Epiphytic algae on Norway spruce needles in Sweden - geographical distribution, time-trends and influence of site factors

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Epifytisk algpåväxt på granbarr i Sverige – geografisk utbredning, tidstrender och inflytande av ståndortsfaktorer

Laura Poggio

PREFACE

This thesis is made as a 20 credit points individual course and fullfills all the requirements for a Master of Science thesis in Soil Science at the department of Forest Soils at the Swedish University of Agricultural Sciences. Ms. Poggios work has been supported by the Erasmus programme financed through the European Commission.

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CONTENTS

SUMMARY. The occurrence of epiphytic vegetation in temperate and boreal forest is a fairly recent phenomenon. Epiphytic algae have increased especially on Norway spruce (*Picea abies* L.Karst.) needles in the southern part of Scandinavia and in Central Europe. The algae present on spruce needles are mainly green algae and take their nutrients directly from rainwater and air. Thick layers of algae may accumulate over several years. The colonisation of the needles by the algae may cause different problems for the vitality of the tree. The most probable repercussion is the reduction of photosynthetic active irradiation available to the needles.

In this report the correlation between the algae and the main site factors, such as climate, atmospheric deposition of nutrients and acidifying compounds, soil properties, site hydrology and indices for vegetation productivity, were evaluated. In addition, the description of the individual tree and its vitality were considered. The algae variables used were the youngest needle colonized and coverage of needle in percent. The data used were obtained from the Swedish National Survey of Forest Soils and Vegetation, the National Forest Inventory and the Swedish Hydrological and Meteorological Institute and collected between 1993 and 2000. The total number of plots was 4055, covering the whole forested area in Sweden. The correlation was evaluated using multivariate statistical analysis, in particular principal component analysis and the analyses were made on three datasets. Each dataset was further divided into four groups, according to the geographic position and to the presence of algae, to study different rapports between the variables. The results showed that the most important factors for algae growth are climatic conditions and atmospheric deposition. Temperature is the most important climatic factor. The growth of algae seems to be inhibited up to a certain temperature sum threshold of between approximately 1100 – 1300 day degrees. Under Swedish climatic conditions, humidity does not seem to be a limiting factor for algae. Many plots with algae were found in areas with low humidity. However, it may act as a contributing factor. In favourable climatic conditions, atmospheric deposition could play the principal role for algae colonisation, acting as a limiting factor and as an accelerator. The correlation with the other variables is quite weak. The local variability of different factors, such as vicinity to nutrient sources or structure of the stand, could also play an important role for the algal colonisation. The algae show a clear geographic distribution that coincides well with climatic and deposition gradients in the country. The northward sharp decline of algae corresponds approximately to *Limes norrlandicus*. In addition to the correlation evaluation between variables, a partial least square regression model was calculated to try to predict the algae growth using measured values of the variables describing site factors. The prediction ability of the model was not very high. This is probably a result of local factors not covered in the present investigation The investigation of the temporal variation of algae showed a slight tendency to decrease over the period 1995 to 2000.

SAMMANFATTNING. Epifytisk vegetation på barr i tempererade och boreala skogar är ett ganska nytt fenomen. Förekomsten av epifytiska alger på barr hos gran (*Picea abies* L.Karst.) har ökat i södra Skandinavien och i Mellaneuropa. Algerna som finns på granbarr är huvudsakligen grönalger som tar sina näringsämnen direkt från regnvatten och atmosfären. Tjocka alglager kan ackumulera på barren över flera växtsäsonger. Algkolonisationen på granens barr kan medföra problem för trädens vitalitet. Den största risken är troligen en reduktion av ljusinstrålningen i de våglängder som används i fotosyntesen.

I denna rapport utvärderas samband mellan och ståndortsfaktorer som klimat, atmosfärisk deposition av näringsämnen och försurande substanser, markegenskaper, den lokala hydrologin och bonitets index. Även eventullt inflytande av egenskaper hos de träd på vilka algpåväxten har bedömts har testats. De algvariabler som använts är dels den senaste årgången med algpåväxt (yngsta barrårgång) och täckningsgrad i % av barrytan. Det data som använts kommer från Ståndortskarteringen (SK) , Riksskogstaxeringen (RT) och Sveriges Hydrologiska och Meteorologiska Institut. Data från SK och RT är från perioden mellan 1993 and 2000. Det totala antalet använda provytor är 4055, och representerar hela arealen med produktiv skogsmark i Sverige. Korrelationerna utvärderades med multivariata statistiska metoder, särskilt principalkomponentanalys (PCA) och analyserna gjordes på tre olika dataset. Varje dataset indelades i fyra olika grupper efter geografisk belägenhet och förekomsten av alger. Resultaten visar att de viktigaste faktorerna för algpåväxt är klimat och atmosfärisk deposition. Temperatur är den enskilt mest betydelsefulla faktorn. Tillväxten av alger verkar hämmas när temperatursumman för växtsäsongen sjunker under 1100 -1300 daggrader. Humiditet verkar inte vara begränsande under svenska förhållanden. Många provytor med algpåväxt hittas även i regioner med låg humiditet. Det går däremot inte att utesluta att en högre humiditet kan gynna tillväxten hos algerna.. Förutsatt att klimatet tillåter, så verkar den atmosfäriska depositionen av näringsämnen styra tillväxten av algerna Korrelationen med andra variabler är ganska svag. Den lokala variationen hos vissa faktorer, som t.ex. närheten till lokala kväveutsläpp eller trädets position i beståndet, kan spela en viss roll men detta har inte kunnat testas. Algerna har en tydlig geografisk fördelning som överensstämmer med klimat och depositionsgradienter i landet. Den skarpa gränsen för den nordliga utbredningen sammanfaller med *Limes norrlandicus*. En PLS (partial least square regression) modell skapades för att kunna förutsäga algpåväxt på yngsta barråtgång. Modellens prediktionsförmåga var inte speciellt hög vilket kan tolkas som att även lokala faktorer som inte ingått i denna undersökning har stor betydelse för algpåväxten. Algpåväxtens förändring över tiden testades också. Resultaten visar en tendens till senare kolonisation och minskande täckningsgrad från 1995 till 2000.

INTRODUCTION

The occurrence of epiphytic vegetation in temperate and boreal forest is a fairly recent phenomenon. Normally, in drier parts of temperate and boreal forests, epiphyllic microorganisms have low species diversity and their development is rather poor. However, in recent decades the needles of evergreens in such climatic regions have become colonised by significant epiphytic vegetation, mainly algal (Søchting, 1997). Epiphytic algal vegetation has changed from being almost non-existent in the early part of this century to the widespread cover seen today, according to information from old foresters and what can be deduced from the lack of information in the early literature (Søchting, 1997). Thick layers of microorganisms may accumulate over several years. Epiphytic algae have increased especially on Norway spruce (*Picea abies* L.Karst.) needles in the southern part of Scandinavia and in Central Europe. It has been proposed that the occurrence of these microorganisms is associated with forest decline (Peveling et al., 1992).

Description of algae

The algae present on spruce needles are mainly green algae, single-cell organisms, which take their nutrients directly from rainwater and the air. Their taxonomy (and their ecology) is still not well known. The most common species of algae on spruce needles belongs to the following four genera: *Protococcus* spp., *Apatococcus* spp., *Desmococcus* spp., *Coccomyxa* spp. There is also a filamentous alga, but its identity is unknown (Bråkenhielm and Quinghong, 1995; Søchting, 1997). Some algae live in symbiosis with lichens and the epiphyllic microbial cover may also include various bacteria and fungi species.

Colonisation

The algae colonies grow vertically from the base region up through the crown and horizontally from the older needles to the end of the branches. The colonisation by algae starts at the end of the first season of a new needle, in the late autumn. Small colonies of algae are scattered on the upper surface of the needle. Algae are very often located close to and even inside the stomata and live in symbiotic and/or parasitic associations with the needle (Peveling et al., 1992). The needle surface is a special habitat where nutrients are provided, partly, by organic and inorganic exudates that are dissolved in throughfall from the canopy above (Søchting, 1997). With increasing age of the needle, the layer of microorganisms becomes increasingly thicker. The algae rapidly propagate and may form thick clusters on the upper side of two-year-old needles. At this stage of the colonisation most of the algae are still alive. Three-year-old needles can be almost totally covered by algae on the upper side, but also large areas of the lateral sides and even parts of the underside are covered. Most of the algae are still alive, but some dead cells can be found at this stage. The layer of microorganisms increases in thickness, as does the proportion of needle surface covered (Peveling et al., 1992). In a study by Søchting (1997), the algae cover increased during the first three to four years to about 55% of the needle surface and then decreased slightly to reach another peak on eight-year-old needles. The thickness of the algae crust increases during the first three years then remains unchanged. A quantitative analysis of algae colonisation showed that the largest amount of needle colonised by algae was normally found in the lower part of the crown, with the highest concentration on the 11^{th}-branch level counted from the bottom. On single branches, the largest amount of algae was found on the oldest needles. A 20-year-old spruce, in the south of Sweden, had about 16 kg, in dry weight, of needles and 200 g (dry weight) of algae. This means that a stand of spruce of the same age may have around 375 kg (dry weight) ha^{-1} of algae (Göransson, 1992).

Possible damage

The colonisation of needles by the algae (and other epiphytic microorganisms) may cause different problems for the vitality of the tree. The most important probable repercussion is light reduction. The quantity of the photosynthetic active irradiation available for the needle is reduced by epiphytic colonisation. The rate of photosynthesis in spruce trees is decreased by about 4% from the optimum, but single needles enveloped in a thick compact layer of algae the reduction can be up to 40% (Burg, 1990 cited in Peveling et al., 1992). The algae could also interfere with gas exchange in the stomata openings (Peveling et al., 1992). The occurrence of all these factors can cause an overall degeneration of the tree and may facilitate the development of secondary infections by more serious pathogens. Furthermore, the algae colonisation has become a problem in some locations for commercial production of ornamental spruces (Søchting, 1997).

Factors facilitating algae growth

According to most of the literature, the algae seem to be influenced mainly by climate and deposition of nutrients or by interaction between nutrients and climate. Some studies (Quinghong and Bråkenhielm, 1995; Quinghong, 1997) have tried to decompose the common variation and to quantify the unique variation belonging to specific variables using techniques of variation partitioning, like partial redundancy analysis. The results showed that the atmospheric deposition of nutrients and acidifying substances increased the explained variance compared to when climate factors were used on their own. The climate, however, seemed to play a major role in the distribution of algae.

Climate

Algae growth seems to be limited by low temperatures and a mean annual temperature of 1° C would appear to be the limit below which the algae no longer occur (Poikolainen et al., 1998). The temperature also influences the length of the vegetation period, another factor that seems to be correlated with algae colonisation possibilities (Bråkenhielm and Qinghong, 1995). The growth of algae is favoured by high humidity. Warm and moist autumns seem to promote the growth of colonies of algae (Søchting, 1997, Poikolainen et al., 1998). There should be enough light for the algae growth but fairly low irradiation (Peveling et al., 1992; Poikolainen et al., 1998). Light winds seem to be favourable for algae growth in comparison to strong winds that may shake the needles and thus wipe off the algae cover (Peveling et al., 1992). The microclimate, assessed mainly by the position of the tree in the stand and by the stand density, seems to have some effects on the growth of algae (Poikolainen et al., 1998).

Atmospheric deposition

Atmospheric deposition of nutrients and acidifying substances, especially nitrogen and sulphur, seems to be very important for the spreading of the algae, which probably obtain the minerals needed for their development from the deposition. Algae that are more directly exposed to precipitation and dry deposition seem to respond by increased growth to deposition changes (Bråkenhielm and Qinghong, 1995).

Nitrogen deposition seems be very important for the spread and the colonisation of algae. Nitrogen seems to be the main limiting nutrient for algal growth (Bråkenhielm and Qinghong, 1995) and increased availability of nitrogen will promote algae growth. The vicinity of various nitrogen sources, e.g. fertiliser factories, fur farms, cattle farms and urban areas seems to be positively correlated to algae occurrence on needles (Poikolainen et al., 1998).

The role of sulphur deposition is not very clear, but it is possible that sulphur deposition, together with ozone, erodes the wax layer and thus prepares a better surface for algae colonisation (Bråkenhielm and Qinghong, 1995).

Climate gradients in Sweden

The Swedish forest climate is the *snow forest climate* and the northern and southern coniferous forest regions lie within this typology of cold-temperate, wet climate with a considerable depth of snow covering the soil every winter (Nilsson, 1990). The boundary between the northern region (with a longer period of ground covered with snow and a shorter summer) and the southern region (with a longer period of bare ground and a summer with an average temperature above +10°C which last more than four months) is the *Limes norrlandicus*, or biological Norrland boundary. The definition of the boundary was made on the basis of vegetation differences by Du Rietz (1952). Hazel is considered a particularly important distinguishing species. A large number of plants have a continuous distribution south of *Limes norrlandicus*, but only occur sporadically north of it. Although *Limes Norrlandicus* is biologically defined, several climate variables coincide closely with it, especially in the west part of Sweden, e.g. mean temperature for most months, duration of the snow cover, and the dates when spring and winter begin (Gustafsson & Ahlen, 1996).

Temperature

The temperature sum is a cumulative measurement of the temperature during the growing season and it is an estimate related to the needs of the vegetation. It is obtained by taking the sum of the daily mean air temperature for all days when the mean air temperature exceeds +5°C. The temperature sum decreases towards higher latitudes and altitudes. The summer temperature has a large impact on the temperature sum, particularly in the north where the growing season is short. The months of June to August account for about 85% of the temperature sum in northern Norrland, 75% in southern Norrland and Svealand, and 65% in the south of Sweden. The difference in the temperature sum between the northernmost and the southernmost parts of Sweden is around 1000 day degrees (Fig. 1).

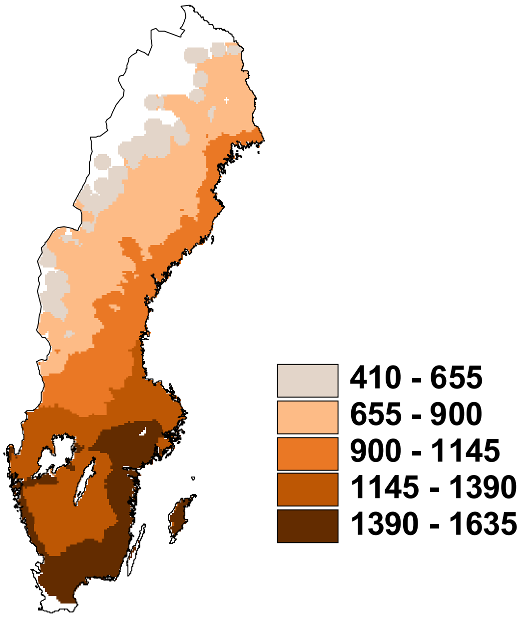

Figure 1. Temperature sum in degree days.

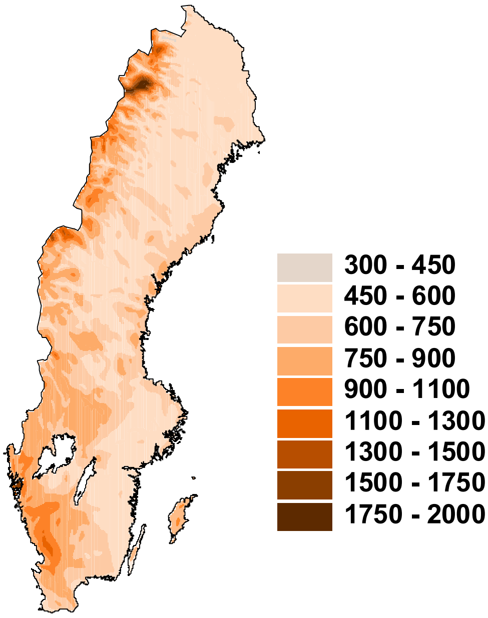

Figure 2. Precipitation in millimetres.

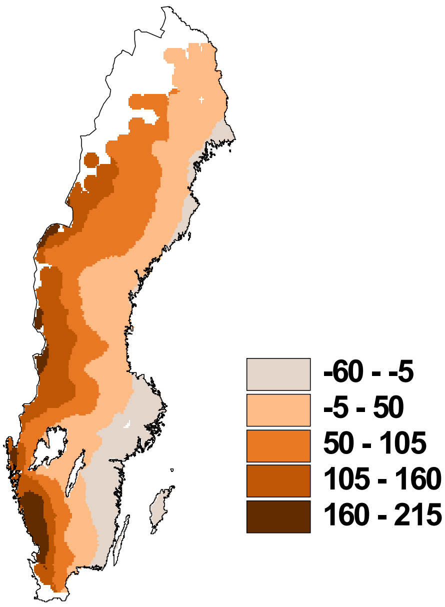

Figure 3. Humidity in millimetres.

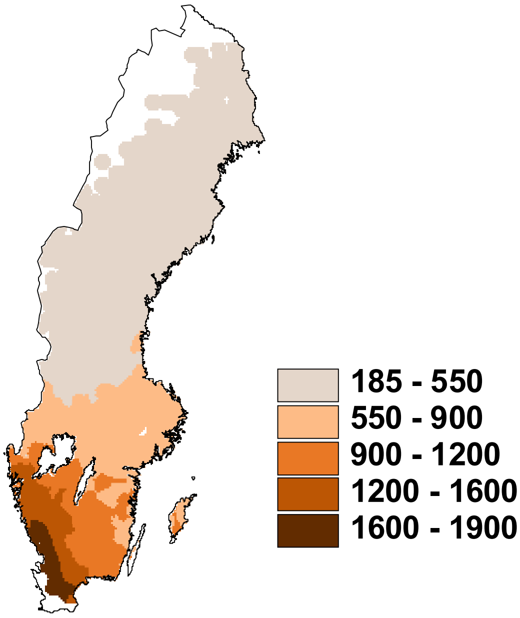

Figure 4. Nitrogen deposition (mg m^{-2}).

At the same latitude, differences in temperature sum are mainly due to the altitude. The temperature sum decreases by 80–120 day degrees for every 100 meters of gained elevation. The distance from cold seawater, mainly along the east coast, also has an impact (Nilsson, 1990; Raab & Vedin, 1995).

Growing season

The growing season is defined as the period during the year when the temperature exceeds +5°C. This is a conventional value, because the relevant critical temperature level varies for different species. The length of the growing season varies from just over 200 days on the west and south coasts to about 100 days in northernmost Lapland where the start coincides almost with the week when the snow disappears. The growing season begins about two months earlier in the southernmost part of Sweden (Scania) than in the northern part of Lapland. The length of the growing season is affected by the same conditions as the temperature sum (Nilsson, 1990; Raab & Vedin, 1995).

Precipitation

The precipitation shows a gradient from west to east, with the highest value along the west coast and in the mountains close to Norwegian border (Fig. 2). The eastern and northern parts get from 1/3 to 1/2 of the precipitation on the west coast and the regions with lowest values are the central mountains and the archipelago areas (Nilsson, 1990; Raab & Vedin, 1995).

Humidity

The humidity is the difference between precipitation and evaporation from a homogenous, even ground covered by vegetation, which is optimally supplied with water. When the humidity is negative, the potential evapotranspiration exceeds the precipitation. These conditions can be found in the eastern part of Sweden and in some areas in Norrland. In the rest of the country, the humidity is positive exhibiting a strong gradient between the west and east of the country (Fig. 3) (Nilsson, 1990; Raab & Vedin, 1995).

Deposition gradients in Sweden

The atmospheric deposition of nutrients and acidifying substances is thought to affect algal growth. Although deposition of nitrogen (Fig. 4) probably has the largest effect on algal growth, the deposition of sulphur and base-forming cations, such as Ca, Mg, K and Na, may also be of importance. The deposition of the above-mentioned substances is fairly evenly distributed all over the country. The highest deposition is in the southwest and the wet deposition (elements dissolved in rainwater) reaches its maximum in southwest Sweden, where the precipitation is highest. The largest wet deposition of sulphur and nitrogen compounds in Sweden occurs in areas with high precipitation along the west side of the southern highlands, although the concentration levels of the substances in the precipitation may be somewhat lower there than in the southernmost part of Sweden. The extent of dry deposition is dependent on the nature of the ground and the vegetation: it varies noticeably from site to site (Gustafsson & Ahlen, 1996; Lövblad, 2000).

Nitrogen deposition decreases from south to north, where the total amount of fallout is only 1/5 of the amount in the south. In central Sweden, as well as along the Norrland coastline, deposition is about 60 – 75 % of the maximum in the south. The lowest deposition is found in the mountainous region where it is 20 – 30 % of that measured in the south. In the most polluted part of southern Sweden nitrogen deposition amounts to more than 2.5 g N m^{-2} yr^{-1}, including wet and dry deposition of oxidised and reduced nitrogen compounds. Of that amount between two-thirds to half of the deposition is wet deposition. The highest deposition of non-marine sulphur in some spruce forest areas can reach values as high as 3 g S $m^{-2}yr^{-1}$. In the northern part of Sweden deposition is considerably lower. Deposition in spruce forests is normally below 0.6 g S $m^{-2}yr^{-1}$. Most of it is in the form of wet deposition (Bernes & Grundsten, 1992).

The total pollutant load should be considerably higher in forests. It has been shown that forested areas receive more deposition than non-forested areas. However, there is less information on deposition to grass and heathland than on deposition to forests. Tree crowns have proved to capture particles and gases very effectively, so the rain under the crown contains not only the initially dissolved pollutants (wet deposition) but also dry deposited pollutants washed off the vegetation (Nilsson, 1990; Westling & Lövblad, 2000). Results from throughfall monitoring (precipitation sampled below the canopy) and different studies show that spruce forests receive more deposition than pine forests and deciduous forests. For instance, the deposition of sulphur in a pine or deciduous forest is around 25% lower than the deposition in a spruce forest (Lövblad et al., 1992).

In recent years, the deposition of nitrogen and, mainly, sulphur has declined. In particular, the dry component of the deposition has decreased, thus reducing the nitrogen and the sulphur present in the throughfall in the forest. Sulphur deposition peaked in the 1970s, showed a decreasing trend and now it is expected to fall considerably in the next few years. Nitrogen deposition has shown a relatively small decline. Deposition of nitrogen oxides culminated around 1990 and a slight decline can now be seen. (Westling & Lövblad, 2000).

Aim

The aim of this report is to describe geographical distribution, time-trends and influence of site factors on the colonisation of epiphytic algae on spruce needles. The correlation with site factors was evaluated using multivariate statistical analysis on data from the National Forest Inventory, the Swedish National Forest Soil and Vegetation Survey and the Swedish Hydrological and Meteorological Institute. The site factors considered are climate, principal atmospheric deposition of nutrients and acidifying compounds, physical and chemical soil proprieties, site hydrology and description indices for the vegetation productivity. Parameters describing the individual tree and its vitality have been considered too.

MATERIAL & METHODS

Data

The data used in this study were obtained from various data sources. The main part of the data is from the Swedish National Survey of Forest Soil and Vegetation (NSFSV) and the National Forest Inventory (NFI). The data on deposition are from the database on deposition chemistry of the Swedish Meteorological and Hydrological Institute

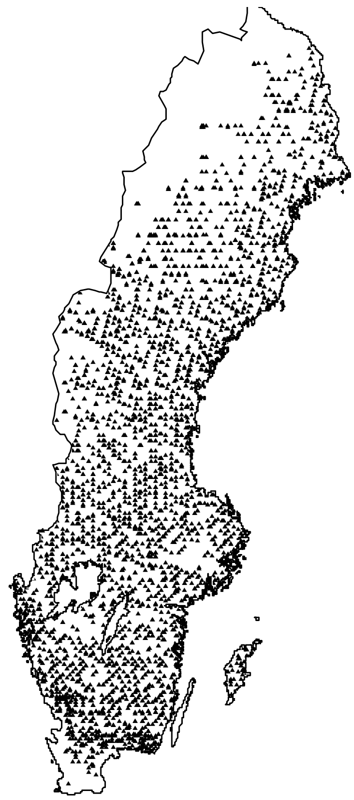

Figure 5. Sample plots of the Swedish National Survey of Forest Soils and Vegetation where information about algae growth were recorded.

(SMHI, 2002). The data on precipitation and temperature presented in Figure 1 and 2 were also obtained from SMHI. The data considered covers the whole forested area in Sweden (Fig. 5) and they were collected between 1993 and 2000. Soil chemistry data were only available between 1993 and 1998. The atmospheric deposition data were modelled for all the plots using data from SMHI for 1998. The total number of plots used was 4055, but not all the plots had complete data for all the different variables (55). Three datasets were prepared to avoid missing values in the data matrix that could affect the statistical analysis (Table

Table 1. Datasets used to avoid missing values and to obtain the maximum number of plots for the variables used. In soil chemistry and sample tree datasets have also been used the general variables that resulted more significant in PCA analysis made on the general dataset

	General	Soil chemistry	Sample tree
Number of plots	3428	496	1918
Number of variables	39	26	22
Type of variable	General site description, climate, atmospheric depositions, soil description	Soil chemistry description	Sample tree description

Table 2. Datasets groups according to geographic position of the plots and to the presence of algae

	plots in Sweden where algae were found	all plots in southern Sweden (below latitude 59° north)	plots in southern Sweden (below latitude 59° north) where algae were found
all plots in Sweden	45 %	30 %	25 %
plots in Sweden where algae were found	-----	65 %	55 %
all plots in southern Sweden (below latitude 59° north)	-----	-----	85 %

1). Each dataset was further divided into four groups according to the geographic position, i.e. all Sweden or only the part below latitude 59° north, and the presence of algae, i.e. all plots or only the plots where algae were found (Table 2).

National Forest Inventory and National Survey of Forest Soil and Vegetation

The main purpose of the Swedish National Forest Inventory (NFI) is to describe the status and change in forest resources in Sweden. However there are numerous fields of application for data from the inventory. For example, a considerable amount of variables can be used for environmental monitoring. The inventory includes 23500 sample plots. Different types of land use are included in the survey, but the most detailed information is from plots that are on forested land. The NFI started in 1923 and until 1983 all the plots were temporary (surveyed once). After 1983 the design was changed and the NFI began to use both temporary and permanent plots (resurveyed regularly) (NFI, 2002a).

The NFI is based on systematic and objective sampling. The observations are made within defined circular plots. The plots are clustered into tracts. These are quadratic and vary in size between different parts of the country. The tracts are systematically distributed over the whole Sweden in an equilateral grid. The distance between the tracts is different in different parts of the country, being shorter in the south than in the north (NFI, 2002b).

The NFI assesses different attributes in each plot in order to describe the vegetation situation. The principal information recorded are the tree species, the diameter for all trees and the description of some average attributes of the trees in the plot, such as species composition, stand age, type of forest treatment, etc. In each plot some sample trees are assessed and measured in detail. For these trees, attributes like age, height, damages, epiphytic vegetation (excluding algae) and defoliation rate are recorded (NFI, 2002c).

The Swedish National Survey of Forest Soil and Vegetation (NSFSV) is a long-term inventory of permanent sample plots of the NFI and it started in 1983, when the NFI changed its design and began to use permanent plots. The plots are identical to the NFI plots. The NSFSV deals specifically with some aspects of the site description like the hydrological conditions, the description of soil types and soil horizons, the soil sampling from organic and mineral horizons for chemical analysis, the description of different vegetation layers with more importance placed on non-timber aspects and the inventory of pendulous lichens and algae on spruce needles. The data are stored in the general database of NSFSV project. The variables can be combined with the NFI data of forest stands from the same plots. All the plots were surveyed for the first time between 1983 and 1987. The second inventory started in 1993 and is expected to be completed in 2002 (NSFSV, 2002).

Dependent variables

The variables that describe the algae characteristics are the youngest needle (YN) and the algal coverage (CA).

The youngest needle variable expresses the age class of the youngest needles on which algae are found and, indirectly, how favourable the conditions are for the algal colonisation. The younger the age at which the needle is colonised with algae, the more favourable are the conditions for algal growth. The original range (1 = needle 1 year old, 10 = needle 10 years old) was inverted to describe this aspect better and more logically in the data analysis. Thus a lower value for the youngest needle means an older needle colonised (1 = needle older than 10 years old) and a higher value means a younger needle colonised (10 = needle younger

Table 3.The climatic variables. The data were not measured in the plot but obtained through map interpolation

	Abbreviation	Short explanation	Units of measurement
Temperature sum	TSUM	sum of degrees of mean air temperature above +5°C, for all days with mean air temperature exceeding +5°C	Degree Celsius
Humidity	HUM	calculated as: precipitation – evapo-transpiration during the vegetation period (the period when the average daily temperature exceeds 5 ° C)	Mm

than 1 year old). It may be considered as an intensity index of algal colonisation.

The algal coverage variable expresses, as a percentage, the maximum upper-side surface of the needle covered with algae.

The youngest needle and the algal coverage variables are recorded on the NFI sample tree of the plot. The tree is chosen systematically. The first spruce on the right when walking from the plot centre that fulfils specific requirements, such as a normal shape for the stand, absence of obvious damage or irregular features and the presence of branches at approximately eye height is selected. Two branches are considered on each sample tree, one on the inside half of the crown, towards the centre of the plot and one on the outside half of the crown, away from the plot centre. The age of the youngest needle with algae or the absence of algae is recorded for each branch. The upper side of the needles of the most colonised age, on the selected branches, are used to record the maximum coverage of algae in percent of the total needle area.

Independent variables

The independent variables, used to try to explain the growth of algae, describe the main site factors and could be divided in groups according to which factors they are related to:

- Climate (Table 3).
- Atmospheric deposition of both acidifying and basic compounds (Table 4).
- General description of the site. Topography, hydrology, fertility and species composition are considered (Table 5).
- Soil description. Physical and chemical parameters are used (Table 6).
- Description of the sample tree (Table 7).

The single variables are briefly described in the tables. Some of the variables were category variables, therefore they are not continuous but discrete. Each category was transformed to a variable with two possible values, +1 for the presence and –1 for the absence, according to the suggestion of Esbensen et al. (1996).

The variables identifying the position of the plots, like the geographic coordinate, altitude and distance from the coast, were only used to identify plots and to create maps and were not used during statistical analysis. The geographic variables are highly correlated with climate factors. The climate variations are a manifestation of the variation of the geographic position, and it is the climate, not the latitudinal or longitudinal position that affects the vegetation. For this reason the geographic variables were not used in the PCA and PLS models.

Statistical analysis

The relations between the different variables were studied with multivariate data analysis methods using the Unscrambler program, version 7.5. Principal component analysis (PCA) was used to describe the data and their structure and partial least square regression (PLS) to make a model to predict algal growth from the site factors. In addition, the correlation coefficients between the variables describing algal growth (dependent variables) and the most significant independent variables were calculated.

The main objective of multivariate data analysis

Table 4. The deposition variables. The data were modeled for all plots using data for 1998

	Abbreviation
Calcium deposition	DepCa
Magnesium deposition	DepMg
Potassium deposition	DepK
Sodium deposition	DepNa
Ammonium deposition	DepNH
Nitrogen deposition	DepNO
Sulphur deposition	DepS

Table 5. The variables for the general description of the site: topographic situation, hydrological description, fertility indices and species composition (limited to the timber aspects)

	Abbreviation	Short explanation	Units of measurement
Topographic position	Top	Top of a elevation	+1/-1 = yes / no (class variable)
	Hillside	Side of a elevation with a slope > 4:20	
	Flat	Flat area (slope < 4:20)	
	Bottom	Concave area	
Slope	Slope	Vertical gain in meters every 20 m horizontally	m
Moving ground water	Never	No mobile ground water	+1/-1 = yes / no (class variable)
	ShortPer	Mobile groundwater for short period	
	LongPer	Mobile groundwater all the time	
Soil moisture	Dry	Dry	+1/-1 = yes / no (class variable)
	Fresh	Fresh	
	Fresh-moist	Fresh – moist	
	Moist	Moist	
	Wet	Wet	
Growing rate	GrowingRate		m^3 sk/ ha
Pine site index	PineSI	Stand productivity for pine	1/10 m^3 sk
Spruce site index	SpruceSI	Stand productivity for spruce	1/10 m^3 sk
Stand height	Height	Average height in the stand	dm
Pine proportion	PropPine	Species proportion in the stand,	1/10 tree number
Spruce proportion	PropSpruce	Species proportion in the stand,	1/10 tree number
Birch proportion	PropBirch	Species proportion in the stand,	1/10 tree number

Site index = site quality classification expressed as wood production in cubic meters per hectare and year during the rotation period (100 years for spruce and pine).

methodology is to find out which part of the data can be used to describe the problem and which part of it is random noise. The different methods use different ways to decompose data, i.e. to divide them into the structure part and in the noise part. The methods used in this report, PCA and PLS, are based on correlation.

The correlation is a scaled covariance measure and it is the most useful measure of interdependence between variables because correlations are directly comparable whatever units the variables are measured in. The covariance is the measure of linear association between variables (Esbensen et al., 1996).

Principal component analysis

The PCA is a method that describes the structure of the data. It is used to detect the interdependence between variables, the patterns and the outliers on the data. The purpose of a PCA analysis is to decompose the data, organised in a X matrix, to create an explorative model of the structure. A PCA model is a transformation in which many original dimensions are transformed into another coordinate system with fewer dimensions. The transformation is achieved through projection into the new coordinate system. The directions of the new coordinate axes, or principal components (PC), are chosen to describe the largest variation in the dataset. In the transformation the information in the dataset is reduced due to projection onto fewer dimensions and the remaining information is stored as residuals, which are used to create the next PC. The difference between the coordinates of the samples in the new and in the old system can be used as a measure of how good the model is (Esbensen et al., 1996). It is important that the model is representative of the real situation. A measure of this is the total residual variance, a measure of error, which indicates the deviation of the model from the real data. The residual variance is calculated from the part of data that cannot be explained by the model and reaches a small value when the model is explicative. The total explained variance is complementary to the residual variance in so far that it is a measure of the part of the data structure that is explained by the different PCs in the model. The explained variance is also useful to define the significance of the variables. Variables with high loading values along PCs with high explained variance are more important than variables with the same loading values along PCs with a low explained variance.

The loadings plots are important for interpreting the model, especially when the main pur-

Table 6. The variables describing the characteristics of the soils. Physical description and chemistry parameters

	Abbreviation	Short explanation	Units of measurement
Thickness O horizon	ThickO		cm
Texture	Stones-gravel	Stones – gravel	+1/-1 = yes / no (class variable)
	Sand	Sand: coarse + medium-fine + fine sand	
	Silt	Silt: coarse + silt	
	Clay	Clay	
	Peat	Peat	
Soil depth	DeptSoil		cm
Humus layer	HumusLayer	Total quantity of material in O or A horizon	ton/ha
pH O horizon calculated in water solution	pHH2OO		pH units
Total carbon in O horizon	CO		% of dry weight
Total nitrogen in O horizon	NO		% of dry weight
pH B horizon calculated in water solution	pHH2OO		pH units
Total carbon in B horizon	CB		% of dry weight
Total nitrogen in B horizon	NB		% of dry weight

pose of the analysis is to investigate the relations between the different variables. Loadings are the coefficient of unit vectors along each axis in the variable space, i.e. the directions of each PC relative to the original coordinate system. Loadings give information about the relationship between the original variables and the PCs (Esbensen et al., 1996).

The loading plots show how much each variable contributes to the explained variance of each PC. Graphically, important variables lie far away from the origin, the further away they are, the more important they are. Numerically, this means that they have large absolute loadings. The loadings plots also show how the variables covary. Graphically, variables close to each other and along the same straight line through the origin are covariant. The covariance is positive if they lie on the same side of the origin, negative if they lie on the opposite sides of the origin. Numerically this means that they have similar loadings in absolute values (Esbensen et al., 1996).

In the PCA analysis, it is important that the variables get equal weighting if they are expressed in different units of measurement. In the calculations used for the models in this thesis the different variables were standardised by scaling each value with the inverse of the standard deviation of the corresponding variables (Camo, 1996).

Partial least square regression

The PLS is a regression method. The main purpose is to create a model to predict the value of one variable (PLS 1) or more variables (PLS 2) using values of other variables. It needs two matrices, one (X) for the independent variables and one (Y) for the dependent variables. The model is created using multivariate calibration between the two matrices. The PLS method can be described as two PCA analyses on two matrices. The PLS uses the y-variance as a guiding hand in decomposing the X matrix, i.e. the X matrix is decomposed using vectors obtained by the Y matrix. Then the Y matrix is decomposed using vectors obtained by the X matrix. The calculation continues by iteration until convergence (Esbensen et al., 1996).

The model should be validated to assure that it will work with new, similar data and to avoid either over or under fitting. The validation is thus a way of testing the modelling and/or the prediction ability of the model. Therefore it is necessary to have a new dataset, or a part of the old one that has not been used in the development of the model. There are three different validation methods: test set, cross validation and leverage correction. In this report the test set method was used because of its high statistical significance.

The test set method requires access to two datasets, calibration and validation. In each dataset both X and Y values are known. The two datasets should be as similar as possible with regard to

Table 7. *The variables describing the sample tree used for the algae inventory*

	Abbreviation	Short explanation	Units of measurement
Tree height	TrHeight		dm
Crown height	CrownHeight	The distance from the ground to the lowest part of the ground	dm
Diameter	Diam	The diameter of the tree at 1.3 m above the ground	mm
Crown condition	CrownCond	Defoliation in percent	%
Decolouration	Decol	Discolouration in percent	%
Distance from stand edge	BordDist		m
Stand age	Age		year

both population and sampling conditions. In addition, they should cover the same range and display the same features. The calibration set is used to calculate the model and it should be representative of the future population and span the X-space as widely and representatively as possible. The modelling error can be calculated by comparing predicted and measured Y values of this dataset.

The validation set is used to verify the predictive ability of the model. The prediction error can be calculated by comparing predicted and measured Y values of the validation data set (Esbensen et al., 1996). In the following analysis, the two datasets were chosen randomly from the main dataset.

Geographic representation

The spatial distribution of some variables was shown with maps. The maps were made by interpolation of grid data for the different variables in the plots. The interpolation is based on the inverse distance weighted (IDW) method. The IDW interpolator assumes that each input point has a local influence that diminishes with distance. This method can be used when the variable being mapped decreases in influence with distance from its sampled locations. The method assigns a greater weighting to points closer to the processing cell than those farther away. The output value for each location was determined using all points within a fixed radius of 20 km (ESRI, 1996).

RESULTS

Distribution patterns of algae

Three different maps show the distribution of algae on spruce needles in the Swedish forests. The first map shows the presence of algae, i.e. if algae were found on the selected tree or not (Fig. 6). The second map shows the age class of the youngest needle colonised by the algae (Fig. 7). These two maps show similar distribution patterns. It is possible to identify two main patterns, one along the north-south direction and one along the east – west direction. The algae decrease considerably towards the north. They disappear almost completely north of a line between latitude 61° north in the east and 63° in the west. The sharp decline in algal distribution coincides roughly with *Limes norrlandicus*. The south-north gradient is not obvious south of 59° north but there seems to be a gradient along the east-west direction. The algae are more widespread and occur at more sites in the west than along the east coast. However the pattern is not consistent. Even on the west coast large areas have a low presence of algae. The distribution in the southern region is quite scattered and could be related to local conditions, such as areas with intensive agriculture or cattle farms.

The map showing algal coverage of needle surface (Fig. 8) also shows the clear north-south boundary. Northwards the coverage is minimal, southwards it can reach high values. The distribution of this variable in the southern region is quite scattered and it is not possible to find a clear gradient. The maximum values of needle surface coverage do not always correspond to the maximal presence or colonisation of algae.

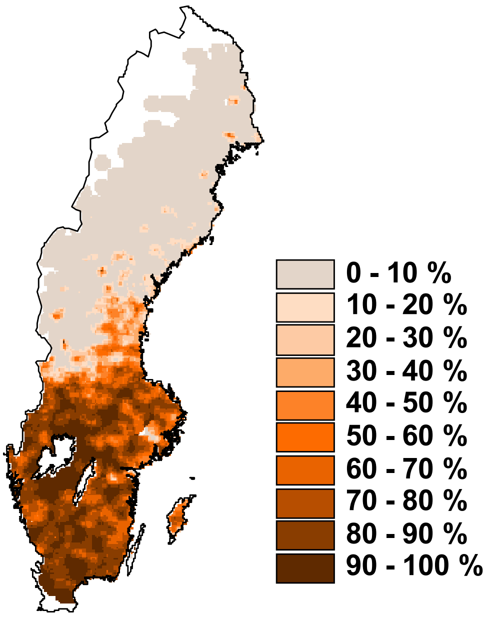

Figure 6. Percentage of plots where presence of algae was found on spruce needles.

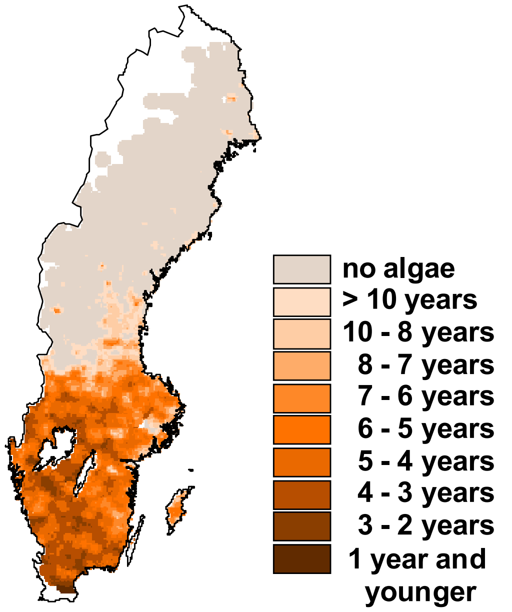

Figure 7. Age class of the youngest needle where algae were found.

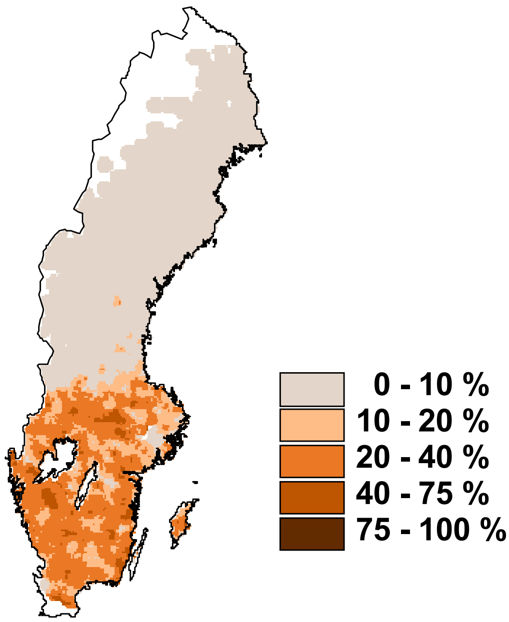

Figure 8. Algae coverage on the upper side surface of the needle with the highest colonisation.

PCA and correlation analysis

Almost all the variables display some degree of covariance with algal growth on Norway spruce needles, but a fairly limited number of variables show a relatively high correlation. This can be seen by analysing the correlation coefficients (Table 8) between the variables expressing the algal presence and the independent variables and by interpretation of loading plots of PCA models. In this way, it is possible to describe the co-variation, i.e. the measure of the interdependence, between the different variables. However, it is not possible to draw any conclusions about the casual relationship that may exist between the variables. The PCA model shows the structure of the data and the relations between the different variables. It is possible to quantify and to interpret the common variation of all the variables, but it is not possible to measure the unique variation belonging to a specific variable.

The PCA analyses were done as 12 different PCA models, four for each of the three different datasets described earlier (Table 1). In all the models, the value of explained variance increases continually with the increased number of PCs. The explained variance for the PC1 is normally around 20%, considerably lower than the values found in other studies (Bråkenhielm and Qinghong, 1995; Qinghong, 1997). This could be related to the high number of variables with low interdependency considered in the following calculations. In fact, when a PCA model with only the most significant variables (9) is made, the explained variance for the PC1 increases to more than 60% without any significant changes in the relations between variables.

The correlation between the youngest needle and the coverage of algae is high. A general observation is that the covariance and the correlation of the independent variables with the youngest needle are higher for the youngest needle than for coverage. This is also underlined by the result of the PLS analysis. It was possible to create a regression model, albeit a weak one, to predict the youngest needle variable, but not the algal coverage variable.

Table 8. Correlation coefficients between dependent variables (youngest needle, YN, and coverage algae, CA) and the most significant independent variables, according to the PCA analysis, for the different groups based on geographic position of the plots and on presence of algae

	All plots in all Sweden		Plots in all Sweden with algae		All plots in southern Sweden		Plots in southern Sweden with algae	
	YN	CA	YN	CA	YN	CA	YN	CA
Temperature sum	0,70	0,51	0,32	0,17	0,02	-0,00	0,02	0,01
Humidity	0,02	0,01	0,13	0,01	0,12	0,01	0,14	0,02
Calcium deposition	0,50	0,33	0,32	0,11	0,06	-0,02	0,10	-0,03
Magnesium deposition	0,51	0,36	0,30	0,09	0,11	-0,00	0,13	-0,03
Ammonium deposition	0,65	0,45	0,36	0,10	0,16	-0,01	0,17	-0,07
Sulphur deposition	0,65	0,46	0,35	0,11	0,14	-0,01	0,16	-0,05
Growing rate	0,24	0,18	0,04	0,03	-0,03	-0,03	-0,03	-0,01
Spruce site index	0,65	0,46	0,25	0,07	0,00	-0,10	0,08	-0,10
Long period for mobile groundwater	-0,18	-0,14	-0,13	-0,03	-0,07	0,00	-0,01	-0,01
Soil depth	-0,16	-0,15	-0,05	-0,05	0,02	-0,05	0,04	0,02
Total C in O horizon	-0,18	-0,10	0,03	0,06	0,10	0,06	0,09	0,03
Total N in O horizon	-0,04	-0,03	0,05	0,01	0,10	0,00	0,08	-0,05
pH O horizon in H_2O	-0,15	-0,15	-0,08	0,06	-0,17	-0,05	-0,14	0,01
Total C in B horizon	0,18	0,18	0,04	0,14	0,22	0,17	0,14	0,10
Total N in B horizon	0,19	0,18	0,02	0,09	0,24	0,12	0,16	0,03
pH in B horizon in H_2O	-0,14	-0,15	-0,14	-0,14	-0,22	-0,11	-0,26	-0,06
Tree height	0,16	0,16	-0,03	0,09	-0,02	0,06	-0,04	0,07
Age	-0,31	-0,17	0,09	0,08	0,02	0,13	-0,03	0,14
Crown conditions	-0,27	-0,14	-0,08	0,08	0,02	0,10	-0,05	0,09

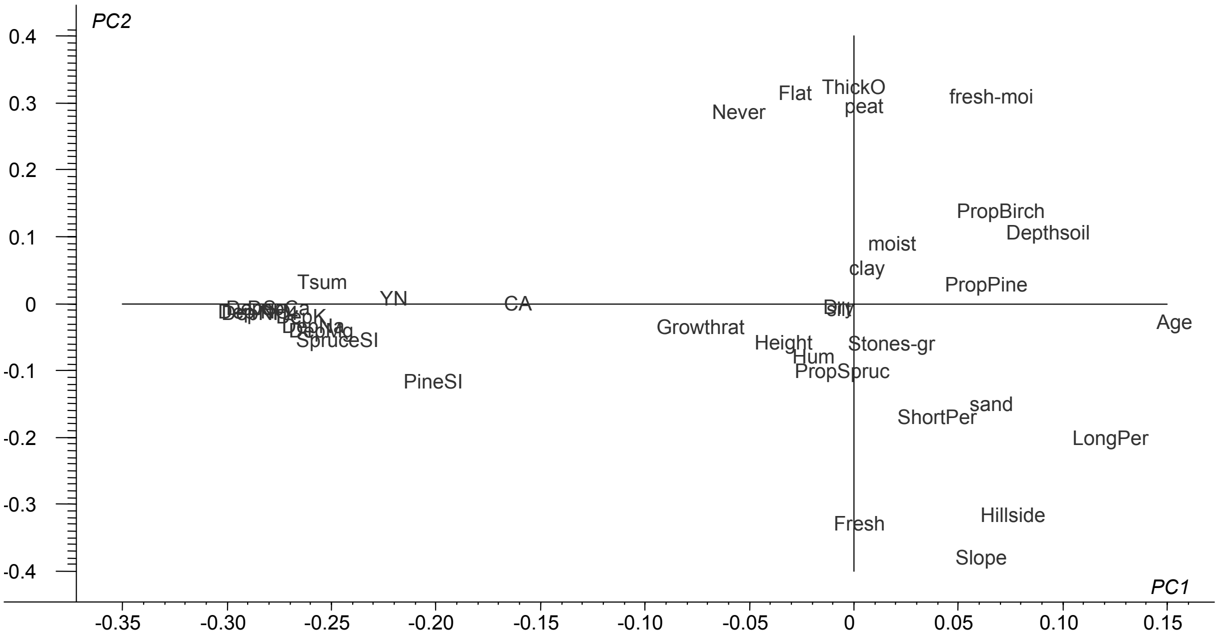

Figure 9. PCA model created using the general dataset with all the plots in Sweden, using all the variables belonging to this dataset. The total explained variance for PC1 and PC2 is 36%.

General dataset

The first PCA model is based on the dataset called general, which contains the variables describing the site, the climate and the atmospheric deposition and is shown in Figure 9. This dataset has the highest amount of plots. In the first PCA model all the available plots throughout Sweden were used. In a PCA analysis the direction of the largest variation in the dataset is described by PC1. In this model the variables describing the algae are found far from the origin along PC1. According to this plot, the variables that seem to co-vary with the algal presence are the temperature, the deposition and the fertility indices, especially the index for spruce. However, the site index for spruce seems less important than the temperature and the deposition. All the variables describing these factors lie at the end of PC1, with high loading values and close to the youngest needle and

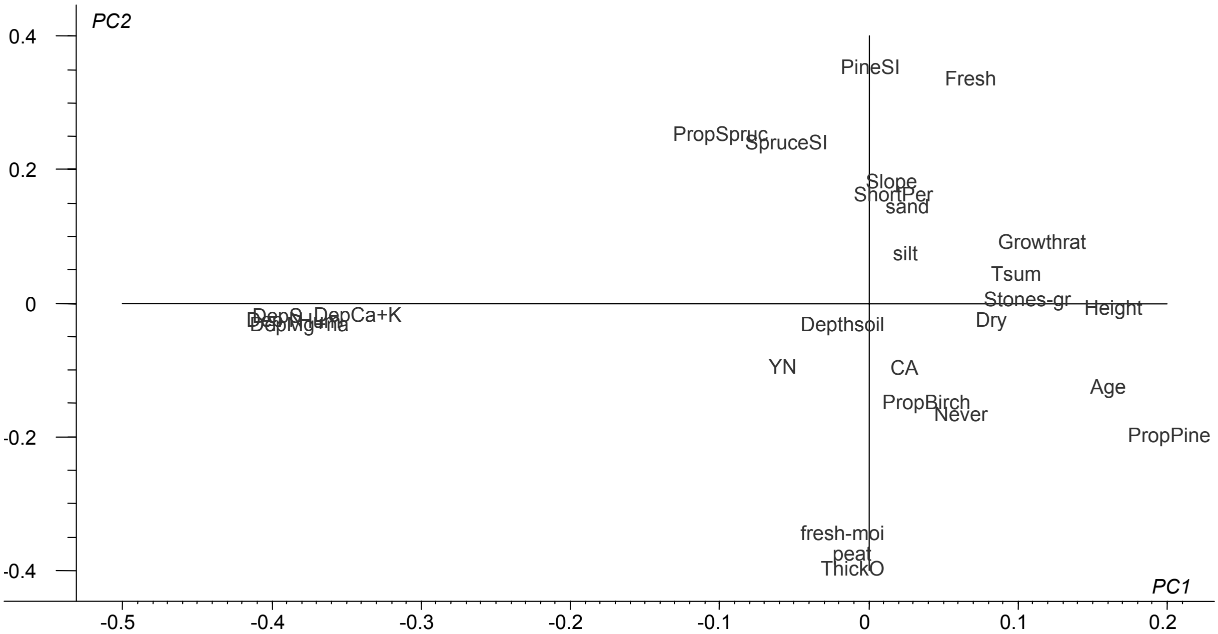

Figure 10. PCA model created using the general dataset with all the plots in southern Sweden (below latitude 59° north), using all the variables belonging to this dataset. The total explained variance for PC1 and PC2 is 33%.

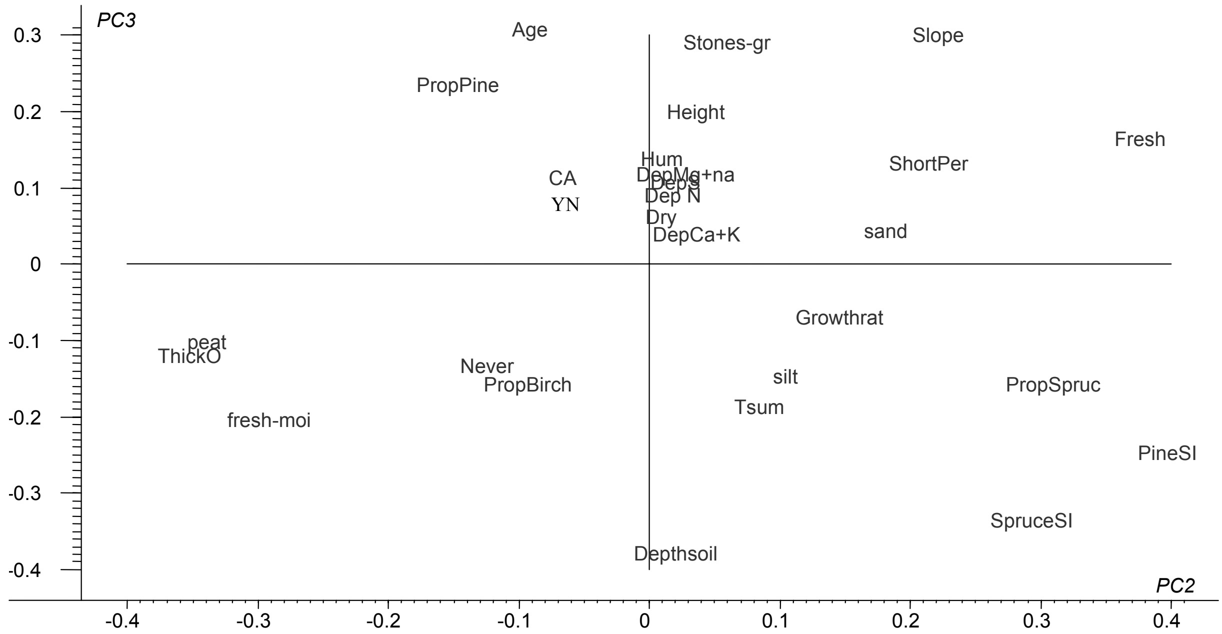

Figure 11. PCA model created using the general dataset with all the plots in southern Sweden (below latitude 59º north), using all the variables belonging to this dataset. The total explained variance for PC2 and PC3 is 24%.

algal coverage variables. They seem to play the same role for algal growth, however, according to the correlation coefficients (Table 8), the temperature and the nitrogen and sulphur depositions are better correlated. The growth rate and the average height of the stand seem also to be correlated with algae, but with a lower significance. A weak negative correlation with algae was found for the variables describing the depth of the soil, the average age of the stand and the presence of water in the soil for a long period. All these relations are confirmed by the correlation coefficients calculated (Table 8). The variables lying along PC2, including the humidity, do not seem to affect the algae.

Since temperature seems to be important for limiting the northward distribution of algae, a number of variables also influenced by temperature will also show a relative strong correlation. This is true for variables like growth rate, age of forest stand and site indices that are all influenced by temperature. The lack of influence from humidity might also be explained by the fact that there are areas with very high humidity that are very cold and thus would not have any algae. Further models were calculated to try to clarify this aspect. In order to diminish the temperature effect only plots south of the latitude 59° north were considered. This PCA model is shown in figure 10. It can clearly be seen that the variables that contribute most to the explained variance of PC1 have changed. The most important climate variable is now humidity and the temperature seems to have lost the most of its significance. The strong southwest gradient for the deposition variables contributes to their strong influence on PC1. However, even the algae do not seem to covary with either humidity or deposition. The covariation between these variables and the algae is shown by plotting PC2 and PC3 (Fig. 11). However, it is a weak correlation because the variables lie close to the origin. The site index for spruce is now mainly explained by PC2 and it does not seem to affect the algae. The relations with the other variables, which are however less significant, do not show any change.

The results for the models using only plots where algae were found and the models calculated only for the southern region are very similar, so no plots for these models are shown. The results from the models calculated using the plots in the south where algae were found were similar to the results for the whole southern region and it was not possible to point out any new information. A possible explanation for these similarities could be the high proportion of plots with algae in the southern part of Sweden.

Soil chemistry dataset

The models based on the soil chemistry dataset (Fig. 12) contain the variables describing some of the chemical properties of the soils and the most important variables from the general dataset. Using data from all the plots, the major variation distribution of variables along PC1 is similar to the first model (Fig. 9). The variation along PC2 is dominated by the soil chemistry variables. It is possible to see a positive correlation with algae for

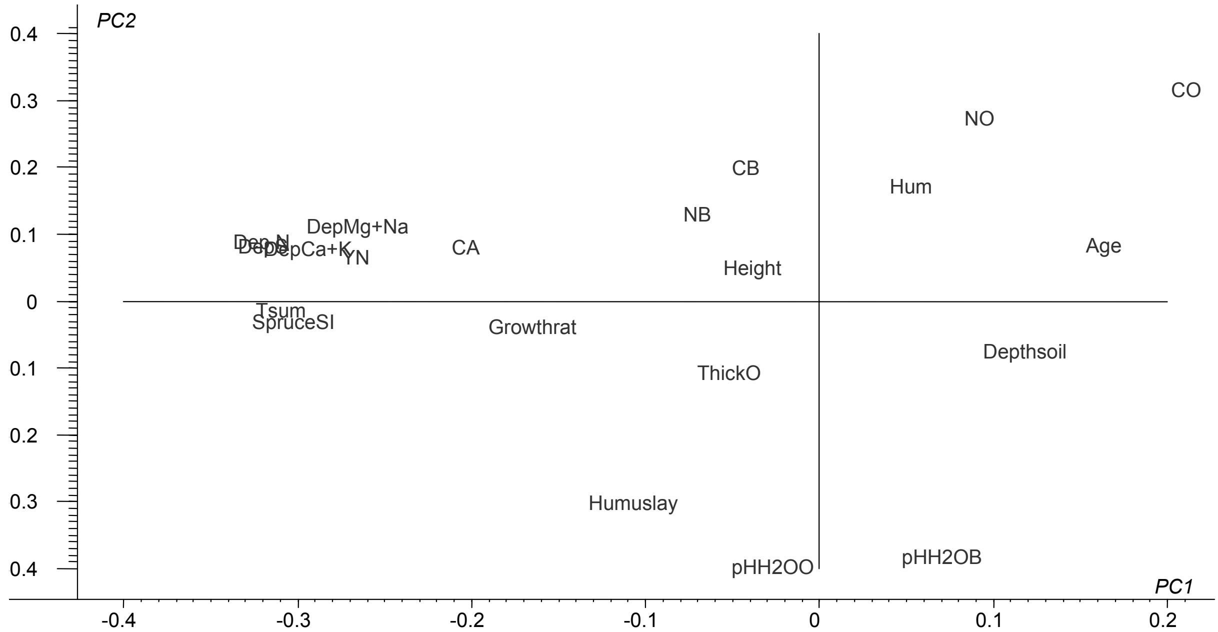

Figure 12. PCA model created using the soil chemistry dataset with all the plots in Sweden, using all the variables belonging to this dataset and the most significant variables from the general dataset analysis. The total explained variance for PC1 and PC2 is 52%.

the carbon and the nitrogen in the B horizon. pH values for both O and B horizons and carbon and nitrogen in O horizon show a negative correlation with algae. However, these correlations are quite weak. The relations between algae and soil chemistry parameters do not show any significant change when the model is calculated only for the plots in the south of Sweden or only with plots where algae were found.

To check if algal growth was influenced by the nitrogen status of the soil, the C/N ratio was compared between plots with algae and plots without. The comparison was made separately for the south and north of Sweden. Even though the results show a distinct pattern for both the north and south of Sweden with lower C/N ratios in the O horizon and higher C/N ratios in the B horizon for plots with algae, the differences are far from significant (Table 9).

Sample tree dataset

In order to evaluate possible influence from the tree on algal growth, the dataset containing the tree data variables was used. To avoid influence from well-known differences between the north and south of Sweden such as higher tree age and bad crown condition along the Scandinavian mountain range in the north, the dataset from all plots in southern Sweden was used.

The PCA model based on the sample tree dataset (Fig. 13) contains the variables describing the sample tree used for the algae inventory and the most important variables from the general dataset.

As in the other models the position of variables along PC1 shows the relation between algae and climate and deposition. It seems clear that none of the tree variables are important for explaining either the presence, or the coverage of algae. The figure also shows that in the south of Sweden there is a correlation between the youngest needle and deposition (they are situated along the same axis from origin), but that it is weak.

Table 9. Mean values, with confidence levels, for the C/N ratio in O and B horizons calculated for plots with algae and plots without algae in the northern part of Sweden (above the 59° latitude north) and in the southern part

	North of Sweden		South of Sweden	
	C/N O horizon	C/N B horizon	C/N O horizon	C/N B horizon
Plots with algae	33,46 ± 3,68	27,92 ± 12,33	29,48 ± 3,31	24,49 ± 3,17
Plots without algae	35,41 ± 3,00	25,52 ± 4,64	33,42 ± 10,22	21,68 ± 4,45

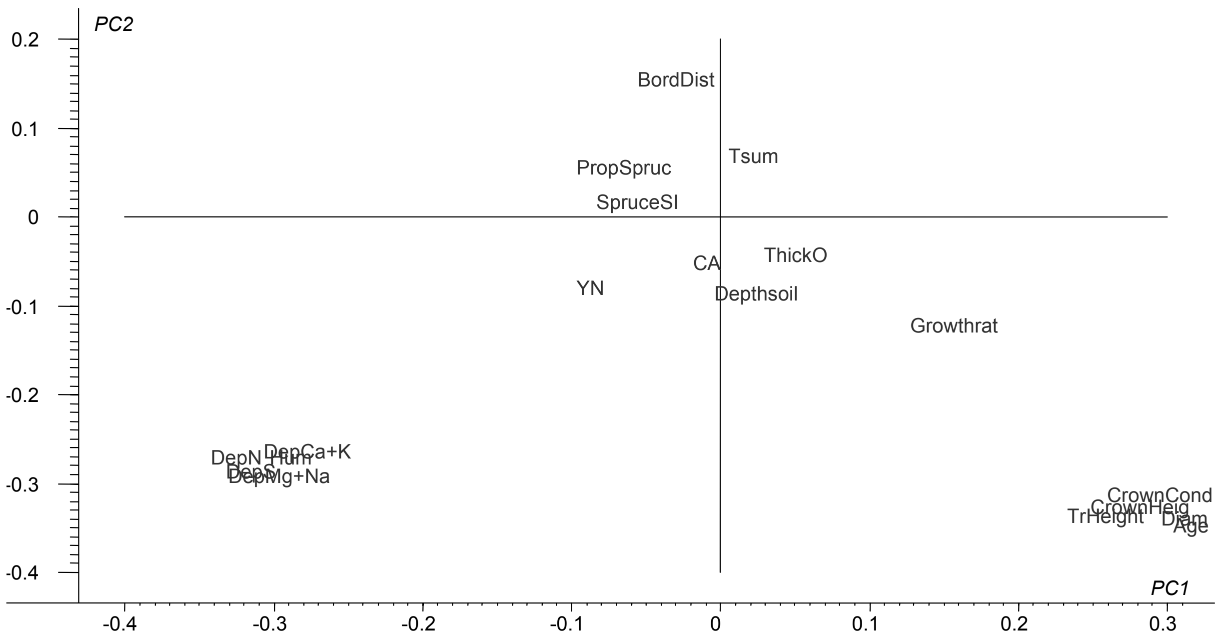

Figure 13. PCA model created using the sample tree dataset with all the plots in southern Sweden (below latitude 59° north), using all the variables belonging to this dataset and the most significant variables from the general dataset analysis. The total explained variance for PC1 and PC2 is 48%.

Temporal variations

To investigate a possible temporal trend, the mean values for the variables describing algae were calculated for the different years with available data. The results, as means with a 95% confidence interval, are shown in Figure 14 for the youngest needle variable, and in Figure 15 for the coverage of algae. A linear trend line has been added to the values distribution. The data for the coverage of algae variable were only recorded from 1995. To avoid bias, the data from 1993 and 1994 for the youngest needle were pooled, since only plots in the south of Sweden were visited in 1993 and only plots in the north were visited in 1994. Both the youngest needle and coverage seem to decrease from 1995 onwards, but the data from 1993 and 1994 show lower values. If this first year is not considered, the r^2 value for the trend line increases from 0.04 to 0.34 (shown as the dotted line in Figure 14). In general, there was a tendency for algae to decrease.

PLS model

The PLS model was calculated to try to predict the values of the youngest needle variable using measured values of variables describing the site factors. In the model the most significant variables for the algal growth possibilities (x variables) according to the previous interpretation of the PCA models are included. These variables are: temperature, humidity, atmospheric deposition, spruce site index, age, height, diameter, crown condition

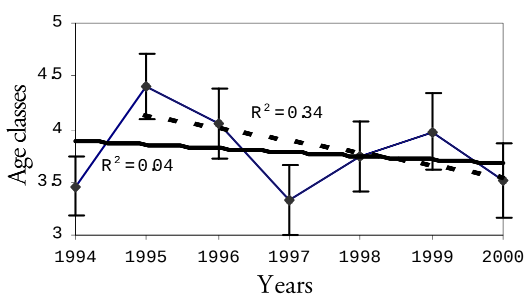

Figure 14. Temporal variation of the youngest needle variable from 1994 to 2000. Error bars denote ± mean confidence level at 95%. The continuous line shows the tendency from 1994 to 2000 (R^2 = 0.04). The dotted line shows the tendency from 1995 to 2000 (R^2 =0.34).

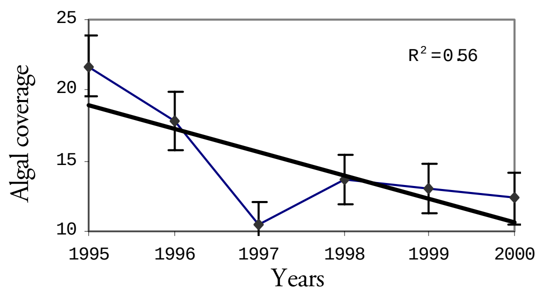

Figure 15. Temporal variation of the coverage of algae variable from 1995 to 2000. Error bars denote ± mean confidence level at 95%. The continuous line shows the tendency from 1995 to 2000 (R^2 = 0.56).

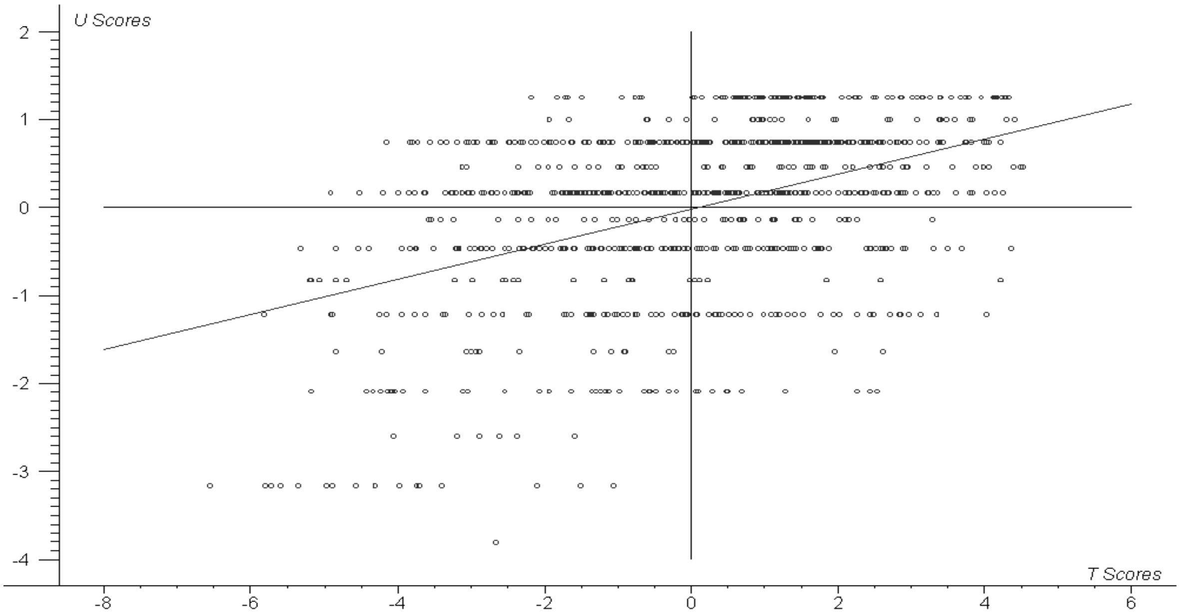

Figure 16. PLS model – T versus U scores. In a good model the samples should lie as close as possible along a straight line. In this model the samples are spread over almost the whole plot.

or defoliation rate and distance from the edge of the stand. A logarithmic transformation of the variables was made to stabilise the variance.

The prediction ability of the model is not very high and can explain only 25% of the youngest needle (y variable) variance. The results could not be improved by adding new variables.

The relationship between the youngest needle variable and the independent variables did not seem to be linear. This is shown by the T versus U scores plot (Fig. 16) where the samples are spread over the whole plot. In a linear model samples should lie as close as possible to a straight line. The quality of the regression model fitted to the data is not very high. In the predicted versus measured y plot (Fig. 17) the predicted values should be as similar as possible to the measured values. This means that the line in the plot should have a slope close to one. In the model the slope is only 0.15.

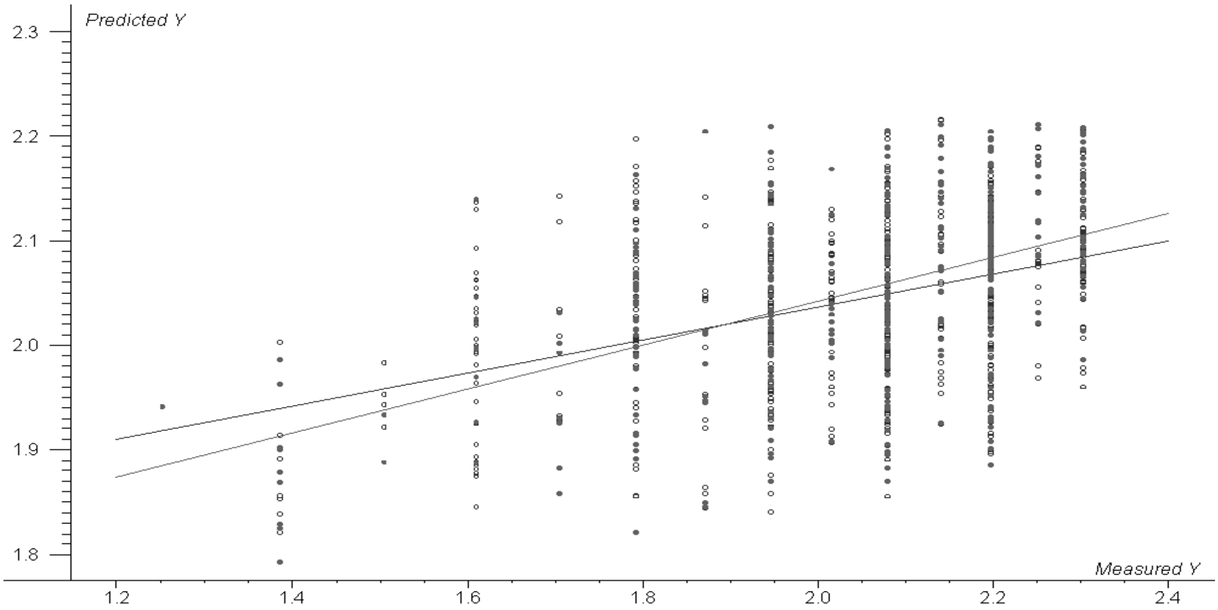

Figure 17. PLS model – Predicted versus measured Y plot. In a good model, the predicted values should be as similar as possible to the measured values, i.e. the angular coefficient of the line should be closed to 1. In this model the angular coefficient is only 0.15.

Discussion

The algae on spruce needle, as all kinds of vegetation, are affected by site factors. The conditions needed for development are created by interaction of the different site factors. All the factors have an influence, but some of them play a more important role. Some of them are limiting factors: if they are not available in a suitable quantity the vegetation can not grow. What are the limiting factors for epiphytic algae on spruce needles?

In this report, many variables describing the different site factors that could affect algal growth have been considered. The most important, according to the results, are the climatic conditions and atmospheric deposition. Furthermore, the quality of the site, expressed as productivity capacity, also seems to affect algal growth, even if it plays a considerably less important role. However, this could also be explained as a climatic influence since the site index changes decrease from south to north.

The results from the first model (Fig. 9) show a high correlation between algae, temperature and deposition. This is similar to what is reported in the literature. In different studies (Bråkenhielm and Qinghong, 1995; Poikolainen et al., 1998; Qinghong and Bråkenhielm, 1995; Qinghong, 1997), a correlation between algae and increasing temperature and deposition has been found. Peveling et al. (1992) assume that algae obtain the minerals they need from air deposition, especially nitrogen, which is considered the main limiting nutrient by Bråkenhielm and Qinghong (1995). The humidity, contrary to what has been suggested in some studies (Bråkenhielm & Qinghong, 1995; Søchting, 1997; Poikolainen et al., 1998), does not seem to affect the algae to the same extent.

The main problem is thus to try to separate the effects of climate from the effect of deposition. The correlation between algae and climate and between algae and deposition are very high. However, algae, climate and deposition have a strong covariation. In these cases a correlation may not indicate a cause and effect relationship. The same problems have been encountered in other studies (Bråkenhielm and Qinghong, 1995; Poikolainen et al., 1998).

A new PCA model was calculated to try to separate the effect of temperature from deposition. This model takes into account a limited area, i.e. the part of Sweden below latitude 59° north. This region presents a narrower range for the temperature sum compared to the overall variation in Sweden, but there is nevertheless a significant gradient due to the central Highland area that has lower temperatures due to higher altitude (Fig. 1). The results show (Fig. 10) that the algae seem to be affected by deposition and humidity. However, in this area the covariance between humidity and deposition is high because the deposition, especially the wet component, is strongly affected by the precipitation (Lövblad, 2000). In fact, when looking at the whole country, where the gradients of humidity and depositions do not correspond so much, the humidity does not seem to affect the algal growth. It is probable then the correlation between humidity and algal growth is caused by the covariation with deposition. These results would suggest that, for Swedish climatic conditions, the humidity is not a limiting factor for algal colonisation, but may act as a contributing factor. The local variation in humidity could play an important role (Søchting, 1997).

The temperature sum does not contribute to the variance of algae in the southern part of Sweden. This result would suggest that the algae are limited by the temperature sum, but only below an ecological optimum. Above this threshold, between approximately 1100 and 1300 day degrees, the variation in temperature does not seem to affect the algae in any significant way that could be controlled by other factors, such as depositions.

Deposition, when the climate conditions are favourable, seems to play the principal role in affecting growth and algal distribution, acting as a limiting factor and as an accelerator.

The local variability of the factors could also play an important role for the growth and distribution of algae. The most important local factors could be the vicinity to nutrients sources, the structure of the stand or the morphology of landscape. All these factors are thought to affect the local variation of the deposition (Näsholm & Persson, 2000). Søchting (1997) emphasises that the presence of algae could be related to the position in the stand, which affects the humidity and the light. While Poikolainen et al. (1998) discuss the presence of more algae in moist sites and close to nitrogen sources, such as fertiliser factories, fur or cattle farms and urban areas. Even though general tendencies regarding the influence of different factors are found in this study, the degree of explanation is quite low. The effect of local factors not described in the available data for the plots could be an explanation for the lack of fit of the PLS model trying to predict algal presence. The maximum explained variance for the Y variable considered, i.e. youngest needle, was only 25%. The part of the variance that cannot be explained by the variables used could be due to local factors that were not considered. This is suggested by the fact that the explained y variance did not increase even when other variables were added.

Temporal variations

The temporal variations in algal growth are not very clear. The occurrence of algae seems to be quite recent, at least in noticeable quantities, in Sweden or in the Scandinavian area. The first studies date back to the 1980s. In Finland the increasing abundance of algae is discussed in Poikolainen et al. (1998) for the period 1985 – 1995 and Bråkenhielm and Qinghong (1995) found an evident temporal variation at some sites in Sweden for the years 1989 –1992, but no clear trend could be seen. The results of this report show a tendency for a slight decrease in both the colonisation index and algal coverage of needle from 1995 to 2000. For the youngest needle variable, when considering the years 1994 –2000, the variation is almost non-existent. This is due to the 1994 value, which, however, could have been more affected by systematic errors in the algae judgements because the inventory had only just started then. If the tendency were confirmed, it could be related to the recent decrease in the deposition of nitrogen, discussed in Westling & Lövblad (2000).

CONCLUSIONS

- The temperature sum seems to prohibit the growth of algae up to a certain level (approximately 1100 – 1300 day degrees). Above this threshold the temperature does not seem to have any negative influence on algal growth.
- Humidity seems to be less important but may act as a contributing factor.
- Atmospheric deposition of nutrients may be the main factor responsible for algal growth. This would also explain the tendency for a decrease in algae in recent years, when depositions of nitrogen started to decrease.
- Local variation, e.g. microclimate and nitrogen emissions, seems to play an important role in growth of algae.

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