Epiphytic Algae and Lichen Cover in Boreal Forests—A Long-Term Study Along a N and S Deposition Gradient in Sweden

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Abstract The aim was to describe spatiotemporal patterns of colonization of spruce branches by algae and lichens and the relationship with decreasing deposition of N and S. Coverage was estimated annually over 10 years for four Swedish Integrated Monitoring catchments with varying deposition levels. Initial hypotheses were that algal coverage would be positively correlated with deposition and that lichen coverage would be negatively correlated with S and positively with N deposition. Data were analyzed using regression, ANOVA, and partial least square regression. The results showed a temporal decrease in the coverage of algae but an increase in colonization rates, while lichens showed less uniform patterns. Within catchments, algae and lichen coverages were positively correlated with mainly S deposition. Across catchments, coverage of algae increased, while the coverage of lichens decreased with increasing N and S deposition. Colonization rates of both algae and lichens showed weak correlations with both spatial and temporal trends in N and S deposition. Thus, while N and S deposition had an effect on the colonization and coverage of algae and lichens, other factors are also important.

Keywords Epiphytes · Algae · Lichen · Nitrogen · Sulfur · Long-term · Indicator

INTRODUCTION

Aerially dispersed green algae are abundant on many substrates. However, the occurrence of algae on Norway spruce needles in boreal forests is a relatively new phenomenon. In recent decades, a number of studies have reported increased occurrence of aerial algae on spruce needles (Liu and Bråkenhielm 1995a; Peveling et al. 1992;

Poikolainen et al. 1998b; Søbcting 1997; Thomsen 1992). Søbcting (1997) concluded, on the basis of interviews with senior foresters, that algae were absent from spruce needles at the beginning of the last century. However, there are no reported scientific studies confirming these observations.

Aerial green algae that colonize spruce needles belong mainly to the species *Desmococcus olivaceus* (Persoon ex Archerson) J.R. Laundon (syn. *Protococcus viridis* C. Agardh) (Søbcting 1997). These algae are single-celled organisms that obtain their nutrients directly from moisture on the surface of the needles. Their abundance is regulated not only by the amount of nutrients available but also by the temperature regime, humidity, and light conditions (Hoffmann 1989). Following colonization of individual spruce needles, an algal crust accumulates for up to 4 years; this crust then peels off over the following 3 years. At this point, if needles are not shed due to aging or other causes, a new crust may start to accumulate (Søbcting 1997). It has been shown that the occurrence of these algal crusts is related to changes in nitrogen and sulfur deposition (Poikolainen et al. 1998b). However, several studies have concluded that at low to intermediate levels of deposition, other factors such as weather and shelter are also of importance for epiphytic algae coverage (e.g., Liu and Bråkenhielm 1995b; Poggio 2002; Søbcting 1997).

Lichens have been considered good indicators of air quality for more than a century (e.g., Hawksworth and Rose 1970; van Dobben and ter Braak 1999). In contrast to aerial algae, the colonization and coverage of foliose lichens on spruce branches show different responses to N and S deposition depending on which species colonize. There are both nitrophobic and nitrophilous lichens (Gries 1996; Hultengren et al. 1991; van Herk 1999). The main atmospheric pollutants affecting lichen colonization are SO₂, NO_x, and NH₃ (Geiser et al. 2010; Krupa 2003; Marti

1983). Lichen sensitivity to pollutants is mainly associated with the lack of a protective cuticle, non-selective nutrient uptake, and preference for more exposed substrates (Hultengren et al. 2004). Some studies have shown that high levels of air pollution cause a decrease in lichen abundance and homogenization of the lichen flora, with only the least sensitive species remaining (e.g., Liska and Herben 2008). Other studies have shown that the lichen community in situations with high N deposition consists of nitrophilous species only (van Herk 2004).

There is an expectation that lichen communities will recover as N and S deposition decreases, but there are presently little empirical data to support this hypothesis (see Hultengren et al. 2004; Sparrius 2007). In Sweden, deposition of both N and S has decreased significantly during the last two decades, with current levels being low from both a historical and a European perspective (Fig. 1). Over the last two decades, S deposition has decreased by 60% and N deposition by 20% (Anon. 2011). However, there is still great regional variation in deposition, with very low levels in the north contrasting with comparatively high levels in the southwest. Despite the decrease in S deposition, it remains unlikely that national environmental quality objectives for acidifying compounds (Anon. 2011) will be met by the target year 2020. It is also likely that the critical load (defined as the level of deposition below which significant harmful ecological effects do not occur; Nilsson and Grennfelt 1998) for sulfur deposition will be exceeded in the southern parts of the country that are subjected to the greatest transboundary air pollution. Thus, although deposition of N and S is likely to continue to decrease, Swedish authorities (SEPA) expect levels to remain above critical loads. The catchments included in this study are located

along a depositional gradient from southwest to north. The initial expectation was that the differences in deposition would be reflected in the distribution and coverages of epiphytic algae and lichens.

Many studies have suggested that lichens can and should be used as bioindicators of atmospheric pollution (Gries 1996; Hawksworth and Rose 1970; Skye 1979; Søbchting 1997). However, Bråkenhielm and Qinghong (1995) found no clear patterns when they analyzed data on the lichen community on spruce branches, obtained from a former Swedish national monitoring program. Other studies have shown that local factors such as localized emissions or tree position in a stand may override large-scale patterns of deposition (Poggio 2002). However, a recent study in Denmark and Wales concluded that epiphytic lichens can provide an early warning of changes in air quality (Larsen Vilsholm et al. 2009).

Some studies have shown a relationship between deposition and epiphytic coverage, using space-for-time substitutions (Göransson 1990; Søbchting 1997). However, there have been few reports of work using real time series to investigate these relationships. In this study, the temporal dynamics of epiphyte coverage on spruce needles were followed and related to deposition of N and S. Spruce needles constitute a substrate that is renewed annually at the tip of each branch. This allows detailed studies of the colonization and growth of algae and lichens on spruce branches. The branches selected for this study were all fully exposed to the air and thus received ambient levels of N and S deposition (cf. Esseen and Renhorn 1998; Hilmo 1994).

The aims of this study were to describe the temporal and spatial patterns of colonization and coverage of epiphytic

Fig. 1 Spatial and temporal patterns in N and S deposition at the IM catchments. Significant regressions are indicated by r^2 -values and solid lines in the diagrams. Hatched lines show mean deposition. All mean lines are significantly different (ANCOVA with year as covariable, followed by Tukey's HSD, $P < 0.05$)

algae and lichens and to evaluate the reliability of these organisms as indicators of N and S deposition. The initial hypotheses were that: (a) coverage of, and colonization by, algae is positively correlated with N and S deposition, (b) lichen coverage and colonization are negatively correlated with S and positively correlated with N deposition, and (c) both algae and lichens can be used as indicators of atmospheric deposition of N and S.

MATERIALS AND METHODS

Four well-defined catchments representing a south–north gradient were monitored as part of the Swedish Integrated Monitoring program [UNECE—International Cooperative Programme on Integrated Monitoring of Air Pollution Effects on Ecosystems (ICP-IM)]: Gårdsjön (3.7 ha, Annual mean temp: 6.7°C, Precipitation: 1000 mm year⁻¹), Aneboda (19 ha, 5.8°C, 750 mm year⁻¹), Kindla (20 ha, 4.2°C, 900 mm year⁻¹), and Gammtratten (45 ha, 1.2°C, 750 mm year⁻¹) (Fig. 2). The catchments are located along a climatic and depositional gradient, with the mildest climate and highest levels of deposition in the southwest. The vegetation is dominated by conifer (*Picea abies*) forest. At each catchment (except for Gårdsjön, where only six trees were used), 20 solitary young (10–20 years) Norway spruce (*Picea abies*) trees within open areas of about 100 × 100 m with no over-story canopy were selected and monitored annually in late July or early August. The time series at Gårdsjön was broken in 1998 when new trees had to be selected, as the original trees had become too large and with few branches left below 2 m. Data from Gårdsjön were therefore divided into two time series for all analyses of coverage and colonization. For analyses focusing on deposition, it was only possible to use the second time series from Gårdsjön due to missing data in the first time series. Algae were only found to be present on spruce needles at the three southern catchments, so the northernmost catchment was excluded from all calculations concerning algae.

On each tree, three branches between 1 and 2 meters above ground and pointing in different directions were selected. The coverage of algae on needles and of foliose lichens as a collective group on each whole branch was estimated using a four-degree scale: 0—absent, 1—small amount, individual colonies, 2—larger colonies, coverage up to 50%, and 3—thick coverage >50%. Colonization rate was assessed by counting the number of annual shoots on the branch from the most recent shoot to that on which the first algal colony or lichen was detected.

Coverage data were stored in a database as one arithmetical mean value per tree, although three branches were surveyed. For analyses of algal and lichen coverage, these mean values were transformed to percent coverage using the formula $7 \times x^2 - x$, where x is the mean estimated

Fig. 2 Location of the study sites

coverage. Using this transformation, coverage degree 1 is transformed to 6, 2–26, and 3–60% coverage, which are more realistic estimates of coverage than the original ordinal values.

Explanatory Data

To help explain the observed patterns, the following variables were also quantified: open field wet deposition of S, NH₄, and NO₃ (all in kg ha⁻¹), precipitation, runoff, evaporation, humidity, and growing season (days with daily mean temperature >5°C). These variables were all quantified as annual sums calculated for the period July 1–June 30 to reflect conditions during the year preceding the sampling of lichens and algae. There are no annual data on dry deposition, but five-year means are available and show that dry deposition ranges from 4 to 12% of wet deposition except at Gårdsjön where dry deposition ranges from 18 to 45% of wet deposition (Löfgren et al. 2011). The N and S content of spruce needles (mg g⁻¹ dry weight) was also measured for six trees evenly distributed over the catchments to provide an annual catchment mean for each component. Data for deposition, hydrology, and meteorology were obtained according to the international manual for the ICP Integrated Monitoring program (Anon. 1998). Deposition measurements were taken monthly using open bulk collectors situated in an open area at a meteorological sampling station within each catchment in the study. Temperature was recorded as daily means.

Statistical Methods

Temporal and spatial patterns in N and S deposition were tested using analysis of covariance with catchment as factor and year as covariate. This method tests for differences between catchments taking possible annual trends into account. Temporal trends in deposition were tested catchment by catchment using ordinary least square regressions.

The independent effect, and its significance, of each explanatory variable on coverage and colonization was tested using partial least square regression (PLS) (Umetrics 2009). PLS with one response variable is a form of multiple regression but without the caveats of co-linearity in the predictor variables that often hamper results in ordinary multiple regressions (Umetrics 2009). To achieve linearity in the PLS analyses, colonization rate was expressed as $\log_{10}(1/x)$, where x is the age (in years) of the most recent annual shoot with visible algae or lichens. Results of PLS analyses are presented as centered and scaled PLS model correlation coefficients for only those variables with a variance importance value (VIP) ≥ 1 . In PLS, variables with a VIP greater than 1 are considered to explain a significant proportion of the response variable (Umetrics 2009).

RESULTS

Deposition Patterns

The results confirmed that the Swedish IM catchments represent a depositional gradient, with deposition of both N and S differing significantly between the catchments after accounting for temporal trends (Table 1; Fig. 1). The levels of N and S deposition decreased from south to north, with very low levels in the north. Open field deposition of both S and N also decreased over time. During the period of investigation, the overall mean deposition of NH₄ decreased by 29% (range 27–52%), and the mean S deposition decreased by 35% (range 22–54%). Despite the wide range of the decrease in deposition, there was no significant interaction between catchment and year. In consequence, the slopes of the annual trends did not differ significantly between the catchments (Table 1).

Colonization

The age of the most recent annual shoot bearing signs of algal colonies differed significantly between catchments (Table 2). The lowest colonization rate after factoring out within catchment temporal trends was found at Gårdsjön before 1999, followed by Kindla and Gårdsjön after 1999, while Aneboda had the most rapid colonization (Table 2). For all three catchments with algae present, there was a significant decreasing temporal trend in colonization rate (Fig. 3), that is, the youngest shoot where algae were found gets older year by year. The slope of the regression lines in Fig. 3 indicates that the colonization rate decreased by, on average, between 0.2 and 0.3 years per year.

The spatial pattern of lichen colonization rates was similar to that of algae, but the average age of shoots at which colonies were first detected was higher for lichens than for algae (Table 2). Colonization was slowest at Kindla and fastest at the northernmost catchment, Gamtratten. There were no temporal trends in lichen colonization (Fig. 3), indicating that the colonization rate was stable over the period of study at all four catchments.

Table 1 Summary of an analysis of covariance testing for differences between catchments and for temporal effects in annual deposition patterns

Source	DF	F ratio	
		SO ₄ -S	NH ₄ -N
Catchment	3	54.7***	74.2***
Year	1	38.3***	19.0***
Catchment $\times$ year	3	0.16 ^{ns}	0.49 ^{ns}

^{ns} $P > 0.05$; *** $P < 0.001$

Fig. 3 Temporal and spatial patterns and relationship with N and S deposition for algae and lichen on spruce needles, for all catchments combined and on a catchment by catchment basis. Significant

($P < 0.05$) regressions are indicated in the graphs (all regression lines have $P < 0.001$)

There was evidence that algae colonize faster than lichens, since the youngest lichens were detected on older annual shoots than the youngest algae (Table 2). However,

the magnitude of this difference was not the same across catchments. At Kindla, the mean difference was 2.4 years, while it was only 0.66 years at Gårdsjön before 1999.

Table 2 Mean age of youngest annual shoot with colonies of algae and lichens on spruce needles, at four catchments

Catchment	Mean age (year) of youngest annual shoot with epiphytes (SE)		
	Algae	Lichens	Difference
Gårdsjön < 1999	5.9 (0.27) ^A	6.4 (0.42) ^A	−0.66 (0.50) ^A
Gårdsjön > 1999	3.3 (0.15) ^C	4.9 (0.23) ^B	−1.6 (0.28) ^A
Aneboda	3.1 (0.079) ^C	4.5 (0.12) ^{BC}	−1.5 (0.15) ^A
Kindla	4.3 (0.077) ^B	6.7 (0.12) ^A	−2.4 (0.14) ^B
Gammtratten	n/a	4.2 (0.13) ^C	n/a

Catchments not sharing the same letter are significantly different (ANCOVA with year as cofactor, Tukey's HSD, $P < 0.05$)

Coverage

The mean algal coverage differed significantly between catchments (Table 3). There was also a significant difference between the two time series from Gårdsjön, with the later series having half the mean coverage of the earlier series. At all catchments, the mean algal coverage decreased significantly during the period of investigation (Fig. 3). The most pronounced decrease was observed after 1999 at Gårdsjön, where the coverage decreased from between 25 and 60% to about 5%.

The quantity of lichens also differed between catchments, with the highest coverage at the northernmost catchment, Gammtratten (Table 3). The lichen coverage at Gammtratten was more than double that at Aneboda, which had the second highest coverage, and twelve times the coverage at Gårdsjön before 1999. The quantities recorded in the two time series from Gårdsjön were of the same order of magnitude. All three catchments in the southern half of the country showed significant temporal trends, with coverage of lichens decreasing over time (Fig. 3), while the northernmost catchment had a stable population with high lichen coverage.

Relationship with Explanatory Variables

Partial least square regression analyses indicate that deposition was of greatest importance for the coverage and colonization rate of algae, while meteorological variables were more important for lichens (Fig. 4). The colonization of lichens showed very low correlation with deposition (Fig. 4). For algae, S deposition was the variable most strongly correlated with both coverage and colonization rate. Algal colonization rate was very weakly related to N and S deposition, but the patterns nevertheless indicate faster colonization with higher deposition (Fig. 3). Both nitrogenous compounds were correlated with algal colonization, but ammonium was more strongly correlated than nitrate. Together, these observations suggest that

Table 3 Coverage of algae and lichens on spruce needles at four catchments

Catchment	Coverage (%) of epiphytes (SE)	
	Algae	Lichens
Gårdsjön < 1999	24.1 (2.03) ^C	14.5 (1.4) ^{CD}
Gårdsjön > 1999	15.9 (1.03) ^A	3.29 (0.99) ^D
Aneboda	12.6 (0.59) ^C	19.1 (0.56) ^B
Kindla	15.9 (0.56) ^B	9.00 (0.69) ^C
Gammtratten	n/a	41.6 (0.80) ^A

Catchments not sharing the same letter are significantly different (ANCOVA with year as cofactor, Tukey's HSD, $P < 0.05$)

Fig. 4 The relationship between coverage and colonization rate for algae and lichens, and various explanatory variables, expressed as PLS coefficients. The figures show only variables with PLS importance values greater than or equal to 1

anthropogenic deposition is an important factor affecting the behavior of epiphytic algae on spruce needles. Latitude and longitude were not important descriptors of algal behavior (note that the northernmost catchment had no epiphytic algae and was thus not included in the analyses relating to algae), but some of the meteorological variables were significantly correlated (Fig. 4). The coverage of algae was negatively correlated with humidity and positively correlated with runoff. Precipitation was also an important factor in the model, but with a very low PLS correlation coefficient (Fig. 4), indicating that catchment characteristics affecting the overall catchment hydrology might be more important than actual precipitation for the coverage of algae.

In contrast to the algal patterns, the quantity of lichens decreased with increasing levels of S and N, when all catchments were analyzed together (Fig. 3). However, two of the catchments showed significantly increasing coverage of lichens with increasing deposition of both S and N when analyzed individually. Lichen colonization was only very weakly related to deposition; it was more strongly related to meteorological variables (Figs. 3, 4). The only exception was a weak positive relationship between N and age of youngest shoot with lichens at Aneboda, that is, faster colonization at lower levels of N deposition. The strong effects of the meteorological variables indicated that precipitation and humidity were more important than N and S deposition.

For both algae and lichens, N and S in needle tissue showed no relationship with coverage or colonization. Thus, needle chemistry is probably a long-term, integrated metric of deposition, which is not directly related to colonization by, or growth of, epiphytes.

DISCUSSION

Abundances of both algae and lichens decreased during the study period. The lack of relationship between needle chemistry and epiphytic patterns indicates that current patterns of deposition and weather rather than historical deposition are more important for epiphyte behavior. Similar results were obtained by Wolseley and Pryor (1999), who concluded that deposition directly affects the epiphytic lichen community. The decreases occurred at all catchments, except for the northernmost catchment, which showed a stable and high abundance of lichens. Decreases in abundance of algae and lichens also coincided with a decrease in S and N deposition, but the relationships were far from strong, and several other factors had major effects on the abundance of epiphytes. PLS analyses separated the anthropogenic N and S stressors from natural climatic factors and clearly identified meteorological factors as

being of the same order of importance as the anthropogenic deposition variables (the analysis did not take into account possible effects of anthropogenic climate change on the meteorological variables measured in this study). This observation is consistent with the results of several other studies investigating epiphyte response to low to intermediate levels of N and S deposition, whose authors also concluded that factors other than deposition are of importance for the epiphytic community (Liu and Bråkenhielm 1995b; Poggio 2002; Poikolainen et al. 1998a). However, although variables related to precipitation were important, the length of the growing season was not important, which was unexpected given the range of variation in the growing season (122–221 days). Poikolainen et al. (1998b) have suggested that warm and moist falls are important for algal growth. This may explain why humidity but not annual temperature regime is important for epiphytic expression.

Algae

Bobbink et al. (2003) have suggested that a critical deposition load for both algae and lichens in boreal forests is $10\text{--}15\text{ kg N ha}^{-1}\text{ year}^{-1}$, which is three to fifteen times higher than the N deposition observed at the Swedish IM catchments. However, effects of N deposition on lichens vary between regions. In a Mediterranean climate, lichens are affected at N deposition levels as low as $3\text{ kg ha}^{-1}\text{ year}^{-1}$ (Fenn et al. 2008). In an experimental study in a boreal forest, Johansson et al. (2010) found that lichen chemistry was affected only at nitrogen loads greater than $12.5\text{ kg N ha}^{-1}\text{ year}^{-1}$. Data from an abandoned Swedish monitoring program suggested that epiphytic algae are absent when the throughfall N concentration is lower than $5\text{ kg ha}^{-1}\text{ year}^{-1}$ (Bråkenhielm 1990). The throughfall at the Swedish IM catchments is currently between 1 and $3\text{ kg ha}^{-1}\text{ year}^{-1}$, except at Gårdsjön where the total throughfall nitrogen concentration was $8\text{--}10\text{ kg ha}^{-1}\text{ year}^{-1}$ before 2005, but thereafter decreased to $6\text{--}7\text{ kg ha}^{-1}\text{ year}^{-1}$. In the present study, no algae were found at the northernmost catchment where the N deposition has always been below $2\text{ kg ha}^{-1}\text{ year}^{-1}$, which is obviously lower than that required for the formation of an algal crust on spruce needles. The decreasing algal coverage at the other catchments further indicates that N deposition limits algal abundance. However, despite N deposition of less than $5\text{ kg ha}^{-1}\text{ year}^{-1}$, all three southerly catchments still had an epiphytic coverage. It can thus be concluded that algae are present and continue to colonize at deposition levels below $5\text{ kg ha}^{-1}\text{ year}^{-1}$ but that coverage and colonization rate both decrease as N deposition decreases.

The importance of S deposition for algae resembled the effects of N; with more S, there were more algae and faster

colonization. The PLS analyses indicated that S deposition was more important than N for the abundance of algae, but of equal importance for colonization. It has been suggested that sulfur deposition together with ozone is beneficial for algal colonization, as it can erode the wax cuticle on spruce needles (Bråkenhielm and Qinghong 1995). If this is the case at intermediate levels of deposition, as in this study, a positive relationship between algal colonization and S deposition would be expected. Ammonium, on the other hand, does not affect the wax cuticle (Bacic et al. 1992). The first hypothesis raised in the introduction, that abundance of, and colonization by, algae is positively correlated with N and S deposition, can be addressed by concluding that deposition of N and S is of importance for the coverage of algae on spruce needles but that other factors play a larger part in determining the extent of colonization of algae. The possible effect of S on the needle wax cuticle was therefore not confirmed in this study.

Algae were not present on needles at the northernmost catchment. This catchment was excluded from the analyses concerning algae since the ecological distance between presence and absence of an organism is often non-linearly related to the multidimensional environmental gradients that cause biological patterns (Økland 1990). Absence could be due to sampling of a biotope either just outside the distributional range or far away from the range of the focal species. Absence of a species may also result from random processes at a catchment where the species could potentially grow (Atmar and Patterson 1993). However, in this case, it is more likely that N is limiting algal abundance, as the catchment is located in an area with low levels of N and S deposition.

Lichens

The most pronounced pattern displayed by the lichens was a decrease in coverage over time; there were also positive relationships between lichen coverage and N and S deposition. The positive correlations between S deposition and lichens at two of the catchments are in contrast to many other studies (e.g., Ellis and Coppins 2010; van Herk et al. 2003) that report a negative relationship. These contradictory results suggest that the abundance of lichens is affected by factors other than S deposition. Ellis and Coppins (2010) suggest that lichen species colonizing following the general European decline in S deposition are nitrophilic rather than acidophilic. There are also indications that under conditions of reduced S deposition, NO_x has a more pronounced effect on the epiphytic lichen community (Cristofolini et al. 2008). The lichens observed in the present study are probably nitrophilous and react positively to N deposition at the investigation catchments. van Dobben and ter Braak (1998) found that nitrophilic

lichens reacted positively to increasing N and decreasing S deposition. They also found that lichens responded differently to NO_2 and NH_3 deposition. In this study, the effects from NH_4 and NO_3 were of different magnitudes, but not contradictory. Taken together, these results suggest that lichens as a collective group are not suitable as indicators of N and S deposition. The variation in response to deposition by different species is the most probable explanation why the first part of the second hypothesis, that lichens are negatively correlated with S deposition, was not supported, while the second part, that there is a positive relationship between lichens and N deposition, gained support from the patterns observed.

Colonization

Within the catchments monitored in this study, over the period of investigation, the colonization rate for algae decreased steadily, while the rate remained at the same magnitude for the lichens. However, for both algae and lichens, the rate differed between catchments. The greatest difference was between Gammtratten and Kindla where the mean age of the most recent shoots bearing lichens differed by 1.5 years. There is thus a catchment effect on colonization rate that is not reflected in either the temporal trend or the relationships with N or S deposition. This raises a question about the origin of propagules. On each branch where epiphytes are present, propagules are produced that could colonize more recent shoots toward the tip of the branch. However, as the age of the most recent shoot with epiphytes detected differed despite a fairly constant colonization rate (i.e., differences in intercepts but not slopes in Fig. 3), the rate must be determined by factors in addition to the supply of propagules from already established epiphytes. A possible explanation could be that when epiphytes are more abundant, more propagules are produced, which would in turn favor higher rates of colonization. However, the relationships between epiphytic abundance and colonization rate were generally weak and not related to differences between catchments in the age of the youngest shoot bearing epiphytes. Nor could differences in N or S deposition explain variation in the ages of the most recent shoots with epiphytes. A plausible explanation, although one that was not tested in this study due to lack of data, concerns the ages and growth rates of the branches. At the northernmost catchment, the branches grow slowly and the branches selected for observation are much older, though not longer, than the branches observed in the more southerly catchments. As a consequence, the epiphytes at the older branches probably developed over longer time periods and therefore had a higher chance of producing propagules. This hypothesis was supported in a study by Esseen and Renhorn (1996), who concluded that the age of

branches was a decisive factor in the development of the epiphytic lichen community. The availability and dispersal of propagules within stands are also important for the abundance of epiphytic lichens (Dettki et al. 2000). Old growth stands generally have larger thalli, which produce more lichen propagules, than young stands.

Indicative Ability

A good indicator should have several important attributes. It should provide early warning of an impact and should preferably indicate the cause of a change rather than its mere existence. It should also be indicative over a wide range of stressor intensity levels and be cost-effective to monitor (Carignan and Villard 2002). Epiphytic algae and lichens fulfill several of these requirements. However, the results of this study do not fully support the suggestions by many authors that both of these groups of organisms are ideal indicators of N and S deposition (Gries 1996; Hawksworth and Rose 1970; Larsen Vilsholm et al. 2009; Skye 1979; Söchting 1997). Some studies have questioned the reliability of lichens as indicators of nitrogen deposition (Jeran et al. 2007; van Dobben and ter Braak 1999), partly due to the different responses to N deposition of different lichen species. The probable main reason why lichens failed to meet the criteria of a good indicator according to the results of the present study is that the monitoring method used did not distinguish between individual species. It is well known that there are both nitrophilic and nitrophobic lichen species (e.g., Gries 1996; Hultengren et al. 1991; Larsen Vilsholm et al. 2009; van Herk 1999), but the present study failed to discriminate between these types. Variation in lichen coverage between branches of different ages, and in the availability of propagules, together with previous findings that position within a stand (Liu 1997) affects the epiphytic community (Hauck 2010; Poggio 2002; Wolseley and Pryor 1999), which further suggests that lichens as a group are far from ideal as indicators of air quality at intermediate levels of deposition in boreal or boreo-nemoral ecosystems.

Epiphytic algae showed more consistent patterns in response to deposition in this study, confirming their value as indicators. Though the relationships between algae and deposition were not strong, they were always consistent throughout the full range of deposition levels. Moreover, in contrast to a report by Hänninen et al. (1993), the field staff in this study did not find it difficult to assess the algal coverage in the field; ease of assessment is another criterion for a good indicator.

The last hypothesis underlying this study, that both groups of species under investigation could be used as indicators of N and S deposition, was thus supported for the epiphytic algae, but not for lichens as a collective group.

CONCLUSIONS

Both N and S deposition decreased gradually during the period of investigation. The expression of epiphytic algae was associated with both deposition and meteorology, while lichen dynamics were mainly described by meteorological variables. The results suggested that epiphytic algae responded in a consistent fashion throughout the depositional gradient, while the epiphytic lichens as a collective group showed less consistent patterns or no relationships at all. The results support the use of epiphytic algae, but not lichens as a collective taxonomic group, as indicators of N and S deposition.

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