

CORRELATION BETWEEN ARTHROPODS AND PHYSICAL AND CHEMICAL CHARACTERISTICS OF WATER AND SOIL RETAINED IN TILLANDSIA VIOLACEA (BROMELIACEAE) IN AN ABIES- QUERCUS FOREST IN CENTRAL MEXICO

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Abstract. The effect of the support tree species and the seasonal and altitudinal variations on the physical-chemical characteristics of the water and soil accumulated in plants of the epiphytic bromeliad *Tillandsia violacea* were studied in “El Chico” National Park, a temperate forest from Hidalgo, in Central Mexico. The relationship of these factors with arthropods living in theme was also studied. It was found that the tree support species influenced the ions concentration in water and soil. The highest values of ions were found in plants from *Abies religiosa*. Altitude and the season of sampling affected calcium concentrations, as well as pH of soil and water accumulated on epiphytic *Tillandsia*. Electrical conductivity, calcium and dissolved organic carbon (DOC) in epiphytic water accounted for more than 60% of the variation in the density of arthropods. In the accumulated soil pH (among 3.4-8.3), organic carbon content (17.16-30.07 mg g⁻¹), sodium and potassium concentrations (0.26-1.43, 0.49-34.87 cmol⁺ kg⁻¹, respectively) were the most important factors correlated with the total fauna abundance. These results showed the role of epiphytic plants as refuges and nutrient source for arthropod communities and their influence on energy flow in this ecosystem.

Keywords: *Altitude, dissolved organic carbon, ions contents, nutrients, suspended soils.*

Introduction

Epiphytic plants are very frequent in tropical ecosystems, representing about 10% of all the vascular plants species in different kinds of forests (Kress, 1986; Nieder, et al., 2001). In such ecosystems, their biomass can represent up to 30% of the total leaf biomass (Nadkarni, 1984; 1992); thus significantly contributing to the diversity of animal and plant species in Ecuador, Peru and Venezuela (Gentry and Dodson, 1987; Ibisch et al., 1996; Barthlott et al., 2001). Their bearing on the nutrient cycle is of great importance because they sequester atmospheric nitrogen and make it available to other levels of the ecosystem (Edwards and Grubb, 1977; Nadkarni, 1984, 1992; Clark et al., 1998).

These characteristics suggest that epiphytic plants are a key resource for their function (Nadkarni, 1994), in specific environments where competition by light, nutrients and space are factors that limited the development of the understory layer. Due to their morphology, most of these plants give shelter and supply food to a variety of arthropods and other animals (Benzing, 1990; Gutiérrez et al., 1993; Richardson, 1999). They accumulate large amounts of organic matter and litter inside, as well as water, which are vital as an energy source for the different animal communities and the maintenance of general moisture of the whole ecosystem (De Buen, 1953; Bohlman et al., 1995; Zotz and Thomas, 1999). In fact, the epiphytic environment represents one of the most nutrient-poor habitats for vascular plants, thus the bromeliads have consequently developed mechanisms to accumulate mineral salts dissolved in rainwater and related canopy fluids, and leach significant amounts from the host plants (Tukey, 1970; Benzing, 1980). An input of nutrients in the canopy of the tropical forest comes from the forest leaching and atmospheric aerosols. Soil ions become available to epiphytic plants microbial mineralization, nitrogen fixation, canopy roots and the plant capacity to accumulate plant and animal remains and litter (Benzing, 1990; Vence and Nadkarni, 1990, 1992).

Many studies have demonstrated that the so-called 'suspended soils' (Delamare-Devouteville, 1948), nevertheless its scarce, have many nutrients and they constitute an important pool of organic matter, sometimes functioning as "buffers" of mineral nutrients from the atmosphere for their further incorporation to the ecosystem (Nadkarni and Matelson, 1991). Despite their importance for the fauna they shelter, few studies have been carried out in these peculiar microcosms concerning their physical and chemical properties, considered as arboreal Histosol by some authors (Bohlman et al., 1995) or arboreal soil (Nadkarni et al., 2002). Recent studies propose that the arboreal soils can be considered as true soils (Enloe et al., 2006).

Most of the studies about the mineral epiphytic nutrition have been conducted in tropical forests (Clarkson et al., 1986; Hietz et al., 1999; Richardson et al., 2000b). Nevertheless, little information is available about temperate forests. Recent studies show that the presence and abundance of vascular epiphytes in temperate forests are more common than has been considered previously, and in some places they are similar to those of tropical forest (Zotz, 2005). An only few studies are focused in the origin and characteristics of the arboreal soils (Enloe et al., 2006, 2009)

In the present study we evaluated the influence of support trees (oak vs. spruce) of *Tillandsia violacea* Baker on the nutrient concentration in the accumulated water and soil in epiphytes, and its relation with arthropods inhabiting on the plants in temperate forests in Central Mexico.

Materials and methods

Study site

"El Chico" National Park (2793 ha) is located on the north-east slope of the Valley of Mexico (Vargas-Márquez, 1984), approximately 24 km north-west of Pachuca City, in the highest part of the Pachuca Range (20°13'45"N, 98°47'23"W). Elevation ranges from 2320 m asl to 3090 m asl (SEDUE, 1988). The soils of the area have very friable consistency, with contents of N, P and S, they has been classified as Andosols, derived from volcanic ash mainly of basaltic composition, with very high organic matter content in the A horizon, which gives them dark colour (Melo and López, 1994). The climate

according to the Köppen classification system, modified by García (1981) in the area, is temperate and humid, with a cold and rainy winter. The annual average temperature ranges between 10° to 14°C, with a minimum of -6° to -9°C; annual rainfall varies between 600 and 1500 mm.

The dominant vegetation is *Abies religiosa* (Kunth.) Schltdl. & Cham. forest (Rzedowski, 1988). This kind of forest grows at elevations between 2700 and 3000 m asl, mainly on slopes, where trees are protected from strong winds and solar radiation. The oak forest varies in architecture and composition. *Quercus* spp. trees reach heights from 20 to 30 m and they often have many epiphytic plants. Dominant species are *Q. laurina* Humb. & Bonpl., *Q. rugosa* Née, *Q. laeta* Liebm., *Q. mexicana* Humb. & Bonpl. and *Q. crassifolia* Humb. & Bonpl. This community is located between 2300 and 3000 m asl, although it occurs as an ecotone with the cloud montane forest at 2600 and 2800 m asl with *Abies religiosa* at its upper limit (Rzedowski, 1988).

The average density (\pm S.E.) of *Tillandsia violacea* Baker on *Quercus* spp. in the study area is about 5.9 ± 4 ind. per tree and in *Abies religiosa* is 7.8 ± 4 ind. per tree (Castaño-Meneses et al., 2003)

Sample collection

One randomly stratified spatio-temporal sampling was done. Sampling units were specimens of *Tillandsia violacea* of two different sizes (plant diameter at the base of the rosette: 25-40 cm and > 40 cm). They were carefully collected to avoid damage and loss of materials such as water, soil and fauna, stored into polyethylene bags and transported to the laboratory. Plants were dissected leaf by leaf, in order to obtain the suspended soil and fauna accumulated. Ten plants of each size were collected in two kinds of support tree (*Quercus* spp. and *Abies religiosa*) at two different altitudes where both tree species were present (2765 and 2900 m asl) during the rainy (September 1998) and dry (April 1999) seasons. The water and soil accumulated on the plants were isolated for chemical analysis. Water was collected when the plants were separated from the support tree, storage in separated plastic jars for their latter quantified and analyzed. That water was filtered to obtain the solid particles, those particles were homogenized and analyzed separately. The litter accumulated in the epiphytes was processed by Berlese-Tullgren funnels to extract the arthropods. To check that the collected material was suspended soil, the presence of minerals was studied by mineralogical qualitative analysis of semipermanent slides mounted in cedar oil using a petrographic microscope.

Water analyses

The water obtained was filtered through Whatman No. 1 paper in order to separate and obtain liquid and solid fractions. Dry solid fraction was quantified and also homogenized by grinding and sieving through 10 mm. Water analyses were expressed on a volume basis, and included: pH, electrical conductivity (EC), soluble cations (Ca^{2+} , Mg^{2+} , K^{+} and Na^{+}) and chloride (Cl⁻). Dissolved organic carbon (DOC) was evaluated by Walkley and Black Method (Jackson, 1982).

Soil analyses

Solid fractions (soil and litter) from the plants processed by Berlese funnels were analyzed for pH in H₂O (1:10), total organic carbon (TOC), by Walkley and Black Method (Jackson, 1982); and exchangeable cations (Ca^{2+} , Mg^{2+} , K^{+} and Na^{+}), Ca^{2+} and

Mg^{2+} were extracted by 1M ammonium acetate pH 7 and quantified by EDTA, whereas K^+ and Na^+ were evaluated using a flame photometer (Page et al., 1982).

Statistical analysis

In order to evaluate the normal distribution of the data, the Kolmogorov-Smirnov test was used, and the variables with percentage values were arcsine-square-root transformed before the analysis (Sokal and Rohlf, 1973). To evaluate the differences between water physical and chemical parameters at the sites of sampling (altitudes), Mann-Whitney U-test was used because not enough water was obtained from all the epiphytic plants to allow the analysis. The effect of (1) the supporting tree type, (2) the size of the epiphytic plants and (3) the altitude and season of sampling on chemical and physical data of the water and also of the soil were evaluated with Multiple Variance Analysis (MANOVA). Season is a qualitative variable that was coded as 0 and 1 for the model. Duncan's test was used to detect differences (Zar, 1984). To compare the value of the parameters of the water and soil during the rainy season, a t-test was run. A multiple regression analysis was used to evaluate the relationship between the physical and chemical parameters and the arthropod densities. Analyses were performed with the program STATISTICA ver. 6.0 (StatSoft, 1995).

A multivariate technique, a Canonical Correspondence Analysis (CCA) was used to evaluate the influence of edaphic variables on faunal composition at the dry and rainy seasons. Explanatory variables include pH, Ca^{2+} , Mg^{2+} , K^+ , Na^+ and TOC. The analysis was performed in CANOCO 4.0 for Windows (ter Braak and Smilauer, 1998). We use 500 permutations under reduced model by Monte Carlo test.

Results

Water analyses

Enough water was obtained to measure chemical properties only during the rainy season. At 2765 m asl, mean diameter of the epiphytic plants was 40.10 ± 11.01 cm (range 26-76 cm). From them, a total of 2743 ml of water was obtained (N = 23). At 2900 m asl, the size of the plants was 45.21 ± 10.95 cm of diameter (range 28.0-64.5 cm), with a total of 3321 ml of accumulated water in plants (N = 32). Average results for the parameters evaluated at the two altitudes are shown in *Table 1*.

Mean values in comparison between the supporting tree and the size of the epiphytic plant are shown in *Tables 2 and 3*. In *Table 4* the results of the MANOVA are shown.

Calcium concentration was affected by altitude (*Table 4*), the highest concentrations occurring at 2765 m asl. For the supporting tree there was a significant statistical value in the amount of calcium, magnesium, sodium and potassium, however calcium was the only element affected by the size of the epiphytic plants (*Table 4*). Significant interactions between the tree species and altitude, and the tree and the size for the pH, and on the amount of calcium, and the altitude were found.

The result of the multiple regression analysis was significant when fauna of the epiphytic plants was correlated with the physical and chemical parameters, with a correlation coefficient of 0.61 ($F_{5,49} = 5.69$; $P = 0.0003$). The parameters better correlated with fauna abundance were the electric conductivity ($r_{49} = 0.94$; $P = 0.006$), DOC ($r_{49} = 0.48$; $P = 0.008$) and the amount of calcium ($r_{49} = 0.37$; $P = 0.03$).

Table 1. Average \pm standard error (range) and U values for physical and chemical parameters for water accumulated in Tillandsia violacea from two altitudes in “El Chico” national Park, Hidalgo State.

Parameter	Altitude 2765 m N = 23	Altitude 2900 m N=32	U	P
pH	5.61 \pm 0.21 (4.10-8.60)	5.22 \pm 0.12 (4.20-6.70)	358	0.17
EC (dS/m)	0.73 \pm 0.31 (0.19-7.60)	0.37 \pm 0.04 (0.1-0.76)	273	0.08
Ca ²⁺ (cmol ⁺ L ⁻¹)	1.72 \pm 0.30 (0.20-6.50)	1.20 \pm 0.12 (0.25-3.50)	303	0.30
Mg ²⁺ (cmol ⁺ L ⁻¹)	1.27 \pm 0.18 (0.50-4.25)	2.19 \pm 0.57 (0.25-15.00)	355	0.88
Na ⁺ (cmol ⁺ L ⁻¹)	4.12 \pm 1.90 (0.24-42.80)	1.37 \pm 0.24 (0.17-4.57)	341	0.70
K ⁺ (cmol ⁺ L ⁻¹)	2.78 \pm 1.34 (0.04-30.77)	1.09 \pm 0.25 (0.10-6.31)	283	0.17
Cl ⁻ (cmol ⁺ L ⁻¹)	7.67 \pm 0.54 (5.00-14.00)	7.60 \pm 0.44 (4.00-13.00)	355	0.89
C (g L ⁻¹)	17.71 \pm 2.08 (1.96-45.24)	16.02 \pm 1.90 (2.78-41.33)	315	0.41
C (soil) (g kg ⁻¹)	19.42 \pm 0.57 (10.43-22.72)	19.80 \pm 0.34 (12.99-22.77)	337	0.65

Table 2. Average \pm SE (range) for physical and chemical parameters for water accumulated in T. violacea from two species of support trees at 2765 m asl (N=23). Different letters in the same row indicated significant differences (Duncan’s test).

Parameter	<i>Abies religiosa</i>		<i>Quercus</i> spp.	
	Medium	Large	Medium	Large
pH	5.97 \pm 0.66 ^a	5.98 \pm 1.56 ^a	5.76 \pm 0.99 ^a	4.55 \pm 0.48 ^a
EC dS/m	0.43 \pm 0.17 ^a	1.95 \pm 3.16 ^a	0.29 \pm 0.08 ^a	0.38 \pm 0.27 ^a
Ca ²⁺ cmol ⁺ L ⁻¹	1.60 \pm 1.34 ^a	3.35 \pm 1.95 ^b	1.04 \pm 0.58 ^a	1.05 \pm 0.82 ^a
Mg ²⁺ cmol ⁺ L ⁻¹	2 \pm 1.37 ^a	1.15 \pm 0.72 ^a	1.12 \pm 0.83 ^a	0.81 \pm 0.24 ^a
Na ⁺ cmol ⁺ L ⁻¹	3.63 \pm 3.08 ^a	11.66 \pm 17.7 ^a	0.36 \pm 0.11 ^a	1.88 \pm 3.15 ^a
K ⁺ cmol ⁺ L ⁻¹	2.07 \pm 2.74 ^a	8.28 \pm 12.76 ^a	0.48 \pm 0.21 ^a	0.77 \pm 0.3 ^a
Cl ⁻ cmol ⁺ L ⁻¹	8.33 \pm 3.58 ^a	7.80 \pm 3.11 ^a	6.67 \pm 2.11 ^a	8.0 \pm 2.58 ^a
C g L ⁻¹	19.63 \pm 4.34 ^a	16.68 \pm 18.61 ^a	19.18 \pm 8.44 ^a	17.47 \pm 6.7 ^a
C (soil) g kg ⁻¹	19.86 \pm 0.76 ^a	19.00 \pm 2.13 ^a	18.07 \pm 4.85 ^a	20.59 \pm 0.9 ^a

When each taxon of arthropods was analyzed separately, comparatively more significant correlations were found for the percentage of DOC and the EC. The correlation coefficient for most abundant groups is shown in Table 5, except for Oribatid and Prostigmatid mites, which were not correlated with any parameter.

Groups which are less abundant but significantly correlated with some of the parameters were the Hexapoda larvae ($r_{49} = -0.34$; $P < 0.05$) and Hymenoptera ($r_{49} = -0.50$; $P < 0.05$), with DOC; Diplopoda with sodium ($r_{49} = -0.96$; $P < 0.05$), ants with pH ($r_{49} = -0.37$; $P < 0.05$) and Crustacea with calcium ($r_{49} = 0.37$; $P = 0.05$).

It is necessary to point out the fact that electric conductivity was significantly related with abundance of total arthropods, illustrating the fact that accumulated water in the epiphytic plants is an important storage of available nutrients for the fauna.

Suspended soil analyses

Suspended soils were obtained from 49 epiphytic plants (1164 g of soil in 4.96 m²) during the rainy season and from other 80 epiphytic plants (2082 g of soil in 7.46 m²)

during the dry season. Between the sampling sites there were differences in the amount of sodium, but for the other seasons there were significant differences in the calcium concentration for the rainy season and for the dry season with pH (Table 6).

Table 3. Average \pm standard error (range) for physical and chemical parameters for water accumulated in *T. violacea* from two species of support trees at 2900 m asl (N=32). Different letters in the same row indicated significant differences (Duncan's test).

Parameter	<i>Abies religiosa</i>		<i>Quercus</i> spp.	
	Medium	Large	Medium	Large
pH	4.77 \pm 0.20 ^a	5.41 \pm 0.83 ^a	5.33 \pm 0.46 ^a	5.34 \pm 0.85 ^a
EC dS m ⁻¹	0.57 \pm 0.15 ^a	0.47 \pm 0.24 ^{ab}	0.29 \pm 0.21 ^b	0.22 \pm 0.10 ^b
Ca ²⁺ cmol ⁺ L ⁻¹	0.92 \pm 0.03 ^{ab}	1.66 \pm 0.88 ^a	1.03 \pm 0.64 ^{ab}	1.05 \pm 0.56 ^b
Mg ²⁺ cmol ⁺ L ⁻¹	3.96 \pm 5.51 ^a	2.87 \pm 2.31 ^a	1.89 \pm 2.85 ^a	0.57 \pm 0.20 ^a
Na ⁺ cmol ⁺ L ⁻¹	1.95 \pm 1.48 ^a	1.71 \pm 1.67 ^{ab}	1.07 \pm 1.45 ^{ab}	0.81 \pm 0.58 ^b
K ⁺ cmol ⁺ L ⁻¹	1.85 \pm 1.63 ^a	0.90 \pm 0.81 ^a	0.61 \pm 0.53 ^a	1.06 \pm 1.80 ^a
Cl ⁻ g L ⁻¹	7.0 \pm 1.26 ^a	6.87 \pm 1.70 ^a	7.43 \pm 3.10 ^a	8.80 \pm 2.60 ^a
C g L ⁻¹	20.20 \pm 14.0 ^a	15.51 \pm 22 ^a	16.71 \pm 11 ^a	14.09 \pm 80 ^a
C (soil) g kg ⁻¹	19.85 \pm 5.8 ^a	20.55 \pm 40 ^a	18.47 \pm 80 ^a	20.04 \pm 2.70 ^a

Table 4. Values of *F* from analysis of variance for the support tree (*T*), altitude (*Al*), and size (*S*) effects on physical and chemical parameters from water accumulated in *T. violacea*. * = significant differences to *P* < 0.05; *df* = 1, 45

Parameter	T	Al	S	T x Al	T x S	Al x S	T x Al x S
pH	1.12	1.81	0.19	4.36*	4.36*	3.30	0.60
EC dS m ⁻¹	3.92	1.78	1.74	1.66	1.06	2.69	1.79
Ca ²⁺ cmol ⁺ L ⁻¹	9.35*	6.06*	4.63*	5.85*	4.58*	1.08*	1.11
Mg ²⁺ cmol ⁺ L ⁻¹	3.87*	1.52	2.54	0.002	1.46	0.26	0.05
Na ⁺ cmol ⁺ L ⁻¹	4.98*	2.25	3.16	1.23	2.78	2.70	1.18
K ⁺ cmol ⁺ L ⁻¹	4.48*	1.78	2.18	1.03	2.73	2.39	2.61
Cl ⁻ cmol ⁺ L ⁻¹	0.09	0.49	0.06	1.33	1.72	0.02	0.02
C g L ⁻¹	0.03	0.60	0.11	0.01	0.37	0.16	0.07
C (soil) g kg ⁻¹	0.01	0.82	0.08	1.78	2.07	1.48	0.28

Table 5. Correlation coefficients between density of main arthropod groups and physical and chemical parameters from water accumulated in *T. violacea*. **P* < 0.05, *N* = 55

Parameter	Mesostigmata	Collembola	Psocoptera	Homoptera
pH	0.11	0.13	-0.02	0.008
EC	0.96*	0.96*	0.50	0.46
Ca ²⁺	0.30	0.12	0.17	0.30*
Mg ²⁺	-0.08	-0.05	0.004	0.01
Na ⁺	-0.37	-0.11	-0.77	0.74
K ⁺	-0.68	-0.48	0.56	-0.71
Cl ⁻	0.05	-0.08	-0.17	0.04
C dissolved	-0.36*	-0.21	-0.47*	-0.31*
C (solid fraction)	0.07	0.19	0.09	0.10

The results of the MANOVA, to evaluate the effect of the altitude, supporting tree and the size of the plant and the interactions between them, are shown in *Table 7*. Supporting tree had a significant effect on the amount of magnesium and organic carbon, whereas the size has effect on the pH. Season and tree species have an interactive effect on the pH, while interaction of tree and the size of the epiphytic plant influenced significantly the amount of total organic carbon (TOC).

Multiple correlations of the chemical parameters and the fauna, including the weight of soil obtained, altitude, season, tree and size of epiphytic were significant for the total abundance and also for the most abundant groups of arthropods (*Table 8*).

Most correlations of the fauna groups were negative with the pH and TOC, whereas with soluble base contents, such as sodium and potassium were positive. There are strong differences between the parameters that affect playing a role on the abundance of arthropods during the seasons that were compared. Percentage of TOC has a significant correlation with ($r = -0.17$, $P < 0.05$) and the season of sampling ($r = -0.33$, $P < 0.05$); we have found higher amount at lower altitude and during the rainy season.

A *t*-test (*Table 9*) was done to evaluate the differences among soil and water parameters. Significant differences were observed in all the parameters. Values were higher in soil samples than in water samples, except for sodium. The pH was more basic in water than in the soil.

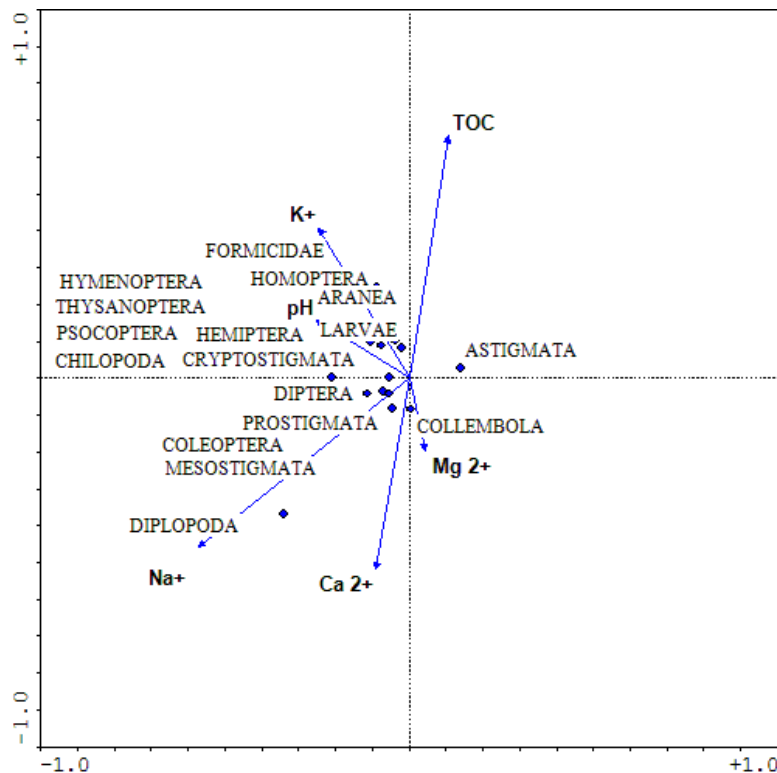


Figure 1. CCA analysis for the edaphic parameters and composition of arthropods in *T. violacea* for the dry season.

The CCA analysis for the dry season show that canonical axes explain 93.75% of observed variance in arthropods composition, with Na^+ best explaining axis 1 ($r = 0.56$) and TOC best correlated to axis 2 ($r = 0.66$; overall Monte Carlo test of significance P

= 0.05 with 500 permutations; *Figure 1*). The two axes explain 65.1% of total variance observed. In general, most of arthropod groups are related with axes 1, while Astigmata and Collembola are better related with axes 2.

For the rainy season, according with CCA analysis, canonical axes explain together 95.86% of the variance in composition. The Na⁺ (r = 0.75) and TOC (r = 0.64) are the best correlated with axis 1, while the axes 2 is better correlated with pH (r = 0.71) and Mg²⁺ (r = 0.55). The overall Monte Carlo test was significant (P = 0.03 with 500 permutations; *Figure 2*). The two axes explain 78.7% of total variance. Collembola, Isopoda, Neuroptera and Thysanoptera, were the groups better related with axes 2.

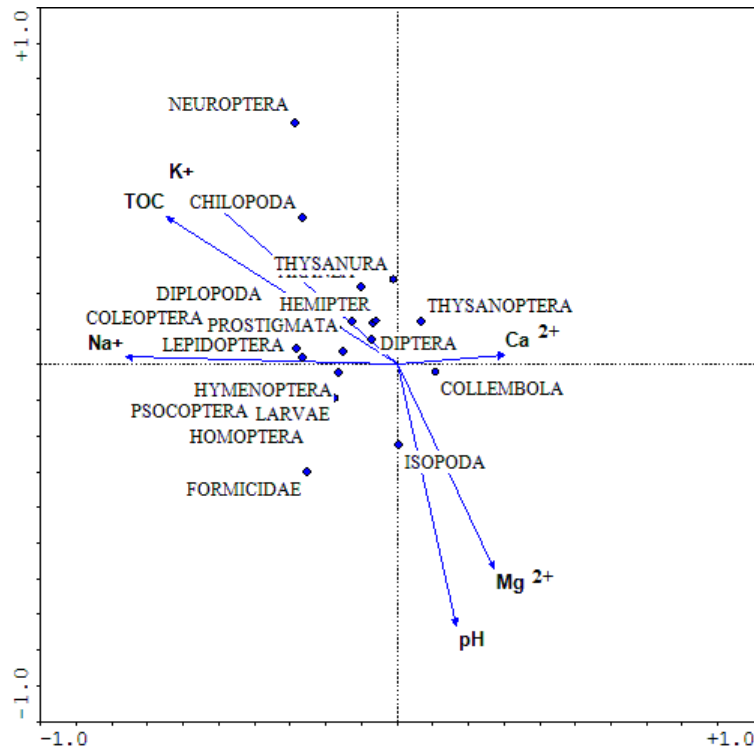


Figure 2. CCA analysis for the edaphic parameters and composition of arthropods in *T. violacea* during rainy season.

Table 6. Average, standard error, range and U values for physical and chemical parameters from accumulated soil in *T. violacea* at two altitudes in “El Chico” National Park, Hidalgo State, during rainy (September 1998) and dry (April 1999) seasons. ns= no significant; *P<0.05, **P<0.005

Parameter	Altitude 2,765		Altitude 2,900		U	P
	Rainy Season N=28	Dry Season N=50	Rainy Season N=21	Dry Season N=50		
pH	4.42±0.43 (3.7-5.1)	4.48±0.5 (3.7-6.9)	4.49±0.43 (3.8-5.3)	4.5±0.77 (3.4-8.3)	2320	rs
Ca ²⁺ cmol ⁺ kg ⁻¹	22.5±7.51 (10.5-42)	30.53±14.02 (13.8-30.5)	27.54±8.93 (14.95-43.05)	29.81±17.91 (9.2-97.75)	2690	rs
Mg ²⁺ cmol ⁺ kg ⁻¹	9.92±6.56 (1.15-22.05)	19.05±21.86 (1.15-97.75)	10.89±5.25 (1.15-20.7)	19.26±17.76 (2.3-103.5)	2336	rs
Na ⁺ cmol ⁺ kg ⁻¹	0.58±0.25 (0.26-1)	0.47±0.07 (0.35-0.7)	0.54±0.21 (0.26-1)	0.66±0.24 (0.3-1.43)	1964	**
K ⁺ cmol ⁺ kg ⁻¹	4.16±2.09 (1.54-9.74)	4.54±3.06 (1.59-19.23)	3.66±2.14 (0.49-7.95)	5.13±5.42 (0.66-34.87)	2634	rs
C g kg ⁻¹	29.33±3.81 (22.18-36.08)	27.68±3.27 (21.04-35.75)	29.52±2.98 (22.08-35.1)	26.47±4.04 (17.16-30.07)	2275	rs

Table 7. *F* values form MANOVA to evaluated the support tree species (*T*), size (*S*) of *T. violacea* (excluding small plants), collect season (*E*), altitude (*Al*), and their interactions effects on physical and chemical parameters for accumulates soils in “El Chico” National Park, Hidalgo State. **P*<0.05 ; *df*= 1,102.

Source	pH	Ca ²⁺ cmol ⁺ kg ⁻¹	Mg ²⁺ cmol ⁺ kg ⁻¹	Na ⁺ cmol ⁺ kg ⁻¹	K ⁺ cmol ⁺ kg ⁻¹	C mg g ⁻¹
T	0.65	0.07	0.21	1.71	2.35	0.23
E	0.17	2.93	6.06*	0.42	0.75	17.42*
S	5.22*	1.85	1.34	1.61	1.36	0.16
Al	0.30	0.90	0.61	0.95	0.0002	1.28
T*E	3.99*	1.13	0.81	0.42	0.60	1.71
T*S	0.09	0.52	1.14	0.09	0.11	8.12*
T*Al	0.28	0.22	1.13	0.21	0.34	0.70
E*S	0.09	0.001	1.51	0.06	0.07	2.26
E*Al	0.06	0.77	0.39	15.48*	0.61	1.70
S*Al	0.02	0.28	0.33	0.22	4.34*	1.81
T*E*S	0.06	0.42	1.43	1.55	0.02	0.58
T*E*Al	0.41	0.15	1.42	0.10	0.01	0.01
T*S*Al	0.08	0.50	2.83	0.07	0.59	0.13
E*S*Al	0.15	0.39	0.63	2.99	0.08	0.27
T*E*S*Al	0.27	3.4*	4.01*	0.004	1.55	0.003

Table 8. Multiple regression coefficients (*r*) between fauna and physical and chemical parameter from soil accumulated in *T. violacea*. *T*= Tree; *S*= Size; *Al*= Altitude; *E*= Collect season; *W*= recuperated soil weight; %*C*= Carbon percentage; *Ca*= Calcium; *Mg*= Magnesium; *Na*= Sodium; *K*= Potassium; *df*= 11,113, **P*<0.05

Taxa	T	S	Al	E	W	%C	Ca	Mg	Na	K	pH	<i>r</i>	<i>F</i>	<i>P</i>
Cryptostigmata	0.16*	0.35*	0.18*	0.17*	0.005	-0.13	-0.26*	-0.15	0.13	0.09	-0.54*	0.68	9.63	0.00001
Prostigmata	0.13	0.31*	0.16	0.17	-0.03	-0.08	0.20	-0.15	0.14	-0.02	-0.41*	0.57	4.89	0.00004
Astigmata	-0.01	0.05	-0.01	0.31*	0.29*	-0.12	-0.20	0.04	0.07	0.28*	-0.08	0.55	4.52	0.00001
Collembola	0.12	0.28*	0.17*	-0.14	0.23*	-0.20*	0.13	-0.05	-0.01	0.03	-0.29*	0.62	6.39	0.00001
Larvae	0.11	0.34*	0.03	-0.20*	0.14	0.03	0.003	0.03	0.01	-0.001	0.06	0.51	3.66	0.0002
Diptera	0.03	0.49*	0.03	-0.28*	-0.16	0.01	-0.06	0.05	-0.09	0.05	0.02	0.54	4.16	0.00004
Homoptera	0.16	0.04	0.002	-0.33*	-0.001	-0.04	-0.16	0.10	-0.13	-0.19*	0.14	0.42	2.26	0.02
Thysanoptera	0.02	-0.14	0.28*	-0.08	0.44*	-0.04	-0.23	0.02	-0.15	-0.11	0.30*	0.52	3.74	0.0001
Araneae	-0.07	0.20*	-0.17*	0.45*	0.08	0.12	0.06	-0.09	-0.07	-0.22*	0.36*	0.61	6.20	0.00001
Coleoptera	0.15	0.40*	-0.10	-0.36*	-0.12	0.05	-0.07	0.07	0.03	0.02	0.03	0.58	5.19	0.00001
Total abundance	0.09	0.24*	0.02	0.15*	0.32*	-0.21*	-0.03	-0.02	0.14	0.22*	-0.10*	0.69	9.63	0.00001

Mineralogical analysis

Mineral content of the soil samples from epiphytic plants varied from 5 to 20 g kg⁻¹ dry weight in all the samples. Feldspars of the plagioclase series and orthoclase; quartz, phytoliths and volcanic glass were the most abundant light minerals with low amounts of apatite and calcium carbonate crystals. Among heavy minerals, we identified pyroxenes of enstatite-hyperstene series and augite, as well as amphiboles like basaltic, green and brown hornblends. These results confirm that this substrate is a real soil, by the presence of minerals.

Table 9. Values of *t* test between the chemical parameters of water and soil from *T. violacea*

Parameter	t	df	P
pH	7.26	106	0.001
Calcium	20.4	103	0.001
Magnesium	9.92	103	0.001
Sodium	2.04	103	0.04
Potassium	3.24	103	0.001
Carbon	125	103	0.001

Discussion

The importance of the epiphytic plants in the uptake, storage and release of nutrients, which represent main processes for the functioning of the ecosystems, has been observed in different vegetation types (Coxson and Nadkarni, 1995). The presence of different rock-derived minerals in the solid fraction confirms that this material is in fact a suspended soil and not just an accumulation of organic matter and detritus.

Our results showed that the ions contents in the water and soil accumulated in *T. violacea* are strongly affected by the supporting tree species, because the storage and soluble nutrients depend on the quality of litter and its decomposing rate. For instance, it has been found that concentrations of phosphorus and potassium are usually larger in *Abies* forest than in other conifers (Kavvadias et al., 2001). Also, the rate of decomposition of oak litter is 50% higher than those of pine as has been documented in central Himalaya (Upandhyay et al., 1989; Usman et al., 2000). The concentration of potassium in water and soil was higher in the epiphytic plants sampled from *Abies religiosa* than those from *Quercus* spp., as found by other authors in localities from Canada and France (Lavigne et al., 2001; Ponette et al., 2001; Elliot et al., 2002).

The presence of different ions and their availability are necessary for various processes of the plants and ecosystems. For example, the potassium gathered with nitrogen and phosphorus have been related to an increase of growth of *Tillandsia guatemalensis* in greenhouses; whereas when they occur separately, they have little effect (Castro-Hernández et al., 1999).

Many studies on nutrient cycling show that, in the tropical forest, primary production could be limited by the availability of potassium (Vitousek, 1984; Tanner et al., 1998; Bedford et al., 1999). The Ca/Mg ratio has been used as an index of the influence of the vegetation in the biogeochemical cycles of the ecosystem (Quideau et al., 1999). The presence of calcium is related to vegetation and it is essential for the development of plant roots.

The concentration of ions in the water is lower than that found in the phytotelm of the Bromeliaceae in tropical forest in Puerto Rico (Richardson et al., 2000a). Nevertheless, in our study in the suspended soil, the calcium, potassium and magnesium concentrations were higher than those reported in plants studied in Puerto Rico. Our explanation of these differences can be related to the rain pattern and the period of time that the plants lack of water. It has been found that the tank bromeliads store large amounts of water together with organic residues (mainly leaves of the host tree) and suspended soils. There is a high concentration of nitrogen, mainly due to the action of the rain, which carries this nutrient from the canopy (Hietz et al., 1999; Zotz and Hietz, 2001). On the other hand, in our work we found a contrasting effect depending on the season of collection which was very important in determining the accumulation of

nutrients. During the dry season, ion concentration and TOC were higher than in the rainy season. Also, we recorded a higher abundance of the arthropods from epiphytic plants during this season. On the other hand, the concentration of the salts was positively related with the abundance of the fauna as it happens in epiphytes at the tropical rain forests (Richardson et al., 2000a).

Epiphytic plant size is a very important factor, as it has been directly related with the water and suspended soil storage capacity (Zotz and Thomas, 1999), as well as with the abundance of the inhabiting fauna. A higher accumulation of detritus and water influences the rate processes for aerial soil formation, and it promotes biological activity to increase the nutrient fluxes in the system and higher amounts of nutrients can be assimilated at shorter or longer periods.

It has been found that the amount of TOC is correlated with the occurrence of some of the microbial heterotrophic processes, such as respiration, denitrification and also with leaching of organic carbon (Andersson et al., 1994).

The value of the quantified parameters is different from those that have been measured in tank bromeliads in tropical forest. Those differences include the water and soil accumulated in *T. violacea* in El Chico; our results (Table 1) shown lower values than those recorded by Richardson et al. (2000b) for *Guzmania* spp. and *Vriesea sintenisii* in a tropical rain forest in Puerto Rico. An explanation to this, is the relationship between pH and DOC. Richardson et al. (2000b) found a pH of 5.6, while ours were around 4 (Tables 1 and 6). It has been observed that an increase in the pH, increases microbial activity, rising the deposition of DOC and dissolved organic nitrogen (DON), due to the production of a higher amount of negative charge colloids in the humus, and also the increase of solubility (Andersson et al. 2000). In this study the pH and the organic carbon were the most significantly correlated factors and it was also found that the highest abundance of arthropods was at pH levels between 4 and 5.

The CCA analysis of both rainy and dry seasons, show that the pH, TOC, and Na^+ and Mg^+ contents are the main factor to explain the variation in the composition of arthropod community associated to *T. violacea*.

Taking into account of this, the function of *T. violacea* in the temperate forest could play an important role in the storage of nutrients, mainly during the dry season, when it is used as a shelter by different groups of insects. However, during the rainy season, many nutrients become available when they are dissolved into the water, in that form where they can still be used by the larvae of several groups as Diptera. The accumulation of litter in *T. violacea* is a very important factor, because litter production and its fall is the largest pathway for nutrient and organic matter flux into the soils, that is fundamental to understand the ecosystem function (Meentemeyer et al., 1982; Barbosa and Fearnside, 1996).

Studies done in a tropical low forest in Puerto Rico have demonstrated that in this environment the highest accumulation of nutrients and fauna is done by other plants with phytohelm, but not the bromeliads (Richardson et al., 2000a). Recent studies about the origin and formation processes of arboreal soils in Northern California, shown that the climate affects the formation of soil in canopies, by their influence on the OM translocation and decomposition (Enloe et al., 2006, 2009). In an environment with strong seasonal changes, such as the forest from "El Chico", the function of the bromeliads, as shelter and supply of nutrients is of great importance for the arthropods communities mainly for the maintenance of the biological diversity.

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REFERENCES

- [1] Andersson, S., Valaaur, I., Nilsson, I. (1994): Influence of lime on soil respiration leaching of DOC and C/S relationships in the mor humus of a Haplic Podsol. – *Environmental International* 20: 81-88.
- [2] Andersson, S., Nilsson, S.I., Saetre, P. (2000): Leaching of dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) in mor humus as affected by temperature and pH. – *Soil Biology and Biochemistry* 32: 1-10.
- [3] Barbosa, R.I., Fearnside, P.M. (1996): Carbon and nutrient flows in an Amazonian forest: fine litter production and composition at Apiaú, Roraima, Brazil. – *Tropical Ecology* 37: 115-125.
- [4] Barthlott, W., Schmit-Neuerburg, V., Nieder, J., Engwald, S. (2001): Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. – *Plant Ecology* 152: 145-156.
- [5] Bedford, B.L., Walbridge, M.R., Aldous, A. (1999): Patterns in nutrient availability and plant diversity of temperate North American wetlands. – *Ecology* 80: 151-2169.
- [6] Benzing, D.H. (1980): The nutritional dynamics of *Tillandsia circinnata* in Southern Florida and the origin of the “air plant” strategy. – *Botanical Gazette* 141: 165-172.
- [7] Benzing, D.H. (1990): Vascular epiphytes. General biology and related biota. – Cambridge University Press, New York.
- [8] Bohlman, S.A., Matelson, T.J., Nadkarni, N.M. (1995): Moisture and temperature patterns of canopy humus and forest floor soil of a montane cloud forest, Costa Rica. – *Biotropica* 27: 13-19.
- [9] Castaño-Meneses, G., García-Franco, J.G., Palacios-Vargas, J.G. (2003): Spatial distribution patterns of *Tillandsia violacea* (Bromeliaceae) and support trees in an altitudinal gradient from a temperate forest in Central Mexico. – *Selbyana* 24: 71-77.
- [10] Castro-Hernández, J.C., Wolf, J.H.D., García-Franco, J.G., González-Espinosa, M. (1999): The influence of humidity, nutrients and light on the establishment of the epiphytic bromeliad *Tillandsia guatemalensis* in the highlands of Chiapas, Mexico. – *Revista de Biología Tropical* 47: 763-773.
- [11] Clark, K.L., Nadkarni, N.M., Gholz, H.L. (1998): Growth, net production, litter decomposition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest. – *Biotropica* 30: 12-23.
- [12] Clarkson, D.T., Kuiper, P.J.C., Lüttge, U. (1986): II. Mineral nutrition: sources of nutrients for land plants from outside the pedosphere. – *Progress in Botany* 48: 80- 96.
- [13] Coxson, D.S., Nadkarni, N.M. (1995): Ecological roles of epiphytes in nutrient cycles of forest ecosystems. – In: Lowman, M.D., Nadkarni, N.M. (eds.): *Forest canopies*. – Academic Press, San Diego, 495-543.
- [14] De Buen, A. (1953): Observaciones ecológicas sobre mosquitos de "El Ajenjibre", Pue. Méx. – *Anales del Instituto de Biología, UNAM, México* 24: 177-204.
- [15] Delamare-Deboutville, C. (1948): Étude quantitative du peuplement animal des sols suspendus et des épiphytes en forêt tropicale. – *Comptes Rendues de l'Academi du Science* 226 : 1544-1546.
- [16] Edwards, P.J., Grubb, P.J. (1977) : Studies of mineral cycling in a montane rain forest in New Guinea. I. The distribution of organic matter in the vegetation and soil. – *Journal of Ecology* 65: 943-969.

- [17] Elliott, K.J., Boring, L.R., Swank, W.T. (2002): Aboveground biomass and nutrient accumulation 20 years after clear-cutting a southern Appalachian watershed. – *Canadian Journal of Forest Research* 32: 667-683.
- [18] Enloe, H.A., Graham, R.C., Sillet, S.C. (2006): Arboreal histosols in old-growth redwood forest canopies, Northern California. – *Soil Science Society of America Journal* 70: 408-418.
- [19] Enloe, H.A., Quideau, S.A., Graham, R.C., Sillet, S.C., Oh, S-W., Wasylishen, R.E. (2009): Soil organic matter processes in old-growth redwood forest canopies. – *Soil Science Society of America Journal* 74: 161-171.
- [20] García, E. (1981): Modificaciones al sistema de clasificación climática de Köppen. Tercera edición. – Enriqueta García, Indianapolis 30, México.
- [21] Gentry, A.H., Dodson, C.H. (1987): Contribution of nontrees to species richness of a tropical rain forest. – *Biotropica* 19: 149-156.
- [22] Gutiérrez, M., Camino, M., Castrejón, F., Jiménez, A. (1993): Arthropods associated with *Bromelia hemisphaerica* (Bromeliales: Bromeliaceae) in Morelos, México. – *Florida Entomologist* 76: 616-621.
- [23] Hietz, P., Wanek, W., Popp, M. (1999): Stable isotopic composition of carbon and nitrogen content in vascular epiphytes along an altitudinal transect. – *Plant Cell Environment* 22: 1435-1443.
- [24] Ibsch, P.I., Boegner, A., Nieder, J., Barthlott, W. (1996): How diverse are Neotropical epiphytes? An analysis based on the 'Catalogue of the Flowering Plants and Gymnosperms of Peru'. – *Ecotropica* 2: 13-28.
- [25] Jackson, M.L. (1982): Análisis Químico de Suelos. 4a ed. – Omega, Madrid.
- [26] Kavvadias, V.A., Alifragis, D., Tsiontsis, A., Brofas, G., Stamatelos, G. (2001): Litterfall, litter accumulation and litter decomposition rates in forest ecosystems in northern Greece. – *Forest Ecology and Management* 144: 113-127.
- [27] Kress, W.J. (1986): The systematic distribution of vascular epiphytes: an update. – *Selbyana* 9: 2-22.
- [28] Lavigne, M.B., Little, C.H.A., Major, J.E. (2001): Increasing the sink: source balance enhances photosynthetic rate of 1-year-old balsam fir foliage by increasing allocation of mineral nutrients. – *Tree Physiology* 21: 417-426.
- [29] Melo, C., López J (1994): Parque Nacional El Chico, marco geográfico-natural y propuesta de zonificación para su manejo operativo. – *Boletín del Instituto de Investigaciones Geográficas, UNAM* 28: 65-128.
- [30] Meentemeyer, V., Box, E.O., Thompson, R. (1982): World patterns and amounts of terrestrial plant litter production. – *BioScience* 32: 125-128.
- [31] Nadkarni, N.M. (1984): Epiphyte biomass and nutrient capital of a neotropical elfin forest. – *Biotropica* 16: 249-256.
- [32] Nadkarni, N.M. (1992): The conservation of epiphytes and their habitats: Summary of a discussion at the International Symposium on the Biology and Conservation of Epiphytes. – *Selbyana* 13: 140-142.
- [33] Nadkarni, N.M. (1994): Diversity of species and interactions in the upper tree canopy of forest ecosystems. – *American Zoologist* 34: 70-78.
- [34] Nadkarni, N.M., Matelson, T.J. (1991): Litter dynamics within the canopy of a neotropical cloud forest, Monteverde, Costa Rica. – *Ecology* 72: 2071-2082.
- [35] Nadkarni, N.M., Schaefer, D., Matelson, T.J., Soleno, R. (2002): Comparison of arboreal and terrestrial soil characteristics in a lower montane forest, Monteverde, Costa Rica. – *Pedobiologia* 46: 24-33.
- [36] Nieder, J., Posperí, J., Michaloud, G. (2001): Epiphytes and their contribution to canopy diversity. – *Plant Ecology* 153: 51-63.
- [37] Page, A.L., Miller, R.H., Kenney, D.R. (1982): *Methods of Soil Analysis. Part II. Agronomy* 9. – American Society of Agronomy, Madison, USA.

- [38] Ponette, Q., Ranger, J., Ottorini, J.M., Ulrich, E. (2001): Aboveground biomass and nutrient content of five Douglas-fir stands in France. – *Forest Ecology Management* 142: 109-127.
- [39] Quideau, S.A., Graham, R.C., Chadwick, O.A., Wood, H.B. (1999): Biogeochemical cycling of calcium and magnesium by ceanothus and chemise. – *Soil Science Society of America Journal* 63, 1880-1888.
- [40] Richardson, B.A. (1999): The bromeliad microcosm and the assessment of faunal diversity in a Neotropical forest. – *Biotropica* 31: 321-336.
- [41] Richardson, B.A., Rogers, C., Richardson, M.J. (2000a): Nutrients, diversity, and community structure of two phytotelm systems in a lower montane forest, Puerto Rico. – *Ecological Entomology* 25: 348-356.
- [42] Richardson, B.A., Richardson, M.J., Scatena, F.N., McDowell, W.H. (2000b): Effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities in a humid tropical forest in Puerto Rico. – *Journal of Tropical Ecology* 16: 167-188.
- [43] Rzedowski, J. (1988): *Vegetación de México*. – Limusa, México.
- [44] Sedue, Secretaría de Desarrollo Urbano y Ecología (1988): *Plan de Manejo del Parque Nacional del Chico*. – Delegación Hidalgo, México, D. F.
- [45] Statsoft, Inc. (1995): *Statistical user guide. Complete Statistical System Statsoft*. – Oklahoma.
- [46] Sokal, R.R., Rohlf, F.J. (1973): *Introduction to biostatistics*. – Freeman and Co., San Francisco, California.
- [47] Tanner, E.U.J., Vitousek, P.M., Cuevas, E. (1998): Experimental investigations of nutrient limitation of forest growth on wet tropical mountains. – *Ecology* 79: 10-22.
- [48] Ter Braak, C.J.F., Smilauer, P. (1998): *CANOCO reference manual and user's guide to Canoco for windows: software for canonical community ordination (version 4)*. – Microcomputer Power, Ithaca, New York.
- [49] Upandhyay, V.P., Singh, J.S., Meentemeyer, V. (1989): Dynamics and weight loss of leaf litter in central Himalayan forests. Abiotic versus litter quantity influence. – *Journal of Ecology* 77: 147-161.
- [50] Usman, S., Singh, S.P., Rawat, Y.S., Bargali, S.S. (2000): Fine root decomposition and nitrogen mineralization patterns in *Quercus leucotrichophora* and *Pinus roxburghii* forest in central Himalaya. – *Forest Ecology Management* 131: 191-199.
- [51] Vargas-Márquez, F. (1984): *Parques Nacionales de México y reservas equivalentes. Pasado, presente y futuro*. – Instituto de Investigaciones Económicas, Universidad Nacional Autónoma de México. México, D. F.
- [52] Vence, E.D., Nadkarni, N.M. (1990): Microbial biomass and activity in canopy organic matter and the forest floor of a tropical cloud forest. – *Soil Biology and Biochemistry* 22: 677-684.
- [53] Vence, E.D., Nadkarni, N.M. (1992): Root biomass distribution in a moist tropical montane forest. – *Plant Soil* 142: 31-39.
- [54] Vitousek, P.M. (1984): Litterfall, nutrient cycling and nutrient limitation in tropical forest. – *Ecology* 65: 285-298.
- [55] Zar, J.H. (1984): *Biostatistical Analysis*. – Prentice-Hall, Englewood Cliffs, New Jersey.
- [56] Zotz, G. (2005): Vascular epiphytes in temperate zones – a review. – *Plant Ecology* 176: 173-183.
- [57] Zotz, G., Hietz, P. (2001): The physiological ecology of vascular epiphytes: current knowledge, open questions. – *Journal of Experimental Botany* 52: 2067-2078.
- [58] Zotz, G., Thomas, V. (1999): How much water is in the tank? Model calculations for two epiphytic bromeliads. *Annals of Botany* 83: 183-192.