Tropical Bryology 3: 29-35, 1990

On the occurrence of bryophytes and macrolichens in different lowland rain forest types at Mabura Hill, Guyana

J.H.C. Cornelissen
Department of Plant Ecology, Lange Nieuwstraat 106, 3512 PN Utrecht, The Netherlands

S.R. Gradstein
Institute of Systematic Botany, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands

(Studies on the flora of the Guianas 53)

Abstract. A floristic and ecological study of bryophytes and macrolichens in different lowland rain forest types around Mabura Hill, Guyana, South America, yielded 170 species: 52 mosses, 82 liverworts and 36 macrolichens. Lejeuneaceae account for about 30% of the species and are the dominant cryptogamic family of the lowland rain forest. Special attention was paid to the flora of the forest canopy, by using mountaineering techniques. It appeared that 50% of the bryophyte species and 86% of the macrolichens occurred exclusively in the canopy. Dry evergreen 'walaba' forest on white sand is particularly rich in lichens whereas the more humid 'mixed' forest on loamy soil is characterized by a rather rich liverwort flora.
More species are exclusive to the mixed forest than to dry evergreen forest due to the 'canopy effect', i.e. the occurrence of xerophytic species in the outer canopy of both dry and humid forests. Furthermore, canopy species have wider vertical distributions on trees in the dry evergreen forest than in the mixed forest, due to the more open canopy foliage of the dry evergreen forest.

Epiphytic bryophytes and lichens are often neglected in rain forest studies as their main occurrence is in the forest canopy (Gradstein et al. 1990). In the Guianas, one of the last areas of the world covered largely by virgin lowland rain forest, floristics and ecology of rain forest bryophytes and lichens were investigated at Moraballi Creek, Guyana, by Richards (1954) and in the Kabalebo area in western Suriname by Florschütz-de Waard & Bekker (1987). These studies were performed at forest ground level and did not include a detailed analysis of the forest canopy. In the present study, focusing on rain forests at Mabura Hill, Guyana, whole standing trees have been inventoried by using mountaineering techniques for access into the canopy (ter Steege & Cornelissen 1988).
The Mabura Hill area is situated between the Essequibo and Demerara River, ca 180 km SSE of Georgetown (5°20' N, 58°10' W) at an altitude less than 100 m. above sea level. Rainfall is between 3000 and 4000 mm annually and mainly in the periods May-August and December-January (Fanshawe 1952). Average air temperatures are between 27 and 30 °C and relative air humidity rarely drops below 60 % in the forest.
The main rain forest types around Mabura Hill are (Richards 1952; ter Steege & Cornelissen 1990):
1. *Walaba forest* (ca 30 m high): dry evergreen

rain forest dominated by *Eperua falcata* Aubl. (walaba) and *Eperua grandiflora* (Aubl.) Benth. This forest type is very common in the Mabura Hill area and occurs on excessively drained white sand soils. The canopy foliage of the walaba forest is rather open as compared to the other forest types.
2. *Greenheart forest* (ca 35 m high): rain forest dominated by *Ocotea rodiaei* (Schomb.) Mez (greenheart). This rain forest type is found on loamy sand soils on hill sides. Density of the canopy foliage is intermediate between that of the walaba forest and the mixed forest.
3. *Mixed forest* (ca 40 m high): typical humid lowland rain forest without dominant tree species. It occurs on lateritic and loamy soils and has a relatively closed canopy foliage.

Bryophyte and lichen collecting was done during February - March 1985 in the three forest types, especially in the walaba forest and the mixed forest, as well as along trails and roads, in riverine *Mora* forest, and along creeks. In the walaba forest five mature *Eperua falcata* and six mature *Eperua grandiflora* trees were climbed and sampled from the tree base up to the outermost canopy twigs (Cornelissen & ter Steege 1989). In the mixed forest five trees of different species were sampled likewise, and in the greenheart forest one *Ocotea rodiaei* tree. Six tree height zones were recognized, following Johannson (1974): 1. tree base; 2. lower trunk; 3. upper trunk; 4. lower canopy; 5. middle canopy; 6. upper canopy.
Over 700 specimens of bryophytes and 150 specimens of macrolichens were gathered. All materials have been named down to species, except for the epiphylls which remain largely unidentified. The collections have been deposited in the cryptogamic herbarium of the University of Utrecht (U) with duplicates in the herbarium of the University of Guyana (GUY).
Nomenclature follows Gradstein & Hekking (1989) for Hepaticae, Florschütz-de Waard (1990) for Musci and Hekking & Sipman (1988) for Lichenes.

Results and discussion

In total 170 species of bryophytes and macrolichens have been identified from the Mabura Hill area (Table 1): 52 mosses, 82 liverworts and 36 macrolichenes**.** The area is richer in liverworts than in mosses and this agrees with findings in other lowland rain forest areas in the Guianas and elsewhere in the equatorial tropics (Richards 1984, Florschütz-de Waard & Bekker 1987, Gradstein et al. 1990).
Lejeuneaceae (51 spp.) account for about 30% of all the species of bryophytes and lichens collected and are by far the most important family in the area. Conspicuous but far less rich in species are the Calymperaceae (11 spp.), Hookeriaceae and Parmeliaceae (9 spp. each), Lepidoziaceae (8 spp.), Plagiochilaceae (7 spp.), Coccocarpiaceae, Frullaniaceae, Orthotrichaceae and Sematophyllaceae (6 spp. each) and Leucobryaceae (5 spp.).

The ecological distribution of the bryophytes and macrolichens in the Mabura Hill area, in terms of their occurrence in microhabitats and in the different lowland rain forest types, is shown in Table 1. It appear that the richest flora is found in the forest canopy, which harbours 122 species (29 mosses, 59 liverworts, 33 macrolichens) or about 70% of the entire bryophyte and macrolichen flora . While some of the species collected in the canopy also occur in the understory, it appears that 50% of the bryophyte species and 86% of the macrolichens were only found in the canopy and on the upper trunks, over 10 m above ground level (see also Gradstein et al. 1990). In contrast, only 14% of the bryophyte species and none of the lichens are exclusive to the understory. It would thus appear that many species might not have been collected when the inventory would have been carried out at ground level only. This is especially true for macrolichens. Our results are therefore not compatible with most other tropical lowland inventories, which were usually carried out at ground level and inferred canopy data from fallen branches.
Among the genera found almost exclusively in the canopy are all Orthotrichaceae (*Macromitrium, Groutiella, Schlotheimia*), *Acrolejeunea, Cylindrocolea, Diplasiolejeunea* spp., *Caudalejeunea, Frullania* spp., *Neurolejeunea, Pycnolejeunea, Thysananthus* and most of the macrolichens.

While the rain forest lichens are mainly found on living bark or leaves, bryophytes may also occur on rotten logs, rocks or soil (Table 1). However, in the present study the latter habitats have been inventoried less intensively than the trees and the list of species occurring on logs, rock and soil should therefore be rather incomplete. Among the terrestrial bryophytes two groups of species occur: those occurring on well-drained white sands and those found on periodically inundated clay soils. *Leucobryum martianum* and *Zoopsis integrifolia* are species of the white sand soils. Species occuring on clay soils include *Campylopus surinamensis, Dicranella hilariana, Fissidens pauperculus* var. *pauperculus* and *Calypogeia miquelii.*

A comparison between the species found in the different forest types (Table 1) shows that 7 mosses, 13 liverworts, and 17 macrolichens are exclusive to the walaba forest, whereas 6 mosses, 22 liverworts and 1 macrolichen species were only collected in the mixed forest. The data indicate that the walaba forest is particularly characterized by species of macrolichens, whereas the mixed forest is characterized by liverworts.
The higher atmospheric humidity and lower light intensities in the mixed forest as compared to the walaba forest should account for the floristic differences in lichen and liverwort floras of the two forest types, liverworts in general being more hygrophytic and skiophytic than lichens. In the Kabalebo area, Suriname, about 200 km SE of Mabura Hill and similar in altitude and vegetation, Florschütz-de Waard and Bekker (1987) also found that a relatively large proportion of the liverworts occurred exclusively in the atmospherically humid forest types.
A closer comparison between the bryophyte floras of the Kabalebo and Mabura Hill areas shows that the following species are characteristic for the humid forest types (mixed forest, marsh forest in each of the areas: *Syrrhopodon incompletus, Callicosta bipinnata, Calymperes afzelii, Pilosium chlorophyllum, Callicostella rufescens* and *Lepidopilum surinamense* among the mosses, and *Lepidolejeunea involuta, Plagiochila laetevirens (=P. hondurensis), P. orbiguniana, Stictolejeunea squamata, Radula flaccida, Cyclolejeunea convexistipa, Lophocolea liebmanniana,* and *Lopholejeunea muelleriana* among the liverworts. Only few species occur exclusively in the dryer savanna forest and scrub in the Kabalebo area and the walaba forest at Mabura Hill: *Macromitrium pellucidum, Syrrhopodon ligulatus* (mosses) and *Cheilolejeunea trifaria* (liverworts). The lower number of species exclusive for the dryer forest types is due to the 'canopy effect' (Cornelissen & ter Steege 1989), i.e. the occurrence of xerophytic species in the upper canopy of a wider range of forest types, whether dry or humid. The 'canopy effect' is demonstrated by the following species: *Syrrhopodon parasiticus* var. *disciformis, Leucodontopsis geniculata, Groutiella obtusa, Orthostichopsis tetragona (*mosses*), Acrolejeunea torulosa, Frullania kunzei, F. nodulosa* and *Mastigolejeunea auriculata (*liverworts*).* All of these are characteristic elements of dry scrubby vegetation in the Kabalebo area but occur in the outer canopy of the mixed (and wallaba) forest at Mabura Hill.

Only one species, *Syrrhopodon cryptocarpos,* was exclusive to the greenheart forest in the Mabura Hill area. This low number may largely be due to the fact that only one tree was sampled in the greenheart forest.

The vertical distribution of the epiphytic bryophytes and lichens on trees in the walaba forest has been discussed in some detail by Cornelissen and ter Steege (1989), who distinguished between 'specialists' (narrow vertical amplitude) and 'generalists' (broad vertical amplitude). When comparing the vertical distributions of species found both in the mixed forest and the wallaba forest, it appears that the amplitudes are often similar in each of the forest types except for canopy species, which may extend lower down in the walaba forest than in the mixed forest. Examples are the canopy 'specialists' *Macromitrium punctatum, Sematophyllum subpinnatum (*mosses*), Acrolejeunea torulosa, Pycnolejeunea contigua, Thysananthus amazonica (*liverworts*), Bulbothrix fungicola, Coccocarpia erythroxyli, C. palmicola, C. filiformis, C. pellita* and *Dictyonema pavonia (*macrolichens*),* and the canopy 'generalists' *Ceratolejeunea*

Table 1: The distribution of bryophytes and macrolichens in the Mabura Hill area, Guyana. Microhabitat categories are: EU = epiphytic in forest understorey (0-3 m height), on saplings, shrubs or lianes; ET = epiphytic on tree trunks (0 -20 m height); EC = epiphytic in canopy of large trees (20-40 m height); EP = epiphyllous; DL = on decaying logs; SA = saxicolous; TE = terrestrial. Very moist habitats are indicated by underlining of records.
Forest types are given only for the epiphytes on trees: W = walaba forest (11 trees); G = greenheart forest (1 tree); M = mixed forest (5 trees). *Lejeunea caespitosa* Lindenb. is new to the Guianas.

	microhabitats							forest types		
	EU	ET	EC	EP	DL	SA	TE	W	G	M
Mosses										
Acroporium pungens (Hedw.) Broth.		x	x		x			x		x
Bryum coronatum Schwaegr.					x					
Callicosta bipinnata (Schwaegr.) C.M.	x	x								x
Callicosta evanescens C.M.	x		x							
Callicostella pallida (Hornsch.) Aongstr.					x					
Callicostella cf. rivularis (Mitt.) Jaeg.					x					
Callicostella rufescens (Mitt.) Jaeg.		x								x
Calymperes afzelii Sw.		x	x			x				x
Calymperes erosum C.M.		x	x		x			x	x	x
Calymperes lonchophyllum Schwaegr.	x	x	x					x		x
Calymperes palisotii Schwaegr. subsp. richardii (C.M.) S.Edwards			x							x
Campylopus surinamensis C.M.							x			
Crossomitrium patrisiae (Brid.) C.M.		x	x	x				x		x
Dicranella hilariana (Mont.) Mitt.							x			
Fissidens guianensis Mont. var. guianensis		x				x				x
Fissidens pauperculus Howe var. pauperculus							x			
Fissidens prionodes Mont.		x				x				
Fissidens similiretis Sull.	x					x				
Groutiella obtusa (Mitt.) Florsch.			x					x	x	x
Holomitrium arboreum Mitt.		x	x		x			x		
Hookeriopsis parkeriana (Hook & Grev.) Jaeg.	x									
Lepidopilum surinamense C.M.		x								x
Leucobryum crispum C.M.					x					
Leucobryum martianum (Horsch.) C.M.		x					x	x		x
Leucodontopsis geniculata (Mitt.) Crum & Steere			x					x		x
Leucoloma cruegerianum (C.M.) Jaeg.		x						x		
Leucomium strumosum (Hornsch.) Mitt.					x	x				
Macromitrium cirrosum (Hedw.) Brid.		x	x					x		
Macromitrium pellucidum Mitt.			x					x		
Macromitrium punctatum (Hook & Grev.) Brid.		x	x					x		x
Mniomalia viridis (Mitt.) Hedw.		x	x					x		x
Octoblepharum albidum Hedw.		x	x					x	x	x
Octoblepharum pellucidum C.M.		x	x					x		x
Octoblepharum pulvinatum (Dozy & Molk.) Mitt.		x								
Orthostichopsis tetragona (Hedw.) Broth.	x	x	x					x		x
Phyllodrepanium falcifolium (Schwaegr.) Crosby	x					x				
Pilosium chlorophyllum (Hornsch.) C.M.	x	x	x		x				x	x
Schlotheimia rugifolia (Hook) Schwaegr.			x					x		
Schlotheimia torquata (Hedw.) Brid.			x					x		
Sematophyllum subpinnatum (Brid.) Britt.			x					x		x
Sematophyllum subsimplex (Hedw.) Mitt.		x	x		x			x	x	x
Syrrhopodon cryptocarpos Dozy & Molk.		x							x	
Syrrhopodon incompletus Schwaegr.		x	x		x			x		x
Syrrhopodon ligulatus Mont.		x	x		x			x	x	x
Syrrhopodon parasiticus (Brid.) Besch. var. parasiticus		x	x			x		x		x
Syrrhopodon parasiticus (Brid.) Besch. var. disciformis (C.M.) Florsch.			x					x		x
Syrrhopodon parasiticus (Brid.) Besch. var. flexifolius (Mitt.) Reese		x	x					x		
Syrrhopodon simmondsii Steere		x	x					x	x	
Taxithelium planum (Brid.) Mitt.		x						x		x
Trichosteleum hornschuchii (Hampe) Jaeg..					x		x			
Trichosteleum papillosum (Hornsch.) Jaeg.					x					
Zelometeorium patulum (Hedw.) Manuel	x	x	x	x				x		x

Liverworts

	microhabitats							forest types		
	EU	ET	EC	EP	DL	SA	TE	W	G	M
Acrolejeunea torulosa (Lehm. & Lindenb.) Schiffn.			x					x		x
Aphanolejeunea diaphana (Evans) Schuster		x								x
Arachniopsis pecten Spruce							x			
Archilejeunea fuscescens (Hampe ex Lehm.) Fulford	x	x	x					x	x	x
Archilejeunea parviflora (Nees) Schiffn.	x		x		x	x				
Bazzania bidens (Nees) Trevis.		x								
Bazzania breuteliana (Lindenb. & Gott.) Trevis		x	x					x		
Bazzania cubensis (Gott.) Pagán		x						x		
Bazzania cuneistipula (Gott. & Lindenb.) Trevis		x	x					x		
Calypogeia miquelii Mont.						x	x			
Caudalejeunea lehmanniana (Gott.) Evans			x							x
Ceratolejeunea confusa Schuster			x					x		
Ceratolejeunea maritima (Spruce) Steph.		x	x	x				x	x	x
Ceratolejeunea patentissima (Hampe ex Gott.) Evans		x	x							x
Ceratolejeunea plumula (Spruce) Steph.			x	x						x
Ceratolejeunea rubiginosa Steph.		x								x
Cheilojeunea adnata (Kunze) Grolle		x	x					x	x	x
Cheilolejeunea rigidula (Mont. & Nees) Schuster		x	x		x			x	x	x
Cheilolejeunea trifaria (Nees) Mizut.		x	x		x			x		x
Colura cylindrica Herz.			x							x
Crossotolejeunea boryana (Mont.) Schiffn.	x									
Cyclolejeunea convexistipa (Lehm. & Lindenb.) Evans			x	x						x
Cylindricolea planifolium (Steph.) Schuster			x					x		x
Cyrtolejeunea holostipa (Spruce) Evans		x	x					x	x	x
Diplasiolejeunea cavifolia (Steph.) Steph.			x					x		x
Diplasiolejeunea cobrensis Gott. ex Steph.			x	x				x		x
Diplasiolejeunea pellucida (Meissn.) Schiffn.			x	x				x	x	x
Diplasiolejeunea rudolphiana Steph.			x					x	x	x
Drepanolejeunea crucianella (Tayl.) Evans		x	x		x			x		x
Drepanolejeunea fragilis Bischler		x	x					x	x	x
Frullania apiculata (Reinw. et al.) Dum.			x					x	x	x
Frullania mucronata (Lehm. & Lindenb.) Lehm. & Lindenb.		x	x					x		
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.		x	x	x				x	x	x
Frullania nodulosa (Reinw., Bl. & Nees) Nees			x					x		x
Frullania obcordata (Lehm. & Lindenb.) Lehm. & Lindenb.		x	x	x				x	x	x
Frullania riojaneirensis (Raddi) Aongst.			x							x
Haplolejeunea cucullata (Steph.) Grolle		x						x	x	x
Harpalejeunea stricta (Lindenb. & Gott.) Steph.		x	x					x		x
Harpalejeunea uncinata Steph.			x							x
Lejeunea caespitosa Lindenb.		x								x
Lejeunea (Microlejeunea) dimorphophylla Schuster		x	x					x	x	x
Lejeunea glaucescens Gott.					x					
Lejeunea laetevirens Mont. & Nees			x					x		x
Lepidolejeunea involuta (Gott.) Grolle		x	x	x				x	x	x
Leptolejeunea elliptica (Lehm. & Lindenb.) Steph.		x	x	x				x		x
Leptoscyphus ovatus (Spruce) Grolle			x					x		
Leptoscyphus porphyrius (Nees) Grolle		x	x					x		
Lophocolea liebmanniana Gott.		x								x
Lopholejeunea muelleriana (Gott.) Schiffn.		x								x
Lopholejeunea quelchii Steph. (=L. howei Evans)		x	x					x		x
Lopholejeunea subfusca (Nees) Steph.			x					x		x
Mastigolejeunea auriculata (Wils.) Schiffn.		x	x					x		x
Microlejeunea acutifolia Steph.		x	x							x
Micropterygium trachyphyllum Reim.					x					
Neurolejeunea seminervis (Spruce) Schiffn.		x	x					x		x
Odontolejeunea lunulata (EWeb.) Schiffn.			x	x				x		x
Odontoschisma denudatum (Mart.) Dum.		x	x					x		
Pictolejeunea picta (Gott. ex Steph.) Grolle		x			x					x
Plagiochila contigua Gott.		x	x							x
Plagiochila disticha (L. & L.) Mass.			x					x		
Plagiochila hypnoides (Willd.) Lindenb.		x	x					x		x
Plagiochila laetevirens Lindenb.		x						x		x
Plagiochila orbiguniana Mass.		x								x
Plagiochila pittieri Steph.		x	x					x	x	x
Plagiochila tenuis Lindenb.		x	x					x		
Prionolejeunea sp.	x	x								x
Pteropsiella serrulata Spruce							x			
Pycnolejeunea callosa (Lindenb.) Steph.			x					x		
Pycnolejeunea contigua (Nees) Grolle		x	x					x	x	x
Pycnolejeunea macroloba (Mont.) Schiffn.		x	x					x	x	x

	microhabitats						forest types		
	EU	ET	EC	EP	DL	SA	TE	W	G	M
Radula flaccida Lindenb. & Gott.		x		x				x		x
Radula caldana Aongstr.		x	x		x			x		x
Rectolejeunea brittoniae Evans		x	x							x
Rectolejeunea flagelliformis Evans		x	x					x	x	x
Riccardia amazonica (Spruce) Schiffn.					x					
Stenorrhipis grollei Gradst.						x				
Stictolejeunea squamata (Willd. ex Web.) Schiffn.		x	x							x
Symbiezidium barbiflorum (Lindenb. & Gott.) Evans		x	x							x
Symbiezidium transversale (Sw.) var. hookeriana		x	x					x		x
Thysananthus amazonicus (Spruce) Steph.			x					x	x	x
Trachylejeunea pandurantha (Spruce) Steph.		x			x			x		x
Zoopsis integrifolia (Spruce) Steph.					x		x			
Macrolichens										
Bulbothrix fungicola (Lynge) Hale			x	x				x		
Coccocarpia domingensis Vainio			x	x				x		x
Coccocarpia cf. epiphylla (Fée) Krempelh.			x	x				x		
Coccocarpia erythroxili (Spreng.) Swinsc. & Krog			x					x		x
Coccocarpia filiformis Arvidss.			x	x				x		x
Coccocarpia palmicola (Spreng.) Arvidss. & Gall.		x	x	x				x		x
Coccocarpia pellita (Ach.) Müll. Arg. emend. Sant.			x					x		x
Coenogonium linkii Ehrenberg ex Nees	x	x	x	x				x	x	x
Cladonia didyma (Fée) Wain.					x					
Cladonia subradiata (Vainio) Scriba		x	x		x			x		x
Collema leptaleum Tuck. var. bilbosum (Mont.) Zegel			x					x		
Crocynia biatorina (Mont.) Hue			x					x		
Crocynia gossypina (Sw.) Nyl.		x	x					x		x
Dictyonema pavonia (Sw.) Parm.			x					x		x
Eschatogonia prolifera (Mont.) Trevis		x	x					x	x	x
Heterodermia galactophylla (Tuck.) Trevis			x					x		
Leptogium coralloideum Vainio			x					x		x
Leptogium cf. marginellum (Sw.) Gray	x		x					x		
Leptogium cf. ulvaceum Malme			x							x
Pannaria isidioidea (Müll. Arg.) Vainio			x					x		x
Pannaria mariana (Fr.) Müll. Arg.			x	x				x		x
Pannaria stylophora Vainio			x					x		
Parmotrema coralliforme (Hale) Hale					x					
Parmotrema cristiferum (Taylor) Hale			x					x		
Parmotrema cf. dilatatum (Vainio) Hale			x					x		
Parmotrema endosulphureum (Hillm.) Hale			x					x		
Parmotrema latissimum (Fée) Hale			x							
Parmotrema mellissii (Dodge) Hale			x					x		
Phyllopsora cf. albicans Müll. Arg.		x	x					x		x
Phyllopsora cf. isidiotyla (Vainio) Riddle		x	x					x	x	x
Phyllopsora santensis (Tuck.) Swinsc. & Krog.		x	x					x		
Physcia fragilescens Zahlbr.			x					x		
Physma byrsinum (Ach.) Müll. Arg.			x					x		x
Pseudoparmelia sphaerospora (Nyl.) Hale			x		x			x		
Relicina subabstrusa (Gyel.) Hale			x					x		
Sticta weigelii (Ach.) Vainio			x					x		

maritima, *Cheilolejeunea rigidula*, *C. trifaria*, *Frullania obcordata*, and *Pycnolejeunea macroloba* (all liverworts). Their broader vertical distribution in the wallaba forest is probably due to the more open canopy foliage in the walaba forest as compared to that in the mixed forest. This assumption is further corroborated by the fact that macrolichens, a known photophilous group, provide many species exclusive to the walaba forest.

Acknowledgements

Thanks are due to H. ter Steege for his stimulating collaboration in the fieldwork and for help with identifications; to A. Thompson, T. Singh, B.J. Sommerfeldt, B.J.H. ter Welle and the Demerara Woods Company for help with the organization of the fieldwork and for providing accomodation in Guyana; and to A. Aptroot, J. Bekker and J. Florschütz-de Waard for help with identifications. The fieldwork was financed by the 'Werkgroep Studiereizen Ontwikkelingslanden', 'Miquel Fonds', 'Utrechts Universiteits Fonds' and the Faculty of Biology, University of Utrecht.

References

Cornelissen, J.H.C. & ter Steege, H. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. Journal of Tropical Ecology 5: 131-150.

Fanshawe, D.B. 1952. The vegetation of Guyana, a preliminary review. Oxford, Imperial Forestry Institute Paper 29: 1-96.

Florschütz-de Waard, J. 1990. A catalogue of the bryophytes of the Guianas II. Musci. Tropical Bryology 3:

——— **& Bekker, J.M. 1987**. A comparative study of the bryophyte flora of different forest types in West Suriname. Cryptogamie, Bryologie Lichénologie 8: 31-45.

Gradstein, S.R. & Hekking, W.H.A. 1989. A catalogue of the bryophytes of the Guianas I. Hepaticae and Anthocerotae. Journal of the Hattori Botanical Laboratory 66: 197-230.

———, **Montfoort, D. & Cornelissen, J.H.C. 1990**. Species richness and phytogeography of the bryophyte flora of the Guianas, with special reference to the lowland rain forest. Tropical Bryology 2: 117-126.

Hekking, W.H.A. & Sipman, H.J. 1988. The lichens reported from the Guianas before 1987. Willdenowia 17: 193-228.

Johannson, D. 1974. Ecology of vascular epiphytes in West African rain forests. Acta Phytogeographica Suecica 59: 1-136.

Richards, P.W. 1952. The tropical rain forest. Cambridge University Press.

———. **1954**. Notes on the bryophyte communities of lowland tropical rainforest, with special reference to Moraballi Creek, British Guyana. Vegetatio 5-6: 319-328.

———. 1984. The ecology of tropical forest bryophytes. In: R.M. Schuster (ed.), New Manual of Bryology Vol. 2, p. 1233-1270. Hattori Botanical Laboratory, Nichinan.

Steege, H. ter & Cornelissen, J.H.C. 1988. Collecting and studying bryophytes in the canopy of standing rain forest trees. In: J.M. Glime (ed.), Methods in Bryology, p. 285-290. Hattori Botanical Laboratory, Nichinan.

———— **&** ———. **1990**. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. Biotropica 21: 331-339.