

Site factors determining epiphytic lichen distribution in a dieback-affected spruce–fir forest on Whiteface Mountain, New York: microclimate

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Relationships between microclimatic site factors and cover of epiphytic lichen species were studied in a dieback-affected forest of *Picea rubens* and *Abies balsamea* on Whiteface Mountain, New York, U.S.A. Canonical correspondence analysis revealed an effect of light and water relations on epiphytic lichen abundance, but these factors only accounted for less than 10% of total variance in species data. Neither light nor evaporation, relative humidity, water-holding capacity of bark, or air temperature differed at the trunks between trees of different species or vitality. These results suggest that microclimate is probably not the main cause of significant differences in the epiphytic lichen diversity of spruce and fir and of living trees and snags. However, as canopy structure at the study site changed recently due to dense young growth of *A. balsamea*, it is possible that past differences in microclimate still exert an influence on present-day within-stand variation of epiphytic lichen abundance.

Key words: epiphytic lichens, evaporation, forest dieback, light (PPFD), relative humidity, temperature, water-holding capacity of bark

Introduction

Epiphytic lichen diversity in montane coniferous forests affected by pollutant-caused forest dieback is usually significantly different from that of comparable healthy forest stands (Hauck 2003). This has been found in stands of *Picea abies* and *Abies alba* in central Europe (Gliemeroth 1990, Legrand & Asta 1995, Hauck & Runge 1999) and of *Picea rubens* in eastern North America (Schmull *et al.* 2002, Schmull & Hauck 2003).

In a case study carried out in the Harz Mountains, northern Germany, lower concentrations of S, Mn and Cu in stemflow and bark, were found to enable higher lichen abundance on dieback-affected versus healthy trees of *Picea abies* (Hauck *et al.* 2001, 2002a, 2002b, Hauck & Runge 2002). The lower concentrations in stemflow and bark are due to needle loss decreasing the interception of substances from the atmosphere and due to damage of the root system reducing the uptake of ions from the soil (Hauck 2003). The potential of excess amounts of S

(Lechowicz 1982, Kershaw 1985), Mn (Hauck et al. 2002c, 2002d, 2003, Paul et al. 2003, 2004) and Cu (Branquinho et al. 1997, Shapiro 2002, Hauck & Zöller 2003) to limit lichen abundance has been shown experimentally. Microclimatic factors, such as light and water supply, appear to be of subordinate significance for the high epiphytic lichen diversity on dieback-affected *P. abies* in the Harz Mountains (Hauck et al. 2000, Hauck 2003). The high atmospheric load of long-distance transported, acidic pollutants in this area (Hauhs 1985, Andreae 1994), apparently lessens the significance of most site factors other than element concentrations (Hauck 2005).

In dieback-affected *Picea rubens* stands of eastern North America, the situation is more complex. Schmull et al. (2002) and Schmull and Hauck (2003) studied the relations between forest dieback and epiphytic lichen abundance on Whiteface Mountain in the Adirondacks, upstate New York, because Whiteface Mountain is the area with the most severe damage to *P. rubens* (Johnson 1987). This is because of low base saturation and acid neutralizing capacity of the soils of the Adirondacks combined with the exposed position of the Whiteface Mountain massif (Civerolo et al. 2003). However, the pollutant load of the atmosphere is significantly lower on Whiteface Mountain than in the Harz Mountains. For example, in 1998–2000, annual mean pH of incident precipitation was 4.5 in the Adirondacks (Driscoll et al. 2003) as compared with 3.9–4.0 in the Harz Mountains (Hauck & Runge 2002, Hauck et al. 2002a).

In contrast to the Harz Mountains, a dominant role of chemical site factors in controlling epiphytic lichen abundance on damaged and healthy *P. rubens* could not be substantiated on Whiteface Mountain. S and Cu concentrations in stemflow or bark were not related to lichen abundance, whereas cover of some lichen species on *P. rubens* decreased with increasing Mn/Fe ratio of bark (Schmull et al. 2002, Schmull & Hauck 2003). Species decreasing with the Mn/Fe ratio included *Hypogymnia physodes*, a species for which Fe has been shown to alleviate Mn-induced chlorophyll degradation and growth inhibition of soredia (Hauck et al. 2003). Whether negative correlations between the cover of several lichen species and the NO_3^- concen-

tration were due to a limitation of epiphytic lichen abundance by high NO_3^- supply is unclear (Schmull et al. 2002, Hauck 2003).

Since chemical site factors may be less significant for differences in the lichen diversity on dieback-affected versus healthy spruce trees on Whiteface Mountain than in the Harz Mountains, it is appropriate to test the hypothesis that microclimate could be a major cause for these differences on *P. rubens*. In other localities, the significance of light, water relations and temperature for epiphytic lichen distribution has been shown repeatedly (Halonen et al. 1991, Campbell & Coxson 2001, Benson & Coxson 2002). Hence, we tested the hypothesis that differences in epiphytic lichen abundance between dead and living trees would be caused by higher photosynthetically active radiation (PAR), higher evaporation, higher temperature, higher water-holding capacity of the substrate and lower relative humidity on dead than on living trees.

Apart from *P. rubens*, living and dead trees of *Abies balsamea* also were included in the study, as both species are associated with each other on Whiteface Mountain. In contrast to *P. rubens*, *A. balsamea* does not suffer from pollutant-caused forest dieback (Johnson 1987, Schmull & Hauck 2003), but a sufficient number of dead fir trees was available from natural mortality.

Material and methods

Study site

Field studies were carried out on Whiteface Mountain in the Adirondacks, Essex Co., New York, U.S.A. The sample plot was located on the northwestern slope of Mt. Esther, which is part of Whiteface Mountain, at an elevation of 1100 m (44°23'23"N, 73°53'76"W). The tree layer consisted of red spruce (*Picea rubens*), balsam fir (*Abies balsamea*) and paper birch (*Betula papyrifera*). Many spruce trees of the area were affected by pollution-caused forest dieback. Though timber was harvested in the lower spruce–fir zone of Whiteface Mountains in the early 20th century (Peart et al. 1992), trees were probably never felled on the sample plot. At 603 m, yearly precipitation is 1100 mm

(National Atmospheric Deposition Program, unpubl.), annual mean temperature is 6.2 °C, and the prevailing winds are westerly. Average length of the growing season is shorter than 105 days (Atmospheric Sciences Research Center unpubl. data). Data on weather conditions on Whiteface Mountain during the investigation period from July to September 2000 is compiled in Table 1.

Selection of sample trees

A 100 × 100 m sample plot was set up and spruce and fir trees with a minimum diameter at breast height of 15 cm and minimum height of 5 m were numbered. Ten trees each of living spruce, dead spruce, living fir and dead fir were randomly selected out of a total of 138 trees for measurements of light influx, evaporation and water-holding capacity of bark. Further, three groups of trees, located in three different subjectively chosen parts of the sample plot, were selected for measuring diurnal variation of relative humidity, evaporation and air temperature. Measurements were carried out on one tree each of living spruce, dead spruce, living fir and dead fir per group so that a total of twelve trees was investigated in this part of the study. The trees of each group should grow as close to one another as possible and should be similar in diameter and height. All investigations were restricted to a standard aspect (west) and height (100–200 cm above the ground) of the tree trunks to be consistent with other studies of our group (Schmull & Hauck 2003).

Vegetation mapping

Epiphytic lichen vegetation was recorded from all sample trees. Cover of all epiphytic lichen species was estimated as a percentage of the studied trunk area (at a height of 100–200 cm in western exposure). Where necessary for identification, lichen samples were qualitatively analyzed for lichen compounds by thin-layer chromatography (Culberson & Ammann 1979). Nomenclature of lichen species is based on Esslinger and Egan (1995). Nomenclature of

Lepraria jackii, which is not included there, refers to Tønsberg (1992).

Light

Photosynthetic photon flux density (PPFD; $\lambda = 400\text{--}700\text{ nm}$) was measured in $\mu\text{mol m}^{-2}\text{ s}^{-1}$ with silicon photovoltaic detectors (LI-190SA, LICOR, Lincoln, Nebraska, U.S.A.) and LI-1000 dataloggers on twelve days with evenly cloudy skies. Sensors were held at a height of 150 cm above the ground at a distance of 10 cm from the trunk surface in horizontal position adjusted with a spirit level. Three replicate measurements were recorded within one minute from each tree per sampling day. Incident PPFD outside the forest was measured at the nearby Whiteface Mountain toll road, simultaneously to data recording at the trees in order to specify tree-PPFD as percentage of incident PPFD.

Water-holding capacity of bark

Five grammes of bark pieces per tree, which were cleared from epiphytes with a toothbrush and which had a maximum diameter of 3 cm, were stored in deionized water for 24 h. After removing the excess water with a paper towel, wet bark weight was determined. Dry weight was measured, after the bark had been stored at 105 °C for 24 h. Water-holding capacity was calculated as wet minus dry weight and specified

Table 1. Weather conditions on Whiteface Mountain at 603 m during the investigation period from July to September 2000. Sum of precipitation from daily measurements; mean values of the other parameters are calculated from daily means of hourly measurements. Source: University at Albany, Atmospheric Sciences Research Center, Whiteface Mountain Field Station, Wilmington, New York.

	July	Aug.	Sep.
Precipitation (mm)	106	80	60
Mean temperature (°C)	15.6	16.3	11.5
Mean relative humidity (%)	76	78	76
Mean wind speed (m s^{-1})	1.2	1.2	1.4
Mean wind direction (°)	214	218	210

as percentage water content related to dry weight (% dw).

Daily evaporation

Evaporation was determined by using Piche evaporimeters (Stoutjesdijk & Barkman 1992) mounted at 150 cm above the ground at a distance of 2 cm from the tree trunk. Deionized water evaporated from a green filter paper with a diameter of 3 cm. Evaporimeters were scaled in steps of 100 μ l. Evaporation was recorded daily between 17:00 and 18:00 for one month from 4 August to 3 September 2000.

Diurnal variation of relative humidity, temperature and evaporation

Relative humidity, air temperature and evaporation were measured hourly from 8:30 (i.e. shortly before direct insolation of the northwest-facing slope with the sample plot) to 18:30 on 5–6 days per tree group consisting each of one living spruce, dead spruce, living fir and dead fir. Air humidity and temperature were determined by using an Assmann psychrometer subsequent to an adjustment time of 3 min, after the wet thermometer of the psychrometer was moistened (Stoutjesdijk & Barkman 1992); the Assmann psychrometer was mounted 150 cm above the ground 2 cm in front of the trunk. Evaporation was measured with Piche evaporimeters as described above.

Statistics

All data were tested for normal distribution with the Shapiro-Wilk test. Significance of differences in vegetation data, which were not normally distributed, was tested with the Kruskal-Wallis test. A two-way analysis of variance (ANOVA) was used to test the influence of the tree species, tree vitality and the interaction between these parameters on PPFD, daily evaporation and water-holding capacity of bark. In a three-way ANOVA that was run to test dependencies of the daily courses of relative humidity, evaporation and air

temperature from stand variables the location of sample trees within the study site was studied in addition to tree species and tree vitality. These analyses were carried out with SAS 6.04 software (SAS Institute Inc., Cary, North Carolina, U.S.A.). Detrended correspondence analysis (DCA) was applied to study differences between tree species and vitality in variation of epiphytic lichen abundance. Canonical correspondence analysis (CCA) was used to relate site factors to variation of epiphytic lichen cover on tree trunks. The significance of correlations between epiphytic lichen data and environmental parameters was tested with a Monte-Carlo permutation test with 1000 iterations. Species occurring on less than five trees were excluded from all ordination procedures. Species names in the ordination diagram (Fig. 2) consist of the first three letters each of the genus and the species epithet; the complete names can be taken from Table 2. DCA and CCA were calculated with the program PC-ORD 4.01 (MjM Software, Gleneden Beach, Oregon, U.S.A.).

Results

Epiphytic lichen diversity

A total of 44 lichen species were found on the sample trees used for measurements of microclimate. Table 1 shows frequency and cover values of the lichen species recorded from the 40 sample trees used for measurements of light, evaporation and water-holding capacity. The main difference in epiphytic lichen abundance was found between the tree species. In DCA ordination, *P. rubens* and *A. balsamea* trees form two distinct groups (Fig. 1). A single dead spruce tree was located in the cluster of fir trees. This is because of the absence of the typical spruce epiphyte *Arthonia caesia*, the scarce occurrence of *Imshaugia aleurites*, and the high cover of the typical fir epiphytes *Hypogymnia physodes*, *Loxospora ochrophaea* and *Micarea melaena*. Two fir trees, which were located in the spruce cluster (Fig. 1), were characterized by high cover values of *Arthonia caesia*, whereas a third fir differed from fir trees by high abundance of *Imshaugia aleurites* and *Lepraria jackii*. Typical spruce

species have low Axis 1 scores in the ordination space of Fig. 2; such species are, aside from *Arthonia caesia* and *Imshaugia aleurites*, e.g.,

Hypocenomyce friesii and *Alectoria sarmentosa*. Species with a preference for fir (and high Axis 1 scores in Fig. 2) are *Loxospora ochrophaea*,

Table 2. Frequency and cover of epiphytic lichen species on *Picea rubens* and *Abies balsamea*. Freq.: frequency defined as number of sample trees ($n = 10$) with occurrence of the respective species. Cover: arithmetic mean $\pm$ standard error. K-W: Kruskal-Wallis test; d.f. = 3; levels of significance: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

	<i>Picea rubens</i>				<i>Abies balsamea</i>				K-W
	Living trees		Dead trees		Living trees		Dead trees		
	Freq.	Cover	Freq.	Cover	Freq.	Cover	Freq.	Cover	
<i>Alectoria sarmentosa</i>	3	0.1 ± 0.1	4	0.1 ± 0.0	3	0.1 ± 0.1	2	0.1 ± 0.0	
<i>Arthonia caesia</i>	8	18.0 ± 5.0	9	22.0 ± 5.0	8	11.0 ± 5.0	3	6.4 ± 5.8	*
<i>Bryoria capillaris</i>	1	0.0 ± 0.0	3	0.1 ± 0.1	3	0.1 ± 0.1	3	0.2 ± 0.1	
<i>Bryoria furcellata</i>	0	0.0 ± 0.0	1	0.1 ± 0.1	2	0.1 ± 0.0	4	0.1 ± 0.1	
<i>Bryoria fuscescens</i>	3	0.1 ± 0.1	4	0.1 ± 0.1	3	0.1 ± 0.1	5	0.4 ± 0.2	
<i>Bryoria nadvornikiana</i>	3	0.2 ± 0.1	4	0.1 ± 0.0	1	0.0 ± 0.0	2	0.2 ± 0.1	
<i>Bryoria subcana</i>	0	0.0 ± 0.0	1	0.0 ± 0.0	2	0.2 ± 0.2	1	0.0 ± 0.0	
<i>Calicium glaucellum</i>	0	0.0 ± 0.0	1	2.0 ± 2.0	0	0.0 ± 0.0	0	0.0 ± 0.0	
<i>Chaenotheca chrysocephala</i>	0	0.0 ± 0.0	2	1.3 ± 0.9	0	0.0 ± 0.0	1	1.8 ± 1.8	
<i>Chaenotheca ferruginea</i>	1	1.0 ± 1.0	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	
<i>Cladonia coniocraea</i>	5	1.9 ± 1.2	8	2.8 ± 1.4	3	0.5 ± 0.4	7	1.1 ± 0.4	
<i>Cladonia digitata</i>	2	0.1 ± 0.0	1	0.1 ± 0.1	1	0.0 ± 0.0	0	0.0 ± 0.0	
<i>Cladonia fimbriata</i>	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.0 ± 0.0	
<i>Cladonia macilenta s. lato</i>	2	0.1 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	
<i>Cladonia pyxidata s. lato</i>	0	0.0 ± 0.0	1	0.0 ± 0.0	0	0.0 ± 0.0	1	0.2 ± 0.2	
<i>Cladonia squamosa</i>	5	1.3 ± 1.0	7	5.9 ± 3.1	3	0.1 ± 0.0	4	0.2 ± 0.1	
<i>Evernia mesomorpha</i>	0	0.0 ± 0.0	2	0.1 ± 0.0	2	0.1 ± 0.1	3	0.1 ± 0.1	
<i>Flavopunctelia soledica</i>	5	0.1 ± 0.0	9	0.4 ± 0.1	7	0.6 ± 0.2	10	0.7 ± 0.1	**
<i>Haematomma ochroleucum</i>	1	0.1 ± 0.1	0	0.0 ± 0.0	3	2.5 ± 1.6	6	6.0 ± 2.8	*
<i>Hypocenomyce friesii</i>	7	5.1 ± 2.3	5	2.7 ± 1.5	1	0.1 ± 0.1	0	0.0 ± 0.0	**
<i>Hypocenomyce scalaris</i>	3	0.4 ± 0.4	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	*
<i>Hypogymnia krogiae</i>	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.5 ± 0.5	2	1.6 ± 1.5	
<i>Hypogymnia physodes</i>	9	1.7 ± 1.0	10	2.6 ± 1.1	10	10.0 ± 2.2	10	9.3 ± 2.4	***
<i>Imshaugia aleurites</i>	10	7.5 ± 3.1	10	5.6 ± 2.4	10	5.1 ± 1.6	5	0.2 ± 0.1	***
<i>Japewia subaurifera</i>	0	0.0 ± 0.0	0	0.0 ± 0.0	5	0.6 ± 0.3	4	1.6 ± 1.5	**
<i>Lecanora impudens</i>	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.5 ± 0.5	0	0.0 ± 0.0	
<i>Lecanora pulicaris</i>	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.1 ± 0.1	0	0.0 ± 0.0	
<i>Lecidea leprarioides</i>	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.0 ± 0.0	
<i>Lecidea nylanderii</i>	9	5.4 ± 2.4	5	2.9 ± 1.4	7	8.9 ± 3.6	5	2.9 ± 1.6	
<i>Lepraria jackii</i>	9	8.2 ± 3.5	10	5.3 ± 1.5	9	6.2 ± 2.5	10	9.1 ± 3.4	
<i>Loxospora cismonica</i>	0	0.0 ± 0.0	0	0.0 ± 0.0	2	0.9 ± 0.6	0	0.0 ± 0.0	
<i>Loxospora ochrophaea</i>	0	0.0 ± 0.0	2	2.9 ± 2.7	2	6.1 ± 4.1	4	12.0 ± 6.0	
<i>Micarea melaena</i>	1	0.4 ± 0.4	5	3.4 ± 2.3	2	2.3 ± 2.2	1	0.3 ± 0.3	
<i>Micarea prasina</i>	2	3.3 ± 2.5	3	4.4 ± 2.8	0	0.0 ± 0.0	1	0.3 ± 0.3	
<i>Mycoblastus alpinus</i>	1	0.8 ± 0.8	0	0.0 ± 0.0	1	0.1 ± 0.1	0	0.0 ± 0.0	
<i>Mycoblastus fucatus</i>	0	0.0 ± 0.0	2	0.1 ± 0.1	4	0.3 ± 0.2	3	0.1 ± 0.1	
<i>Mycoblastus sanguinarius</i>	1	0.0 ± 0.0	3	0.2 ± 0.2	9	6.4 ± 2.8	4	2.3 ± 1.0	**
<i>Parmelia saxatilis</i>	0	0.0 ± 0.0	3	0.4 ± 0.2	7	2.2 ± 1.1	8	2.4 ± 1.1	**
<i>Parmeliopsis capitata</i>	1	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	
<i>Platismatia glauca</i>	4	0.1 ± 0.0	8	0.3 ± 0.1	10	2.7 ± 0.8	10	1.9 ± 0.8	***
<i>Pseudevernia cladonia</i>	3	0.1 ± 0.1	4	0.1 ± 0.0	6	0.2 ± 0.1	8	0.4 ± 0.1	*
<i>Pseudevernia consocians</i>	1	0.0 ± 0.0	4	0.3 ± 0.2	7	0.4 ± 0.1	3	0.1 ± 0.0	*
<i>Ropalospora chlorantha</i>	0	0.0 ± 0.0	0	0.0 ± 0.0	2	0.6 ± 0.5	5	3.2 ± 1.9	***
<i>Usnea sp.</i>	1	0.0 ± 0.0	6	0.2 ± 0.0	7	0.4 ± 0.2	10	2.8 ± 1.7	***

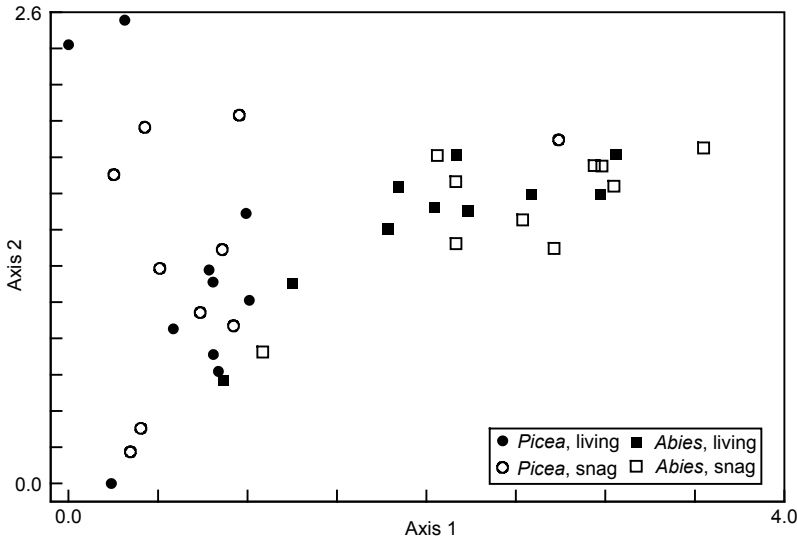


Fig. 1. DCA ordination of 40 living or dead trees of *Picea rubens* and *Abies balsamea*. Included are cover values of 28 lichen species with occurrence on more than five sample trees. Total variance in species data: 3.335. Eigenvalues: 0.608 (Axis 1), 0.306 (Axis 2). Length of gradient: 3.654 (Axis 1), 2.361 (Axis 2).

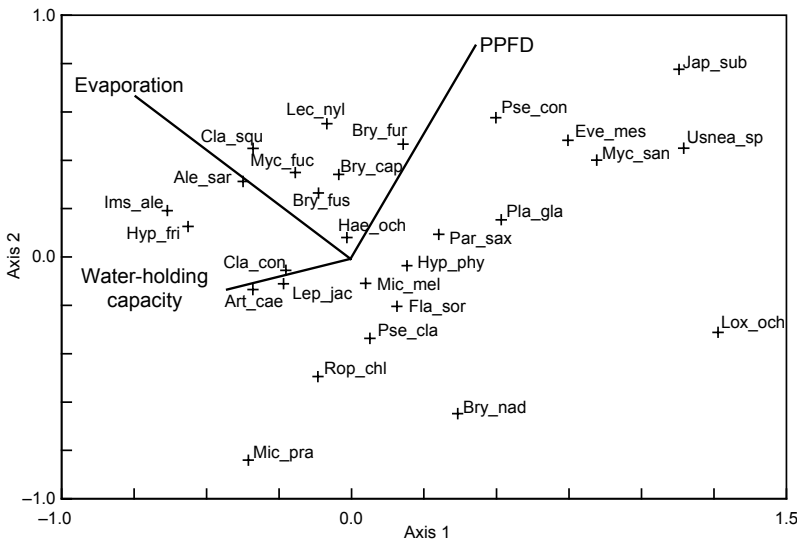


Fig. 2. CCA ordination of cover data of 28 lichen species with occurrence on more than five out of 40 living or dead sample trees of *Picea rubens* and *Abies balsamea*. Total variance in species data: 3.445. Eigenvalues: 0.286 (Axis 1), 0.093 (Axis 2). Cumulative percentage variance of species data explained: 8% (Axis 1), 11% (Axis 2). Pearson correlation coefficients between species and environmental data: $r = 0.74$ (Axis 1), $r = 0.56$ (Axis 2). Monte Carlo permutation test: $p \leq 0.05$ (Axis 1).

Japewia subaurifera, *Usnea* sp., *Mycoblastus sanguinarius*, and *Evernia mesomorpha*. Further species, with a less marked preference for fir, are *Flavopunctelia soredica*, *Haematomma ochroleucum*, *Hypogymnia physodes*, *Platismatia glauca*, *Pseudevernia cladonia* and *P. consocians* (Table 2 and Fig. 2). *Flavopunctelia soredica*, *Haematomma ochroleucum*, *Hypogymnia physodes*, *Pseudevernia cladonia*, *Platismatia glauca*, and *Usnea* sp. are more abundant on snags than on living trees, whereas *Hypoconomyce friesii*, *Imshaugia aleurites* and *Mycoblastus sanguinarius* are more frequent on living than on dead trees (Table 2).

Microclimatic measurements

Mean light intensity, evaporation and water-holding capacity of bark did not differ between living spruce, dead spruce, living fir and dead fir (Table 3 and Fig. 3). An effect of tree species and tree vitality was not observed either on diurnal variation of evaporation, air temperature and relative humidity (Figs. 4–5). ANOVA further shows that the location of the sample trees within the 100×100 m sample plot did not exert an influence on the results (Figs. 4–5). Evaporation and air temperature reached the maximum values in the afternoon hours, whereas at the same time rela-

Fig. 3. Daily mean evaporation on the trunk surfaces of ten trees each of living or dead spruce and fir from 4 August to 3 September 2000.

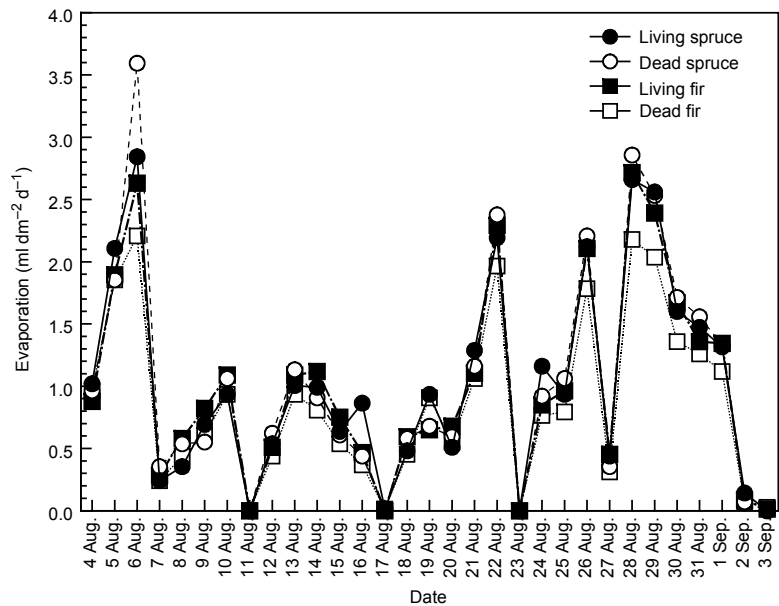


Fig. 4. Diurnal variation of evaporation on the trunk surfaces of living and dead trees of *Picea rubens* and *Abies balsamea* ($n = 3$). No significant differences according to three-way ANOVA considering the potential impact of tree species, tree vitality and location of the sample tree within the 100×100 m study plot ($F = 0.87$, d.f. = 9).

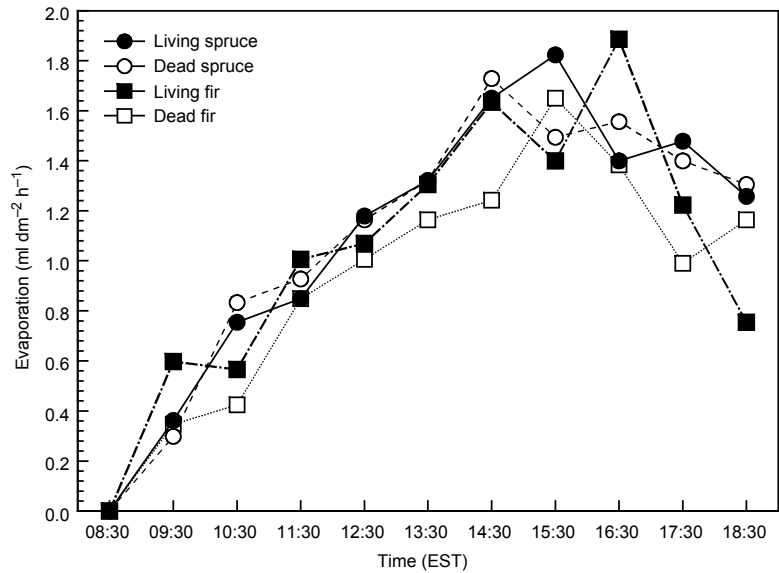


Table 3. Mean light influx, daily evaporation and water-holding capacity on living or dead spruce and fir trees. Arithmetic mean $\pm$ standard error ($n = 10$). PPFD at tree trunk is given in percent of PPFD from outside the forest (mean values of 12 days). Evaporation was measured daily for one month. WHC: water-holding capacity. F values represent results from a two-way ANOVA testing the effect of tree species and tree vitality on the parameters measured; all results not significant (n.s.; d.f. = 3).

	<i>P. rubens</i>		<i>A. balsamea</i>		<i>F</i>
	Alive	Dead	Alive	Dead	
PPFD (%)	17.0 $\pm$ 1.0	16.4 $\pm$ 1.6	18.6 $\pm$ 2.0	19.4 $\pm$ 1.2	1.38 n.s.
Evaporation (ml dm ⁻² d ⁻¹)	10.3 $\pm$ 0.6	10.5 $\pm$ 0.8	10.1 $\pm$ 0.6	8.7 $\pm$ 0.7	0.88 n.s.
WHC (% dw)	68.5 $\pm$ 6.1	61.3 $\pm$ 3.2	66.4 $\pm$ 8.1	70.1 $\pm$ 6.7	0.36 n.s.

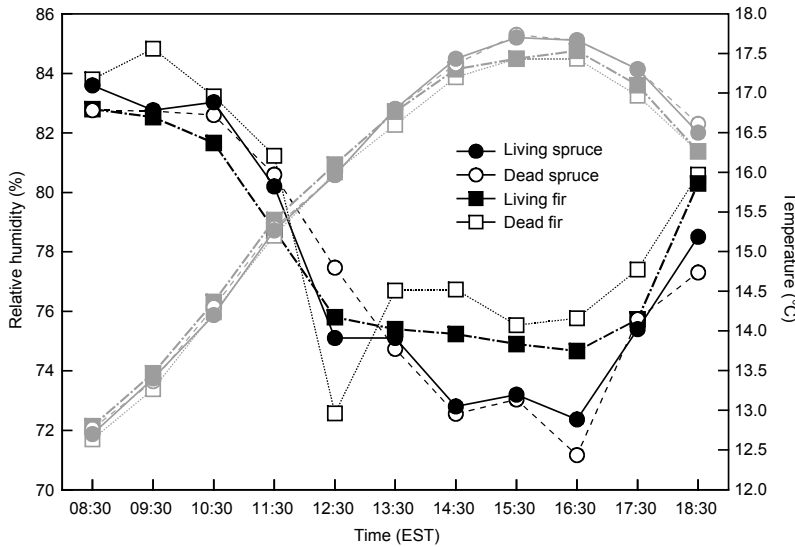


Fig. 5. Diurnal variation of relative humidity (black) and air temperature (grey) on the trunk surfaces of living and dead trees of *Picea rubens* and *Abies balsamea* ($n = 3$). No significant differences according to three-way ANOVA considering the potential impact of tree species, tree vitality and location of the sample tree within the 100×100 m study plot ($F = 1.07$, relative humidity; $F = 2.91$, air temperature; d.f. = 9).

tive humidity reached the minimum value (Figs. 4–5).

Correlation between microclimatic parameters and epiphytic lichen abundance

CCA ordination reveals that PPFD, evaporation and, to a lesser extent, water-holding capacity of the substrate are correlated with epiphytic lichen cover (Fig. 2). However, the Monte Carlo permutation test shows that correlation is only significant for Axis 1, which explains no more than 8% of total variance in species data (Fig. 2). Species correlated with high PPFD are, first of all, *Evernia mesomorpha*, *Japewia subaurifera*, *Mycoblastus sanguinarius*, *Pseudevernia consocians*, and *Usnea* sp. *Hypocenomyce friesii* and *Imshaugia aleurites* have the lowest scores on Axis 1 representing species from microsites with high evaporation. Low Axis 2 scores indicate species of shady and humid sites, such as *Bryoria nadvornikiana*, *Loxospora ochrophaea*, *Micarea prasina*, *Pseudevernia cladonia*, and *Ropalospora chlorantha*. *Arthonia caesia*, *Cladonia coniocraea* and *Lepraria jackii* are primarily correlated with the water-holding capacity of the substrate. As demonstrated by the Monte Carlo test, no significant correlation was found between epiphytic lichen cover and values of relative humidity and air temperature shown

in Figs. 4–5; the corresponding CCA ordination diagram is, therefore, not shown.

Discussion

CCA ordination (Fig. 2) revealed a significant impact of light and water relations on epiphytic lichen abundance in the spruce–fir forests of Whiteface Mountain. The position of the species in Fig. 2 is very plausible judged from published ecological preferences of these species that derive from field experiences (Purvis *et al.* 1992, Wirth 1995, Brodo *et al.* 2001). This concerns lichens of light-flooded microsites, such as *Evernia mesomorpha*, *Pseudevernia consocians* and *Usnea* sp., as well as species from shady and humid micro-environments, such as *Bryoria nadvornikiana*, *Micarea prasina* and *Ropalospora chlorantha*. The correlation with water-holding capacity of the substrate might, at least partly, be due to other properties of bark that intercorrelate with water-holding capacity. This is inferred from the correlation of cover of *Lepraria jackii* with water-holding capacity, as water uptake in this lichen is apparently only from air humidity (Tønsberg 1992). An interesting correlation that supports causality of correlations shown in Fig. 2 is that most lichen species with yellow or brown pigments have positive scores on Axis 2, which is correlated with PPFD. This applies to most species that contain usnic acid (*Alectoria*

sarmentosa, *Evernia mesomorpha*, *Usnea* sp.) or melanins (*Bryoria capillaris*, *B. furcellata*, *B. fuscescens*) or to species that contain unknown brown (*Hypocenyomyce friesii*, Timdal 1984) or brown and yellow pigments (*Japewia subaurifera*, Tønsberg 1990). Only one melanin-containing (*Bryoria nadvornikiana*) and one usnic acid-containing species (*Flavopunctelia soledica*) have negative Axis 2 scores. Yellow, brown (and orange) pigments are widespread sun-screening agents in lichens (Gauslaa & Solhaug 2001, Solhaug *et al.* 2003, Nybakken *et al.* 2004).

Despite such convincing correlation, it may not be overlooked that microclimate accounts for less than 10% of the total variance in the epiphytic lichen cover data (Fig. 2). Two explanations can be found for the overall low significance of microclimate for epiphytic lichen distribution on Whiteface Mountain that is suggested by Fig. 2. First, it is conceivable that significance increases when measurements are carried out over longer periods and with more sophisticated methods. Second, it is possible that other factors than present-day climate account for most of the variation in epiphytic lichen abundance. The second assumption is supported by the fact that none of the microclimatic parameters studied differed between living and dead trees or between spruce and fir. This is surprising, at first glance, because defoliation should result in higher light influx, higher evaporation, higher summer temperatures and lower humidity at the tree trunks. Dense young growth of *Abies balsamea* may explain why the loss of needles and branches of the dead trees did not result in brighter, drier and warmer microhabitats on the studied areas of the trunks. In undisturbed forests of *Picea rubens* and *Abies balsamea*, the number of fir trees prevails over spruce in lower size classes, whereas spruce is more common than fir among the largest trees of a stand (Peart *et al.* 1992). One reason for its dominance in young growth is that *A. balsamea* produces large seed crops more often than *P. rubens* (White & Cogbill 1992). Pollution-sensitivity of *P. rubens*, but not of *A. balsamea*, increased the dominance of the latter among young growth even more during forest decline (Johnson 1987); half of the large canopy spruce trees died in the Adirondacks since the 1960s (Driscoll *et al.* 2003). Therefore,

the stand structure of dieback-affected stands differs considerably from that of dieback-affected *P. abies* forests in central Europe. In Europe, soil acidification strongly reduces young growth of *P. abies*, and dieback-affected spruce stands become increasingly more open with increasing damage (Niedersächsisches Umweltministerium 1992). Hence, light availability on the trunk surface increases with increasing needle loss (Hauck 2003). However, increasing lichen diversity on damaged trees could not be attributed to this increasing light influx in the Harz Mountains, because element concentrations in stemflow and bark were apparently more effective in limiting epiphytic lichen abundance (Hauck 2003, 2005).

Though significant differences in microclimatic conditions on the trunk surface of trees of different species or vitality were not observed at present, it is possible that such differences occurred in the past when *P. rubens* started to decline. It is possible that, for example, light availability was formerly higher on the trunks of damaged trees, before the surrounding young growth reached its present size of several meters. Thus, it is conceivable that present differences in epiphyte vegetation between dead and living trees are not due to present-day conditions, but to former differences in microclimate. Whether this hypothesis comes true depends on the speed of epiphytic lichen succession in the spruce–fir forests of the Adirondacks. Knowledge on the dynamics of epiphytic lichen vegetation is generally scanty. Recording the size of individual thalli on permanent plots, Wirth *et al.* (1999) found little change in lichen communities on *Abies alba* or on several species of deciduous trees in southern Germany during 10 years. Under changing environmental conditions, however, epiphytic lichen vegetation of a tree can change significantly in one or two decades (Fisher Stone 1989, Seaward & Letrouit-Galinou 1991, Kirschbaum & Hanewald 2001).

Changes in epiphytic lichen vegetation caused by the deterioration of the chemical environment can be expected to be quick because of lichen thalli that die, as soon as a toxic substance exceeds a certain threshold level. Effects of improvements of chemical or microclimatic site conditions on epiphytic lichen vegetation may take more time, because the colonization of new

thalli or species is involved. A gradual change of microclimate due to young growth of trees has perhaps little effect on epiphytic lichen vegetation for a transitional period. Changes to less favorable microclimatic conditions may reduce carbon gain and growth of lichen species adapted to open habitats step by step, but as long as more shade-tolerant species have not yet been successful in colonizing the trees, open-habitat species would probably still be able to survive for a limited time under suboptimal microclimatic conditions. So, it is conceivable that epiphytic lichen vegetation on damaged trees on Whiteface Mountains is just in such a transitional period and that past microclimatic conditions have been involved in causing the higher lichen diversity on dead than on living trees. As initial stages of forest dieback cannot be studied anymore, the only way to test this hypothesis would be to continue studies on Whiteface Mountain with a long-term monitoring of epiphytic lichen dynamics.

Conclusions

Light and water relations were found to exert an influence on small-scale distribution of epiphytic lichen species in spruce–fir forests of Whiteface Mountain. However, the influence is rather small, as microclimatic parameters studied accounted for less than 10% of total variance in species data. This result suggests that light and water relations are one of several causes controlling epiphytic lichen distribution in the investigated stand. The Mn/Fe ratio of bark has already been established as another relevant site factor for epiphytic lichens in the study site (Schmull & Hauck 2003). The results agree with an hypothesis of Hauck (2005) that the influence of chemical site factors on epiphytic lichen diversity decreases with increasing air purity, as both chemical and microclimatic parameters were shown to affect lichen vegetation in the medium-polluted area of upstate New York. The initial hypothesis that the trunks of dead trees are characterized by higher solar irradiation, higher evaporation, higher temperature, higher water-holding capacity of the substrate and lower relative humidity does not apply to the *Picea rubens*–*Abies balsamea* forests of Whiteface Mountain.

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