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Diversity of subaerial algae and cyanobacteria on tree bark in tropical mountain habitats*

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Abstract: We report the species composition of subaerial epixylic algae and cyanobacteria from a South-East Asian mountain rainforest locality in Cibodas, West Java. Green algae (*Trebouxiophyceae, Chlorophyceae, Trentepohliales*) were dominant and *Cyanobacteria* were the second most frequent group. We specifically concentrated on the comparison of species composition of closed primary forest and open antropogenic spaces. *Trentepohliales* and *Cyanobacteria* dominated in open spaces with higher light intensities, whereas closed forest localities were dominated by trebouxiophycean coccal green algae. There was a significantly higher algal diversity in open spaces than in closed forest samples indicating the limiting effect of light on subaerial algal communities of closed tropical forests. A number of isolated strains and morphotypes probably represent undescribed taxa.

Key words: subaerial algae; Trebouxiophyceae; Chlorophyceae; Trentepohliales; Cyanobacteria; diversity

Abbreviations: ANOSIM, analysis of similarities; NMDS, non-metric multidimensional scaling

Introduction

Since the 19th century the diversity of tropical subaerial algae growing on tree bark and leaves has been investigated in different localities and habitats (Hariot 1889; de Wildemann 1890, 1897; Printz 1939). In addition, there are several more recent detailed taxonomic and floristic studies dealing with tropical subaerial algae. However, these works are almost exclusively concentrated on *Trentepohliales* – a physiognomically most prominent algal group forming the subaerial growths on tropical trees (Thompson & Wujek 1997; Salleh & Milow 1999; Neustupa 2003, 2005; Rindi et al. 2005). Information on the distribution of other algae and cyanobacteria in these habitats is extremely scarce – and mostly concentrates on descriptions of new species rather than on the diversity and dynamics of species composition (Neustupa & Šejnohová 2003; Neustupa 2004; Rindi et al. 2006a; Neustupa et al. 2007). Thus, we still do not know which algal groups (apart from *Trentepohliales*) actually constitute the growths on tree bark in tropical ecosystems and, at the same time, we do not have a real idea on the microalgal diversity of these tropical habitats.

In this study, we concentrated on the analysis of differences in species composition of epixylic algae and cyanobacteria in samples from mountainous habitats of Cibodas area (West Java, Indonesia). Using cultivation methods we especially attempted to characterize the diversity of unicellular green algae that had been overlooked in previous studies. Our samples comprised epixylic growths from 10 tree specimens of a closed primary mountainous rainforest and adjacent anthropogenic open spaces of a mountainous garden. Primarily, we aimed at the identification of differences between closed forest and open spaces localities. We also investigated the possible differences in algal species composition that could be ascribed to the species identity of the host tree, to bark roughness and to the types of cultivation media. Using microscopic methods, we were not able to identify many taxa of coccal green algae and cyanobacteria. Rather than trying to assign all of our isolates to traditional species names, we concentrated on the characterization of individual morphotypes in order to compare the composition and diversity of samples in ecologically different habitats. Thus, this study deals primarily with the ecology of algal diversity in subaerial epixylic habitats of a mountainous tropical forest. The taxonomic identifications in individual taxa were left to detailed studies involving molecular analyses and other methods (see e.g. Neustupa et al. 2007; Eliáš et al. this volume).

Material and methods

The samples were collected in Cibodas Botanical Garden

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Table 1. List of investigated samples.

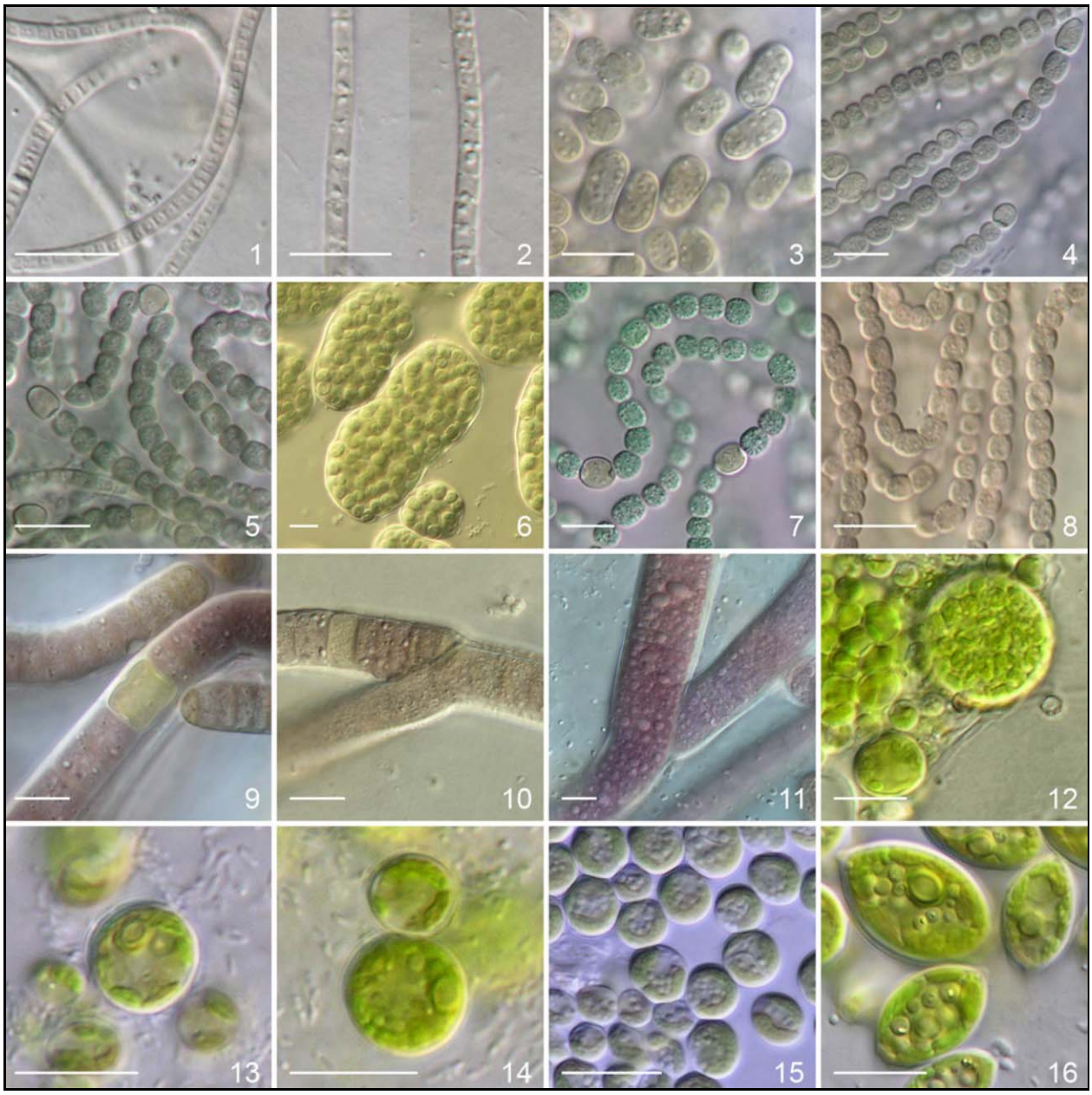
Sample no.	Tree species	Habitat	Bark roughness	Proportion of open sky (%)
1	*Ehretia javanica* Bl.	forest	2	15
2	*Ehretia javanica* Bl.	forest	1	10
3	*Manglietia glauca* Bl.	forest	1	15
4	*Cleistocalyx operculata* (Roxb.)Merr. & Perry	forest	1	20
5	*Schima wallichii* (DC.) Korth.	forest	2	10
6	*Agathis dammara* (Lamb.) Rich. & A. Rich.	garden	1	30
7	*Altingia excelsa* Noroña (Rasamala)	garden	2	45
8	*Schima wallichii* (DC.) Korth.	garden	3	50
9	*Livistona decipiens* Becc.	garden	2	30
10	*Altingia excelsa* Noroña (Rasamala)	garden	2	40

Table 2. A list of species from investigated localities. Different cultivation media are indicated as A – BBM and B – DY IV.

	1		2		3		4		5		6		7		8		9		10	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Cyanobacteria																				
Leptolyngbya sp. 1								2						1	2	2				
Leptolyngbya sp. 2								1												
Nostoc sp. 1																1				
Nostoc sp. 2														1						
Nostoc cf. *entophytum* Bornet & Flahault					1	1		1					2	2	2	1				
Nostoc cf. *punctiforme* (Kütz.) Hariot													1	2	2	2	1		1	
Scytonema ocellatum Lyngbye ex Bornet & Flahault														1		2				
Scytonema sp.							1													
Chlorophyceae																				
Bracteacoccus sp.																	2	2		
Coelastrella sp.								1												
Mychonastes homosphaera (Skuja) Kalina & Punčochářová													1	2					1	1
Scotiellopsis rubescens Vinatzer		1					1	2												
Trebouxiophyceae																				
Chlorella sp. 1															1					
Chlorella sp. 2						1										1				
Chlorella sp. 3																	1			
Chlorella sp. 4								1												
Dictyochloropsis sp.					2			1		1			2	2	1					1
Elliptochloris sp.							1			1								2		
Pseudococcomyxa simplex (Mainx) Fott	1	2	2	2	2	2	1	2	2	2	1	1			1	2	2	2	2	2
Pseudococcomyxa sp.	2	1					1													
Stichococcus bacillaris Näg.																1				1
Watanabea sp.													2							
Ulvophyceae																				
Printzina bossei (De Wildeman) Thompson & Wujek														2					2	2
Printzina effusa (Krempelhüber) Thompson & Wujek									1	1			2	2	1				1	
Printzina cf. *lagenifera* (Hildebrand) Thompson & Wujek									1										1	2
Trentepohlia aurea (L.) Martius											2	2					2	2		
Trentepohlia monilia De Wildemann												1								
Trentepohlia sp.												1								

(geographical coordinates 6°45′30″S and 107°00′10″E) of the Indonesian Institute of Science (L.I.P.I.) at an altitude of 1290–1350 m a.s.l. in a climatically homogenous area of approximately 4 km^2 (Table 1). The bark of 10 trees with a trunk diameter of more than 30 cm was sampled for surface microbial growths at a height of 120–40 cm above the soil level, evenly around the trunk perimeter (collected in February 2001). Bark roughness was estimated into three categories (smooth, undulated, strongly wrinkled). The proportion of an open sky was used as an estimate of illumination in individual microlocalities (Niinemets 1998; Nifinluri et al. 1999). The homogenized samples were placed in Petri dishes within 72 h after the collection. They were cultivated on BBM (Bischoff & Bold 1963) and DY IV (Sandgren et al. 1996) agar media at a temperature of 25 °C and an illumination of 40 μmol m^{-2} s^{-1} provided by 18W cool fluorescent tubes (Philips TLD 18W/33). Microphotographs were taken with Olympus BX51 light microscope and Olympus Z5060 digital equipment using Nomarski differential interference contrast optics. Quantities of individual species were estimated as two categories (rare species – one to three colonies on Petri dishes, more frequent species – higher number of colonies). For identification we used relevant taxonomic and identification monographs and papers (Printz 1939; Komárek & Fott 1983; Sarma 1986; Ettl & Gärtner 1995; Komárek & Anagnostidis 2005; Rindi et al. 2005).

Statistical analyses involved the non-metric multidimensional scaling (NMDS) of species composition data using the Manhattan distance measure in PAST, ver. 1.67. software (Hammer et al. 2001). NMDS ordination was used

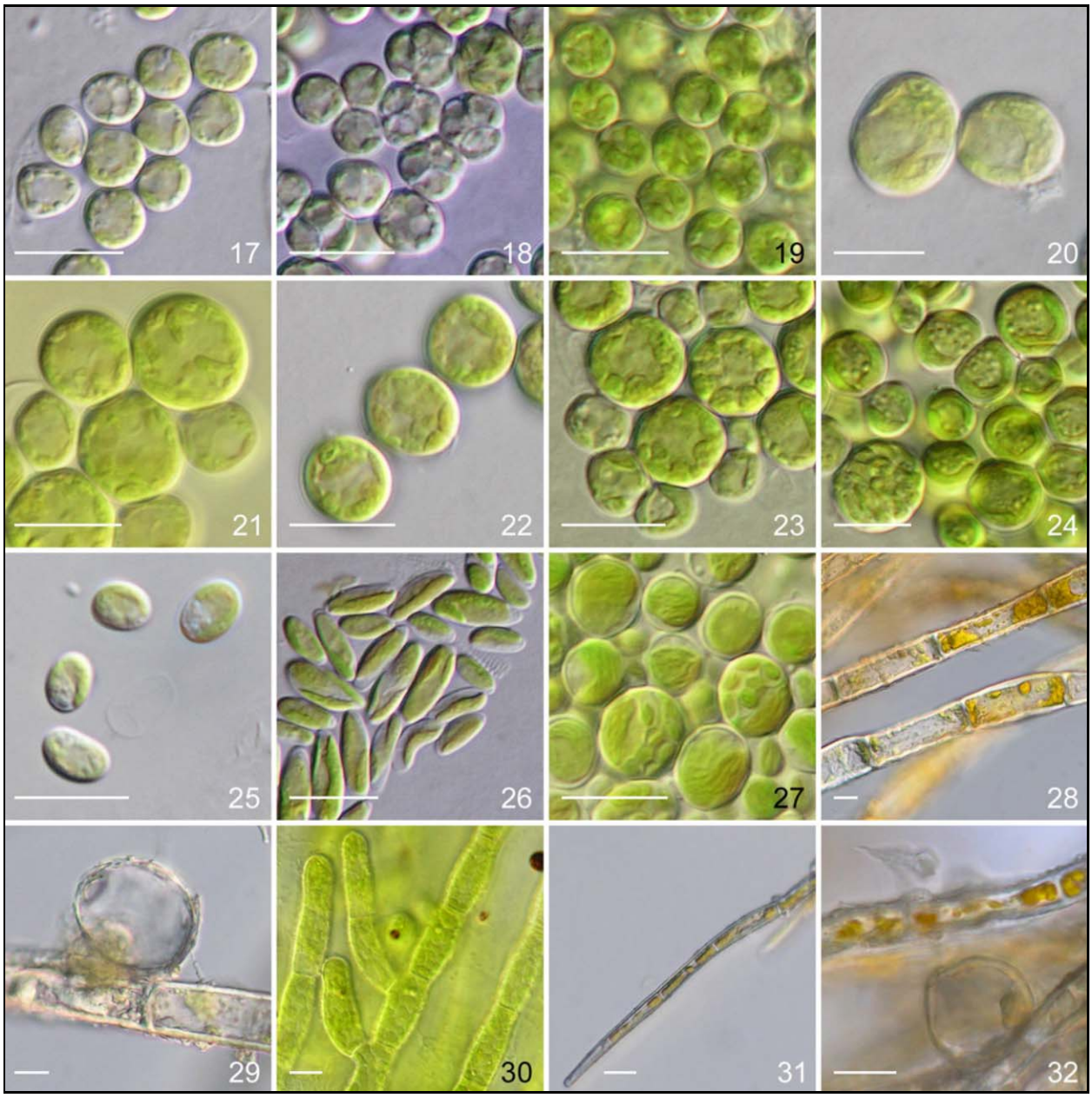


Figs 1–16. 1 – *Leptolyngbya* sp. 1; 2 – *Leptolyngbya* sp. 2; 3, 4 – *Nostoc* cf. *entophytum*; 5, 6 – *N.* cf. *punctiforme*; 7 – *Nostoc* sp. 1; 8 – *Nostoc* sp. 2; 9, 10 – *Scytonema ocellatum*; 11 – *Scytonema* sp.; 12 – *Bracteacoccus* sp.; 13, 14 – *Coelastrella* sp.; 15 – *Mychonastes homosphaera*; 16 – *Scotiellopsis rubescens*; scale bar 10 μm.

for the visualization of similarities in species composition of samples with a scatter plot of the first two axes (stress factor 0.1775). The significance of differences in algal composition between forest and open spaces samples and between both types of cultivation media was assessed using Manhattan distances by non-parametric two-group ANOSIM permutation tests with 10,000 permutations (Clarke 1993; Hammer et al. 2001; Carballo et al. 2002; Rico & Gappa 2006). The differences in species diversity between closed forest and open spaces samples were evaluated using permutation test on Shannon diversity index of data sets pooled from both habitat types. Two-matrices and partial Mantel tests of matrix correlations were used for evaluation of effects of cultivation medium type, host tree species, bark roughness and illumination on algal composition indicated with Manhattan distance in pairs of samples (Mantel 1967; Cayuela et al. 2006). Significance was assessed by 10,000 permutations of original matrices. Mantel tests were conducted in PAST ver. 1.67. and *zt* ver. 1.0. software (Bonnet & Van der Peer 2002).

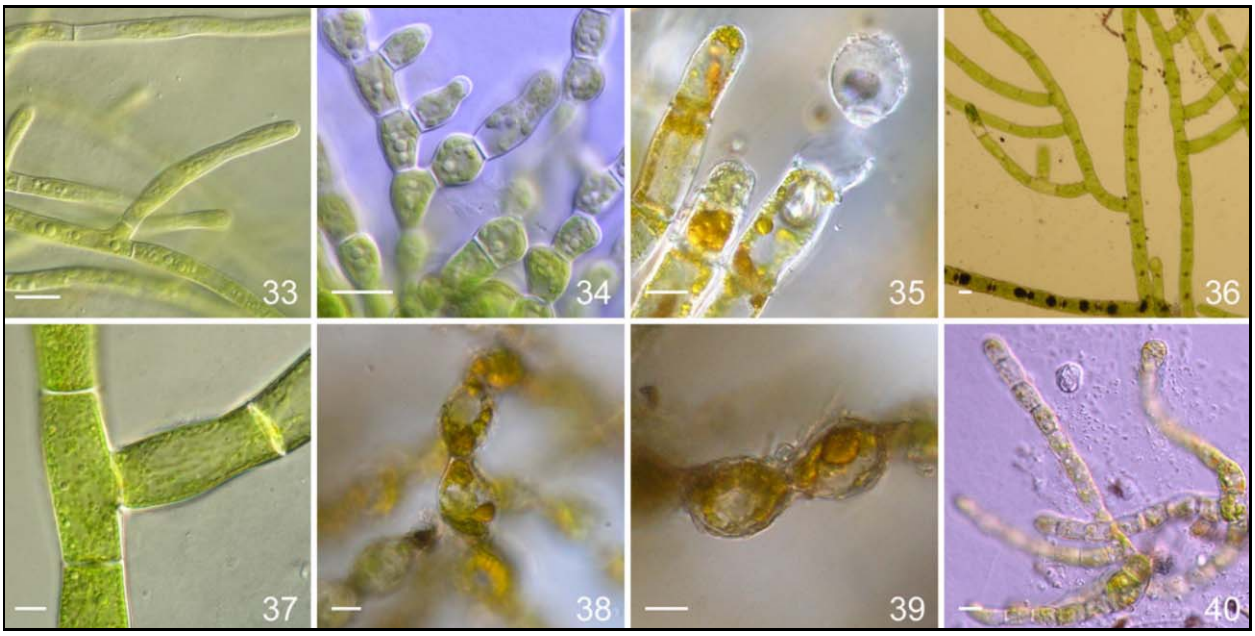
Results

In the investigated samples, we identified 28 taxa of algae and cyanobacteria (Table 2, Figs 1–40). The average species number was 4.8 in closed forest and 7.8 in open spaces. The permutation test on Shannon index between these two habitat types revealed significant differences ($p = 0.006$) indicating a higher algal diversity in open spaces samples. The NMDS ordination diagram (Fig. 41) illustrated the similarity in species composition of forest samples, whereas there was higher variation in composition of open spaces



Figs 17–32. 17, 18 – *Chlorella* sp. 2; 19 – *Chlorella* sp. 3; 20 – *Chlorella* sp. 4; 21–23 – *Dictyochloropsis* sp.; 24, 25 – *Elliptochloris* sp.; 26 – *Pseudococcomyxa* sp. 2; 27 – *Watanabea* sp.; 28–30 – *Printzina bossei*; 31, 32 – *P. effusa*; scale bar 10 μm.

samples. The ordination diagram suggested close similarity in algal composition obtained from samples by cultivation on different media. This relation was confirmed by the Mantel test of the species composition distance matrix (Manhattan distances) vs. matrix of sample identity ($r = 0.7816$, $p = 0.0004$). Thus, the cultivation on different media types did not impose a significant change on the species composition identified from individual samples. Two-group ANOSIM revealed a clear difference in species composition of forest vs. open spaces samples (mean rank within groups 87.38, mean rank between groups 102.8, $r = 0.1623$, $p = 0.0027$). Not surprisingly, the forest/open space affiliation closely correlated with the proportion of open sky as an indirect measure of irradiation ($r = -0.8946$, $p = 0.0001$) and the Mantel test of species composition matrix vs. proportion of open sky difference matrix revealed a significant correlation ($r = 0.3484$, $p = 0.0284$). There were some clear group preferences in the occurrence of individual major algal and cyanobacterial groups in the two habitat types. The distribution of *Trentepohliales* and cyanobacteria correlated positively with the proportion of open sky ($r = 0.5334$, $p = 0.0155$ in *Trentepohliales*; $r = 0.6818$, $p = 0.0009$ in cyanobacteria). On the other hand, the distribution of green microalgae, taken as a single physiognomic group, did not correlate with this measure ($r = 0.1953$, $p = 0.4092$). There were several species occurring in at least two samples only in open space habitat, e.g. *Nostoc* cf. *punctiforme* (Fig. 4), *Scytonema ocellatum* (Fig. 10), *Mychonastes homosphaera* (Fig. 15), *Stichococcus bacillaris, Printzina bossei* (Figs



Figs 33–40. 33 – *Printzina effusa*; 34 – *P.* cf. *lagenifera*; 35–37 – *Trentepohlia aurea*; 38, 39 – *T. monilia*; 40 – *Trentepohlia* sp.; scale bar 10 μm..

28–30), *Trentepohlia aurea* (Figs 35–37). On the other hand, there were two species (both of them coccal green algae) that exclusively occurred in at least two separate samples from forest habitat – *Pseudococcomyxa sp. 2* (Fig. 26), *Scotiellopsis rubescens* (Fig. 16). A common subaerial coccal green alga *Pseudococcomyxa simplex* was a single most frequent species occurring in all but one sample. In addition, *Nostoc* cf. *entophytum* (Figs 3, 4) and *Dictyochloropsis sp.* (Figs 21–23) frequently occurred in at least four samples including both forest and open space habitats, indicating their wide distribution in the investigated area.

We did not observe a correlation between the host tree species and the algal composition (complete Mantel test of species composition distance matrix vs. matrix of a host tree identity – $r = 0.0342$, $p = 0.4043$; partial Mantel test with proportion of open sky as a covariate – $r = 0.015$, $p = 0.4585$). At the same time, there was no significant relationship between the total algal species composition and the bark roughness of samples (complete Mantel test – $r = 0.0757$, $p = 0.3151$; partial Mantel test with proportion of open sky as a covariate – $r = -0.0097$, $p = 0.4864$). However, looking at group preferences in distribution of major groups in relation to bark roughness, we encountered significant positive correlation for cyanobacteria ($r = 0.5288$, $p = 0.0165$). The correlations in other two major groups were insignificant.

Discussion

Subaerial habitats of tropical rainforests represent one of the least known algal habitats world-wide (Thompson & Wujek 1997; Neustupa 2005; Rindi et al. 2006b). The estimated proportion of possibly undescribed and new taxa of green microalgae unidentifiable according to the traditional criteria was about 60%. However, given the overall high proportion of pseudocryptic and cryptic species among these groups (Henley et al. 2004; Krienitz et al. 2004; Neustupa et al. 2007), the real proportion of new species might be even higher. Likewise in *Trentepohliales*, cryptic diversity seems to led to a considerable underestimate of the presumed total species numbers in tropical habitats (López-Bautista et al. 2006). In this respect, taxonomic conclusions should only be made using combination of molecular and phenotypic approaches. However, comparing several epixylic microlocalities, we used the microscopic and cultivation methods for enumeration of individual morphotypes, even if they could not be identified to a species level. Using comparable methods, Mikhailyuk (1999) and Mikhailyuk et al. (2001) estimated the average species number of algae and cyanobacteria per sample of living tree bark in temperate and subtropical habitats. In the Kaniv Nature Reserve (Ukraine) representing a natural temperate forest, there were on average 1.7 species per sample (Mikhailyuk 1999; Mikhailyuk et al. 2001). In subtropical localities in Israel (Canyon Nahal Keziv and Mt. Carmel Nat. Park) the average number was 4.0 species (Mikhailyuk et al. 2001). Handa & Nakano (1988) reported average number of 1.9 species of algae and cyanobacteria on the tree bark of subtropical forests from Miyajima Island in Japan. Nakano et al. (1991) found on average 5.9 species in a similar study from south-western Japan. Cox & Hightower (1972) reported an average number of 3.8 algal species from tree bark in intermediate temperate to subtropical climate of Tennessee, U.S.A. In our samples, we revealed average 4.8 species in shaded forest undergrowth and 7.8 species in open space habitat. Thus, we can possibly presume that this increase of a species number in a tropical, especially the non-shaded

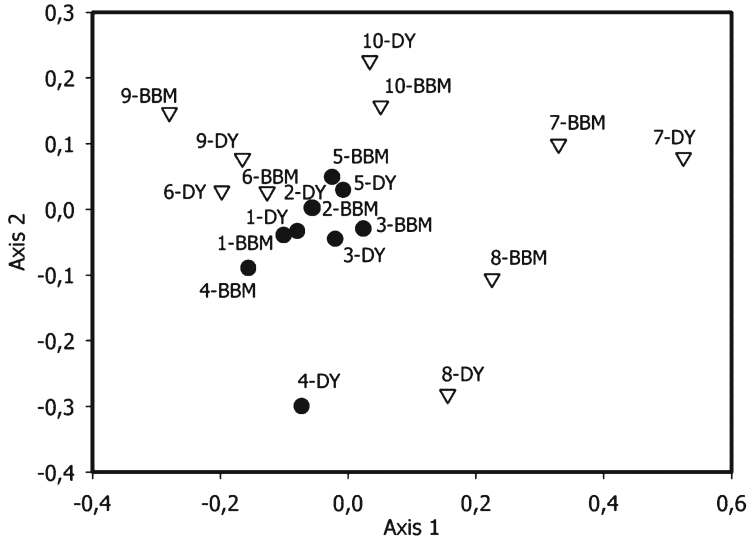


Fig. 41. NMDS ordination diagram of individual samples based on a matrix of Manhattan distances in species composition. Circles (●) indicate forest localities, triangles (▽) open space localities.

habitat might indicate a higher total algal diversity in subaerial epiphytic habitats of the tropics, in comparison to drier seasonal ecosystems. Of course, we suppose that the numbers reported in the literature and our species numbers are lower than the real diversity in natural localities, as the cultivation methods do not capture non-cultivable cyanobacteria and algae. Thus, these organisms remain mostly excluded from species lists of such studies. In this respect, the environmental sequencing approaches (Romari & Vaulot 2004; Lefranc et al. 2005) will provide extremely useful comparative data sets in the future.

The light conditions were found to be a principal factor for influencing diversity and species composition. Two major groups, cyanobacteria and *Trentepohliales*, occurred mostly only in open non-shaded microhabitats. On the other hand, the undergrowth of primary mountain rainforest had a lower diversity and most of the species were green microalgae. However, a lot of these green microalgae were non-identifiable using traditional methods and they probably represent undescribed species awaiting future molecular characterizations and taxonomic descriptions. In this respect, epixylic algae of primary rainforest undergrowth certainly represent a very important and valuable source of diversity. The algal growths in open spaces (that correspond to forest edges and gaps in non-antropogenic landscape), on the other hand, probably include most of the trentepohliacean tropical diversity. These green algae which are a prominent and characteristic feature of tropical subaerial growths seem to be almost excluded from distinctly shaded undergrowth of primary rainforest.

In comparison with the subaerial epixylic algal communities of non-tropical ecosystems (Brand & Stockmayer 1925; Laundon 1985; Gärtner & Ingolić 2003), our samples did not include some of the "flagship" taxa of these habitats *Apatococcus lobatus*, *Desmococcus* spp. and *Klebsormidium flaccidum* which often form macroscopically visible growths on tree bark in temperate samples. On the other hand, species of *Trentepohliales*, heterocytous cyanobacteria and, in shaded forest samples, unicellular green algae were physiognomically dominant. Whether the dominant species of temperate algal bark growths are completely missing from similar tropical microhabitats, or whether they simply occur in smaller numbers in tropical ecosystems, is a question that future studies involving a wider selection of localities and areas need to address.

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