Cryptogamie, Mycologie, 2016, 37 (2): 205-215

Effects of microclimate on species diversity and functional traits of corticolous lichens in the Popayan Botanical Garden (Cauca, Colombia)

Luis Gerardo CHILITO LÓPEZ[a], *Edier Alberto SOTO MEDINA*[*b] *& Adriana Marcela PEÑA*[a]

[a] *Unidad de Investigación en Ecología Tropical – UNIET, Programa de Ecología, Fundación Universitaria de Popayán. Sede Campestre Los Robles km. 8 vía al sur E-mail: chilo_1226@hotmail.com, adriana.pena@docente.fup.edu.co*

[b] *Grupo de Ecología y Diversidad Vegetal, Universidad del Valle, Facultad de Ciencias Naturales, Departamento de Biología, Cali, Colombia, Calle 13 Nº 100-00*

Abstract – The aim of this study was to evaluate the taxonomic and functional diversity of corticolous lichens under the influence of different micro-climatic conditions in the Botanical Garden of Popayán. We considered 11 contrasting stations distributed in the area, selecting five individuals of *Cecropia angustifolia* per station. We worked with quantitative sampling locating a quadrant of 0.50 ξ 0.20 m^2 on the trunk of each tree, where the percentage of cover for each species was estimated. Microenvironmental parameters, such as light, temperature and relative humidity, CAP and the pH of the bark were evaluated. A total of 63 lichen species was recorded. The results showed that light and temperature had positive correlation with species richness and cover of fruticose and foliose lichens, while relative humidity was negatively related to richness and positively with crustose cover. Lichen distribution at the Popayan Botanical Garden is mainly affected by light, temperature and relative humidity

Corticolous lichens / distribution / cover / micro-climatic parameters

INTRODUCTION

Lichens have a slow metabolism and slow growth, and are affected by various environmental factors, especially the soil, air quality, and lighting conditions, which can restrict their distribution (Marcelli 1992, Barreno & Perez-Ortega 2003). Climatic variables such as solar radiation, temperature, humidity, among others related to light and water availability, are considered as constraining factors that can lead to a major change in the composition and colonization processes of lichens in a limited area (Auger & Perez Ortega 2003). Epiphytic lichens are particularly sensitive to climate change (Nash & Olafsen 1995; Rivas-Plata *et al.* 2008, Soto-Medina *et al.* 2012), because the factors that have the greatest influence over lichen

* Corresponding author: e-mail: ediersot@gmail.com

doi/10.7872/crym/v37.iss2.2016.205

physiology are abiotic (De los Rios 2003), as well as the substrate to which they belong, such as pH, texture and physiognomy (Brodo 1973, Marcelli 1996, Purvis 2000, Aptroot & Herk 2007, Seaward 2008, Benitez *et al.* 2013). Human intervention alters the microclimate and soil conditions, which affect the growth and distribution of lichens (Barreno & Perez-Ortega 2003, Diaz *et al.* 2016, Benitez *et al.* 2013). Because of this, lichens have been used as bioindicators.

To better understand the response of a community to different anthropogenic or natural effects, it is necessary to go beyond the taxonomic diversity and see the changes in functional traits of communities and functional diversity (Webb *et al.* 2005). These aspects are important because there are rules of assembly within the communities which can be understood only by approaching various components of communities (taxonomic, functional, and phylogenetic diversity). Furthermore, it has been found that environmental gradients act as filters of functional traits in plants, which demonstrates the existence of assembly rules (Diaz 1999). Recently it has been documented that functional traits and functional diversity respond to environmental changes differently than taxonomic and phylogenetic diversity. Knowledge of these patterns for lichens is almost absent (Giordani *et al.* 2012), but there are some studies relating lichen functional traits, such as the type of photobiont and thallus morphology, to forest structural change (Johansson *et al.* 2007, Lewis and Ellis 2010, Giordani *et al.* 2012, Koch *et al.* 2013) and with climate changes (Matos *et al.* 2015). Recent studies show that these traits can act as surrogates for the diversity of species as indicators of states of ecological succession, anthropogenic disturbance, and air pollution (Koch *et al.* 2013, Cardenas *et al.* In press).

In Colombia, there have been investigations in the study of lichens in various fields, such as bioindicators, ecology, biogeography, systematics and diversity in nature reserves, urban areas, and rural areas (Lücking 2009, Moncada & Forero 2006, Sipman *et al.* 2006, Chaparro & Aguirre 2002, Cáceres *et al.* 2007, 2008, Corner 2011, Soto-Medina *et al.* 2012, 2015). However, few ecological studies have been conducted in Cauca, mainly focused on functional ecology of lichens (Diaz *et al.* 2016). This work is focused on evaluating the effects of microclimate on species diversity, species composition, and functional traits of corticolous lichens in the Botanical Garden of Popayan (JBP), in order to establish whether the functional traits can serve as surrogates for the diversity of lichens.

MATERIALS AND METHODS

Area of study: The University Foundation of Popayan (FUP), Campus los Robles is located 8 km from the city of Popayan, on the road to Timbío, Department of Cauca. This area also includes the Botanical Garden, comprising 8 ha of the 46 ha held by the institution. It is located on the western flank of the Cordillera Central at 1850 m, with an average temperature of 18 °C and geographical coordinates 2°23' N and 76°40' W (Méndez & Vallejo 2003). The area corresponds to the Subandina Forest life zone (Cuatrecasas 1958).

Sampling: In total, 11 stations were chosen in different types of vegetation within the Botanical Garden and lichens were sampled in 55 phorophytes. Five individuals of *Cecropia angustifolia* Trécul, the most common species in the study area were selected in each station. Specimens were collected between March and April and a method of quantitative sampling (Cáceres *et al.* 2007, 2008) was used,

in which in each phorophyte a quadrant of 0.50 ξ 0.20 m^2 was placed, 1.3 m high from the base (Soto *et al.* 2012). The thalli were collected using a knife and stored in paper bags.

The microclimatic parameters were taken between April and May. In this phase the relative humidity, ambient temperature and luminosity were measured, with a sampling intensity of three measurements per week (Soto-Medina *et al.* 2012). In addition, the diameter at breast height (CBH phorophytes > 20 cm) and the bark pH (Portable Waterproof pH meter solid Skin pH Meter) were recorded. For light measurements, a spherical densiometer (Forestry Suppliers) was used, with four readings per position in north, south, east, and west directions, in each phorophyte, and averaging the results (Lemmon 1956; Nascimbene & Marini, 2015). Relative humidity and temperature were measured with a Portable Digital Thermo bulb (Brixco). The stations were classified as follows:

Open microsite: Clear areas or open forest. Station 1 – Arboretum, station 10 – Pasture, station 11 – Pasture.

Closed microsites: Forest edges to dense forest. Station 4 and 5 – Corazones creek belonging to the wooded area, station 6, 7, 8 and 9 – Mano de Oso creek belonging to wooded area, Station 2 and 3 – belonging to the Renacer creek wooded area.

Identification: The collected specimens were included in the Herbarium Alvaro Fernández Perez-AFP, and in the Herbarium of the Universidad del Valle-CUVC. The identification was carried out in the laboratory of chemistry at the University Foundation of Popayan, where the morphological, anatomical characteristics and chemical tests for identification and characterization were studied, using available literature, such as Sipman *et al.* (2006), Lücking *et al.* (2009), and with expert advice.

Data Analysis: Species richness was used as a measure of alpha diversity (McCune *et al.* 2002). To evaluate the efficiency of sampling, a first-order Jackknife estimator was used (Gotelli & Colwell 2010). Functional traits were evaluated based on literature and field measurements. We evaluated the coverage of crustose, foliose, and fruticose lichens, presence of apothecia, perithecia, and lirellae, single spores or spores with several septa, ascomata colour. These traits were used as binomial variables. To estimate the traits for sampling unit two matrices were used: a matrix of species per sampling unit (W) and another of traits by species (B). From these matrices, a standard trait matrix was obtained by sampling unit (T), which was used to compare open and closed areas. This analysis was made in the Syncsa program (Debastiani & Pillar 2012).

To compare diversity, functional traits, and microclimatic parameters between stations and microsites, t-tests were made. We also performed Spearman correlation analysis among climatic variables, functional traits, and species richness. Additionally, a non-metric multidimensional scaling (NMS) was conducted to see grouping patterns of sampling units according to the microsite. The analysis was performed with 100 replicates, with a stability criterion of 0·00001 and 100 iterations per replicate (McCune *et al.* 2002). Microsite preferences by lichen species were assessed using an analysis of indicator species (Monte Carlo Simulation) (McCune *et al.* 2002). Correspondence analysis (DCA) was also made with matrix T, in order to see if there were differences in traits between areas and relations with the environmental variables. All analyses were performed with PC-ORD 5.0 (McCune *et al.* 2002) and Statistica 7.1 (Statsoft 2005).

RESULTS

Species diversity. A total of 63 morphospecies was recorded, of which 39 were identified to species, 21 to genera and three were not determined because they were sterile. According to the first-order Jackknife estimator of richness, 83 lichen species was estimated, indicating a sampling efficiency of 76%. In addition, 62% of phorophytes presented between three and seven species of lichens. The sampled species were distributed in 29 genera and 17 lichen families; Physciaceae (nine species), Parmeliaceae (eight species) and Graphidaceae (seven species) were the most representative families.

The highest species richness was found at stations 1, 10 and 11. These stations had a higher light intensity, while the remaining stations were more shaded and wet (Table 1). Bark pH was between 6.17-7.07. Stations 6 and 8 had the lowest DBH, but it was homogeneous among the remaining stations.

Diorygma sp. (42 out of 55 phorophytes), *Coniarthonia* sp. (30), *Herpothallon rubrocinctum* (22), and *Bacidia medialis* (19) had the highest frequency, whereas *Graphis rimulosa* (6), *Sticta subfilicinella* (5), *Leptogium phyllocarpum* (4), *Teloschistes flavicans* (3), *Sticta* sp.1 (2), *Parmeliella triptophylla* (2), *Herpothallon rubroechinatum* and *Haematomma flexuosum* (1) had the lowest frequency. Thus, most of the samples (73%) ranged between 1 and 6 occurrences per phorophyte. In terms of coverage, *Diorygma* sp. (4042 cm^2), *Coniarthonia* aff. *cinnabarina* (2071 cm^2), *Graphis scripta* (756 cm^2), *Usnea* sp. (696 cm^2) and *Herpothallon pustulatum* (628 cm^2) were dominant. Crustose lichens were dominant with 47.6% (30 species), followed by foliose lichens with 36.5% (23 species), fruticose lichens with 6.3% (4 species), and gelatinous and squamulose lichens with 9.6% total for both growth forms.

Table 1. Average Richness and microclimatic variables per station

Station	*Richness (S)*	*DBH (cm)*	*pH*	*Light (%)*	*Temperature (°C)*	*Relative humidity*
1	9	20	6.92	62	21.9	63.3
2	5	23	7.00	32	21.6	75.5
3	5	20	6.67	29	22.8	67.9
4	4	22	6.79	30	17.3	88.2
5	4	27	6.97	34	19.2	92.2
6	6	9	7.07	38	22.1	64.2
7	5	11	6.69	31	22.1	60.2
8	5	12	6.91	33	21.3	61.8
9	6	19	6.17	38	23.5	56.3
10	10	24	6.74	49	27.4	40.9
11	10	22	6.42	71	28.3	35.7

Microclimate effect on diversity and species composition

The results show that the variables of light and temperature, had a positive correlation with species richness (Table 2), while relative humidity was negatively correlated. Thus, phorophytes with more light and lower relative humidity tended to have higher species richness. The pH and DAP had not correlate significantly with richness.

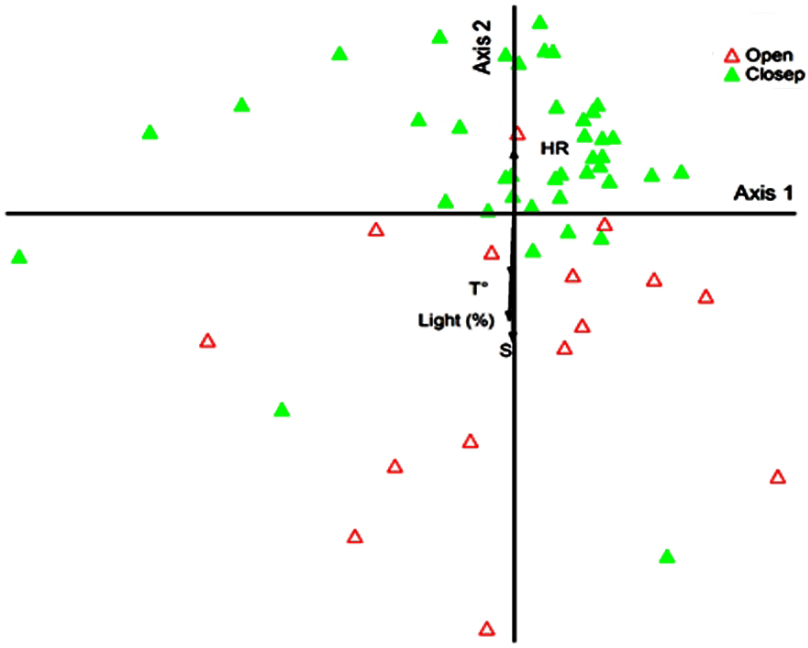

Fig. 1. NMS for the sampling units based on species composition. Lichen communities of open areas (open triangles) are separated from the closed sites (closed triangles). T° is temperature, S richness and HR relative humidity.

The non-metric multidimensional scaling (NMS) showed some associations between stations, but were most notable between closed and open microsites (Fig. 1); this means that the sampling units tended to cluster more because they had similar conditions of light and humidity, due to their spatial proximity. Significant correlations between the variables light, temperature, and relative humidity, with the axes of the NMS, indicate that these clusters are related to these variables. *Canomaculina* sp., *Heterodermia leucomela*, *Hypotrachyna* sp. 1, *Herpothallon* sp., *Physcia* sp. 2, *Lecanora* sp., and *Usnea* sp. preferred open microsites, whereas *Coccocarpia palmicola, Coccocarpia sp. Phyllopsora sp. 2* and *Sticta subfilicinella* preferred closed microsites. Similarly, nine species showed marginal preference ($0.05 < p < 0.1$), such as species, *Graphis aurita, Graphis* cf. *rimulosa, Haematomma* sp., *Heterodermia pseudospeciosa, Heterodermia japonica, Physcia* sp. And Haematomma sp. for open microsites and *Coniarthonia* aff. *cinnabarina, Herpothallon rubrocinctum* and *Phyllopsora nigrocincta* for closed microsites.

Microclimate effect on functional traits

With regard to functional traits, we found that the microsites presented contrasting patterns: closed microsites tended to have a greater cover of crustose lichens, while in open sites, foliose and fruticose lichens dominated (Table 4). With regard to color of ascomata, it was found that in the open area there was a higher incidence of ascomata with dark colors and hyaline spores, while in closed microsites lirellate lichens predominated. Light and temperature were positively correlated with

the incidence of dark ascomata and foliose and fruticose thalli, while the crustose and lirellate lichens presented a negative relationship (Table 2). The DCA indicates that trees are grouped according to the microsite and these clusters were correlated with light, temperature and relative humidity (Fig. 2). Thus, functional traits evaluated in this study correspond to differences in microclimatic parameters.

Table 2. Correlations between microclimatic parameters, lichen species richness and functional traits

	Crustose	*Foliose*	*Fruticose*	*S*	*Light (%)*	*Temperature*	*Relative Humidity*
>1 septa	0.37	– 0.52	– 0.34	– 0.36	– 0.23	– 0.19	0.17
Hyaline spore	– 0.40	0.14	0.34	0.44	0.42	0.31	– 0.31
Ascoma	0.15	– 0.40	0.04	– 0.06	– 0.01	0.09	– 0.04
Ascoma Color	– 0.45	0.33	0.11	0.25	0.27	0.33	– 0.28
Lirellae	0.62	– 0.47	– 0.36	– 0.59	– 0.43	– 0.35	0.39
Perithecia	– 0.01	0.13	– 0.02	0.15	0.06	0.21	– 0.15
Crustose		– 0.78	– 0.46	– 0.59	– 0.46	– 0.42	0.37
Foliose	– 0.78 *		0.23	0.61	0.45	0.43	– 0.41
Fruticose	– 0.46 *	0.23		0.49	0.53	0.51	– 0.44
Richness	– 0.59 *	0.61 *	0.49 *		0.61	0.60	– 0.64

* significant correlations

Table 3. Results analysis of indicator species for microsites. Importance value index (IV), standard deviation (S.Dev) and probability associated with the montecarlo test (p)

Species	*Group*	*IV*	*S.Dev*	*p*
Herpothallon sp.	Open	12	5.87	0.0006
Canomaculina sp.	Open	13.3	5.82	0.0014
Usnea sp.	Open	21.7	4.45	0.0016
Physcia sp. 2	Open	12.5	4.2	0.0044
Lecanora sp.	Open	14.9	4	0.0044
Haematomma flexuosum	Open	14.9	4.78	0.0048
Phyllopsora sp.2	Closed	17.3	6.19	0.005
Coccocarpia sp.	Closed	13.1	3.69	0.0108
Hypotrachyna sp.1	Open	14.5	3.9	0.0286
Sticta subfilicinella	Closed	14	5.82	0.0302
Heterodermia leucomela	Open	13	3.13	0.038
Coccocarpia palmicola	Closed	15.2	3.18	0.0446
Heterodermia japonica	Open	19.4	3.25	0.0614
Graphis cf. *rimulosa*	Open	13.1	3.37	0.0632
Herpothallon rubrocinctum	Closed	18.6	3.54	0.0656
Coniarthonia aff. *cinnabarina*	Closed	15.5	6.16	0.0672
Heterodermia speciosa	Open	13	2.07	0.0724
Physcia sp.1	Open	13.2	2.07	0.0724
Graphis aurita	Open	15.3	3.74	0.0738
Phyllopsora nigocincta	Closed	16	3.99	0.0778
Haematomma sp.	Open	19.2	2.27	0.0782

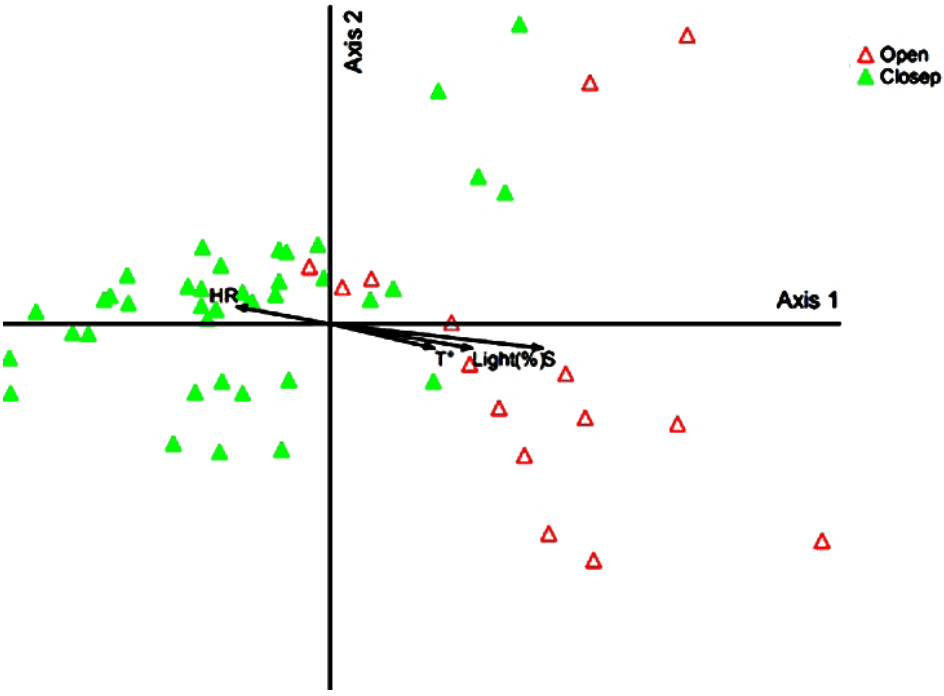

Fig. 2. DCA for functional traits, showing that the phorophytes grouped according to ligth, temperature (T°) and relative humidity (HR).

Table 4. Comparison of functional traits between open and closed microsites

	Open mean	*Closed mean*	*t-value*	*df*	*p*
>1 septa	0.60	0.72	−1.48	53.00	0.14
Hyaline spore	0.72	0.47	3.33	53.00	<0.05*
Apothecia	0.84	0.85	−0.21	53.00	0.84
Ascoma Color	0.26	0.13	2.62	53.00	0.01*
Lirellae	0.14	0.44	−4.64	53.00	<0.05*
Perithecia	0.05	0.04	0.19	53.00	0.85
Crustose	0.48	0.84	−5.02	53.00	<0.05*
Foliose	0.32	0.08	4.82	53.00	<0.05*
Fruticose	0.12	0.00	4.25	53.00	<0.05*
Richness	9.73	4.93	8.22	53.00	<0.05*
pH	6.69	6.78	−0.66	53.00	0.51
Light (%)	60.77	33.18	9.95	53.00	<0.05*
Temperature	25.83	21.24	6.36	53.00	<0.05*
Relative humidity	46.63	70.81	−5.84	53.00	<0.05*

DISCUSSION

With 6.3 species/phorophyte, the average richness of lichen species per phorophyte found in the area of the Botanical Garden of Popayan is high compared with other sites with higher sampling areas, similar to studies of Cáceres *et al.* (2007) in Brazil (8.6 species) in an area of 50 ha and Soto-Medina *et al.* (2012) in Colombia (5.4 species) in 14 ha. Similarly, the report highlights a new record for the Neotropical species *Graphis inversa* RC Harris, which is distributed in seven states in the United States (Lücking *et al.* 2009).

A likely explanation for the high diversity of crustose lichens is that with decreasing altitude, these lichens to have an adaptive advantage to the high humidity in these areas (Sipman & Harris 1989, Lakatos *et al.* 2006). The physiological adaptations presented by these thalli to the high concentrations of humidity and low light intensity, include layers that repel water to prevent it from overwhelming the thallus and permit normal photosynthesis (Lakatos *et al.* 2006, Rincón-Espitia *et al.* 2011).

The high number of species of foliose lichens of the families Parmeliaceae and Physciaceae is explained by they are optimally adapted to forests of middle elevations in sub-Andean and Andean regions (Aguirre 2008, Rincon-Espitia *et al.* 2011), in open microsites. Furthermore, the presence of foliose corticolous lichens is correlated with the complexity of the environment (Méndez & Vallejo 2003). Similarly, the presence of the families Lobariaceae and Collemataceae in closed microsites is explained by their preference for areas of high humidity and low light intensity, typically at the bottom of the phorophytes (Aptroot & Sipman 1997, Diaz-Escandón *et al.* 2016).

Microclimatic variables that influenced the distribution of lichens in the JBP were light and temperature, in accord with the statement made by De Los Rios (2003), which supports the idea that factors, such as light, humidity and temperature, have the greatest influence on lichen physiology. McCune *et al.* (2002) state that lichens are strongly influenced by both macro and micro environmental variables that affect their richness, abundance, and distribution at different scales.

Species richness was related to the intensity of light and humidity; the phorophytes that had more light intensity and lower relative humidity had the highest species richness. This is possibly because the lichens are photophilic and shaded sites with high relative humidity are scarce; in the shaded sites, bryophytes dominate, which have high water requirements and are very sensitive to high solar irradiation (Sillett & Antoine 2004, Gradstein 2008, Benitez *et al.* 2012, Pardow & Lakatos 2013, Soto-Medina *et al.* 2015, Benitez *et al.* 2015). The patterns observed in the NMS suggest that the composition of lichens in open and closed microsites are different and that these patterns match the parameters of light intensity and relative humidity. There are species or genera typical of each microsite; in open microsites the families Arthoniaceae, Parmeliaceae, Physciaceae and Ramalinaceae, typical of sites of high solar irradiation, were dominant, while in the closed microsites Coccocarpiaceae, Collemataceae, Pannariaceae and the genus *Phyllopsora,* typical of sites of high penumbra and relative humidity, were dominant (Sipman & Harris 1989). This is also supported by the analysis of indicator species, which showed that 12 species of lichens of different kinds of development showed significant preferences, and nine showed marginal preferences for different microsites. Preferences for open microsites of fruticose species of lichens, such as *Ramalina, Usnea* and *Teloschistes flavicans*, can be explained, since this type of development is adapted to solar radiation, wind and low relative humidity (Rosabal *et al.* 2012, Cabrera-Amaya *et al.* 2015).

Regarding functional traits, it was found that lichens of closed microsites differ in some traits relative to open microsites. The DCA suggests a functional gradient related traits irradiance and relative humidity. In open microsites, where the temperature is higher and the relative humidity is low, with foliose and fruticose lichens predominated. This is because these types of thallus are favoured under high light and low water, and capturing more efficient water from the environment by having a larger area of contact with air (thallus raised of substrate, presence of cilia and rhizines). In addition, the foliose and fruticose thalli loose moisture faster in open microsites, preventing the thallus becomes supersaturated and thus inhibits photosynthesis. On the other hand, the crustose lichens have a higher tolerance for low light conditions and high relative humidity of closed microsites (Sipman & Harris 1989, Koch *et al.* 2013). This is because these lichens have adaptations in the shape of water repellent layers which prevent the thallus become saturated with water (Lakatos *et al.* 2006).

With regard to reproductive traits, it was found that in open sites ascomata was dominated by dark colors and hyaline ascospores, whereas in closed places there was a higher incidence of lichens with lirellae. A greater abundance of lichen with reproductive structures of dark colors may be due to the presence of photoprotective compounds (*e.g.* melanine) that protect the spore DNA in hymenial tissue from damage by harmful radiation (Rikkinen 1995, Boustie *et al.* 2011). Although it has been found that lirellae are associated with open areas (the lips protect spores and light is required for the dispersal of spores) (Koch *et al.* 2013), the increased incidence of lirellae in closed sites in this case may be caused by the greater cover of crustose lichen on these sites.

In conclusion, a significant difference was observed in diversity, functional traits and composition of lichens when comparing open stations with closed dense forest stations, because of the marked differences between variables of light, temperature and relative humidity. Foliose and fruticose types preferred areas of high solar radiation and low relative humidity or open microsites; in contrast, the crustose lichens were more abundant in sites with high moisture concentrations and low light intensity or closed microsites. The pH and DAP showed no significant correlation with richness, therefore, the distribution of lichens in the Popayán Botanic Garden is affected by light, temperature and relative humidity. This highlights the importance of lichenized fungi as environmental indicators, both in terms of taxonomic diversity and functional traits.

Acknowledgements. The authors thank the professors of the University Foundation of Popayan (FUP), the Herbarium Alvaro Fernandez Perez (HAFP), Herbarium Luis Sigifredo Espinal-Tascon (CUVC), to Colombian group Lichenology (GCOL), and other colleages who assisted with this research.

REFERENCES

AGUIRRE J., 2008 — Diversidad y Riqueza de líquenes en Colombia. En: J.O. Rangel-Ch. (Ed.) Colombia Diversidad Biótica VI Riqueza y diversidad de los musgos y líquenes en Colombia. Universidad Nacional de Colombia, Bogotá D.C. 598 p.

APTROOT A. & SIPMAN H.J.M., 1997 — *Diversity of lichenized fungi in the tropics*. In: Hyde KD, editor. Biodiversity of tropical microfungi. Hong Kong: University Press.

APTROOT A., VAN HERK C.M., 2007 — Further evidence of the effects of global warming on lichens, particularly those with Trentepohlia phycobionts. *Environmental Pollution* 146: 293-298.

BARRENO E. & PÉREZ-ORTEGA S., 2003 — Líquenes de la Reserva Natural Integral de Muniellos, Asturias: Líquenes y el medio. Consejería de Medio Ambiente, Ordenación del Territorio e Infraestructura del Principado de Asturias: KRK ediciones, pp. 83-112.

BENITEZ A.R., PRIETO M., GONZÁLEZ X.Y. & ARAGÓN G., 2012 — Effects of tropical montane forest disturbance on epiphytic macrolichens. *Science of the Total Environ*ment 441: 169-175.

BOUSTIE J., TOMASI S. & GRUBE M., 2011 — Bioactive lichen métabolites : Alpine habitats as an untapped source. *Phytochemistry Reviews* 10(3): 287-307.

BRODO I., 1973 — Substrato Ecology. In: V. Ahmadjian & M.E. Hale (Eds.). *The Lichens*: Academic Press. New York. London, pp. 401-440.

CABRERA-AMAYA D., FAJARDO-GUTIÉRREZ F. y ROJAS-ZAMORA O., 2015 — Diversidad de líquenes, musgos y hepáticas en el Corregimiento de Pasquilla (Bogotá-Colombia). Presentación en VIII Congreso Colombiano de Botánica, Manizales, Colombia.

CÁCERES M.E.S., LÜCKING R. & RAMBOLD G. 2007 — Phorophyte specificity and environmental parameters versus stochasticity as determinants for species composition of corticolous crustose lichen communities in the Atlantic rain forest of northeastern Brazil. *Mycological Progress* 6: 117-136.

CÁCERES M., LÜCKING R. & RAMBOLD G., 2008 — Efficiency of sampling methods for accurate estimation of species richness of corticolous microlichens in the Atlantic rainforest of northeastern Brazil. *Biodiversity and Conservation* 17(6): 1285-1301.

CHAPARRO M. & AGUIRRE J., 2002 — Hongos liquenizados. Bogotá: El Malpensante S.A., 220 p.

CUATRECASAS J., 1958 — Aspectos de la vegetación natural de Colombia. *Rev. Acad. Col. Cs. Ex. Fis. Nat.* 10 (40): 221-268.

DEBASTIANI V. y PILLAR V., 2012 — SYNCSA - R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. *Bioinformatics* 28 (15): 39-54

DE LOS RÍOS A., 2003 — *Estudio ultraestructural y enzimático de los simbiontes liquénicos: aspectos microclimáticos y relaciones talo–sustrato*. Universidad Complutense de Madrid, Madrid, España.

DÍAZ A., 1999 — Diseño estadístico de experimentos. Medellín: Ed. Universidad de Antioquia, 347 p.

DÍAZ-ESCANDÓN D., SOTO-MEDINA E., LÜCKING R. & SILVERSTONE-SOPKIN P., 2016 — Corticolous lichens as environmental indicators of natural sulphur emissions near the sulphur mine El Vinagre (Cauca, Colombia). *The Lichenologist* 48: 147-159.

DÍAZ S., CABIDO M. & CASANOVES F., 1998 — Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 113-122.

GIORDANI P., INCERTI G., RIZZI G., NIMIS P.L. & MODENESI P., 2013 — Functional traits of cryptogams in Mediterranean ecosystems are driven by water, light and substrate interactions. *Journal of Vegetation Science* 25: 778-792.

GOTELLI N.J. & COLWELL R.K., 2010 — Estimating species richness. In MAGURRAN A.E. & MCGILL B.J. (Eds.): Frontiers in measuring biodiversity. — Oxford University Press, New York, pp. 39-54.

GRADSTEIN S.R., 2008 — Epiphytes of tropical montane forests - impact of deforestation and climate change. In: *The Tropical Mountain Forest*. Patterns and Processes in a Biodiversity Hotspot. GRADSTEIN S.R., HOMEIER J. and GANSERT D. (Ed.). University Press, pp. 51-65.

JOHANSSON P., RYDIN H. & THOR G., 2007 — Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. *Ecoscience* 14 (1): 81-91.

HAWKSWORTH D., ITURRIAGA T. & CRESPO A., 2005 — Líquenes como bioindicadores inmediatos de contaminación y cambios medio-ambientales en los trópicos. *Revista Iberoamericana de Micología* (1): 71-82.

KOCH N.M., MARTINS S.M. DE A., LUCHETA F. & MÜLLER S.C., 2013 — Functional diversity and traits assembly patterns of lichens as indicators of successional stages in a tropical rainforest. *Ecological Indicators* 34: 22-30.

LAKATOS M., RASCHER U., & BÜDEL B., 2006 — Functional characteristics of corticolous lichens in the understory of a tropical lowland moist forest. *New Phytologist*, 172: 679-695.

LEMMON P., 1956 — A Spherical Densiometer for Estimating Forest Overstory Density. *Forest Science* 2(4): 314-320.

LÜCKING R., ARCHER A. & APTROOT A., 2009 — A Word–wide key to the genus *Graphis* (Ostropales: Graphidaceae). *The Lichenologist* 41(4): 363-452.

MARCELLI M.P., 1992 — Ecologia liquênica nos manguezais do Sul-Sudeste brasileiro. *Bibliotheca Lichenologica* 47: 1-310.

MARCELLI M.P., 1996 — *Biodiversity assessment in lichenized fungi: the necessary naive roll makers.* In: C.E. Bicudo & N.A. Menezes (eds.). *Biodiversity in Brazil: A first approach*. Conselho Nacional do Desenvolvimento Científico e Tecnológico, São Paulo, pp. 93-107.

McCUNE B., GRACE J. & URBAN D., 2002 — Analysis of ecological communities. Oregon: MjM Software, Gleneden Beach.

MATOS P., PINHO P., ARAGÓN G., MARTÍNEZ I., NUNES A., SOARES A.M.V.M. & BRANQUINHO C. 2015 — Lichen traits responding to aridity. *Journal of Ecology* 103: 451-458.

MÉNDEZ P. & VALLEJO M., 2003 — *Evaluación de la presencia o ausencia de líquenes foliosos corticícolas en las especies Pinus oocarpa y Heliocarpus popayanensis en el Jardín Botánico de Popayán, Cauca*. Tesis de pregrado en Ecología. Fundación Universitaria de Popayán. Facultad de Ciencias Naturales. Programa de Ecología.

MONCADA B. & FORERO E., 2006 — El género *Pseudocyphellaria* Vain. (Lobariaceae-Ascomycetes Liquenizados) en Colombia. *Caldasia* 28 (2): 197-215.

NÖSKE N., 2004 — Effekte anthropogener Störung auf die Diversität Cryptogamischer Epiphyten (Flechten, Moose) in einem Bergregenwald in Südecuador. Ph.D. Thesis, Mathematisch-Naturwissenschaftliche Fakultät, Georg-August-Universität zu Göttingen, Alemania.

NASCIMBENE J. & MARINI L., 2015 — Epiphytic lichen diversity along elevational gradients: biological traits reveal a complex response to water and energy. *Journal of Biogeography* 42: 1222-1232.

NASH T. & OLAFSEN A., 1995 — Climate change and the ecophysiological response of Arctic lichens. *The Lichenologist* 27: 559-565.

PARDOW A. & LAKATOS M., 2013 — Desiccation tolerance and global change: implications for tropical bryophytes in lowland forests. *Biotropica* 45: 27-36.

PURVIS O.W., 2000 — *Lichens*. Natural History Museum, London

RIKKINEN J., 1995 — What's Behind the Pretty Colours? A Study on the Photobiology of Lichens. Bryobrothera 4, Helsinki. 239 p.

RINCÓN-ESPITIA Á, AGUIRRE J. & LÜCKING R., 2011 — Líquenes corticícolas de Caribe Colombiano. *Open Journal System Caldasia* (33) 2: 331-347.

ROSABAL D., BURGAZ A. R. & REYES O. J., 2012 — Diversidad y distribución vertical de líquenes corticícolas en la pluvisilva montana dela Gran Piedra, Cuba. *Bot. Complut.* 36: 19-30.

SILLETT S.C. & ANTOINE M., 2004 — Lichens and bryophytes in forest canopies. In Forest Canopies. Lowman, M.D. and Rinker, H.B. (Ed.). Elsevier Academic Press, pp. 151-174.

SIPMAN H.J.M. & HARRIS R.C., 1989 — Lichens. In: *Tropical Rain Forest Ecosystems*. Lieth, H. & Werger, M.J.A. (Ed.). Elsevier, pp. 303-309.

SIPMAN H., HEKKING W. & AGUIRRE J., 2006 — Checklist of lichenized and lichenicolous fungi from Colombia. In: Biblioteca José Jerónimo Triana, pp. 235.

SOTO-MEDINA E., LÜCKING R. & BOLAÑOS-ROJAS A., 2012 — Especificidad de forófito y preferencias microambientales de los líquenes cortícolas en cinco forófitos del bosque premontano de finca Zíngara, Cali, Colombia. *Revista de. Biología Tropical* (60): 843-856.

SOTO-MEDINA E., LONDOÑO V. & DÍAZ-ESCANDÓN D., 2015 — Epiphytes from a forest type transition zone in the Choco biogeographic region, Valle del Cauca, Colombia. *Revista de Biología Tropical* 63(4): 915-926.

STATSOFT., 2005 — STATISTICA (data analysis software system), Version 7.1. Tulsa: Statsoft, Inc. Retrieved from http://www.statsoft.com.

WOLF J., 1993 — Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Annals of the Missouri Botanical Garden* 80: 928-960.