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Patterns in arbuscular mycorrhizal biomass in Venezuelan and Cuban ecosystems

Patrones de biomasa micorrízica arbuscular en ecosistemas de Venezuela y Cuba

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Palabras clave: continuum *r-K,* fitomasa de raicillas, gradientes ecológicos, hongos micorrizógenos arbusculares

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ABSTRACT

Functional tendencies of the arbuscular mycorrhizal functioning in different ecosystems were studied, from desertic paramos to open and closed savannah in Venezuela and evergreen seasonal forest to grasslands in Cuba. Several mycorrhizal variables were assessed in soil samples taken along an altitude and moisture gradients, considering two variants with contrasting environments with regard to water availability. The clustering of different ecosystems according its mycorrhizal and physical chemical variables was performed by means of multivariate analysis, being the cophenetic correlation the principal criteria for the resulting clustering. The humidity performed a marked influence over the rootlets phytomass, mycorrhizal colonization percentage, arbuscular visual density percentage and arbuscular endophyte mycomass values, which were higher generally in the wetter plots. The higher moisture in the plots yielded a diminishing of the ectophyte mycomass, as soon as ectophyte mycomass:endophyte mycomass ratio and ectophyte mycomass:rootlets phytomass. The two principals functional tendencies of exuberance and austerity, comprehended in the *r-K* continuum, previously observed in the insular ecosystems, were also demonstrated at the continental ecosystems.

RESUMEN

Se estudiaron las tendencias del funcionamiento micorrízico arbuscular en diferentes ecosistemas, desde páramos hasta sabana abierta y cerrada en Venezuela y bosque siempreverde estacional y pastizal en Cuba. Se midieron numerosas variables micorrízicas en muestras de suelo tomadas a lo largo de un gradiente de altitud y humedad, considerando dos variantes con ambientes contrastantes con relación a la disponibilidad de agua. El agrupamiento de los diferentes ecosistemas de acuerdo a sus variables físico-químicas y micorrízicas fue desarrollado mediante análisis multivariados, resultando la correlación cofenética el principal criterio para el agrupamiento resultante. La humedad ejerció una marcada influencia sobre la fitomasa de raicillas, el porcentaje de colonización micorrízica, el porcentaje de densidad visual arbuscular y los valores de micomasa de endófito arbuscular, los cuales resultaron generalmente mayores en las parcelas más húmedas. La mayor humedad en las parcelas produjo una disminución de las micomasas de ectófito así como la relación micomasa de ectófito:micomasa de endófito y micomasa de ectófito:fitomasa de raicillas. Las dos principales tendencias funcionales, comprendidas en el continuum *r-K,* previamente observadas en los ecosistemas insulares fueron también demostradas en los ecosistemas continentales.

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INTRODUCTION

Fungi of the phylum Glomeromycota are ubiquitous hypogeous microorganisms living in symbiosis with approximately 70–90% of the world's vascular land plants (Smith and Read, 2008; Brundrett, 2009). The intimate relationship between arbuscular mycorrhizal (AM) fungi and plants has existed for at least 400 million years (Redecker *et al*., 2000) and this co-evolution has involved numerous interactions at the ecological, physiological and molecular levels between these organisms during the long development of the symbiosis (Taylor *et al*., 2009; VanKuren *et al.,* 2012).

Advanced research on plant ecology and ecophysiology recommends to select functional groups of species preferably to species treated separately (Herrera *et al*., 1990; McDade *et al*., 1994). However, relatively little is known about the AM holistic functioning when tropical ecosystems or species are considered.

Some papers have been devoted to the AM important role for tropical forest succession (Janos, 1980 a, b) or to explain the AM responsiveness of tropical forest tree seedlings (Huante *et al*., 1993; Herrera *et al*., 1997). In a successional context, AM fungi have been commonly found associated with plants in late-successional stages whereas pioneer plants tend to be facultative or nondependent on AM (Reeves *et al.,* 1979; Janos 1980a). However, there is contrasting evidence showing that plants from early successional stages benefit from the symbiosis with AM fungi (Allen and Allen, 1992; Allen *et al.*, 2003). This contradictory evidence suggests that AM prevalence in plant roots could be driven by plant intrinsic attributes, such as root morphology, rather than for their temporal occurrence during the successional process, although these factors could not be easily disentangled, like has been proposed by Pezzani *et al.* (2006).

The functional diversity of tropical forest tree successional groups and tropical forest ecosystems have been characterized in terms of exuberant and austere strategies (Herrera *et al*., 1988a,b; 1997). Herrera *et al*. (1997) grouped 221 forest trees according to their habitat preferences into species preferring humid or dry and/or saline habitats or indifferent to the habitat type. They established that according as succession move forward exist a tendency to increase the *K* selection while *r* selection decrease on the basis of *r-K* continuum, and all at once recognized seven strategies groups: Early Pioneers, Late Pioneers, Exuberant, Colonizers, Opportunists, Invasive and Austere. These strategies resemble the widely applicable *r-K* continuum described by MacArthur and Wilson (1967).

In Cuban tropical forests it has been demonstrated (Herrera *et al*., 1988a; 1997; Herrera-Peraza *et al*., 2004) that the *r-K* continuum can be applied to AM fungi in relation to significant changes in endophyte (ED) and ectophyte-external mycelium-EC mycomass. In ‘exuberant’ systems (*K*-AM), biomass in the symbiosis is more fungal whereas in ‘austere’ systems, the symbiosis is more plant-dominated. Exuberant functioning occurs when necromass turnover and/or photosynthesis rates are high, so that a costly symbiosis (high endophyte mycomass) is easily maintained. Austere functioning occurs when necromass turnover and/or photosynthesis rates are low, necessitating a less costly symbiosis (low endophyte mycomass) for the plant.

It is known that along altitudinal gradients, plant growth conditions have fundamental shifts because of changes in temperature, precipitation, and soil conditions like stated by Ruotsalainen *et al.* (2004). Changes in temperature conditions, nutrient availability, and vegetation coverage are known to affect mycorrhizal colonization (Genney *et al*., 2001; Gai *et al.,* 2012). On the other hand, most of the research on the altitudinal patterns of mycorrhizas has focused on root colonization along environmental gradients in high-alpine regions and the common patterns indicate that mycorrhizal colonization decreases with increasing altitude (Haselwandter, 1987).

Thus, we are using the gradient approach that consists of studying the changes that take place along environmental gradients such as altitude, humidity, nutrients etc. and along gradients of human disturbance from very little use to intense exploitation. These analyses are performed at several different scales, from the landscape to organisms. The present report aims to show how AM exuberant and austere tendencies manifest along a wide ecological gradient of tropical Venezuelan and Cuban ecosystems functioning.

MATERIALS AND METHODS

Study area

Arbuscular mycorrhizas (AM) were studied along an altitudinal and climatic gradient at 6 Venezuelan (VZ) and 2 Cuban ecosystems (Table 1):

Table 1. Characteristics of the study ecosystems.

ECOSISTEMS	LOCALITY	ALTITUDE (msnm)	DOMINANT SPECIES	SOIL TYPE	ANNUAL MEAN TEMPER. (^{0}C)	ANNUAL MEAN RAIN (mm)
Desertic Paramo (DP)	Mifafí, S. La Culata, Mérida (8º 52' N, 70º 48'W)	4200-4400	*Espeletia timotensis Cuatrec.*	Coluvial deposits with gravel	2.8	798
Andean Paramo (AP)	Mucubají, Sierra Nevada, Mérida (8º 48' N, 70º 49'W)	3400	*Espeletia schultzii* Wedd. *Hypericum laricifolium* Juss	Inseptisols	5.4	968
Cloudy forest (CF)	La Mucuy, Sierra Nevada, Mérida (8º 38' N, 71º 02'W)	2300	*Guettarda steyermarkii* Standley *Clusia multiflora* H.B.K., *Oreopanax moritzii* Harms.	Entisols	14	2800-3300
Cloudy grassland (CG)	LaMucuy, Sierra Nevada, Mérida(8º 38' N, 71º 02'W)	2300	*Pennisetum clandestinum* Hochst. ex Chiov.)	Entisols	14	2800-3300
Open Savannah (OS)	Calabozo, Llanos centrales, VZ (8º 56' N, 67º 25'W)	At the sea level	*Trachypogon plumosus* (H. et B. ex Willd) Nees *Axonopus canescens* (Nees) Pilg. *Leptocoryphium lanatum* Kunth (Nees)	Tropical Ferruginous (Ultisols)	28.5	1300
Closed Savannah (CS)	Calabozo, Llanos centrales, VZ (8º 56' N, 67º 25'W)	At the sea level	*Paspalum plicatulum* Michx. *Anonna jhanii* Safford *Jacaranda obtusifolia* Humb. et Bonpl.	Tropical Ferruginous (Ultisoles)	28.5	1300
Evergreen Seasonal Forest, Cuba (CU-EF)	Macizo El Salón, Estación Ecológica SR. (22º 45' N, 82º 50'O)	400	*Pseudolmedia spuria* Sw.) Griseb. *Matayba apetala* (Macf.) Radlk. *Trophis racemosa* L. Urb.	Yellow fersialitic lithic (Cambisol)	23	2300
Grassland-Potrero, Cuba (CU-GP)	La Pastora, El Establo, Carr. del Jobo a las Terrazas (22º 36' N, 83º 16'O)	400	*Axonopus compresus (Sw.) P. Beauv.* *Sporobolus indicus*(L) R. Br. *Hyparrhenia rufa* (Nees) Stapf	Yellow fersialitic lithic (Cambisol)	24.4	2014

Six transects per ecosystem, divided into two variants, dry and wet, according to water availability (D and W) were sampled and analyzed together (ecosystem AM allocation: 6 transects) or separately (water availability AM allocation: D and W, 3 transects each). Each transect composed by 5 soil sub-samples. Soil chemical and physical analyses were carried out (see Table 2). In order to characterize AM fungal community allocation a group of mycorrhizal variables were analyzed: MC, percentage of mycorrhizal colonization VD, percentage of mycorrhizal visual density; RDW, rootlet dry weight; EC, ectophyte (external mycelium); ED, endophyte (internal mycelium); EC:ED, ectophyte:endophyte ratio; EC:RDW, ectophyte:rootlet dry weight ratio were assessed according to Herrera-Peraza *et al*. (2004).

Endophyte mycomass was estimated from rootlet dry weight, considering cortical tissue as 20% by weight and AM visual density data (Herrera-Peraza *et al*., 2004).

Statistical Analysis

Statistical analysis was carried out by 3 factors ANOVA (plots, ecosystems and water availability). The homogeneity of variances was estimated for each case separately using Hartley F-max, Cochran C and Bartlett Chi-sqr tests. Newman-Keuls test was used for *post-hoc* comparison of mean values. When necessary, regressions (line tendencies) were estimated using Excel for Windows. For multivariate analysis the software NTSYS-pc, version 2,8 was used (Rohlf, 1993).

Table 2. Chemical analyses of soils from the studied sites.

	pH	OC %	N%	C:N	P	K	Mg	Na	Ca	H %
DPD	4.70	2.24	0.11	20.3	14.0	0.09	0.11	0.16	0.30	15.98
DPW	4.70	4.74	0.27	17.5	23.0	0.19	0.32	0.19	0.51	30.67
APD	4.70	8.64	0.47	18.3	13.0	0.16	0.22	0.17	0.50	44.41
APW	4.60	15.63	0.74	21.1	25.0	0.20	0.53	0.21	0.49	73.30
CFD	4.30	10.30	0.72	14.3	18.0	0.20	0.63	0.22	0.19	104.73
CFW	4.20	17.23	0.81	21.2	30.0	0.34	1.23	0.39	0.55	145.40
CGD	4.90	3.99	0.22	18.1	9.0	0.28	0.77	0.25	0.43	31.52
CGW	4.90	8.71	0.51	17.1	24.0	0.23	0.57	0.18	0.52	55.54
OSD	5.00	1.75	0.04	43.7	traces	0.15	0.58	0.21	0.65	11.20
OSW	4.80	1.33	0.05	26.6	traces	0.05	0.31	0.21	0.15	11.10
CSD	5.00	1.80	0.13	13.8	traces	0.10	0.56	0.24	0.29	10.63
CSW	5.00	1.35	0.07	19.2	traces	0.06	0.31	0.23	0.19	11.97
EFD	6.60	3.70	0.30	12.33	14.0	0.42	5.04	0.50	33.21	32.82
EFW	6.50	3.21	0.32	10.03	22.0	0.42	9.15	0.42	27.37	38.08
GPD	7.50	2.18	0.20	10.90	29.0	0.70	6.38	0.65	35.99	23.02
GPW	7.80	1.90	0.18	10.55	28.0	0.60	5.12	0.30	37.87	30.07

pH, 1:2,5 v/v in water; OC (Organic Carbon, by oxidation with sulphuric acid and potassium dichromate); N (Kjeldahl); P (Olsen); K, Mg, Na and Ca (Schachabel). P in $\mu g.g^{-1}$, K, Mg, Na and Ca in $cmol/kg^{-1}$

RESULTS AND DISCUSSION

Rootlet phytomass (RDW)

There was a tendency to obtain the highest values of rootlet phytomass in the wetter plots (Table 3). The maximal values were obtained in Cloudy Forest followed by grasslands plots and ecosystems. The Evergreen Forest and paramos plots and ecosystems show reduced values, which are minimal in savannah. Relatively few roots show root hairs; cloudy forest and grassland and evergreen forest show maximal values. However, the average pecentage of root hairs not tends to increase significantly under wetter conditions.

Similar results were obtained by St John *et al*. (1983a,b), Herrera *et al*. (1985, 1988a) and Herrera-Peraza *et al*. (2004) who observed both external mycelium mycomass either rootlet phytomass were significantly stimulated by elevated values of organic matter in the soil, and more exactly by the level of the nutrients derived from its decomposition. This is clearly noticeable in the wetter plot of Cloudy Forest, where the highest values of detritus, organic carbon, nitrogen, phosphorus, potassium and calcium were observed among all the studied Venezuelan ecosystems. On the other hand, Rodriguez *et al*. (1985) studying the mesofauna and the rootlets decomposition process in a grassland of Reserve of the

Biosphere Sierra del Rosario found a highest decomposition of the rootlet phytomass in this kind of ecosystem, because of is probably that a high production of rootlets obey to the necessity of this ecosystem to renew a higher quantities of them.

Percentage of rootlets with root hairs (RHP)
In general there was not evident a regular behavior of the percentage of root hairs in function of the moistening levels of the ecosystems (Table 3). The highest percentage of rootlets with roots hairs in the Cloudy Forest could be a consequence of the high availability of nutrients in this study site.

Table 3. Results of bi-factorial ANOVA for mycorrhizal variables. MC, mycorrhizal colonization; VD, mycorrhizal visual density; RDW, rootlet dry weight; EC, ectophyte (external mycelium); ED, endophyte (internal mycelium); EC:ED, ectophyte:endophyte ratio; EC:RDW, ectophyte:rootlet dry weight ratio;. Means with similar letter in the same column are not significantly different for $p<0.05$.

	RDW	RH	MC	VD	ED	EC	EC:ED	EC:RDW
DPD	0.5efg	2.2 c	84.1 a	13.3 a	14.1 cd	10.6 g	0.8 g	20.4 fg
DPW	0.7 efg	0.4 c	69.4 ab	10.9 ab	14.5 cd	49.1 efg	3.8 f	74.3 de
APD	0.5 efg	1.2 c	69.6 ab	8.1 ab	8.6 de	108.6 abcd	13.9 cd	216.0 abc
APW	1.2 cde	0.0 c	43.7 bc	5.9 b	14.8 cd	20.4 fg	1.7 fg	19.7 g
CFD	3.2 b	27.0 a	63.7 ab	6.9 ab	44.5 b	105.4 abcd	2.5 f	33.4 fg
CFW	6.7 a	29.7 a	68.4 ab	7.5 ab	96.7 a	54.1 efg	0.6 g	9.6 h
CGD	1.5 cde	1.6 c	57.1 ab	5.2 b	14.7 cd	31.0 fg	2.1 f	21.5 fg
CGW	2.2 cde	12.7 ab	66.4 ab	5.7 b	24.9 c	56.1 defg	2.3 f	25.7 fg
OSD	0.4 fg	0.0 c	20.1 d	1.2 c	0.8 f	131.5 a	163.9 a	388.1 a
OSW	0.3 fg	2.7 bc	57.6 ab	7.0 ab	4.4 e	113.6 abc	26.9 b	363.2 a
CSD	0.2 g	1.0 c	18.9 d	0.9 c	0.4 f	68.0 bcdef	182.4 a	314.3 ab
CSW	0.4 fg	1.5 c	34.9 cd	6.2 b	4.6 e	80.8 abcde	17.8 bc	215.1 abc
EFD	1.0 def	12.3 ab	59.3 ab	6.1 b	11.5 cd	109.1 abcd	10.0 de	113.0 cde
EFW	0.7 efg	9.8 ab	63.5 ab	12.8 a	17.3 cd	114.8 ab	6.6 e	169.2 bc
GPD	1.6 cd	0.0 c	66.8 ab	6.8 ab	22.4 c	72.6 bcdef	3.3 f	44.4 ef
GPW	1.7 cd	0.0 c	68.0 ab	6.0 b	20.4 cd	42.7 efg	2.1 f	25.3 fg

Although it has been reported that AM symbiosis and root hairs are excluding organs, as they compromise similar physiological functions (Chilvers and Daft, 1981) some authors (Ferrer and Herrera, 1988; Allen, 1991) have considered that results as contradictory. In accordance with the formers, in spite of the high mycotrophy observed in the forest of Reserve of the Biosphere Sierra del Rosario, the excluding functional role of roots hairs and the AM symbiosis could not be clearly established for the 58 trees, shrubs, vines, grasses and herbs species examined.

Allen (1991) reported that the mycorrhizal activity between tropical tree species was correlated with the root hairs reduction, but in some cases, species with numerous root hairs shown an intense mycorrhizal activity. In our study, the excluding functional role of roots hairs and the AM symbiosis resulted difficult to demonstrate newly. While this behavior was evident for the Cuban grassland, followed by the desertic paramo, it resulted practically inexistent for the cloudy forest, Andean paramo and the closed savanna of Venezuela.

Herrera-Peraza *et al.* (2004) studying the excluding functional role of roots hairs and the AM symbiosis in different biological types as trees, shrubs, vines, grasses and herbs observed that this process were shown when all the species were analyzed together, since separately only the grasses and herbs shown this behavior. They suggested then the use of the "root hair index" (RHI) through to rank the root hairs according to different categories of abundance, length uniformity and mean length, and recognized the wide rank of variation for grasses and herbs as the responsible of the negative correlation observed between these variables.

Mycorrhizal colonization rate (MC)

In general, colonization and visual density values behave similarly (Table 3). However, fungal occupancy significantly increases in wetter plots, particularly in savannah and evergreen forest plots. Arbuscular mycorrhizal colonization was higher in the desertic paramo, followed by the CU GP and the cloudy forest. Some species of *Espeletia* very common in the Andean paramos accumulates significatives levels of organic matter under its canopy, if is compared with the adjacent naked soil (Perez, 1992).

As consequence, the mycorrhizal roots would be particularly important in an efficient nutrient cycling mechanism in this extreme ecosystems, by the rosettes near to the to the steam base, where generally occur a leaching of nutrients from the leaf litter toward the deepest layers of the soil. It would explain the high values of mycorrhizal colonization found in these ecosystems, as were observed by Barnola and Montilla (1997), also given the existence of very low values of rootlets phytomass and external mycelium, as well as intermediate values of radical hair, structures all in charge of assimilating nutrients for the vegetable.

According as suggested by Allen (2001) this variable is dependent as the plant habit as the environmental conditions, derived of the growth of two interdependent organisms, but different among them, each one of them trying to reach its maximum survival and development.

Visual density rate (VD)

At ecosystem level, desertic páramo and evergreen forest show higher fungal occupancy (VD values), and these values tend to increase significantly under wetter conditions (Table 3). From our results, it could be established the existence of a gradient of variation in the values of fungal occupancy clearly related with the topography of the studied ecosystems, and as consequence with the levels of moistening in each ecosystem, as well as a marked diminishing of the values of this variable was observed with the diminishing of the height above sea level.

Gibson and Hetrick (1988) and Khalil and Loynachan (1994) have observed differences in the composition and abundance of the AM fungi along some topographic gradients. As supported by Gibson and Hetrick (1988), the topography of a site constitutes a complex gradient of soil moisture, nutrients and texture; therefore detailed studies about the relation AM-plant-soil are necessary to elucidate the processes and mechanisms involved in them.

At the well drained soils observed in the deserted paramo, distinguished by a low nutrient availability, and subjected to noticeable frost concentrations during the dry season as consequence of the high nocturnal re-irradiating, the internal environment of the root, could represent an adequate protection to the mycorrhizal fungi, if we know that Gai *et al.* (2012) reported that AM establishment was more difficult at higher altitudes, whilst constitutes a site where across the arbuscules, the symbiotic interchange is produced to improve the development of the both partners involved in this relation. It is could not be odd if it is well established that the fungus obtains benefits for its root occupancy provided by a highest access to the root exudates, is the first organisms in obtain the organic substrates once died the host and on the other hand, avoid the competence, predation and parasitism of other soil microorganisms (Brundrett, 2002).

Montilla *et al.* (1992) obtained similar values of percentage of visual density for the Gavidia paramo at 3300 m.a.s.l. in plots with *Espeletia schultzii* as dominant species therefore it could be supposed that the vegetal species also must be take into consideration if you are going to interpret this variable.

Endophyte mycomass (ED)
ED values are significantly larger in cloudy forest whereas they are conspicuously minimal for savannah (reduced rootlet phytomass and VD values) and commonly low for the remaining plots and ecosystems (Table 3). Wetter conditions significantly increase ED values.

Given that this variable is directed related with the rootlet phytomass, the high values of the latter in the in cloudy forest also determined the highest values of ED mycomass in this plot. At the same time, the highest values of rootlets phytomass, root hair percentage, and high values of external mycelium in this plot put in function of the nutritional richness observed in it, should be correspond with adequate levels of endophyte mycomass that guide all the activity of nutrient capture by these components before mentioned.

According with Herrera *et al.* (1994) in this plot should be favored the exuberant functioning of AM symbiosis, which to manifest in plots with larger moistness, higher photosynthetic rates and larger decomposition velocities, that in the first place should be related probably with larger availability of photosynthetic carbon, whereby it is necessary an adequate level of endophyte mycomass.

Ectophyte mycomass (EC)
There was not observed a uniform behavior of the ectophyte mycomass values in function of the moistening degree in the studied plots (Table 3). EC values are particularly high for savannah, cloudy and evergreen forest and Andean paramo, wetter conditions significantly decrease EC values.

Miller *et al.* (1995) established that plants can survive to ecological disturbances partially due to the plasticity of answers of the roots and arbuscular mycorrhizal fungi associated with them. As defined by St. John *et al.* (1983a,b), Marschner (1995) and Smith and Read (1997) the capacity of searching nutrients by the present AM fungi include an extensive dispersion through different substrates, the answer to temporary nutrient sources, the competence with others microorganisms of soil and the production of enzymes in order to loose organic nutrients.

According to Fitter (1987) under growth conditions characterized by moisture deficits (and in the Venezuelan savannahs were registered the lowest values of soil moisture from all the studied ecosystems), the cost for produce rootlets could be bigger than the cost for produce or support external hyphae of AM fungi. It could justify the highest values of EC mycomass observed in this ecosystem, which contrast with the low values of rootlets found.

The high values of EC mycomass observed for the evergreen forest in Vallecito are in accordance with previous results reported by Herrera *et al*. (1985). The existence of a root mat in this type of forest, where are concentrated the rootlets and the external hyphae of the AM fungi justify this high values of EC mycomass. Also the accumulated necromass in this type of ecosystems should be exert an direct influence over the larger EC mycomass, since that has been demonstrated that the organic matter influence noticeably over the EC production.

In the cases of the desertic paramo and Venezuelan cloudy grassland and closed savannah, the larger degree of substrate moistening determined increases of the EC mycomass, though not significatively. The former results could be due that in the Andean paramos, cloudy forest and open savannah the fungal community functionally more important, could be adapted to the less moist conditions that is the exaggerated moistening of the substrate, in this cases, can counterwork the adequate functioning of mycorrhizas. At the same time, en this ecosystems a greater moistening can determine anaerobic conditions that reduce the ectophyte production, as effectively have demonstrated Barnola and Montilla (1997), Janos (1987) and Van Duin *et al*. (1991).

Among other possible causes of the previous obtained results could be think that are selected different mycorrhizal fungal species depending the greater o lower moistening degree. Analyzing these results could be suggested that in case of happens any significative global change, the most fragile ecosystems would be the desertic paramos, Venezuelan cloudy grassland and closed savannah if the change is towards more long drought and the contrary if is toward more moistening.

EC: ED ratio

The ectophyte mycomass : endophyte mycomass (EC:ED) ratio decrease commonly in wet plots; values are higher in savannah and intermediate in Andean paramo and evergreen forest (Table 3). EC:ED values decrease under wetter conditions. The behavior of this relation can not only be explained analyzing the increases of EC and ED separately but this relation must have increases by own balances of this relationship in each site. The high values of this relation obtained in the closed (many trees) savannah yield to the observed extremely low values of endophyte as the values of ectophyte mycomass can be considered intermediate among all the obtained values. The Venezuelan savannahs and specially the cloudy savannah showed practically null values of asimilable phosphate, and among the lowest of organic carbon, nitrogen, potassium, calcium, etc. At the same time, in this ecosystem were registered the lowest values of rootlets phytomass, percentage of root colonization, percentage of visual density, endophyte mycomass, and among the lowest in hairy roots.

In presence of so adverse conditions, where is really difficult to the vegetal species to accede to nutrients, the native AM fungi should exhibit a high specificity or fungal fitness with the vegetal species, making possible to optimize up to a maximum degree the fungus-plant symbiosis, in order to obtain a maximum nutrients profit. This idea is supported by evidences obtained from some studies in temperate and tropical zones Furrazola (unpublished data) and Bever (2001). Furrazola (unpublished data) studying grasslands and evergreen forest at the Reserve of Biosphere Sierra del Rosario in western Cuba observed the differenced existence of three AMF groups: one of them whose role seems to be to stabilize the ecosystems. A second one whose maintaining is few expensive to the host and a third group whose maintaining is very expensive to the host (more photosynthesis derived carbon compounds consumer).

Commonly it has been consider that the AMF show a low association specificity by the host plant, but according to Bever (2001) such conclusions has been established almost exclusively in experiments in which the isolated fungal species grow separately from the others, excluded therefore from the competitive interactions between them. As expressed by this author, when the AMF are analyzed like a community, several evidences are found for to demonstrate that growth rates show a high specificity by the host. This pattern of specificity by the host has been observed in different ecosystems, from sand dunes (Koske, 1981), as far as grasslands in California (Nelson and Allen, 1993) and also in agricultural lands (Douds and Millner, 1999), phenomena that could be expressed in the cloudy savannah.

EC:Rootlet ratio

EC:Rootlet values are higher for savannah, evergreen forest and Andean paramo (Table 3). Cloudy forest and grassland show minimal EC:Rootlet ratios. Wetter conditions tend to significantly decrease EC:Rootlet ratio. This rate like the EC:ED ratio, seems to depend more from the own symbiosis characteristics in each site. When the relation EC:ED was analyzed previously, was made a reference to the poor conditions of the Venezuelan savannahs. Under that conditions, result in extremely advantageous for the plants root system to count upon with a external mycelium network more efficient, suitable to take the scarce nutrients in the substrate matrix. In the case of the evergreen forest, the growth of the external mycelium independent from the colonized root physiology, in a rich organic matrix, should influence over the high values of the EC:Rootlet rate in this plot. It could be beneficial for an ecosystem where the nutrients are very slowly released and the high values of this rate determine that in such conditions the substrate be continuously explored in benefit of the plants.

General and particular tendencies of the arbuscular mycorrhizae functioning in ecosystems with drier and humid variants from Cuba and Venezuela

As resulted of the Correspondence Analysis applied, three types of configurations appear to predominate in the bidimentional space defined by the two primer axis which explained more than 75% of data variance (Fig. 1).

The results showed a gradient of ecosystems, from the mountain cloud forests to the drier savannas. Three groups are clearly separated, the mountain forests and grasslands from Cuba, the mountain systems and the savannas from Venezuela. The horizontal axis is correlated to the type of symbiosis: the predominant endophytic on the right, with higher endomycelium (ED), and rootlets, and the predominantly exophytic symbiosis on the left, with higher EC:ED and EC:Rootlets. The vertical axis is related to nutrients, particularly calcium and also Mg, K, Na that separates the Cuban forest from the rest.

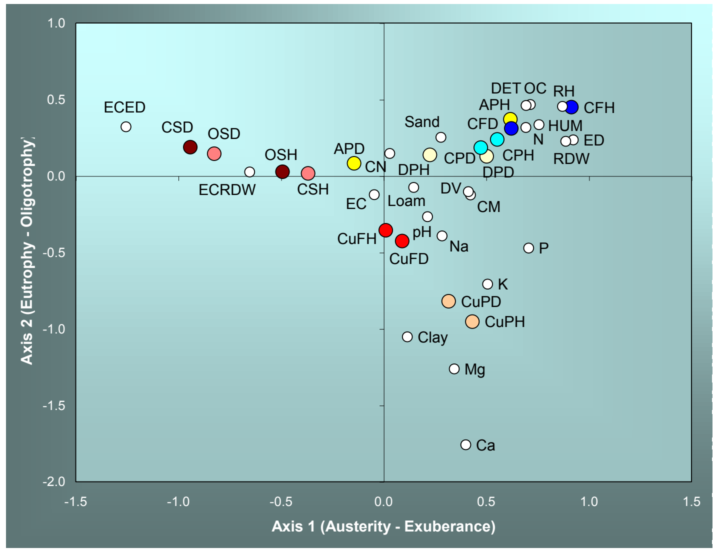

Fig. 1. Dual graphic of the plots and the variables, conforming to the Correspondence Analyses. (see abbreviators in Materials and Methods).

The level of Ca and Mg determined the separations of the Cuban ecosystems in one group, as in these places were reported the higher values of this elements. It has been recognized by several authors that the chemical basis of the soils such as Ca and Mg to play an important role as much over the root colonization as in arbuscular mycorrhizal fungi sporulation (Gryndler *et al*., 1992; Jarstfer *et al*., 1998). Also Anderson and Liberta (1992) found that plants treated with Ca showed a higher colonization but lower sporulation that those not treated, as soon as previous experiences situated the Ca ion as a good predictor of AM fungi sporulation.

Respect to the group constituted by the mountain Venezuelan ecosystems at higher altitude above sea level (paramos and cloudy forest with its grasslands), this behaviour is not difficult to explain. According to Monasterio (1980) the almost ecuatorial situation and the altitude at which the Venezuelan paramos are situated, have important ecological implications because to firmly resolve environment rhythms which determine a distinctive and unique habitat: “the tropical paramo”. Also should be to take a thing into consideration that this ecosystems are characterized by possess climates of low daily medium temperatures along all the year, but with relatively broad temperature cycles and almost constant photoperiods (Azocar and Monasterio, 1980). Also these ecosystems are also related by the highest values of clay percentage, among the lowest of sand percentage and medium values of the relation EM:Rootlets.

The separation of the savannas from Venezuela from the other studied ecosystems to obey at the higher values of the EC:Rootlets and EC:ED ratios found in this plots, as soon as also to the high values of EC observed in both savannas. As has been shown, under wetter conditions, where should be logical a higher velocity of the necromass decomposition, rootlet phytomass, mycorrhizal colonization, ED and VD tend to increase significatively, meanwhile EC, EC:ED and EC:Rootlets ratios significantly decrease in such conditions (Table 3).

The behaviour of these variables coincide with the results obtained by Herrera *et al*. (1994) whose observed an increase of the endophyte MA as well as a decrease of the values of ectophyte MA and the relation EC: Rootlets in plots with higher moistening in an evergreen forest at Biosphere Reserve Sierra del Rosario in Pinar del Rio, western Cuba.

According to Herrera *et al*. (1994) can be considered that a glomeromycetes fungal community, with higher values of arbuscular endophyte and low arbuscular ectophyte mycomass, could be functionally associated with mycorrhizas more expensive to the host, but at the same time more efficient for the vegetal growth, its could represent the “exuberant” tendency of the mycorrhizal functioning. At the same time, this tendency results common in sites with such as higher photosynthetic and turnover rates as with higher availability of water and nutrients.

On the contrary a community of these fungi with a lower fungal occupation and higher ectophyte mycomass could be functionally associated with mycorrhizas less expensive to the host and would represent the “austere” tendency of the mycorrhizal functioning. In this case, such tendency is manifested in sites with such as lower photosynthetic and turnover rates as with lower availability of water and nutrients.

The fact that the percentage of visual density and the endophyte mycomass be significative lower in the driest plots confirm the hypothesis of the austere tendency of the mycorrhizal functioning in presence of necromass accumulations, perhaps due to a improve in the mechanism of nutrient conservation and a slower capture of them (determined by the lower turnover rates and as consequence a smaller nutrients liberation and capture of them).

According to our measurements, the raw humus (particle size 0.5 – 2.0 mm remaining after wet sieving) correlates with substrate water content (Fig. 2), i.e., the higher humidity is, the faster organic matter decomposition (turnover rate) occurs. The particles that compound raw humus are the necromass fragments more difficult to decompose (more lignified), therefore a higher quantity of such humus evidence a process of high necromass decomposition. At once, such detritus are one of the principal causes of the humidity percentage on dry basis increase, then if true such particles are difficult to decompose, its perform an important function as absorbent and very light water reservoirs.

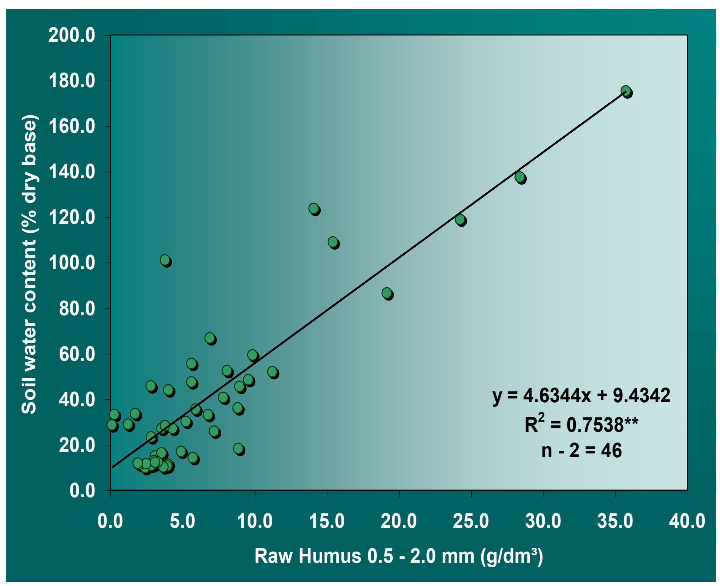

Fig. 2. Correlation between substrate water content and the raw humus particles.

Just as the ideas exposed before, ED values correlate positively and EC:Rootlet values correlate negatively with increasing turnover rate (Fig. 3 and 4). Therefore, arbuscular mycorrhizae tend functionally to allocate as a preferentially endophytic symbiosis under higher turnover rates, i.e., higher water and nutrient availability (exuberant or r-strategy of AM symbiosis). Whereas, they tend to functionally allocate as a preferentially ectophytic symbiosis under lower turnover rates, i.e., lower water and nutrient availability (austere or *K*-strategy of AM symbiosis).

In presence of exhuberant functioning of MA symbiosis, (where exist a greater humidity and a fast nutrient decomposition) the nutrimental attributes of

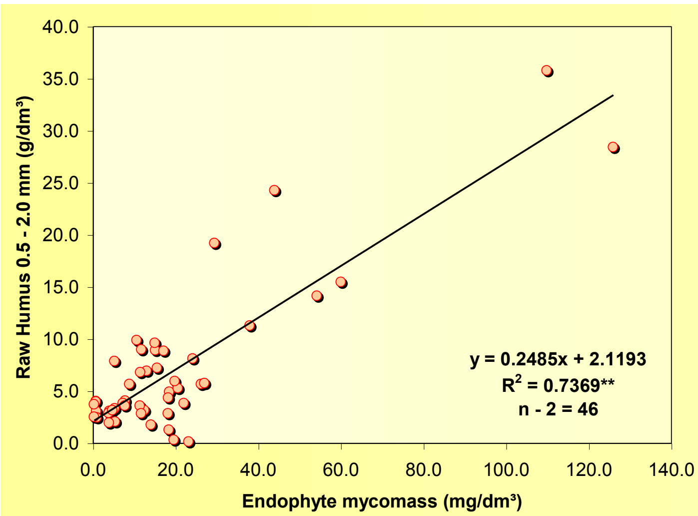

Fig. 3. Correlation between raw humus particles and endophyte mycomass.

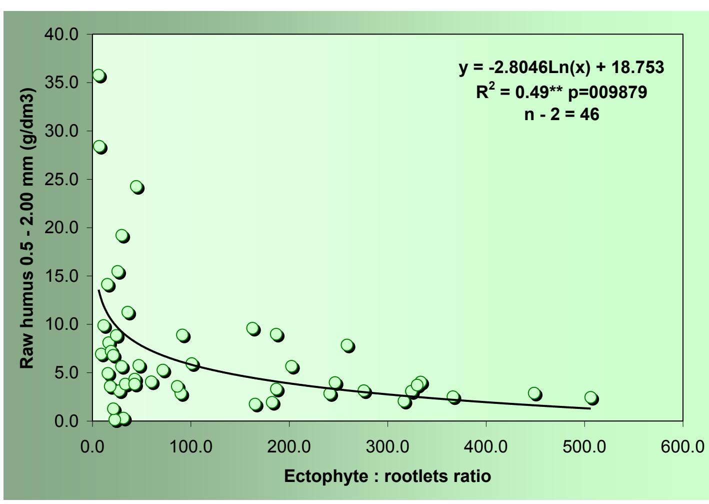

Fig. 4. Correlation between raw humus and ectohyte:rootlets ratio.

the mycorrhizae (ectophyte and its relations with the endophyte and the rootlets) are not so necessary due to the necromass decomposing it more fast, the nutrients are gradually released and consumed more efficiently, thanks to a greater mycorrhizal colonization rate. According with our results, as the same for all living organisms, the two principal tendencies, exuberant and austere can be identified for the arbuscular mycorrhizal functioning conceived inside the *r*-*K* continuum.

The austere ectophytic functional allocation might represent the typical mycorrhizal functioning prevailing under extreme soil or climatic stress. We lack still explanations to the austere mycorrhizal behavior. However, the reduced ectophyte carbon cost vs. the rootlets carbon cost, the probable saprophytic abilities of the ectophyte hyphae, and significant changes in AM fungal community composition, need to be further investigated.

CONCLUSIONS

The humidity performed a marked influence over the rootlets phytomass, mycorrhizal colonization percentage, arbuscular visual density percentage and arbuscular endophyte mycomass values, which were higher generally in the wetter plots. On the other hands, the higher moisture in the plots yielded a diminishing of the ectophyte mycomass, as soon as ectophyte mycomass : endophyte mycomass ratio and ectophyte mycomass : rootlets phytomass. The two principals functional tendencies of exuberance and austerity, comprehended in the *r*-*K* continuum, previously observed in the insular ecosystems, were also demonstrated at the continental ecosystems.

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