainforest, where the highest primary productivity among the forests of southern and southeastern of Brazil is found.

3.7. Upper Montane Soil Water Retention Potential in Caratuva Peak. The high-saturated permeability of the histic horizons (reaching 319.5 cm h⁻¹, Table 3) was considerably reduced to 3 to 7.2 cm h⁻¹ with depth, favoring higher water retention in the soil volume. The hemic and fibric characteristics of superficial horizons, which include their low densities (0.108 to 0.117 kg dm⁻³), high macroporosity and aeration, and considerable pore connectivity, contribute to very high permeability. Although the histic horizons had high water retention capacity, the available water concentrations were low (Table 3). The gleyic horizons, such as the Big horizon representing regosols, showed lower total porosities. They also presented with lower percentage of macropores leading to lower aeration capacity and saturated permeability, which is related to structural and textural changes (Table 3). Like

the estimated carbon stocks, the potential water retention capacities of the histosols (profiles 1 and 2; 2048 and 4976 m³ ha⁻¹, resp.) were similar to those calculated for the Igreja Mountain Range [7]. The regosols of the forest showed a capacity of 3188 m³ ha⁻¹.

4. Conclusions

Soils from the ridge of the Caratuva, as in other upper montane environments of southern Brazil, are dystrophic, extremely acidic, and highly saturated with Al and TOC. Upper montane forests of the Sea Mountain Range of southern Brazil were strongly established by physical impacts from valleys and peaks. Additionally, these forests were influenced by slopes susceptible to higher action of morphogenetic processes, which result in soils with mineral horizons containing higher amounts of clay (such as gleysols and regosols). The high density of these horizons also promoted better conditions to the development of tree species. Therefore, in the upper montane environments, the thickening of mineral horizons and the thinning of histic horizons contribute to the growth of forests. High-altitude grasslands occupy ridges of folic and haplic histosols found on divergent convex ramps, resulting in thicker histic horizons. The low density and lack of consistency of these horizons associated with seasonal hydromorphy and strong winds hinder the development of forests in these environments.

Considering the studies at Sea Mountain Range of southern Brazil, the soil carbon stocks in the high-altitude grasslands are higher by unit area than the stocks of the upper montane forests. However, both values are higher, when compared to soils from other ecosystems including the above-ground biomass of submontane dense rainforests, which exhibited high primary productivity. The high potential of soil water retention of upper montane environments is strongly related to the high total porosities of histic horizons associated with the gleyic horizons. These characteristics, in addition to the filter capacity of these soils, must also be recognized as environmentally functional and worthy of preservation.

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