

# Variation in epiphytic lichen and bryophyte composition and diversity along a gradient of productivity in *Populus tremuloides* stands of northeastern British Columbia, Canada<sup>1</sup>

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**Abstract:** The influence of site productivity on epiphyte diversity on aspen (*Populus tremuloides*) trunks was examined in 19 stands from northeastern British Columbia, whose site indices (dominant tree height at 50 y) ranged from 6.7 to 27.9 m. Canopy epiphyte communities responded strongly to gradients in site productivity. Correlations between plot scores along the axes of non-metric multidimensional scaling ordinations and environmental variables indicated that site index, diameter at breast height, tree age, bark cation concentrations (K, Ca, Mg, and Mn), canopy cover, and bark roughness were significant explanatory variables for epiphyte community composition at trunk base and at breast height. Less productive sites (site indices below 17.25) were dominated by crustose lichens. Indicator species in these sites included *Caloplaca cerina*, *C. holocarpa*, and *Catillaria glauconigrans*. Closed-canopy environments in the more productive stands were dominated by mosses. Associated indicator species included *Brachythecium* spp., *Pylaisiella polyantha*, and *Eurhynchium pulchellum*. Cover of epiphytic species at breast height was higher in stands with low site indices, whereas cover of epiphytic species at trunk base was higher in stands with high site indices. These findings would suggest that management for epiphyte community diversity in aspen dominated landscapes will necessitate the retention of mature aspen stands from across a range of site productivities.

**Keywords:** aspen, bryophytes, forest productivity, lichens, site index.

**Résumé :** L'influence de la productivité du site sur la diversité des épiphytes sur les troncs de peupliers faux-trembles (*Populus tremuloides*) a été examinée dans 19 peuplements forestiers du nord-est de la Colombie-Britannique ayant des indices de qualité de station entre 6,7 et 27,9 m (hauteur dominante à 50 ans). Les communautés épiphytes de la canopée répondaient fortement aux gradients de productivité du site. Des corrélations entre la position des parcelles sur les axes d'ordination axes d'ordination de cadrage multidimensionnel non-métrique et les variables environnementales indiquaient que l'indice de qualité de station, le diamètre à hauteur de poitrine, l'âge de l'arbre, les concentrations de cations dans l'écorce (K, Ca, Mg et Mn), le couvert forestier et la rugosité de l'écorce étaient des variables explicatives significatives de la composition des communautés d'épiphytes à la base des troncs et à hauteur de poitrine. Les sites moins productifs (avec des indices de moins de 17,25) étaient dominés par des lichens crustacés. Les espèces indicatrices de ces sites incluaient *Caloplaca cerina*, *C. holocarpa* et *Catillaria glauconigrans*. Les sites ayant un couvert forestier fermé dans les peuplements plus productifs étaient dominés par les mousses. Les espèces indicatrices associées incluaient *Brachythecium* spp., *Pylaisiella polyantha* et *Eurhynchium pulchellum*. Le recouvrement des espèces épiphytes à hauteur de poitrine était plus élevé dans les sites ayant un faible indice de qualité de station alors que le recouvrement des espèces épiphytes à la base des troncs était plus élevé dans les sites à fort indice. Ces résultats suggèrent que dans les paysages dominés par le peuplier faux-tremble, la gestion de la diversité des communautés épiphytes nécessitera de conserver des peuplements matures de peupliers, et ce, à l'intérieur d'un gradient de productivité de sites.

**Mots-clés :** bryophytes, indice de qualité de station, lichens, peuplier faux-tremble, productivité forestière.

**Nomenclature:** Anderson & Crum, 1990; Esslinger, 2006.

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## Introduction

Boreal and mixedwood forests of western Canada are experiencing ongoing high rates of deforestation, estimated at between 1.21 and 1.76% annually, especially in productive sites that support conversion to agriculture (Fitzsimmons, 2002; Hobson, Bayne & Wilgenburg, 2002). At the same time the utilization of aspen forests (*Populus tremuloides*) as an industrial wood supply has accelerated greatly in recent years, particularly in northeastern British Columbia (BC), reflecting the development of processing capacity for oriented strand board and other commercial products (Peterson & Peterson, 1995). This has led to conservation biology concerns about the retention of aspen stands, especially those that contain large-diameter trees, which could be of higher conservation value (Blood & Backhouse, 1998; Harding, 1994; Stelfox, 1995).

Although the development of epiphyte communities in aspen stands can be treated along a successional gradient from young to old stands, when examined over regional landscapes large even-aged aspen patches of fire origin also incorporate a large range of variation, reflecting gradients of both climate and site productivity (Chen, Krestov & Klinka, 2002). The resultant diversity of abiotic conditions and stand structural characteristics such as abundance of large-sized trees or canopy openings may be an important factor in structuring epiphyte communities. Preliminary evidence from montane coniferous forests in BC also suggests that epiphyte lichen communities respond strongly to site-specific factors such as those that provide enrichment of throughflow precipitation or changes in bark chemistry (Goward & Arsenault, 2000). Thus, the integration of site factors in habitat models might constitute a significant step towards a rational management of lichen communities.

In this study we hypothesize that aspen stands located on productive sites support a greater diversity of epiphytes compared to aspen stands of similar age located on less productive sites. We examined the response of epiphyte communities (lichens and bryophytes) in aspen-dominated stands from the boreal white and black spruce bioclimatic zone of northeastern BC. Changes in abundance of epiphytes were assessed against major stand structural and substrate characteristics, including site index, canopy opening, bark structure, bark pH, bark cation availability, and diameter at breast height.

## Methods

### STUDY AREA

The study was undertaken in the boreal white and black spruce (BWBS) bioclimatic zone in northeastern British Columbia (Figure 1). This zone represents the core of the natural distribution of trembling aspen (*Populus tremuloides*) in British Columbia (Meidinger & Pojar, 1991). The study sites were placed in fully stocked, even-aged trembling aspen stands of fire origin, with an occasional presence of balsam poplar (*Populus balsamifera*) on moist sites. Black spruce (*Picea mariana*) and white spruce (*Picea glauca*) also occasionally occurred as a minor component (Chen, Légaré & Bergeron, 2004).

Data (means for the period of 1951–1980) from the 4 closest weather stations (Dawson Creek, Dawson Creek A, Fort St. John, and Fort Nelson) indicate that precipitation during the warmest month ranges from 445 to 504 mm, mean annual temperature ranges from –1.4 to 1.3 °C, mean temperature of the warmest month ranges from 14.9 to 16.6 °C, and mean frost free period ranges from 78 to 115 d (Environment Canada, 1982). The soils of the *Populus* ecosystems in the study area are primarily fine-textured Grey Luvisols, with some Brunisols, Gleysols, and Regosols. Lamimoder and Mormoders are the most common humus forms in these trembling aspen ecosystems (Fons, Klinka & Kabzems, 1998).

### FIELD DATA COLLECTION

Nineteen aspen-dominated stands were selected for this study from a set of 60 stands previously studied by Chen, Klinka and Kabzems (1998), Chen, Krestov and Klinka (2002), and Chen, Légaré and Bergeron (2004). For each stand, site index (dominant trees height at age 50 y) was calculated based on the growth pattern of the 3 largest dominant trees present in the stand (details on the methodology and algorithms used to calculate the site index are available in Chen, Légaré & Bergeron, 2004). Thus, site index represents a productivity measure. Site index varied with latitude, elevation, aspect, slope position, edatopes, floor and mineral soil and physical and chemical properties, and concentration of foliar nutrients (Chen, Klinka & Kabzems, 1998). The stands were grouped into 4 equidistant site-index classes, representing site indices ranging from 6.7 to 27.9 m (Chen, Légaré & Bergeron, 2004) (Table I). The site-index classes were as follows: I: 6.65 to 11.95 m; II: 11.96 to 17.25 m; III: 17.26 to 22.55 m; and IV: 22.56 to 27.86 m. Mean elevation and slope of the selected stands were 666.8 m (range: 450–750 m) and 7.6% (range: 0–40%), respectively.

In each stand, 5 centre points were selected within a 20- × 20-m square, one at the centre and one at each corner. A plot constituted the 6 co-dominant aspens that were closest to each centre point, for a total of 5 plots per stand. Epiphytic bryophyte and lichen species were recorded on the north face of selected trees in 2 quadrats, one at breast-height (*ca* 1.4 m) and the other one at the base of the trunk, using a 10- × 30-cm grid subdivided in 1-cm<sup>2</sup> squares. For all sampled trees (6 trees per plot, 30 trees per stand, and 570 trees in total), percent cover of bryophytes and lichens (divided into crustose, foliose, and fruticose groups) was assessed by counting the number of 1-cm<sup>2</sup> squares covered by each group in each quadrat. From a subsample of 3 trees per plot (285 trees in total), epiphytes were identified to species or group of species (see Appendix I), evaluating cover of each taxon within the 10- × 30-cm grid. Epiphyte samples were collected for later determination where field identification was not possible. The roughness of the bark at breast height and at the base of each trunk was recorded on a 4-point scale (adapted from Gustaffson & Eriksson, 1995; 1 = smooth; 2 = rather smooth; 3 = rough; and 4 = very rough). The diameters at breast height (DBH) of all sampled trees were measured, and canopy cover was quantified with a densiometer at each plot centre.

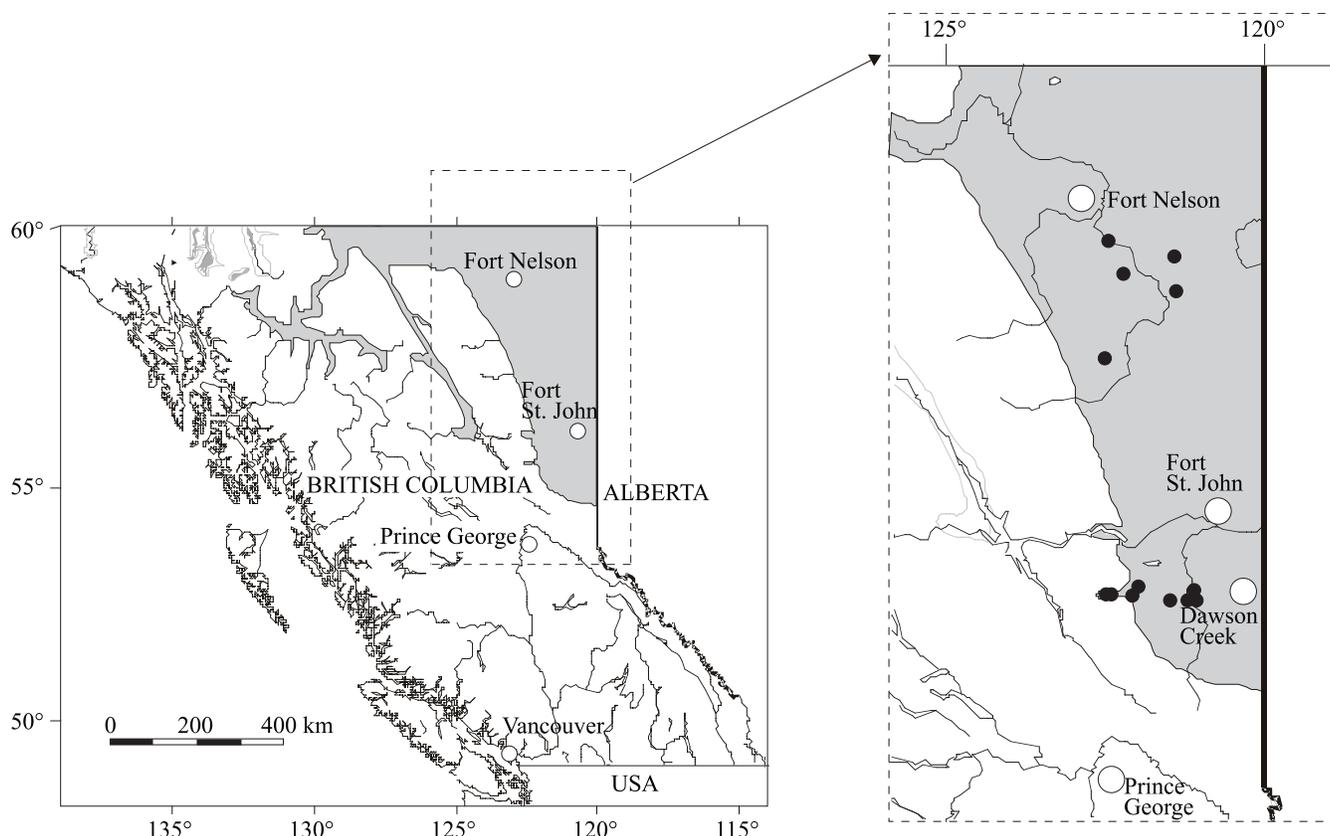


FIGURE 1. Site locations (closed circles) in northeastern British Columbia. The grey area represents the boreal white and black spruce bioclimatic zone.

TABLE I. Site, plot, and bark characteristics (mean  $\pm$  SE) for each site-index class<sup>a</sup>.

	Class I	Class II	Class III	Class IV	<i>F</i> <sup>a</sup>	<i>P</i>
<b>SITE CHARACTERISTICS</b>						
	( <i>n</i> = 4)	( <i>n</i> = 5)	( <i>n</i> = 6)	( <i>n</i> = 4)		
Site index (m)	8.52 $\pm$ 1.58	14.84 $\pm$ 1.6	20.51 $\pm$ 1.24	24.35 $\pm$ 1.79		
Tree age at breast height (y)	53.83 $\pm$ 0.65 <sup>a</sup>	50.47 $\pm$ 1.73 <sup>a</sup>	54.72 $\pm$ 3.93 <sup>a</sup>	46.17 $\pm$ 4.83 <sup>a</sup>	1.26	0.325
Dominant tree height (m)	8.76 $\pm$ 0.94 <sup>c</sup>	15.07 $\pm$ 0.80 <sup>b</sup>	21.39 $\pm$ 0.97 <sup>a</sup>	22.94 $\pm$ 1.68 <sup>a</sup>	31.84	< 0.0001
<b>PLOT CHARACTERISTICS</b>						
	( <i>n</i> = 20)	( <i>n</i> = 25)	( <i>n</i> = 30)	( <i>n</i> = 20)		
Diameter at breast height (cm) <sup>b</sup>	8.27 $\pm$ 2.06 <sup>d</sup>	12.41 $\pm$ 3.27 <sup>c</sup>	17.01 $\pm$ 5.39 <sup>b</sup>	20.90 $\pm$ 7.64 <sup>a</sup>	117.92	< 0.0001
Canopy cover (%) <sup>b</sup>	34.07 $\pm$ 27.03 <sup>c</sup>	58.73 $\pm$ 11.21 <sup>b</sup>	74.56 $\pm$ 13.13 <sup>a</sup>	70.10 $\pm$ 11.59 <sup>a</sup>	28.93	< 0.0001
<b>BARK CHARACTERISTICS</b>						
	( <i>n</i> = 20)	( <i>n</i> = 25)	( <i>n</i> = 30)	( <i>n</i> = 20)		
Ca concentration ( $\mu\text{l}^{-1}$ )	14 208.70 $\pm$ 2505.80 <sup>b</sup>	17 080.20 $\pm$ 3324.51 <sup>a</sup>	13 097.70 $\pm$ 3782.12 <sup>b</sup>	10 133.30 $\pm$ 1787.71 <sup>c</sup>	41.06	< 0.0001
Mg concentration ( $\mu\text{l}^{-1}$ ) <sup>b</sup>	79.27 $\pm$ 46.79 <sup>a</sup>	64.50 $\pm$ 15.76 <sup>b</sup>	51.95 $\pm$ 17.28 <sup>c</sup>	18.13 $\pm$ 11.64 <sup>c</sup>	15.89	< 0.0001
K concentration ( $\mu\text{l}^{-1}$ )	2574.23 $\pm$ 298.07 <sup>b</sup>	3205.96 $\pm$ 531.22 <sup>a</sup>	2897.21 $\pm$ 769.16 <sup>ab</sup>	3195.92 $\pm$ 677.34 <sup>a</sup>	8.58	< 0.0001
Mn concentration ( $\mu\text{l}^{-1}$ ) <sup>b</sup>	1144.17 $\pm$ 275.99 <sup>a</sup>	936.83 $\pm$ 88.28 <sup>a</sup>	900.35 $\pm$ 400.25 <sup>b</sup>	812.10 $\pm$ 189.37 <sup>c</sup>	51.78	< 0.0001
Basal bark roughness	2.12 $\pm$ 0.15 <sup>c</sup>	2.81 $\pm$ 0.10 <sup>b</sup>	3.02 $\pm$ 0.06 <sup>ab</sup>	3.27 $\pm$ 0.10 <sup>a</sup>	42.83	< 0.0001
Breast height bark roughness	2.25 $\pm$ 0.10 <sup>b</sup>	2.11 $\pm$ 0.10 <sup>b</sup>	2.21 $\pm$ 0.12 <sup>a</sup>	2.77 $\pm$ 0.16 <sup>a</sup>	8.61	< 0.0001
pH	6.00 $\pm$ 0.19 <sup>c</sup>	6.56 $\pm$ 0.14 <sup>a</sup>	6.30 $\pm$ 0.15 <sup>ab</sup>	6.11 $\pm$ 0.20 <sup>bc</sup>	7.74	0.000

<sup>a</sup>ANOVAs were used to compare mean values between different site-index classes. Values with the same letters are not significantly different ( $P > 0.05$ ). For nested analyses with plots and bark characteristics, only *F* and *P* values of the main factor (site index-class) are shown, but the nested effect [stand (site-index class)] was significant ( $P < 0.0001$ ) in all analyses.

<sup>b</sup>Rank transformation was performed.

#### CHEMICAL ANALYSIS

Two 5-  $\times$  5-cm pieces of bark were collected at breast height (on north-facing trunk aspects) with a wood chisel on 3 trees in each plot (the same trees that were used for epiphytic species determination). Two pH values were taken with a flat surface pH electrode using 0.5 mL of

distilled water placed on each bark sample (a total of 570 bark samples analyzed). A mean bark H<sup>+</sup> concentration was calculated for each tree by taking the anti-log of the pH values. The use of distilled water instead of a buffering solvent such as 0.1 M KCl tends to give higher pH values (Kricke, 2001), although the impact of this difference in methodol-

ogy may be reduced at these sites, where parent substrates (and dry deposition) are generally calcareous in nature. One bark sample per tree was subsequently dried for 24 h at 70 °C (285 bark samples analyzed). Between 0.25 and 0.3 g of dried bark from each sample was microwave digested in 5 mL of HNO<sub>3</sub> and 1.5 mL of H<sub>2</sub>O<sub>2</sub>. After digestion, this solution was diluted in distilled water to obtain a 50-mL solution, which was analyzed by inductively coupled plasma atomic emission photometer (ICP) for Ca, K, Mg, and Mn.

#### DATA ANALYSIS

We identified indicator species for the 4 site-index classes with the method of Dufrêne and Legendre (1997) in PC-ORD software version 4.34 (McCune & Mefford, 1999). Analyses were performed at the plot level (mean values from the subsample of 3 trees). The indicator values were calculated using the relative abundance and percent cover of species for each plot. Indicator values fell between 0 and 100, where 100 was given to a species found exclusively in all plots of a single site-index class. Significance of these indicator values was tested by permutation. The analyses were performed separately for tree base quadrats and breast height quadrats.

We used non-metric multidimensional scaling ordinations (NMS) performed with PC-ORD software version 4.34 (McCune & Mefford, 1999) to describe the species composition of moss and lichen communities along the productivity gradient and to explore relations between environmental variables and community structure. We conducted 2 different analyses, one on quadrats located at tree base and a second one on quadrats located at breast height. Analyses were performed at the plot level (mean values from the subsample of 3 trees). Only the species present in more than 5 plots out of 95 were incorporated into the ordination. Sorenson's similarity index was used as a distance measure. Analyses were run with 3 axes for the first ordination and with 2 axes for the second one as the reduction in stress was small when additional axes were added. For the first ordination, only results for the 2 axes with the higher coefficients of determination (estimates of amount of variation in the original data matrix represented on an axis) are given since they expressed more than 86% of the variation. We performed Spearson correlations between plot scores on the ordination axes, species scores, and environmental variables. Environmental variables considered were site index, age of the stand, canopy cover, and the mean values of bark

roughness, bark pH, bark cations, and DBH from each plot. Only the significant variables ( $P < 0.05$ ) were illustrated on the vector plot diagram. Each site-index class was represented by a different symbol on the plot position diagrams to facilitate the interpretation.

We performed 1-way ANOVAs to evaluate differences between stand characteristics (stand age and dominant tree height) among the site-index classes (site-index class:  $df = 3$ ; error:  $df = 15$ ). Nested ANOVAs were used to find differences between site-index classes for plot characteristics (DBH and canopy cover), bark characteristics (bark cations, bark roughness, and bark H<sup>+</sup> concentration [the means were log transformed and reported as pH]), species richness and species cover (mean values from the subsample of 3 trees), and mosses and foliose, fruticose, and crustose lichen abundances (mean values from the 6 sampled trees per plot). Site-index class was treated as a fixed factor and stand location as a random factor nested within site-index class (site-index class:  $df = 3$ ; stand [site-index class]:  $df = 15$ ; error:  $df = 76$ ). When the variables did not follow the assumptions of parametric ANOVAs, nested ANOVAs were performed on ranks of the variables. Comparisons of means were made by using the Tukey HSD multiple comparison test. Separate analyses were conducted for quadrats located at breast height and at trunk base.

## Results

### STAND, PLOT, AND BARK CHARACTERISTICS

Stand, plot, and bark characteristics of the sampled stands according to their site-index classes are shown in Table I. Dominant tree height and canopy cover were highest in classes III and IV, and DBH was highest in class IV. Tree age did not vary significantly according to site-index classes. Mg and Mn were lower in class IV and higher in classes I and II. Ca was also lower in class IV but higher in class II, while K was higher in classes II and IV. pH was lower in classes I and IV than in classes II and III. Bark roughness at trunk base and at breast height were higher in classes III and IV.

Table II shows correlations between environmental variables included in this study. Site index was positively correlated with DBH, canopy cover, bark roughness, and K concentrations and negatively correlated with Ca, Mg, Mn, and tree age. pH, Ca, Mg, and Mn were positively correlated, and all these variables were negatively correlated

TABLE II. Spearman correlations between environmental variables ( $n = 95$ ; \*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$ ; \*  $P < 0.05$ ).

	Site index	Ca	K	Mg	Mn	pH	Basal bark roughness	Breast height bark roughness	Tree age	DBH
Bark Ca	-0.550***									
Bark K	0.232*	0.03								
Bark Mg	-0.404***	0.551***	0.287**							
Bark Mn	-0.626***	0.628***	-0.042	0.404***						
Bark pH	0.084	0.367***	0.263**	0.240*	0.206*					
Basal bark roughness	0.577***	-0.292**	0.166	-0.337***	-0.476***	-0.202*				
Breast height bark roughness	0.230*	-0.420***	-0.139	-0.378***	-0.434***	-0.578***	0.570***			
Tree age	-0.213*	-0.050	-0.179	-0.097	0.162	-0.468***	0.19	0.287**		
DBH	0.816***	-0.515***	0.280**	-0.441***	-0.570***	-0.104	0.737***	0.415***	0.094	
Canopy cover	0.560***	-0.290**	0.187	-0.120	-0.436***	-0.017	0.557***	0.209*	-0.095	0.553***

with bark roughness and, except for pH, with DBH. Ca and Mn also showed a negative correlation with canopy cover. Canopy cover and DBH were positively correlated. Bark roughness at tree base and at breast height were also positively correlated to DBH and canopy cover, and roughness at breast height was positively correlated to tree age.

#### NUMBER OF SPECIES AND INDICATOR SPECIES

A total of 54 taxa were observed during this study: 41 epiphytic lichens and 13 epiphytic mosses (Appendix I). *Catillaria glauconigrans* was the most abundant lichen while *Brachythecium* spp. were the most abundant mosses. Seven cyanolichens were present: *Leptogium saturninum*, *Nephroma bellum*, *Peltigera canina*, *P. didactyla*, *P. leucophlebia*, *P. membranacea*, and *P. praetextata*. Except for *P. canina* and *P. didactyla*, they all occurred in classes III or IV.

Indicator species (Table III) were present in each site-index class. *Caloplaca cerina* and *C. holocarpa* were lichen indicator species of class I, while *Catillaria glauconigrans* was a lichen indicator of class II. *Pleurozium schreberi* was detected as a moss indicator species for class I. Classes III and IV were characterized by foliose lichens (*Physcia adscendens* and *Peltigera praetextata*), fruticose lichens (*Cladonia coniocraea*), and by mosses (e.g., *Brachythecium* spp., *Pylaisiella polyantha*, *Eurhynchium pulchellum*, and *Hylocomium splendens*). For class IV, indicator species were only found at the base of trees.

#### SPECIES COMPOSITION OF THE EPIPHYTIC COMMUNITY

The first axis of the NMS ordination conducted with quadrats at tree base explained 50.5% of the variance in the community and the second axis 35.6%. The first axis was positively correlated with site index, DBH, canopy cover,

and bark roughness and negatively correlated with Ca, Mg, Mn, and tree age (Figure 2c, Table IV). Less-productive plots (classes I and II) were clustered on the lower left-hand part of the ordination, while more-productive plots (classes III and IV) were clustered on the upper right-hand part of the ordination (Figure 2a). Characteristics associated with less-productive plots, such as higher bark cation concentrations and open canopy environments, favoured the lichens *Caloplaca holocarpa* and *Catillaria glauconigrans* and the moss *Pleurozium schreberi* (Figure 2b). The mosses species *Mnium* spp., *Pylaisiella polyantha*, and *Brachythecium* spp. and the lichen species *Bacidia* spp. and *Cladonia coniocraea* were more abundant in plots with closed-canopy environments characterized by trees with a larger DBH, a rougher bark texture, and lower bark cation concentrations (Figure 2b).

The first axis of the NMS ordination performed with quadrats at breast height explained 73.6% of the variance and the second axis 16.9%. The first axis was positively correlated with DBH, canopy cover, and site index and negatively correlated with Ca, K, Mg, and Mn (Figure 3c, Table V). Less-productive plots (classes I and II) can be observed in the left part of the graph, while more-productive plots (classes III and IV) can be observed in the right part of the graph (Figure 3a). Species with a preference for higher bark cation concentrations and open canopy environments such as *Caloplaca holocarpa*, *Catillaria glauconigrans*, and *Lecanora impudens* characterized less-productive plots (Figure 3b). Inversely, plots with closed canopy, larger trees, and lower bark cation concentrations favoured the moss *Pylaisiella polyantha* (Figure 3b).

#### COVER AND DIVERSITY OF EPIPHYTES

Epiphytic cover at breast height and at tree base differed significantly across site-index classes (breast height:  $F = 26.50$ ;  $P < 0.001$ ; tree base:  $F = 26.98$ ;  $P < 0.001$ ). The cover at breast height was lower and the cover at tree base was higher in site-index classes III and IV (Figure 4a). Richness at breast height was lower in class IV but was not significantly different from richness observed in class II ( $F = 9.61$ ;  $P < 0.001$ ) (Figure 4b). Richness at tree base did not vary among site-index classes ( $F = 1.98$ ;  $P = 0.124$ ) (Figure 4b). Stand factor was significant for richness and cover at breast height and at tree base (results not presented).

Mosses at tree base and crustose lichens at breast height were the most abundant groups across the site-index classes (Figure 5). Cover of mosses at tree base and at breast height differed significantly across classes (breast height:  $F = 69.20$ ;  $P = 0.011$ ; tree base:  $F = 91.23$ ;  $P < 0.0001$ ), with highest values in site-index classes III and IV. The abundance of crustose lichens at tree base and at breast height was significantly higher in classes I and II and lowest in classes III and IV (breast height:  $F = 81.64$ ;  $P < 0.0001$ ; tree base:  $F = 21.83$ ;  $P < 0.001$ ). Fruticose lichen at tree base ( $F = 9.09$ ;  $P < 0.001$ ) and foliose lichen at breast height ( $F = 12.75$ ;  $P < 0.001$ ) were significantly more abundant in class III (Figure 5). Stand factor was significant for all group abundances but foliose lichens at tree base (results not presented).

TABLE III. Mean percent cover values for indicator species within site-index classes.

Indicator species	Class I <i>n</i> = 20	Class II <i>n</i> = 25	Class III <i>n</i> = 30	Class IV <i>n</i> = 20
TREE BASE QUADRATS				
<i>Brachythecium</i> spp.	1.8	11.6	<b>18.2</b>	16.2
<i>Caloplaca cerina</i>	<b>0.5<sup>a</sup></b>	0	0	0
<i>Caloplaca holocarpa</i>	<b>0.4</b>	0.2	0.1	0
<i>Catillaria glauconigrans</i>	8.2	<b>13.4</b>	0.7	0.8
<i>Cladonia coniocraea</i>	0	0	<b>0.4</b>	+
<i>Eurhynchium pulchellum</i>	+ <sup>b</sup>	0	1.2	<b>5.1</b>
<i>Hylocomium splendens</i>	0.6	0	<b>1.8</b>	0.2
<i>Mnium</i> spp. <sup>c</sup>	0	0.4	2.5	6.2
<i>Peltigera praetextata</i>	0	0	<b>0.5</b>	0
<i>Pleurozium schreberi</i>	<b>0.5</b>	0	0	0
<i>Pylaisiella polyantha</i>	10.1	20.2	31.0	<b>35.4</b>
DIAMETER AT BREAST HEIGHT QUADRATS				
<i>Caloplaca cerina</i>	<b>2.7</b>	0.2	0.2	0
<i>Caloplaca holocarpa</i>	<b>3.0</b>	2.5	2.0	+
<i>Catillaria glauconigrans</i>	23.7	<b>42.1</b>	16.8	13.2
<i>Orthotrichum obtusifolium</i>	0	+	<b>0.1</b>	+
<i>Physcia adscendens</i>	0.2	0.3	<b>1.4</b>	0.2
<i>Physcia aipolia</i>	<b>0.3</b>	+	0.2	+

<sup>a</sup> Values in bold are significant at  $P < 0.05$ .

<sup>b</sup> % cover values  $< 0.1$  are indicated as +.

<sup>c</sup> *Mnium* spp.: *Mnium spinulosum*, *Plagiomnium drummondii*, *Plagiomnium cuspidatum*.

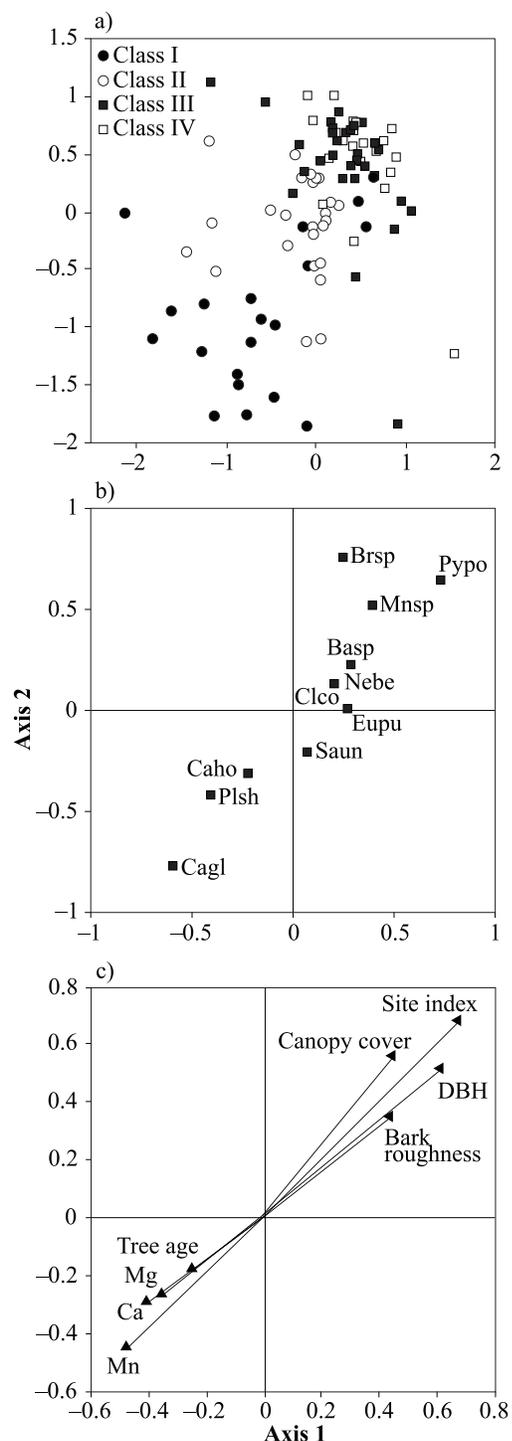


FIGURE 2. Non-metric multidimensional scaling on tree base quadrats showing a) the position of plots according to their epiphytic species composition; b) the position of epiphytic species (species codes are as follows: Basp: *Bacidia* spp.; Brsp: *Brachythecium* spp.; Cagl: *Catillaria glauconigrans*; Caho: *Caloplaca holocarpa*; Clco: *Cladonia coniocraea*; Eupu: *Eurhynchium pulchellum*; Mnsp: *Mnium* spp.; Nebe: *Nephroma bellum*; Plsh: *Pleurozium schreberi*; Pypo: *Pylaisiella polyantha*; Saun: *Sanionia uncinata*); and c) vector plot showing the relationships between the environmental variables and the ordination axes (environmental codes are as follows: DBH: diameter at breast height; Mn: bark manganese concentration; Mg: bark magnesium concentration; Ca: bark calcium concentration); only variables that were significantly correlated ( $P < 0.05$ ) with one or both ordination axes are shown.

Moss cover at tree base and at breast height were positively correlated to site index, DBH, canopy cover, and bark roughness and negatively correlated to Ca, Mg, and Mn (Table VI). On the other hand, lichen cover at tree base and at breast height were negatively correlated to site index and canopy cover and positively associated to Mn content. Lichen cover at breast height showed a positive correlation with Ca and Mg and a negative correlation with DBH. Richness at breast height (mosses and lichens) was negatively related to site index and pH, while richness at tree base (mosses and lichens) was negatively related to Ca and pH and positively related to bark roughness (Table VI). Tree age was positively correlated to lichen cover and richness at tree base and at breast height and negatively correlated to moss cover at tree base.

## Discussion

In the studied stands, site index has a clear effect on the abundance of individual lichen and bryophyte species and on the composition of epiphytic assemblages. However, the exact explanations behind these variations are difficult to determine, because potentially important factors such as tree size, bark characteristics, and canopy cover are all strongly and linearly correlated with site productivity and are thus difficult to separate from one another. The potential effects of these different factors are discussed in detail in the following sections.

### TREE AND STAND CHARACTERISTICS

The importance of light and humidity conditions for epiphytic vegetation is well known (Barkman, 1958). Most

TABLE IV. Spearman correlations between environmental variables, species, and plot locations along the 2 axes with the higher coefficients of determination of the non-metric multidimensional scaling ordination performed on abundance data of quadrats located at the base of the trees ( $n = 95$  plots, 18 species)<sup>a</sup>.

	Axis 1 $R^2 = 0.505$	Axis 2 $R^2 = 0.356$
ENVIRONMENTAL VARIABLES		
Site index	0.676***	0.675***
Diameter at breast height	0.616***	-0.512***
Tree age	-0.256*	-0.190
Bark Ca	-0.403***	-0.294**
Bark K	-0.039	-0.304**
Bark Mg	-0.357***	-0.272**
Bark Mn	-0.477***	-0.453***
Canopy cover	0.454***	0.558***
Bark roughness	0.444***	0.353***
SPECIES		
<i>Pylaisiella polyantha</i>	0.733***	0.641***
<i>Bacidia</i> spp.	0.292**	0.222*
<i>Brachythecium</i> spp.	0.256*	0.748***
<i>Cladonia coniocraea</i>	0.208*	0.131
<i>Mnium</i> spp.	0.396***	0.517***
<i>Sanionia uncinata</i>	0.070	-0.213*
<i>Nephroma bellum</i>	0.209*	0.128
<i>Caloplaca holocarpa</i>	-0.220*	-0.317**
<i>Catillaria glauconigrans</i>	-0.585***	-0.768***
<i>Eurhynchium pulchellum</i>	0.276**	0.005
<i>Pleurozium schreberi</i>	-0.397***	-0.426***

<sup>a</sup> Only those variables with significant correlations ( $P < 0.05$ ) with one or both axes are shown. \*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$ ; \*  $P < 0.05$ .

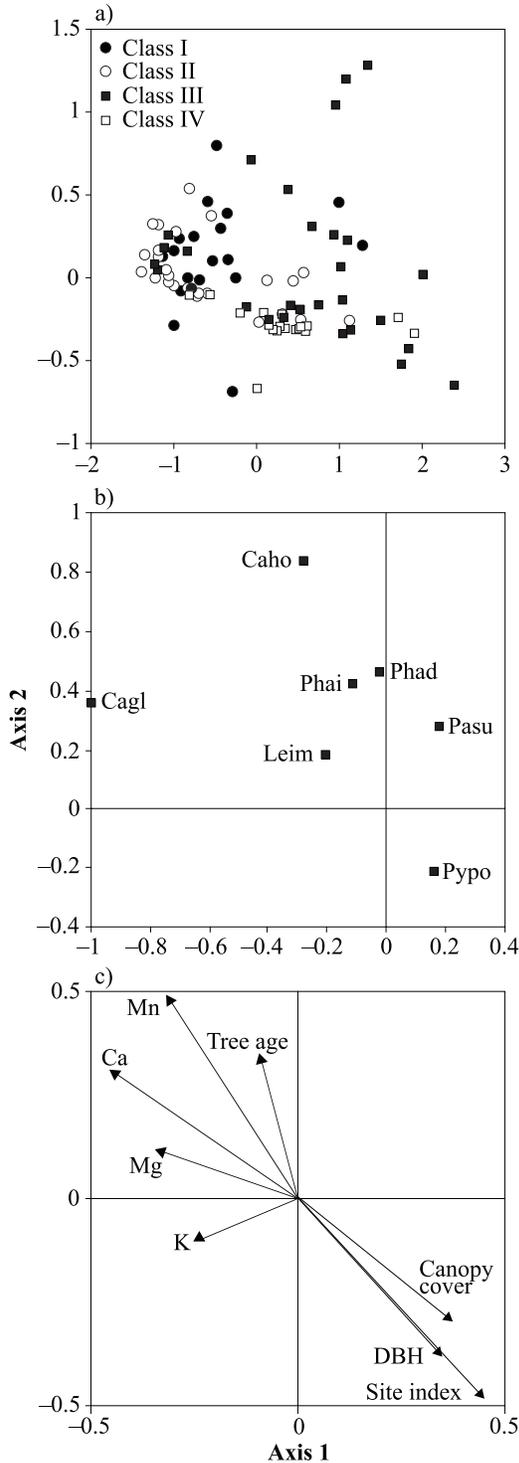


FIGURE 3. Non-metric multidimensional scaling on breast height quadrats showing a) the position of plots according to their epiphytic species composition; b) the position of epiphytic species (species codes are as follows: Cagl: *Catillaria glauconigrans*; Caho: *Caloplaca holocarpa*; Leim: *Lecanora impudens*; Pasu: *Parmelia sulcata*; Phad: *Physcia adscendens*; Phai: *Physcia aipolia*; Pypo: *Pylaisiella polyantha*); and c) vector plot showing the relationships between the environmental variables and the ordination axes (environmental codes are as follows: DBH: diameter at breast height; Mn: bark manganese concentration; Mg: bark magnesium concentration; K: bark potassium concentration; Ca: bark calcium concentration); only variables that were significantly correlated ( $P < 0.05$ ) with one or both ordination axes are shown.

TABLE V. Spearman correlations between environmental variables, species, and plot locations along the 2 axes with the higher coefficients of determination of the non-metric multidimensional scaling ordination performed on abundance data of quadrats located at breast height ( $n = 95$  sites, 10 species)<sup>a</sup>.

	Axis 1 $R^2 = 0.736$	Axis 2 $R^2 = 0.169$
ENVIRONMENTAL VARIABLES		
Site index	0.432***	-0.461***
Diameter at breast height	0.334**	-0.363***
Tree age	-0.090	0.332**
Bark Ca	-0.433***	0.298**
Bark K	-0.240*	-0.103
Bark Mg	-0.323**	-0.114
Bark Mn	-0.311**	0.479***
Canopy cover	0.356***	-0.278**
SPECIES		
<i>Catillaria glauconigrans</i>	-0.996***	0.358***
<i>Caloplaca holocarpa</i>	-0.278**	0.840***
<i>Physcia aipolia</i>	-0.019	0.462***
<i>Lecanora impudens</i>	-0.205*	0.179
<i>Physcia adscendens</i>	-0.112	0.421***
<i>Parmelia sulcata</i>	0.181	0.280**
<i>Pylaisiella polyantha</i>	0.164	-0.214*

<sup>a</sup> Only those variables with significant correlations ( $P < 0.05$ ) with one or both axes are shown. \*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$ ; \*  $P < 0.05$ .

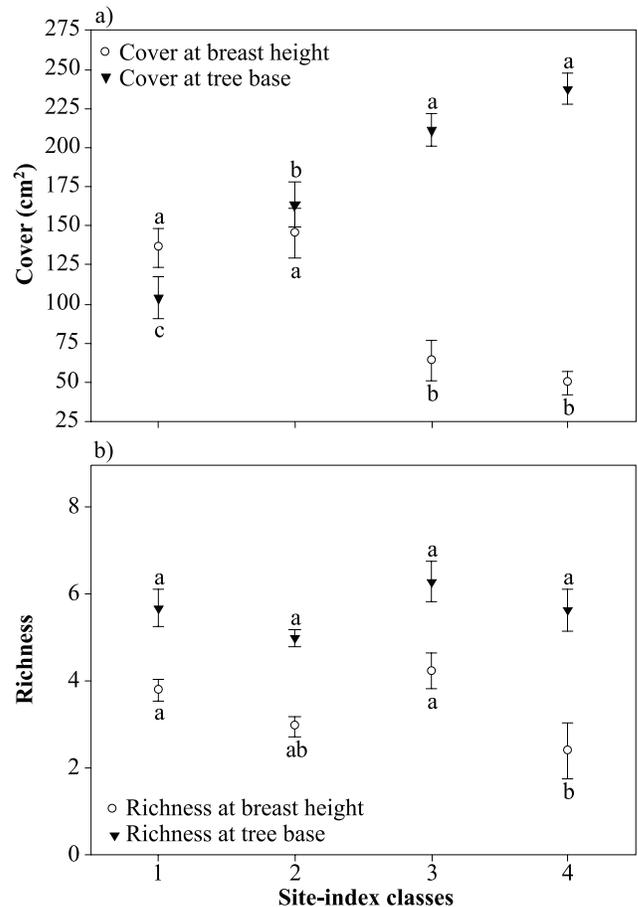


FIGURE 4. Mean and standard errors (from the subsample of 3 trees) within each site-index class and according to the position of the quadrats of a) cover of mosses and lichens and b) richness of mosses and lichens. Classes with different letters are significantly different at  $P < 0.05$  based on nested ANOVAs.

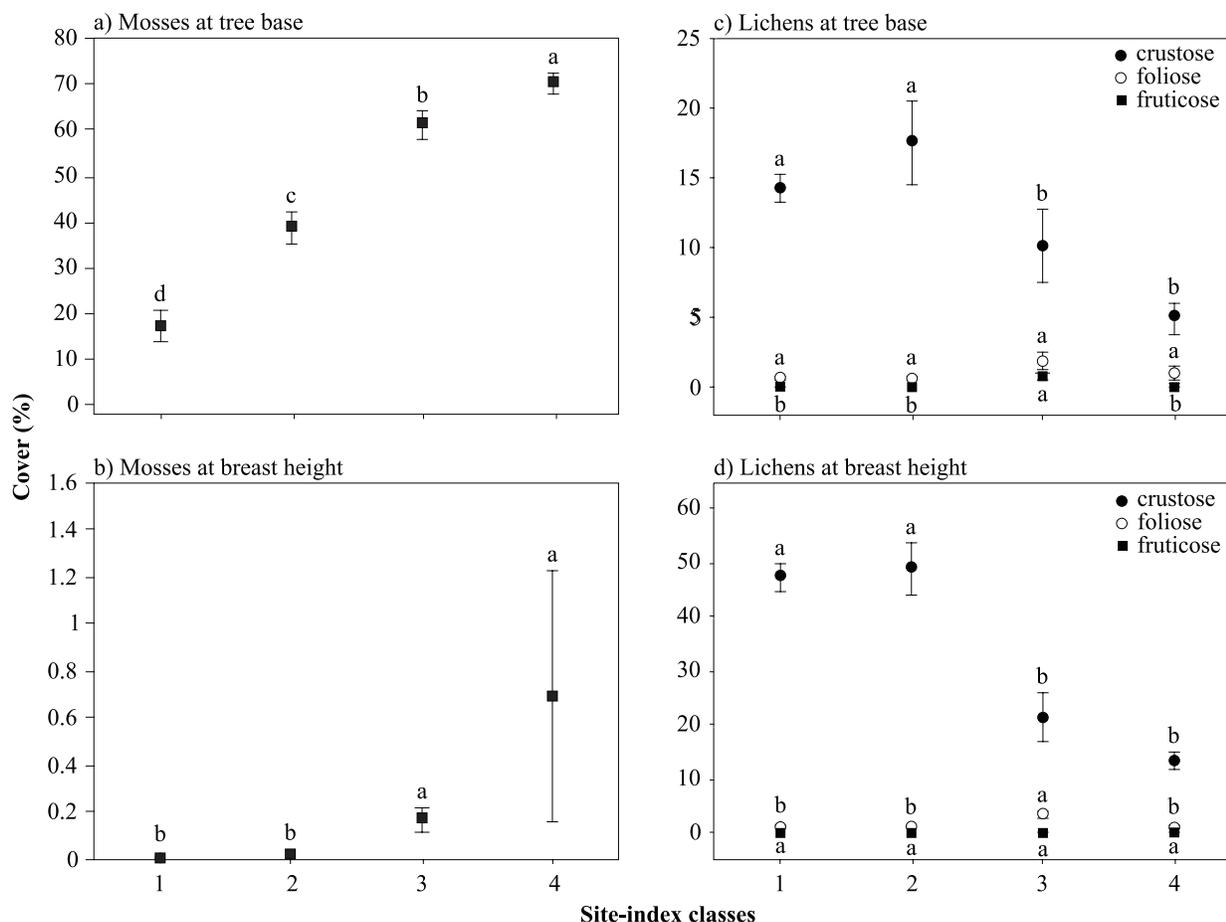


FIGURE 5. Mean  $\pm$  SE (from the 6 sampled trees per plot) within each site-index class of a) mosses at tree base, b) mosses at breast height c), crustose, foliose, and fruticose lichens at tree base, and d) crustose, foliose, and fruticose lichens at breast height. Classes with different letters are significantly different at  $P < 0.05$  based on nested ANOVAs performed on ranks.

TABLE VI. Spearman correlations between richness and cover indices and environmental variables ( $n = 95$ ; \*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$ ; \*  $P < 0.05$ ).

	Site index	Ca	K	Mg	Mn	pH	DBH	Canopy cover	Basal bark roughness	Breast height roughness	Tree age
Moss cover at tree base	0.775***	-0.409***	0.111	-0.450***	-0.539***	0.125	0.586***	0.509***	0.408***	-	-0.351***
Moss cover at breast height	0.341***	-0.287**	-0.131	-0.406***	-0.223*	-0.195	0.469***	0.246*	-	0.288**	0.183
Lichen cover at tree base	-0.377***	0.11	-0.07	0.064	0.278**	-0.225*	-0.156	-0.281**	-0.113	-	0.330**
Lichen cover at breast height	-0.579***	0.447***	0.171	0.295**	0.425***	-0.004	-0.402***	-0.416***	-	-0.078	0.291**
Richness at tree base	0.096	-0.228*	-0.037	-0.081	0.004	-0.207*	0.192	0.007	0.215*	-	0.375***
Richness at breast height	-0.251*	0.048	-0.115	-0.027	0.16	-0.201*	-0.149	-0.074	-	-0.001	0.375***

epiphytic bryophytes are favoured by shaded conditions with high air humidity, whereas lichens are more abundant in sunny environments, although some groups such as cyanolichens require high humidity (Gustafsson & Eriksson, 1995). At the tree level, relative humidity also tends to be higher at the trunk base and decrease with height (Barkman, 1958; McCune, 1993). The dominance of bryophytes at trunk base and the dominance of lichens at breast height in our study is thus related to different humidity levels.

At the stand level, high tree density and canopy cover are often beneficial for the occurrence of bryophyte species because the shade provided by neighbouring trees creates better microclimatic conditions; however, a deficit of light may restrict many epiphytes (Ojala, Mönkkönen & Inkeröinen, 2000), especially lichen species. We hypothesize that the reduced canopy cover in our classes I and II stands may create more xeric microclimatic conditions, similar to those resulting from edge effects in the small

patch stands examined by Gignac and Dale (2005). Gignac and Dale (2005) studied the bryophytes and lichens from sub-humid low-boreal forest environments in northern Alberta in large patches (interior forest habitat) and in small patches (edge habitat) of mature aspen stands. Comparisons with our less productive aspen stands (e.g., class I or II), show few species in common with interior forest habitats. Interestingly, cryptogams that were characteristic indicators of our least productive stands (*Caloplaca cerina*, *Caloplaca holocarpa*, *Physcia aipolia*) had relatively high indicator values in the small patch (edge habitat) plots of Gignac and Dale. Many moss indicators of our classes III and IV are also indicators of interior forest habitat in large patches. According to Hazell *et al.* (1998), weft-forming species such as *Pylaisiella polyantha* (indicator species of class IV) have a low tolerance to low humidity. Thus, the light gradient appears to be an important factor at the stand scale.

The differences observed between stands along the stand productivity gradient may have been attenuated by the relatively young age of the stands in our study. Old-growth stands may accumulate greater species diversity than younger stands because (1) they possess unique structural attributes, (2) they have a longer history of forest continuity, increasing the probability that a propagule reaches a stand, and/or (3) there is a longer period of time for bryophyte and lichen vegetative and sexual expansion. For example, a much greater species richness was observed in a 278-y-old *Populus tremuloides* stand in western Québec when compared against stands that were 70 and 125 y in age (Boudreault, Gauthier & Bergeron, 2000). The stands sampled in the present study, though characterized by a well-developed overstory, fell well below the old-growth threshold of 100 y used by Ojala, Mönkkönen, and Inkeröinen (2000) and 122 y by Crites and Dale (1998). In spite of this, there were differences along the productivity gradient that parallel changes usually observed along a chronosequence. Epiphyte communities of less-productive forests are close in composition to those found in young stands, having a higher proportion of green-algal lichen than moss cover (Lesica *et al.*, 1991; McCune, 1993). More-productive forests with closed canopy are more similar to old-growth forests, with a greater abundance of bryophytes and cyanolichens. In many respects, this change in community composition also parallels successional trends observed in pine forests from adjacent sub-boreal montane environments (Coxson & Marsh, 2001).

Not surprisingly, tree size was significant in explaining epiphyte diversity. Because the age of our trees did not differ among site-index classes, it is clear that the greater cover of mosses and foliose and fruticose lichens on our larger trees (classes III and IV) are not explained by a longer period of time for epiphyte establishment or expansion. These larger trees (DBH measurements) had sizes similar to those observed in the old-growth stands of Ojala, Mönkkönen, and Inkeröinen (2000) and Crites and Dale (1998). Several authors have noted that the number of epiphytic species on Fennoscandian *P. tremula* is strongly correlated with trunk diameter (Gustafsson & Eriksson, 1995; Hazell *et al.*, 1998; Ojala, Mönkkönen & Inkeröinen, 2000). For instance, large-diameter aspens favoured the mosses *Orthotrichum speciosum*, *Orthotrichum obtusifolium*, and *Pylaisiella polyantha*,

which in turn were correlated with rough bark (Hazell *et al.*, 1998). In a study undertaken in Finland, Rolstad and Rolstad (1999) found that occurrence of the rare epiphytic lichen *Usnea longissima* in *Picea abies* forests was better predicted by tree size than tree age. Our results seem to confirm the predictions of Hazell *et al.* (1998), who stated that independent of tree age, large aspens are important for epiphytes because (1) they provide a different environment based on bark structure, bark chemistry, and moisture conditions than small aspens and (2) their rougher bark has a better chance to intercept moss and lichen propagules.

#### BARK CHARACTERISTICS

Bark structure influences epiphyte colonization and growth (Brodo, 1973). Trees with a very smooth bark provide a more xeric substrate for epiphytic species than trees with a thick bark (Sheard & Jonescu, 1974). Thick and fissured bark has high water interception and retention (McGee & Kimmerer, 2002), can trap more diaspores than smooth bark (Brodo, 1973), and constitutes a special microhabitat that is moist and sheltered against wind (Barkman, 1958; Brodo, 1973). Bark thickness also increases with age and diameter in aspens (Gustafsson & Eriksson, 1995). Bates (1992) notes that moisture relations at the bark surface, obtained from correlations with bark slope and bark roughness, were the primary factor in structuring epiphyte communities on *Quercus* and *Fraxinus* in western Scotland. Our results show that bark roughness can also vary according to site productivity. The direct correlation between increasing moss cover and bark roughness showed that bark structure was a major variable in structuring epiphyte communities on aspen.

Bark pH and bark chemistry have been shown to be of major importance in determining the composition of epiphyte communities (Barkman, 1958; Gauslaa, 1985; Bates, 1992). For instance, lichens from the *Lobarion* and *Xanthorion* alliances are associated with barks with high pH and high cation levels (Bates, 1992). The *Lobarion* alliance comprises many cyanolichens that are rare on trees with acid bark (Kuusinen, 1996). Cyanolichens occur more frequently on aspen in late-successional stands (Kuusinen, 1996; Hedenås & Ericson, 2000) because they require high levels of atmospheric moisture as well as liquid water for photosynthetic activity and growth (Lange, Kilian & Ziegler, 1986) and are susceptible to high irradiance (Gauslaa & Solhaug, 1996). Seven cyanolichen species were observed in this study, and they mainly occurred in more-productive closed canopy stands from classes III and IV. Although the presence of *Lobaria pulmonaria* has previously been used as an indicator of stand continuity (Kuusinen, 1996; Hedenås & Ericson, 2000; Ojala, Mönkkönen & Inkeröinen, 2000; Gu *et al.*, 2001; Campbell & Fredeen, 2004; Radies & Coxson, 2004), it was absent from sampling plots in the present study. However, *Lobaria* was observed growing on large-diameter trunks of *P. balsamifera* near adjacent watercourses; the larger bark crevices on these trees may provide more favourable microsites for establishment. The more continental climate of northeastern BC compared to maritime Fennoscandian climate may restrict *L. pulmonaria* growth to these more humid microsites, irrespective of stand

age. This same factor of greater continentality may explain many of the observed differences between the bark epiphyte assemblages found on *P. tremuloides* in northeastern British Columbia and on *P. tremula* in Fennoscandian climates.

The *Xanthorion* alliance is characterized by pioneer photophilous lichen species (e.g., *Caloplaca* spp., *Physcia* spp., and *Xanthoria parietina*) (James, Hawksworth & Rose, 1977) occurring on thin smooth bark (Kuusinen, 1994). The higher light level of class I and the thinner and smoother barks in this class favoured some species of the *Xanthorion* alliance, such as *Caloplaca holocarpa*, *C. cerinea*, and *Physcia aipolia* (indicator species of class I); these species were almost absent from class IV. Thus, for the epiphytic species for which preferences for particular conditions in bark chemistry are known, other factors such as bark texture, general light or humidity conditions appear to have been more limiting in the context of the present study.

### Conclusion

These findings show that site productivity may be just as important a variable in predicting landscape-level diversity of epiphytic lichens and bryophytes as is successional status. This has important implications for the development of spatially explicit landscape models, such as those used by Dettki and Esseen (2003), and points to the importance of retaining mature aspen stands that represent a range of site productivities in regional landscapes.

### Acknowledgements

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APPENDIX I. Number of aspen trunks (*n*) on which each species was recorded (out of 285 total) and mean % cover for epiphytic lichen and moss species in respective basal and breast height sampling plots<sup>a</sup>.

	Plot location on trunk			
	Base		Breast height	
	<i>n</i>	%	<i>n</i>	%
EPIPHYTIC LICHENS				
<i>Bacidia carneoalbida</i>	1	+	0	0
<i>Bacidia obscurata</i>	1	+	0	0
<i>Bacidia</i> spp.	85	3	0	0
<i>Caloplaca cerina</i>	4	+	29	0.7
<i>Caloplaca holocarpa</i>	22	0.2	124	1.9
<i>Catillaria glaucograna</i>	116	5.6	268	24.1
<i>Cladonia chlorophaea</i>	3	+	0	0
<i>Cladonia coniocraea</i>	10	0.1	0	0
<i>Cladonia fimbriata</i>	1	+	0	0
<i>Cladonia pyxidata</i>	1	+	0	0
<i>Cladonia</i> spp.	5	0.1	0	0
<i>Cladonia subulata</i>	3	+	0	0
<i>Cladonia umbricola</i>	1	+	0	0
<i>Collema furfuraceum</i>	0	0	1	+
<i>Collema</i> sp.	0	0	2	+
<i>Crustose</i> sp.	0	0	3	+
<i>Lecanactis</i> sp.	0	0	1	+
<i>Lecania dubitans</i>	0	0	1	+
<i>Lecanora impudens</i>	6	0.1	19	0.4
<i>Lecanora</i> sp.	1	+	3	+
<i>Lecidella euphorea</i>	2	+	3	+
<i>Leptogium saturninum</i>	1	+	0	0
<i>Melanelia subaurifera</i>	0	0	2	+
<i>Melanohalea olivaceoides</i>	0	0	1	+
<i>Melanohalea septentrionalis</i>	0	0	3	+
<i>Nephroma bellum</i>	6	0.1	1	+
<i>Parmelia sulcata</i>	0	0	7	0.1
<i>Peltigera canina</i>	8	0.3	0	0
<i>Peltigera didactyla</i>	2	+	0	0
<i>Peltigera leucophlebia</i>	1	+	0	0
<i>Peltigera membranacea</i>	1	+	0	0
<i>Peltigera praetextata</i>	4	0.2	0	0
<i>Physcia adscendens</i>	0	0	70	0.6
<i>Physcia aipolia</i>	3	+	28	0.1
<i>Physconia perisidiosa</i>	0	0	2	+
<i>Ramalina dilacerata</i>	0	0	1	+
<i>Ramalina farinacea</i>	0	0	1	+
<i>Ramalina</i> sp.	0	0	1	+
<i>Usnea</i> sp.	1	+	5	+
<i>Usnea substerilis</i>	0	0	1	+
<i>Vulpicida pinastri</i>	1	+	0	0
EPIPHYTIC MOSSES				
<i>Brachythecium</i> spp.	223	12.6	2	+
<i>Bryum</i> sp.	1	+	0	0
<i>Eurhynchium pulchellum</i>	11	1.5	0	0
<i>Hylocomium splendens</i>	18	0.7	0	0
<i>Mnium</i> spp. <sup>b</sup>	57	2.2	0	0
<i>Orthotrichum elegans</i> Nees	1	+	0	0
<i>Orthotrichum obtusifolium</i>	5	+	19	+
<i>Pleurozium schreberi</i>	8	0.1	0	0
<i>Ptilidium pulcherrimum</i>	3	+	0	0
<i>Ptilidium crista-castrensis</i>	2	+	0	0
<i>Pylaisiella polyantha</i>	221	24.8	6	+
<i>Sanionia uncinata</i>	38	1.8	0	0
Other epiphytic mosses <sup>c</sup>	123	2.4	0	0

<sup>a</sup> + denotes a mean value of < 0.1%.

<sup>b</sup> *Mnium* spp.: *Mnium spinulosum*, *Plagiomnium drummondii*, *Plagiomnium cuspidatum*.

<sup>c</sup> Other epiphytic mosses are *Campylium* spp., *Platydictya* spp., *Amblystegium* spp., and *Platygyrium repens*.