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Soil microbial dynamics and the condition of Norway spruce on the Bothnian land-uplift coast

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– Nullus est liber tam malus, ut non aliqua parte prodesset –

Parkano, November 2002,

Päivi Merilä

Original publications

The thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I Merilä, P., Lindgren, M., Raitio, H. & Salemaa, M. 1998. Relationships between crown condition, tree nutrition and soil properties in the coastal *Picea abies* forests (Western Finland). Scandinavian Journal of Forest Research 13(4): 413–420

II Merilä, P. & Ohtonen, R. 1997. Soil microbial activity in the coastal Norway spruce [*Picea abies* (L.) Karst.] forests of the Gulf of Bothnia in relation to humus-layer quality, moisture and soil types. Biology and Fertility of Soils 25(4): 361–365

III Merilä P., Smolander, A. & Strömmer, R. 2002. Soil nitrogen transformations along a primary succession transect on the land-uplift coast in western Finland. Soil Biology & Biochemistry 34(3): 373–385

IV Merilä, P., Strömmer, R. & Fritze, H. 2002. Soil microbial activity and community structure along a primary succession transect on the land-uplift coast in western Finland. Soil Biology & Biochemistry 34(11): 1647–1654

Päivi Merilä was responsible for the idea, preparation and writing of all the papers (I, II, III, IV). Rauni Strömmer (former Ohtonen) was the supervisor of this thesis and performed the soil microbial activity measurements (II, IV). Hannu Raitio was the coordinator of the research project under which Papers I and II were carried out, and was also responsible for the needle chemistry data (I). Martti Lindgren and Maija Salemaa were responsible for the crown condition data (I, II). Aino Smolander provided advice in performing the net N mineralisation experiments and in interpreting the results. Hannu Fritze performed the phospholipid fatty acid analyses and gave advice on their interpretation.

Abstract

Merilä, P. 2002. Soil microbial dynamics and the condition of Norway spruce on the Bothnian land-uplift coast. Finnish Forest Research Institute, Research Papers 877.
55 p. + 4 appendices.

The poor condition of Norway spruce (*Picea abies* (L.) Karst.) forests growing in the coastal area of the Gulf of Bothnia, western Finland, has been a cause of concern for several decades. In this study, the crown condition of spruce in the coastal area was compared with that of spruce growing in other parts of southern Finland. The variability in the crown condition of coastal spruce was evaluated in relation to foliar chemistry, soil type, and the mineral nutrient and moisture status of the organic layer in 30 forest sites. Relationships between the chemical, physical and microbial properties of the organic layer were also studied in a survey covering the same 30 coastal sites and 12 sites in the coastal region of Västerbotten, Sweden. None of the studied stands were growing on acid sulphate soils, which is a type of soil that occurs sporadically in the coastal region of the Gulf of Bothnia.

The spruce stands older than 60 years were more defoliated in coastal Ostrobothnia than in other parts of southern Finland. Defoliation and discoloration increased with increasing stand age. Old spruce stands that were strongly defoliated and discoloured also had low needle nitrogen and copper concentrations and the highest boron concentrations. Total nitrogen and extractable sulphur concentrations in the organic layer decreased with increasing stand age, and degree of defoliation and discoloration.

The most common soil types in the stands on the Ostrobothnian coast were carbic podzols and dystric gleysols, which develop in sporadically waterlogged soil conditions. Crown condition was found to be the poorest in old stands growing on these soil types. The carbic podzols and dystric gleysols also differed from the ferric podzols as regards certain microbial activities and the physico-chemical properties of the organic layer. The organic layer of the carbic podzols had lower basal respiration (BASAL) and substrate-induced respiration (SIR), and the gleysols had lower SIR than the ferric podzols. The results support the assumption that, especially on carbic podzols and dystric gleysols, poor nutrient status, acidity and a lack of oxygen due to sporadic periods of excess moisture in the organic layer, result in low microbial activity, impaired water and nutrient uptake and, consequently, poor condition of the spruce trees.

In this study, attention was also focused on successional changes in a forest ecosystem along a primary successional transect, located in the archipelago of Raippaluoto (Björkö and Replot; 63°20’N, 21°15’E). The transect represented a spatial continuum at right angles to the coastline as a result of ongoing post-glacial isostatic rebound (8 – 9 mm yr^{-1}). The transect comprised four forest sites: alder/rowan [70-year-old *Alnus incana* (L.) Moench/*Sorbus aucuparia* L.], birch (mainly 80-year-old *Betula pubescens* Ehrh.), birch/spruce [75-year old *B. pubescens* Ehrh. and *B. pendula* Roth./*Picea abies* (L.) Karst.] and spruce I (95-year-old *P. abies*). In order to extend the age sequence, a fifth forest site (spruce II; 130-year old *P. abies*) was chosen 12.2 km to the south of the transect.

Hypothesizing that a reduction in the availability of nutrients (especially nitrogen) during forest succession contributes to the poor condition of aged spruce crowns, I focused attention on the changes occurring in carbon (C)- and nitrogen (N)-related microbial activities (net and gross N mineralisation, microbial biomass N, BASAL and SIR) in the organic layer along the successional transect. Phospholipid fatty acid (PLFA) analysis was used to detect concurrent changes in the microbial community structure.

The soil C/N ratio along the primary successional transect increased from 16 to 37, and the $pH(H_2O)$ decreased from 5.1 to 4.0. Net N mineralisation decreased substantially. The young alder/rowan site was the only site to show net nitrification. BASAL and SIR remained mainly stable although, during the most favourable temperature and moisture conditions in the field, they tended to increase along the transect from the alder/rowan site to spruce I, and decreased again in spruce II. Microbial biomass N, measured once during the most favourable conditions in the field, also increased along the transect from the alder/rowan site to spruce I. Concurrently, gross N mineralisation showed a tentative increasing trend along the transect, although the differences between the sites were non-significant. The lower net N mineralisation in the spruce sites compared to the alder/rowan site was thus due to higher microbial immobilisation of N, rather than to a lower gross N mineralisation. It may also further be hypothesized that, in late successional spruce sites, a higher proportion of the N in the microbial pool will be further transformed to the more stabile N pool, i.e. to humic substances, resulting in a decreasing net N mineralisation along the transect. As shown by NMS (non-metric multidimensional scaling) ordination of the PLFA data, the microbial community structure showed clear differences along the transect and was closely related to the C/N ratio and pH of the organic layer.

The transect study provided evidence of distinctive changes in organic matter quality and decreasing availability of mineral N during forest succession. Low N availability may contribute to the poor crown condition and growth of the aged Norway spruce stands on the land-uplift coast in western Finland.

Key words: *Alnus incana*, *Betula sp.*, defoliation, discoloration, forest condition, forest soil, land uplift, needle analysis, nitrification, nitrogen mineralisation, phospholipid fatty acids, *Picea abies*, primary succession, soil fertility, soil respiration, substrate-induced respiration

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1. Introduction

1.1. Background

In the late 1970's and 1980's reports of decline in forest condition became headline topics in many parts of the world (Schütt & Cowling 1985, Huettl & Mueller-Dombois 1993, Innes 1993a). The deterioration in tree condition not only occurred in highly polluted areas close to industrial regions, but also in areas located at considerable distances from emission sources. In Central Europe the forest damage was initially characterized as needle loss and chlorosis in silver fir at high elevations, but reports of decline affecting a number of other species, including Norway spruce, Scots pine, and European beech, quickly followed (Augustin & Andreae 1998). Later on this phenomenon also affected oak species (Augustin & Andreae 1998). Long-range transboundary air pollution (primarily NO_x, SO_x, more recently also O_3) was suspected to be the main cause of the reported damages. This aroused widespread concern about the current state and future development of forest condition throughout the industrialised countries. These events prompted a considerable volume of research into cause-effect mechanisms, and highlighted the urgent need to follow, at regular intervals, possible changes in forest condition over large geographical areas. At the present time, forest condition is being monitored in ca. 30 countries using common methods in accordance with the UN/ECE recommendations (Müller-Edzards et al. 1997).

A number of multidisciplinary, regional forest condition surveys were carried out during the1990's in response to concern that the vitality of forests in Finland and in neighbouring areas may also be threatened (Tikkanen & Niemelä 1995, Raitio 1996, Lumme et al. 1997). This thesis originates from a survey conducted on the condition and growth of Norway spruce stands along the coastal areas of the Gulf of Bothnia (Raitio 1996). On the Finnish side of the Gulf, the issue was discussed as early as during the 1940's (Appelroth 1948) suggesting that natural factors rather than anthropogenic pollutants could be the primary cause of the poor crown condition of aged spruce stands in the area. In addition, several earlier studies (Kuusela 1977, Nyyssönen & Mielikäinen 1978, Tamminen 1993) indicated poor growth of coniferous stands in the coastal region of Ostrobothnia compared to other parts of southern Finland. However, more comprehensive ecological studies on the condition of coastal forests were lacking.

1.2. Forest condition vs. external appearance of the tree crowns

Forest condition - also synonymously termed as vitality, vigour and the health status of the forest - is a general expression and, consequently, vaguely defined. It has clearly been used in many different meanings, and often synonymously with defoliation and discoloration of the tree crowns. On the one hand, visual crown condition is considered as one of the most obvious indicators of the health status of forests (UN/ECE 2000), while, on the other hand, the relevance of defoliation and discoloration as forest health indices has also been criticized by several authors (Innes 1993c, Ferretti 1998, Helmisaari 1998).

The definition formulated by Andersson (1995) expresses the ultimate complexity of the concept in question: ‘vitality is the ability of an organism to survive, grow and produce new generations when exposed to various stress factors: climatic factors, soil chemical factors, competition, consumers/ pathogens, air pollutants’. Functionally, the foliage is the assimilative apparatus of the tree, absorbing light energy and converting it into chemical energy, which is the physiological process on which all the other vital functions of the tree depend. A decrease in the amount of foliage biomass, or changes in pigment composition that appear as discoloration, can be assumed to reduce the photosynthesising capacity of the tree, which further impairs its other functions. Furthermore, disturbances in the uptake of water and nutrients, or their reduced/excess availability, are reflected in the biomass and physiological processes in the needles and, consequently, the appearance of the crown. These fundamental arguments have been used to rationalize the use of defoliation and discoloration as indicators of the general condition of the tree (Salemaa & Lindgren 2000).

1.3. Factors affecting tree crowns

Site conditions, spatial status and tree age greatly influence the external appearance of tree crowns. The aboveground biomass of trees is determined by climate and soil fertility, which can be defined as the ability of soil to provide plants with the nutrients they require (Kimmins 1987). Aboveground productivity in nutrient-poor sites is less than that in fertile sites, and a larger root system is needed to meet the water and nutrient demands of the trees (Keyes & Grier 1981). Within a forest stand, the size of the living tree crown is also greatly modified by competition for light. Crown defoliation is known to increase with increasing age (Thomsen & Nellemann 1994, Lindgren et al. 2000), although it is difficult to determine whether this relationship results from natural aging processes or whether older trees are more susceptible to the stresses that promote defoliation (Innes 1993c).

The tree foliage is susceptible to a range of biotic agents (herbivores, pathogens), episodes of extreme weather conditions (wind, frost, drought, excess water, soil frost) and anthropogenic factors (air pollutants, harvesting damage), which may cause foliage loss or premature foliage fall, as well as discoloration of the crown. The effect of these factors is pronounced in evergreen, coniferous tree species that have a long needle retention time, such as Norway spruce. In a Finnish study on the dynamics and covariation of defoliation and biotic and abiotic damages of conifers during 1986-1998, the most marked change on the spruces was reported to be the increase in damage caused by *Chrysomyxa ledi* (Alb. & Schw.) deBary in 1988-1989 and the increase in frost injuries in 1993 (Nevalainen & Heinonen 2000). The overall contribution of damage to defoliation was, however, difficult to demonstrate.

The damaging effects of air pollutants on forest condition are strikingly evident around certain point sources, primarily energy production plants and metallurgical industries. The pollutants of primary concern around these point sources are sulphur dioxide, particulate and gaseous fluoride compounds, and numerous heavy metals (Smith 1990). Smith (1990) mentions that regional-scale air pollutants include ozone (and other oxidants), heavy metals and other trace metals (cadmium, cobalt, copper, lead, mercury, molybdenum, nickel, vanadium, and zinc), and acidic deposition (sulphuric and nitric acids). Of the anthropogenic air pollutants, the effects of mineral nitrogen compounds (ammonium and nitrate) are more complex, because nitrogen (N) is also the factor limiting productivity in many natural terrestrial ecosystems (Tamm 1991). Consequently, atmospheric N deposition can initially result in higher biomass production and increased nutrient uptake (Bauer et al. 2000). However, when so-called nitrogen saturation is reached, cronic N deposition has a number of adverse effects on forest ecosystems (e.g. van Breemen & van Dijk 1988).

Although harmful effects of air pollutants on forest ecosystems are indisputable (Smith 1990, Godbold & Hüttermann 1994), the degree to which these air pollutants contributed to the impaired crown condition in background areas in Europe and in North America in the late 1970's and during the 1980's is still a matter of controversy. In surveys conducted across Europe, a clear correlation between defoliation and air pollution was found only in Norway, although only a few countries could totally exclude long-range air pollution as a factor affecting crown condition (Müller-Edzards et al. 1997). Skelly & Innes (1994) clearly stated that 'connecting air pollution with the diverse symptoms of supposed forest declines over the last several decades is unjustified'. Impaired forest condition has, in many cases, been related to nutritional disorders caused by natural soil properties, forest management, adverse climatic episodes (drought) and their interaction (Landmann 1992, Huettl 1993).

1.4. Indicators for assessing tree/forest condition

1.4.1. Defoliation and discoloration

By definition, the degree of defoliation is assessed as the relative leaf or needle loss in the crown as compared to a reference tree (UN/ECE 1998). The reference tree can be either a real, non-defoliated tree of the same age, same type of crown and growing under similar conditions in the vicinity of the sample tree, or an imaginary tree with a degree of defoliation of 0% (Salemaa & Lindgren 2000). When assessing the degree of defoliation, the influence of normal tree aging and its social status, as well as the effect of natural permanent site conditions on needle/leaf biomass, should be recognized and omitted. In order to avoid the effects of shading on tree defoliation, only predominant, dominant, and co-dominant trees without significant mechanical damage qualify as sample trees (UN/ECE 1998). The effect of natural pruning is excluded by limiting the assessment of Norway spruce to the upper half of the living crown. In the case of Norway spruce especially, the phenotypic branching type (comb, brush and plate types and their combinations) greatly influences the appearance of the crown and should to be taken into account while making the assessment.

Needle discoloration is defined as deviation from the usual colour of the living foliage of the species in question (UN/ECE 1998). The variation in the nature, extent and location of discoloration is a source of important diagnostic information since, in principle, many fungal diseases, nutritional disorders and exposure to certain air pollutants such as ozone, produce relatively clear visible symptoms (Skelly et al. 1987, Kurkela 1994, Marschner 1995). In practice, however, reliable diagnoses that are based solely on visible symptoms are often unsuccessful because the symptoms are not specific enough and several damaging agents may occur simultaneously. The description, and especially, the quantification of diverse symptoms, are problematic and limit the possibilities of further analysing the data. In order to make the visual observations consistent, repeatable and comparable between different observers and different observation years, comprehensive regular training is necessary (Salemaa & Lindgren 2000).

The implementation of the large-scale surveys of forest condition was primarily governed by practical considerations. Defoliation and discoloration of the tree crowns were chosen as the primary indicators of forest condition because they were the most clearly visible symptoms of the observed forest damages (Schütt & Cowling 1985). The assessments of defoliation and discoloration can be carried out rapidly over large areas at low cost and without destructive sampling (Lorenz 1995). The value of defoliation degree as an indicator of the overall condition of the tree crown has proved to be reasonably good (Innes 1993b). However, both defoliation and discoloration of the crown are unspecific symptoms, caused by different processes induced by a number of factors. In order to make a precise diagnosis of the causes of the symptoms observed, additional information is undoubtedly needed.

1.4.2. Elemental composition of the foliage

Nutrient deficiencies, excesses and imbalances in plants can be diagnosed on the basis of the elemental composition of the foliage (Kimmins 1987, Walworth & Sumner 1988). Foliar analysis is a quick, relatively inexpensive diagnostic tool that is also suitable for large-scale monitoring purposes. Conventionally, the nutritional status of a tree or site is assessed by comparing the nutrient concentration in a foliar sample with a standard value or range for the nutrient in question (Ahrens 1964, Morrison 1974, Jukka 1988, Walworth & Sumner 1988). The essential importance of nutrient ratios was demonstrated by Ingestad (1971, 1979, 1981), who postulated that the optimum growth of higher plants was achieved when the ratios of macronutrients were ascertained to a certain range (N:K:P:Ca:Mg 100:50:16:5:5, respectively (Ingestad 1979)). Since nitrogen is frequently the limiting nutrient in boreal forest ecosystems, it is appropriate to consider the sufficiency of other nutrients in relation to the nitrogen concentration.

Because several factors cause considerable fluctuation in the elemental concentrations in needles, foliar diagnosis based on standard values and ranges should be considered as being merely tentative. The application of empirically derived standard values and ranges may be misleading since they are valid only in the conditions in which they have been determined (Timmer 1991). Rapid growth may result in a dilution effect, i.e. low concentrations of certain elements owing to the incorporation of carbohydrates in the biomass. The elemental concentrations in needles fluctuate according to variations in the dry matter content of the needles, which varies seasonally and increases with the age of the needles. In the study of Linder (1995), for example, most of the seasonal variation in the nutrient concentrations of Norway spruce needles could be explained by the variation in the concentration of starch in the needles. Therefore, sampling is generally recommended to be carried out during the dormant period. The increase in the dry matter content with spruce needle age results in a decrease in the element concentrations, with the exception of

Ca and Mn (Linder 1995, Raitio & Merilä 1998). The decrease in N, P, K and Mg with needle age may also, in part, be due to retranslocation of these nutrients (Meier et al. 1985, Helmisaari 1992, Marschner 1995). Finally, the root/shoot dry weight ratio generally increases as the nutrient availability decreases. This relationship is most obvious for nitrogen and less distinct for phosphorus (Marschner 1995). Decreased nutrient availability can also lead to reduced leaf size (Linder 1987). To some extent the foliage biomass is thus in balance with the supply of essential nutrients, while the nutrient concentrations in the needles remain relatively constant. Consequently, slight deficiencies may have minimum if any effects on the needle concentrations.

Bearing in mind the limitations of the method, determining the elemental composition of the foliage provides valuable information on the plant's overall nutritional condition (Walworth & Sumner 1988, Marschner 1995). In the case of surveys and monitoring studies, the comparability of the results is of extreme importance. Some sources of variation (seasonal variation, canopy layer, section of the crown, age of the needles, analytical errors) can be standardized by means of sampling design and consistent analysis (Raitio 1993).

1.4.3. Physical and chemical properties of the soil

Numerous physical and chemical soil analyses are available for describing the conditions in which plants grow: conditions for anchorage of roots, the supply of water, air (oxygen) and nutrients, and buffering against adverse changes in temperature and pH (Wild 1993). The physical properties of the soil, such as texture, structure, porosity and temperature, have a great influence on these basic necessities. Basically, the chemical properties of the soil (e.g. cation and anion exchange capacity, pH, and the forms and availability of nutrients) regulate the availability of nutrients to plants. The total amount and the "availability" of nutrients in the soil can be measured analytically. However, it is not clear which of the extraction methods that are used provides the most useful measure of the amount of available nutrients in different situations. Difficulties in estimating the amounts of plant-available nutrients are not only restricted to chemical aspects. All soils are characterized by extremely high spatial variability, and the error arising from field sampling is typically much larger than that associated with sample preparation, handling, or analysis (Crépin & Johnson 1993). In order to make accurate measurements of nutrient availability we should in fact extract the nutrients that are root available. In practice, however, the analyses are usually made on the bulk soil samples. The roots are able, by means of root exudates, to actively modify the chemical conditions, such as pH, in the rhizosphere, thus affecting nutrient availability. Moreover, chemical soil analysis, being a one-off measure, does not take into account dynamics of the cycling of the nutrients.

The prevailing soil conditions results from the interaction of physical, chemical and biological factors. The upper part of the soil is exposed to soil formation processes, the course of which depend on the parent material, climate, topography, biota (mainly vegetation) and human activities. In the course of time, soil formation processes result in the development of characteristic horizons which, in boreal coniferous forests, typically means podzolization (Duchaufour 1982). Definition of the soil type may give valuable information about the prevailing conditions such as the long-term moisture status of the site.

1.5. The role of surface organic matter in nutrient dynamics of boreal forests

Boreal forest ecosystems are characterized by the accumulation of organic matter at the soil surface. The organic layer, also referred to as the forest floor, mainly originates from plant residues, consisting of above- and below-ground litter, and root exudates. The greatest microbial activity and highest density of nutrient-foraging roots are found in the organic layer (Van Cleve & Moore 1978). The physical and chemical composition, as well as the temperature and moisture conditions and the abundance and composition of soil microbial and faunal communities, are considered to be the key factors controlling the decomposition processes and, consequently, the type of forest floor that is formed (Kimmins 1987). Decomposition can be described as a two-phase process (Berg & Staaf 1980). The initial flush of decomposition is controlled by the climate and the concentrations of major nutrients and water-soluble organic compounds. The later, much slower phase of decomposition, is regulated by the decomposition of lignin compounds. The formation of stable humic substances further contributes to the retarded rate of decomposition.

In the boreal region, the slow rate of decomposition is primarily due to the cool, humid climate and the presence of relatively recalcitrant coniferous litter. In these conditions, the organic layer forms an important reservoir of carbon and nutrients; nitrogen (N), being the main limiting nutrient, regulates the site productivity. In undisturbed mature ecosystems, the supply of N is largely controlled by the rate at which plant-available N is produced from soil organic matter via decomposition, ammonification and nitrification (Tamm 1991). In addition to the rates of ammonification and nitrification, N availability to plants is also influenced by the rate at which inorganic N is consumed in microbial immobilisation. The mycorrhizal and non-mycorrhizal uptake of organic N have also been demonstrated (Kielland 1994, Raab et al. 1996, Näsholm et al. 1998).

The organic matter in the soil makes many beneficial contributions to the stability of the forest ecosystem. It plays a vital role in the establishment of soil structure and in the maintenance of its stability. One important property of soil organic matter is that it improves the water-holding and cation exchange capacity of the soil. However, in conditions that are too cold, too wet or where the litter is unsuitable for faunal degradation, the progressive accumulation of organic matter on the surface of the soil leads to the immobilization of nutrients in the organic layer, paludification and a reduction in site fertility (Prescott et al. 2000).

1.6. The coastal chronosequence - a tool for studying successional changes

Due to isostatic rebound, the coastline along the Gulf of Bothnia between Finland and Sweden is continuously rising at a rate of 8–9 mm per year (Mäkinen et al. 1986). New land is becoming exposed to the combined effect of soil formation (Starr 1991) and other ecosystem processes that are controlled by the prevailing climate. The successional stages of the forest ecosystems thus appear as a spatial continuum running at right angles to the coastline (e.g. Ericson 1982, Svensson & Jeglum 2000). The succession of forest vegetation on stony, fine-textured till soils starts from alder-dominated (*Alnus incana* (L.) Moench) deciduous shoreline vegetation, and ends in almost pure Norway spruce stands (Appelroth 1948, Svensson & Jeglum 2000). On gently sloping shores the succession sere also includes a birch-dominated (mostly *Betula pubescens* Ehrh.), intermediate stage (Svenonius 1945). The ecological change from the dinitrogen-fixing alder stage to the frequently paludified, nitrogen-deficient spruce stands with a thick humus layer is considerable. A chronosequence of this kind offers an opportunity to study the inter-relationship between vegetational succession and the microbial processes that affect organic matter decomposition, N transformations, and thus N availability to plants. In the coastal region along the Gulf of Bothnia such studies are scarce (Aikio et al. 2000), but comparable successional ecosystems have been studied intensively in Alaska at Glacier Bay National Park (Bormann & Sidle 1990, Chapin et al. 1994), and in the Tanana river floodplain (Klingensmith & Van Cleve 1993, Van Cleve et al. 1993, Clein & Schimel 1995, Schimel et al. 1998).

In chronosequence studies conducted in Alaskan conditions, the rate of net N mineralisation has been shown to decline with advancing succession from the poplar-alder (*Populus balsamifera* L. – *Alnus tenuifolia* Nutt.) stage towards the mature white spruce (*Picea glauca* (Moench) Voss) stage (Klingensmith & Van Cleve 1993, Van Cleve et al. 1993). Aboveground net primary productivity of *Picea* has been shown to decrease by 50% over a 160-year, *Picea*-dominated portion of a chronosequence studied by Bormann & Sidle (1990). The changes in N availability, and hence productivity, are concluded to be related to changes in organic matter quality, through the control of microbial activity (Van Cleve & Yarie 1986, Bormann & Sidle 1990). Net N mineralisation was clearly related to significant increases in the lignin/N and C/N ratios in the organic layer, suggesting that early and mid-successional deciduous vegetation types produce litter that is less recalcitrant to decomposition in comparison to the litter of the late successional coniferous forest stages (Van Cleve et al. 1993, Van Cleve et al. 1996). Soil temperature also declined with advancing succession, but its relationship with net N mineralisation was not as clear as that between net N mineralisation and organic matter chemistry (Van Cleve et al. 1993). Plants may also affect N cycling by producing secondary compounds that directly influence microbial activity, acting as substrates, inhibitors or inducers (Van Cleve et al. 1991, Schimel et al. 1996, 1998, Pellissier & Souto 1999). In the study of Schimel et al. (1996), for instance, balsam poplar tannins were found to act as general microbial inhibitors, while low-molecular-weight phenolics functioned as substrates for microbial growth. In addition, monoterpenes have also been found to inhibit N mineralisation (White 1986) and nitrification (White 1986, Paavolainen et al. 1998) in coniferous forest soil.

Based on the C/N ratio of heterotrophic microbial cells and losses of C due to respiration, a C/N ratio of 30 has been proposed as the critical C/N value for detritus, above which heterotrophic micro-organisms are N limited and below which they are C limited (Tate 1995). From this it can be inferred that the microbes in the N-rich alder dominated stage may be relatively the most C limited, resulting in lower microbial biomass and activity in comparison to the subsequent stages of succession (Clein & Schimel 1995). During the succession a reduction in the N pool leads to N limitation of the microbial community. In the late successional spruce stages, recalcitrant C sources may also result in reduced microbial biomass and activity, and affect community composition (Flanagan & Van Cleve 1983, Mikola 1985, Bradley & Fyles 1995, Priha & Smolander 1999, Saetre et al. 1999, Hobbie et al. 2000, Priha et al. 2001).

1.7. Approach and aims of the study

The main objective of this study was to investigate the nutritional status and the physical, chemical and microbiological soil properties of coastal spruce forests in order to elucidate their relationship with the crown condition of spruce. At first, the crown condition of coastal spruce stands was assessed and compared to that of stands in other parts of southern Finland (I). Since any direct cause and effect responses between environmental factors and crown condition may be diverse and elusive to prove experimentally, the work was focused on producing information about correlative patterns between crown condition, tree nutrition and soil properties using sitewise data (I). The possible processes behind the patterns were then considered, i.e. they were inductively interpreted. It is important to bear in mind that this approach is not sufficient for proving causalities and, therefore, the interpretations should merely be taken as an introduction to reasonable theories. A similar approach was further applied in II, in which the variability in soil microbial activity was evaluated in relation to the quality and moisture regime of the organic layer, and soil types. Microbial activity in relation to crown condition was also investigated.

In the second part of the study (III, IV), I utilized the approach provided by post-glacial land-uplift, which allow the successional history of a coastal spruce ecosystem to be followed along a chronosequence. Hypothesizing that a reduction in the availability of nutrients (especially nitrogen) during forest succession contributes to the poor condition of the aged spruce crowns in the study area, I focused attention on the changes occurring in C- and N-related microbial activities in the organic layer along a primary successional transect (III, IV).

The specific objectives of the papers were:

- to investigate the variability in crown condition of coastal spruce in relation to foliar chemistry, soil type, and the mineral nutrient and moisture status of the organic layer (I)
- to study microbial activity in the organic layer of the coastal spruce stands growing on different soil types and with a different soil nutrient and moisture status (II)
- to investigate N transformations, and microbial activity and community structure in the organic layer along a primary successional transect on the land-uplift coast (III, IV)

2. Material and methods

The methods applied are described in detail in original papers I-IV.

2.1. Sites and study area

2.1.1. The surveys (I, II)

The Norway spruce stands studied in I and II were located along the Straits of the Gulf of Bothnia between Finland and Sweden (Raitio 1996; Fig. 1).

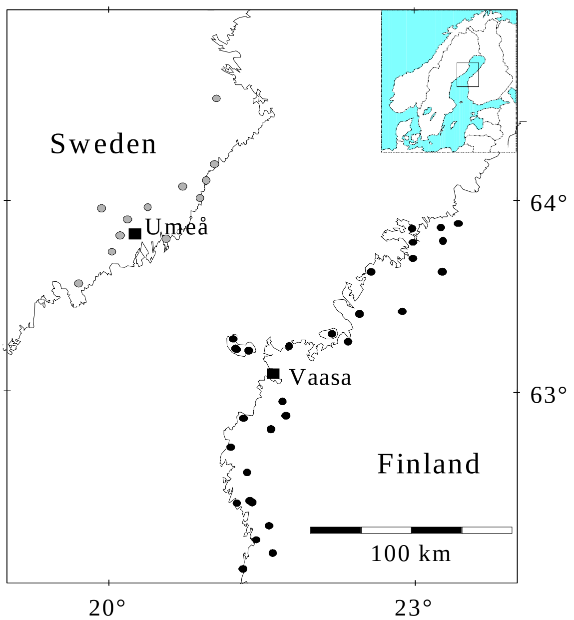

Fig. 1. The location of the sample plots studied in I (black circles) and II (black and grey circles).

Paper I focused on sites (n = 30) on the Finnish Ostrobothnian coast characterized by rapid land-uplift (Ristaniemi et al. 1998), while in II sites on both the Finnish and Swedish sides were included (n = 42). The sites were selected from the plots of the national forest inventories of Finland and Sweden, located less than 33 km from the coastline, and classified as Myrtillus (mesic) or Oxalis-Myrtillus (herb-rich) forest site types according to the Finnish forest type classification by Cajander (1949). On the Finnish side, three stand age classes were represented: 38–59 (n = 9), 60–89 (n = 11) and 90–135 (n = 10) years old. The range in altitude of these sites was 5–45 m. On the Swedish side the number of stands in age classes 60–89 and 90–135 years were 4 and 8, respectively, and the altitude of the stands varied 10–220 m.

The topography of the coastlines of the Straits of the Gulf of Bothnia is characterized by flatness and minor regional variation in altitude, especially on the Ostrobothnian (i.e. Finnish) side of the Gulf (Björklund et al. 1996, Rinkineva & Bader 1998). Glacial till deposits (De Geer moraines, drumlins and hummocky moraines) result in a special fragmented feature of the landscape in the archipelago and near the coastlines (Zilliacus 1987, Kujansuu & Niemelä 1990, Rinkineva & Bader 1998). Because of bouldering of the Vaasa granite bedrock, the soils in the northern Ostrobothnian region are generally very stony (Björklund et al. 1996). None of the studied stands were growing on acid sulphate soil, which is a type of soil that occurs sporadically in the coastal region of the Gulf of Bothnia (Merilä et al. 1996).

The annual precipitation on the Finnish side of the area ranges from 450 to 550 mm (Solantie 1987), and the effective temperature sum (threshold value of +5°C) from 1000 to 1200 d.d. (Helminen 1987).

2.1.2. The transect study (III, IV)

The transect study (III, IV) was conducted in the archipelago of Raippaluoto (Björkö and Replot) in western Finland (63°20'N, 21°15'E). The surficial deposits of the area are characterized by De Geer moraines (Zilliacus 1987). The primary successional transect was located in a nature reserve, and the impact of human activities on the development of the vegetation can be considered minor although some logging and sheep grazing might have occurred in the past. The transect comprises the following four forest sites (Fig. 2):

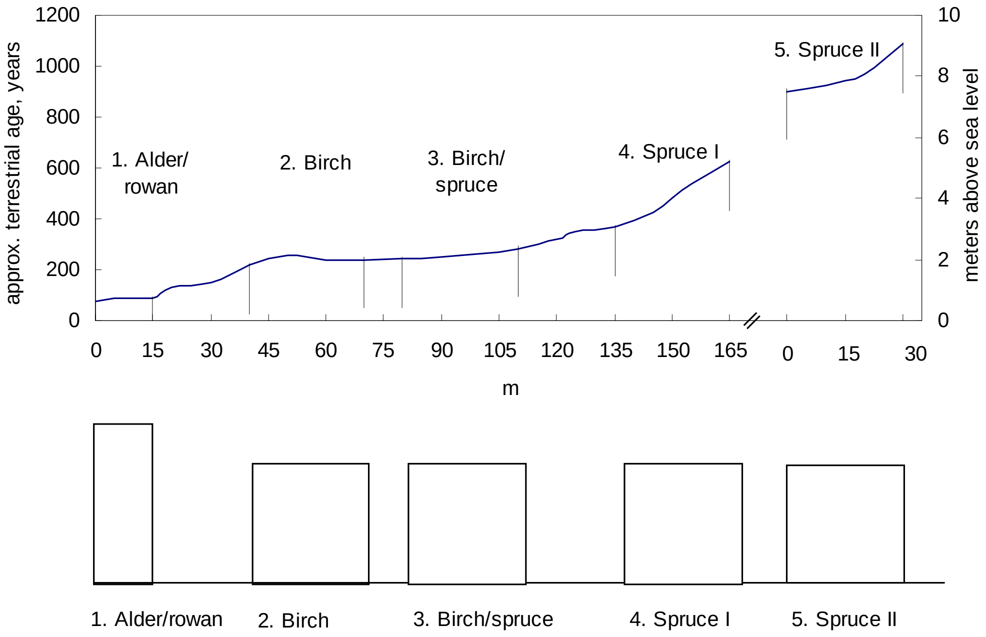

Fig. 2. The profile (above) and map (below) of the primary successional transect (III, IV). X axis refers to both figures. Terrestrial age refers to the number of years elapsed since the site rose above sea level.

(1) Alder/rowan: 70-year-old alder/rowan stand (*Alnus incana* (L.) Moench and *Sorbus aucuparia* L.)
(2) Birch: 80-year-old birch stand (mainly *Betula pubescens* Ehrh.)
(3) Birch/spruce: 75-year-old birch/spruce stand (*B. pubescens* Ehrh., *B. pendula* Roth., and *Picea abies* (L.) Karst.)
(4) Spruce I: 95-year-old spruce stand (*P. abies*)

In order to extend the age sequence, a fifth forest site was chosen 12.2 km to the south of the transect:
(5) Spruce II 130-year-old spruce stand (*P. abies*)

One sample plot (area 30 x 30 m, except for the alder/rowan site 15 x 40 m, see Fig. 2) was established in each of the forest stages. For further information see Table 1.

Table 1.
Stand characteristics, nutrient concentrations (mean ± S.E., number of trees = 10) in previous-year (c+1) needles, and thickness, loss in weight on ignition, pH($CaCl_2$), pH(H_2O), C:N ratio and total and acid ammonium acetate extractable nutrients (Halonen et al. 1983) of the organic layer of the successional forest sites studied. Measurements were carried out in 1997 or 1998.

	Alder/rowan	Birch	Birch/spruce	Spruce I	Spruce II
Stand characteristic					
Stem number ha^{-1}	1617	978	1411	589	1244
Mean diameter at breast height (cm)	13.0	23.4	20.4	26.4	22.1
Mean height (m)	7.5	14.1	14.7	16.8	16.0
Basal area (m^2 ha^{-1})	9.9	20.3	26.9	19.7	26.7
Stem volume (m^3 ha^{-1})	38.2	128.4	186.6	149.5	203.8
Crown defoliation of spruce (stand mean %)	–	–	18	31	32
Percentage of spruce with >5% of the needles discolored	–	–	10	20	25
Spruce c+1 needles					
N (mg g^{-1} dwt)	–	–	11.9 (0.3)	10.5 (0.3)	10.7 (0.2)
P (mg g^{-1} dwt)	–	–	2.3 (0.1)	1.9 (0.1)	1.5 (0.1)
K (mg g^{-1} dwt)	–	–	6.9 (0.2)	7.3 (0.3)	6.7 (0.3)
Ca (mg g^{-1} dwt)	–	–	4.9 (0.3)	5.0 (0.3)	5.2 (0.4)
Mg (mg g^{-1} dwt)	–	–	1.8 (0.1)	1.2 (0.1)	1.2 (0.1)
S (mg kg^{-1} dwt)	–	–	980 (30)	880 (30)	870 (30)
Cu (mg kg^{-1} dwt)	–	–	1.6 (0.1)	1.2 (0.1)	1.2 (0.1)
B (mg kg^{-1} dwt)	–	–	17.1 (0.9)	16.2 (1.2)	16.7 (1.6)
Organic layer					
Thickness (cm)	6.5	6.6	7.4	6.6	6.8
Loss in weight on ignition (OM) (%)	87.2	87.0	90.2	84.9	84.7
pH ($CaCl_2$)	3.9	3.2	3.1	3.1	3.0
pH (H_2O)	5.1	4.3	4.0	4.1	4.0
C:N ratio	15.9	20.2	21.4	31.7	37.3
Total nutrients					
N (mg g^{-1}OM)	33.0	25.7	25.1	16.0	14.3
P (mg kg^{-1}OM)	1310	1500	1690	1110	960
K (mg kg^{-1}OM)	1050	940	860	950	810
Ca (mg kg^{-1}OM)	4540	2800	1730	2980	3660
Mg (mg kg^{-1}OM)	2740	1000	650	760	720
Cu (mg kg^{-1}OM)	22.9	24.7	33.9	12.7	11.6
Extractable nutrients (mg kg^{-1}OM)					
P	200	240	160	350	200
S	150	180	200	160	140
K	840	850	750	880	650
Ca	3010	1900	1150	1980	2450
Mg	1920	760	480	550	480

2.2. Crown condition and elemental composition of the needles

The crown condition of spruce was investigated by estimating the degree of defoliation and needle discoloration (I, II; Manual on methodologies… 1989) On the Ostrobothnian (i.e. Finnish) side (I) the level of defoliation in the study area was compared with that of corresponding forest site types and stand age classes in southern Finland (demarcation line along latitude 65°). Data for this comparison were obtained from the results of the annual monitoring of forest condition carried out by the Finnish Forest Research Institute under the Pan-European Forest Condition Monitoring Programme (Forest condition… 1993).

Tree-specific samples of current (C) and previous year (C+1) needle age classes were collected from ten trees on each sample plot in December 1992 (I). The elemental concentrations of the needles were determined as described by Raitio (1991).

2.3. Soil description and sampling

In I and II the soils of the stands were described by determining the thickness of the organic layer, the soil type (FAO 1988) and the humus type (classified as mor, moder, undisturbed peat layer or disturbed peat layer). On the Finnish side, the majority (75%) of the sites were classified as stony or very stony till soils (Viro 1952). The dominant particle size was silt, fine sand and medium sand in 30%, 33% and 33% of the sites, respectively.

In the surveys (I and II), twenty-eight subsamples were collected systematically from the upper 5–7 cm of the organic layer with a stainless steel auger and combined to give one bulk sample per plot. In the transect study (III, IV), the organic layer was sampled five times (Jun –97, Jul –97, Aug –97, Sep –97 and Jul –98) by taking systematically 24 soil cores, and combining three adjacent cores to give eight subsamples per plot. In the laboratory, the samples were mixed, and litter and roots >1 mm in diameter removed.

2.4. Chemical soil properties

Total C and N were determined on a CN analyser (LECO CHN) and the organic matter content (OM) as loss in weight on ignition (485-500°C, 4 h). pH was measured after suspending a subsample in deionised water or in 0.01 $CaCl_2$ overnight (sample/liquid suspension = 1:3 v/v). Phosphorus, S, Ca, Mg, K, Na, Al, Fe, Mn, and Cu were extracted with 1 M ammonium acetate at pH 4.65 (Halonen et al. 1983) and analysed by inductively coupled plasma atomic emission spectrophotometry (ICP, ARL 3580). Total P, K, Ca, Mg and Cu were determined by ICP after dry ashing and extracting the ash with HCl (III; Halonen et al. 1983). All the concentration data were converted to a dry organic matter basis.

2.5. Microbial activity and biomass (II, IV)

Measurement of the microbial activity of organic layer samples was conducted in constant moisture (250% of OM) and temperature conditions (+20°C) using an automated respirometer (Nordgren 1988). The samples were kept frozen prior to analysis. Basal respiration rate (BASAL), i.e. evolution of CO_2 from the sample, was first measured. Substrate-induced respiration (SIR), known to be correlated with microbial biomass (Anderson & Domsch 1978), was then determined as the respiration rate after addition of a specific substrate (glucose, N as $(NH_4)_2SO_4$ and P as KH_2PO_4). The metabolic quotient of the soil microbes (qCO_2) (Anderson & Domsch 1985a, Anderson & Domsch 1985b) was calculated as the BASAL:SIR ratio (IV), or as the relationship between BASAL and microbial biomass (II), derived from SIR values using the equation of Anderson and Domsch (1978). The additional microbial activity variables determined were Lag-time (Lag) and specific respiration increment (μCO_2), the first being estimated as the time period from substrate addition to the start of exponential growth of the microbial community, and the latter as the slope of the respiration curve during the growth.

2.6. Nitrogen transformations and microbial biomass N (III)

The estimates of net N ammonification and nitrification were determined from the change in the size of the corresponding soil inorganic-N pool over time (Hart et al. 1994). They were measured in 5-week incubation experiments *in situ* using intact soil cores, and in the laboratory on sieved, fresh organic layer samples at constant temperature (14±1°C) and moisture (250% of OM). The laboratory incubations on homogenized soil samples were intended to identify differences in substrate quality that are important for N ammonification, nitrification and immobilisation. The aim of the field incubations was to estimate the importance of environmental factors (temperature, moisture) affecting N transformations.

Total dissolved nitrogen (TDN), NH_4-N and $(NO_2 + NO_3)$-N concentrations in the reference (non-incubated) and incubated samples were determined from extracts (1 M KCl) on a flow injection analyser (FIA Star 5020, Tecator).

Net ammonification and nitrification were calculated by subtracting the initial NH_4-N and $(NO_2 + NO_3)$-N concentrations from the final (post-incubation) NH_4-N and $(NO_2 + NO_3)$-N concentrations, respectively. Net N mineralisation was calculated as the sum of net ammonification and net nitrification. The concentration of dissolved organic nitrogen (DON) was calculated by subtracting the NH_4-N and $(NO_2 + NO_3)$-N concentrations from the TDN concentration.

Gross rates of N mineralisation were estimated in the laboratory on sieved, fresh organic layer samples by the isotope-dilution technique (Hart et al. 1994). This method involves the addition of $^{15}NH_4^+$ to the sample and determination of the rate at which the atom % ^{15}N enrichment of the NH_4^+ pool decreases as microbes mineralise native soil organic ^{14}N to $^{14}NH_4^+$. It is assumed that consumptive processes do not significantly alter the ^{15}N enrichment of the NH_4^+ pool, allowing calculation of gross mineralisation from the dilution rate of $^{15}NH_4^+$ in the sample (Kirkham & Bartholomew 1954).

Soil microbial biomass N (microbial N) was determined using the fumigation-extraction method (Smolander et al. 1994). In this method, N bound in microbial cells is rendered extractable due to lysis of the chloroform-sensitive microbial cells. Microbial N is determined as from the difference in the N concentration between fumigated and unfumigated samples.

2.7. Microbial community structure (IV)

The structure of the microbial communities was estimated by determining the phospholipid fatty acid (PLFA) composition of the cell membranes. PLFA analysis was considered advantageous because it is a quick, quantitative method and does not require isolation of the microbes from the soil substrate (Balkwill et al. 1988, Frostegård et al. 1991). The total amount of PLFAs can also be used as an indicator of the living microbial biomass (Balkwill et al. 1988, Frostegård et al. 1991). Moreover, the relative amounts of PLFAs considered to be primarily of bacterial or fungal origin provide measures of the bacterial and fungal biomass (Frostegård & Bååth 1996). The PLFA composition also allows more detailed interpretations of microbial community structure, even though the indicative value of most of the single PLFAs is not clear. For example, the relative amount of PLFA16:1w5 has been reported to be higher in soil containing arbuscular mycorrhizal fungi (Olsson et al. 1995), and the methyl group in the tenth carbon atom from the carboxyl end of the chain has been found to be characteristic of actinomycetes (Kroppenstedt 1985).

2.8. Statistics and ordinations

The Pearson (r) or the Spearman rank correlations (r_S) were calculated in order to evaluate the covariation between the variables studied (I-IV). The analysis of variance and nonparametric Kruskal-Wallis test were used to distinguish differences between the groups. Pairwise differences were tested with Tukey's test and, in case where the equality of variances between the groups was not met, pairwise comparisons were made for mean ranks (rejection level 0.05).

Because the transect studies (III, IV) were conducted on a single transect and the successional stages were thus not replicated, statistical comparisons can be made to distinguish statistically significant differences between sites but not between the successional stages. Differences in the variables between the plots and between the 1997 incubations were tested with repeated measures analyses of a general linear model. When the assumption of sphericity was not violated according to Mauchly's test (Crowder & Hand 1990), contrasts were used to test the differences among variables between subsequent incubations (SPSS® version 9.0.1).

In III the linear mixed model analysis (PROC MIXED procedure SAS 6.12 software package) was used to investigate the degree to which certain properties of the organic layer accounted for differences in net N mineralisation between the forest sites, and between the incubations in the laboratory (alder/rowan site excluded). The incubations were treated as repeated measures.

In I, principal component analysis (PCA), based on the correlation matrix (Jongman et al. 1987), was applied to sum up the variation of intercorrelated original variables into one principal component. The input variables in PCA were: N in current needles, B in previous-year needles, and the total N and extractable S concentrations, pH, and moisture content of the organic layer at the time of sampling. The site scores along the first PCA axis were interpreted to reflect increasing fertility and decreasing moisture and named as the site fertility index.

In II, the relationships between variables depicting microbial activity and site and organic layer characteristics layer characteristics were investigated by redundancy analysis (RDA), which is a multivariate linear method and a canonical form of PCA, designed to detect the main relationships between two sets of variables (Jongman et al. 1987). RDA analyses were performed on a correlation matrix using CANOCO version 3.10 (ter Braak 1990). Variables describing soil microbial activity, i.e. BASAL, SIR, Lag, μCO_2 and qCO_2, were entered as dependent variables ("species") in the program, and organic layer chemistry and site variables were entered as independent (environmental) variables.

In IV the PLFA data were ordered by global non-metric multidimensional scaling (NMS) using PC-ORD software 4.14 (McCune & Mefford 1999). Prior to NMS, the mole percentages of the PLFA values were double-square root transformed ($y^{0.25}$) in order to down-weight the influence of the very abundant PLFAs. Sørensen (Bray & Curtis) distance was applied as a measure of dissimilarity in microbial community structure between the samples. The C/N ratio and pH in the organic layer, BactPLFA, TotPLFA and the FungPLFA/BactPLFA ratio were given as vectors in the ordination graph, the direction of each arrow indicating the direction of the gradient and the length indicating the strength of correlation. The final configuration was rotated by pH.

3. Results

3.1. The surveys (I, II)

The most common soil types on the sites studied on the Finnish coast were carbic podzols and dystric gleysols, and crown condition was found to be the worst in old stands growing on these soil types (Fig. 4 in I). Defoliation and discoloration correlated positively with stand age (Table 2 in I). The spruce stands older than 60 years were more defoliated in coastal Ostrobothnia than in other parts of southern Finland (Fig. 3 in I).

Old stands in which the spruces were highly defoliated and discoloured had low needle N and Cu concentrations. Boron needle concentrations were highest in these stands. Total N and extractable S concentrations in the organic layer decreased with increasing stand age, defoliation and discoloration.

Principal component analysis (PCA) was applied in order to sum up the variation in the intercorrelated needle chemistry and organic layer variables. The input variables were N in current needles, B in previous-year needles, and total N, extractable S, pH(H_2O) and the moisture content in the organic layer at the time of sampling (Table 3 in I). The site scores along the first PCA axis were used as the site fertility index (increasing fertility, decreasing soil moisture gradient). Consistently with the input variables, this index showed significant (negative) correlation with crown defoliation, crown discoloration and stand age. Stand age-adjusted partial correlation coefficients of the elemental needle concentrations and soil properties with crown defoliation and discoloration were insignificant, apart from the correlation between site fertility index and crown discoloration ($r = -0.41$, $p = 0.03$, $df = 27$).

The organic layer of the ferric podzols had higher BASAL and SIR than the carbic podzols and higher SIR than the gleysols (Table 4 in II). BASAL and SIR were positively related to organic layer fertility factors such as pH and extractable K, Mn and P, but negatively associated with the organic matter content of the organic layer (Fig. 2 in II). A short Lag was associated with organic layer fertility and a long Lag with crown defoliation. μCO_2 was lowest at sites with a high field moisture and discoloured crowns. qCO_2 was situated near the centre of the ordination space, thus indicating poor, if any, correlation with the environmental variables. No correlations were found between microbial activity variables and stand age.

3.2. The transect study (III, IV)

Along the primary successional transect (alder/rowan, birch, birch/spruce, spruce I, spruce II), the C/N ratio in the organic layer increased from 16 to 37 and the pH(H_2O) decreased from 5.1 to 4.0 (III). Concurrently, net N mineralisation decreased substantially (III). The alder/rowan site was the only site to show net nitrification.

Net N mineralisation per unit area summed from the four field incubations (3 Jun – 21 Oct 1997) was 7.4, 7.4, 7.0, 3.6 and 2.8 g m^{-2} in the alder/rowan, birch, birch/spruce, spruce I and spruce II sites, respectively. It was significantly lower in spruce sites I and II than in the other sites.

The average N mineralisation coefficient (net N mineralisation during Jul –98 laboratory incubation: total N) was 0.008, 0.009, 0.010, 0.005 and 0.005, in the alder/rowan, birch, birch/spruce, spruce I and spruce II sites, respectively. The average N mineralisation coefficient thus tended to show lower values in the spruce sites, but the differences between the sites were only tentative.

BASAL and SIR remained mainly stable although, at the time of the most favourable temperature and moisture conditions (BASAL Jul –97; SIR Jul –97 and Jul –98), they tended to increase along the transect from the alder/rowan site to spruce I, and decreased again in spruce II (IV). qCO_2 showed no consistent trend along the transect.

In contrast to the clear decline in the net N mineralisation rate along the transect, the average gross N mineralisation rate showed a slight increasing trend, although the differences between the forest sites were not significant (Fig. 6a in III).

Microbial biomass N was the lowest at the alder/rowan site, and differed significantly from that in spruce I (Fig. 6b in III). The proportion of microbial biomass N out of total N in the organic layer was 2.4, 4.1, 4.1, 6.7 and 5.7% in the alder/rowan, birch, birch/spruce, spruce I and spruce II sites, respectively. The response of microbial N to the C/N ratio was concavely curvilinear, with the lowest microbial biomass N at the lowest (alder/rowan) and the highest (spruce II) C/N ratios.

The organic layer of the birch site had the highest total PLFA and bacterial PLFA concentrations, while that of both spruce sites had the lowest (IV). The ordination configuration of the PLFA data in non-metric multidimensional scaling was clearly related to the C/N ratio and pH, and separated the forest sites relatively well (Fig. 1a in IV). It was possible, on the basis of the similarities in the variation pattern along the transect, to divide the PLFAs into 6 groups (Fig. 1b and Table 3 in IV). The PLFAs of Group 1(16:1w5, cy17:0, 18:1, 18:1w7, 10Me18:0, 19:1a) were relatively more abundant in the alder/rowan site in comparison to the other sites. Group 2 (i14:0, a15:0, i17:0, br18:0) also showed the highest relative amounts in the alder/rowan site and, in addition, gradually decreased along the transect. Group 3 consisted of seven PLFAs (i16:0, i16:1, 10Me16:0, 10Me17:0, 17:0, br17:0, 18:0), which were the most abundant either in the birch site or in the birch/spruce site, and three of them (i16:0, i16:1 and 10Me17:0) were present in minimum amounts in spruce sites I and II. Group 4 (i15:0, cy19:0, c16:0) was characterized by a relatively low abundance in the alder/rowan site compared to the other sites. The feature common to the PLFAs of Group 5 (13 PLFAs, see Table 3 in IV) was that each of them showed the highest relative abundance in either of the spruce sites. Group 6 included PLFAs showing stable or inconsistently variable amounts along the transect (Table 3 in IV).

4. Discussion

4.1. Crown condition vs. site conditions

Study (I) showed, as in several earlier studies (Thomsen & Nellemann 1994, Müller-Edzards et al. 1997, Lindgren et al. 2000), that crown defoliation and discoloration are clearly associated with stand age. However, the fact that the spruce stands older than 60 years were more defoliated in the studied coastal sites than in other parts of southern Finland (I) indicates that the crown condition of coastal spruce is affected by factors other than only the aging of the stand. The old stands with the worst crown condition were growing on infertile sites on periodically waterlogged soil types (dystric gleysols and carbic podzols; I). This result indicates that changes in the microclimate and nutrient cycling during the succession of spruce forests leads to paludification (cf. Sirén 1955) and to a deterioration in site fertility (cf. Ranger & Nys 1994), resulting in impaired crown condition. Changes occurring in the properties of the organic layer and in the ground vegetation along the primary succession transect support this interpretation (III). The rather drastic conclusion of ‘suicide succession’ of the coastal spruce stands should, however, be avoided. The result may be biased by the fact that old stands growing on infertile, paludified sites are not very attractive subjects of felling and regeneration activities, and are therefore readily left uncut. In actual fact, such sites became selected in this study as representatives of old coastal spruce stands. Our results are consistent with the results obtained in more extensive surveys in Finland (Lindgren et al. 2000) and in Norway (Thomsen & Nellemann 1994), according to which the defoliation degree of spruce increases with decreasing site fertility, in addition to the evident relationship between defoliation and stand age. The results suggest that the poor crown condition of the coastal spruce stands is related to natural soil factors such as periodic water-logging and low fertility. These factors are likely to affect the condition of spruce in the region, since infertile, stony and paludified sites are more common on the western coast than in the inland parts at the same latitudes of Finland (Karlsson 1996). Fertile and productive spruce sites do, however, also exist on the Ostrobothnian coast, especially near the coastline where the soil nitrogen capital has been amended by nitrogen-fixing alder species (*Alnus incana* (L.) Moench and *Alnus glutinosa* (L.) Gaertner) (Erikslund 1997).

Crown discoloration in the studied stands appeared in most cases as yellowing of the older needles in the upper part of the crown, the younger needles in the topmost part of the crown remaining symptom-free (Salemaa et al. 1996). Even after adjustment for stand age, this symptom showed significant negative correlation with the site fertility index. The site fertility index was created from the site scores of the first axis of principal component analysis (‘increasing fertility, decreasing moisture’), in which needle N and B concentrations and total N, extractable S, pH and moisture content of the organic layer were used as input variables. This result indicates that soil properties play a significant role in crown condition.

Stoniness has often been mentioned as a factor having a significant influence on the growing conditions of forests along the land-uplift coast in western Finland (Appelroth 1948, Kuusela 1977). Most of the sites sampled on the Finnish coast were classified as stony or very stony (I), but there was, however, no significant covariation between the stoniness index and crown condition, needle chemistry or properties of the organic layer (data not shown). Karlsson (2000) presented height curves for coastal Scots pine and Norway spruce in western Finland, and found that stony sites showed a growth pattern of stronger stagnation over age than stone-free sites, but only for pine. He concluded that the poor rooting conditions on stony sites increase the susceptibility of trees to climatic factors such as strong winds and summer drought, which are characteristic of the weather conditions prevailing in the coastal area (Heino 1987, Solantie 1987). In the spruce data, part of which was collected from the same sites as those studied in I and II, Karlsson (2000) found a stronger stagnation of growth over age at sites with a thick humus layer compared to those sites with a thin humus layer. This probably reflected the slower rate of nutrient cycling in paludified sites with a thick humus layer.

Since acid sulphate soils occur sporadically in the coastal regions of the Gulf of Bothnia, excessive acidity is another factor that may have an influence on the growing conditions in the study area. These soils, formed during the early stages of the Litorina Sea, have been estimated to cover over 2000 km^2 of land in Finland (Palko & Lakso 1991). However, there were no indications to suggest that the forest sites studied included acid sulphate soils. For example, the sulphur concentrations in mineral soil layers of the study sites did not correspond the high levels reported for the soil horizons of acid sulphate soils (0.2–3.7% dw.; reviewed by Palko 1994). In fact, the sulphur concentrations in the mineral soil layers of the study sites were very similar to those reported for spruce forest soils in southern Finland (Merilä et al., 1996, Tamminen, unpublished results).

4.2. Possible effects of waterlogging and low soil temperature

Waterlogged, anaerobic soil conditions impair the nutrient cycling of forest ecosystems in several ways. Such conditions impede the growth and respiration of the roots and, consequently, the uptake of water and mineral nutrients (Marschner 1995), especially NH_4^+ (Lévy 1981), which is the dominant form of mineral N in acidic, sporadically waterlogged soil conditions (Smolander et al. 1995, Stark & Hart 1997, III). The nitrogen deficiency in the spruce stands studied here might thus be due to impaired N uptake. One factor which probably further hinders nutrient and water uptake in the study area is the low soil temperature or even soil frost at the beginning of the growing season. The key climatological factors determining the depth of soil frost are the winter index (sum of the mean daily air temperatures below 0°C) and thickness of the insulating snow cover (Huttunen & Soveri 1993). The Ostrobothnian region is characterized by low winter precipitation: the long-term average for the winter maximum snow cover depth is circa 40 cm, while, for example, the snow cover at the same latitudes in eastern Finland is twice as thick (Solantie 1987). Due to the thin snow cover, the soil freezes down to a greater depth and persists for a longer period on the western coast compared to inland areas, even though the winter index is lower in western Finland than in the eastern part of the country (Huttunen & Soveri 1993). The efficient interception of snowfall in a closed spruce canopy further reduces the thickness of the snow cover and delays soil warming in the spring (Mustonen 1966, Wulff 1996, Merilä 2000). The spruce stands in the coastal Ostrobothnian region are thus susceptible to desiccation injury during sunny days in early spring when the leaf temperature rises above freezing and transpiration increases, but water cannot be absorbed through the roots fast enough to replace transpirational losses (Kozlowski et al. 1991).

Waterlogging and low temperatures also decrease soil microbial activities (Mikola 1960, Van Cleve et al. 1990, Blume et al. 1991). These environmental conditions, together with the acidic soil and recalcitrant needle litter, evidently result in the immobilisation of essential nutrients, especially N, in the forest floor (Flanagan & Van Cleve 1983, Bormann & Sidle 1990). This conclusion is supported by the results of II showing a lower basal respiration (BASAL) in the organic layer of carbic podzols, and a lower microbial biomass (SIR) in both the carbic podzols and dystric gleysols, compared to the BASAL and SIR in the organic layer of ferric podzols. The ratio of BASAL and SIR ($q\mathrm{CO}_2$), i.e. the index of carbon use efficiency (Wardle & Ghani 1995, Wardle et al. 2001), showed no significant differences between the soil types, nor any covariation with the properties of the organic layer. The factors contributing to the value of this ratio thus remained unclear (see also chapter 4.5.4). Although no significant differences between the soil types were apparent in $\mu\mathrm{CO}_2$, it seemed to respond to excess soil moisture. The lowest values were found in samples with the highest field moisture content, although the actual respiration measurements were conducted in ideal moisture conditions (250% OM). This may also be a consequence of the fact that, in wet conditions, the microbial community is to some extent adapted to anaerobic conditions and, consequently, not as much CO_2 is released as in well aerated conditions.

The results of the transect study (III, IV) offered some support for the hypothesis that excess soil moisture and consequent paludification result in reduced nutrient availability, which further contributes to the reduced crown condition observed in the study area. The old paludified spruce II site repeatedly had the lowest net N mineralisation rates along the primary successional transect, and the N mineralisation coefficient (net N mineralisation during Jul –98 laboratory incubation : total N in the organic layer) tentatively declined along the transect (III; see also chapter 4.5.). Since gross mineralisation concurrently remained relatively stable, the decrease in net N mineralisation was interpreted to be primarily due to the increase in microbial immobilisation.

4.3. Microbial activity and biomass vs. nutrient concentrations in the organic layer

BASAL and SIR correlated positively and Lag correlated negatively with the concentration of extractable K of the organic layer (II). Potassium is characterized by a high mobility in plants; it is not metabolised, and forms only weak complexes (Marschner 1995). Consequently, potassium is rapidly released from plant detritus, e.g. from needle litter (Staaf & Berg 1982, Bockheim et al. 1991), which also indicates that K does not limit microbial growth. The correlation between microbial activity and K may reflect the proportion of mineral soil material in the organic layer, which in this material can be assumed to increase with increasing fertility. Furthermore, Palmborg (1997) found a similar positive correlation between K concentration and respiration rate in the mor layer, and proposed that this relationship might reflect the abundance of bilberry (*Vaccinium myrtillus* L.), the leaves of which are rich in potassium and are also easily decomposed (Johansson 1993). Microbial activity and biomass were also rather highly correlated with Mn. Mn has been shown to be essential for the activity of the lignolytic enzymes (Archibald & Roy 1992, Perez & Jeffries 1992), and decomposition activity may even be regulated by the availability of Mn (Berg et al. 1995).

4.4. Crown condition vs. needle elements

Of all the measured mineral elements in the needles, B had the strongest relationship with crown condition, being positively correlated with crown defoliation (I). Similar correlation has been found in another Finnish study covering 43 Norway spruce stands in southern Finland (Lindgren et al. 2000). Elevated foliar B concentrations have also been reported earlier in studies on reduced living crowns of Scots pine caused by browsing moose (Löyttyniemi 1985), Scleroderris canker (*Gremmeniella abietina* (Lagerb.) Morelet) infections and manual pruning (Nuorteva & Kurkela 1993, 1998). The distribution of B in plants is primarily governed by the transpiration stream: the regulation of B uptake and translocation is rather limited compared to that of other mineral nutrients (Marschner 1995). One possible explanation for the elevated B concentrations might thus be that B simply accumulates in remaining needles of a defoliated crown, but further studies would be necessary in order to test this hypothesis.

The N and Cu concentrations in the needles were negatively correlated with crown defoliation and discoloration (I). Needle N and Cu concentrations were also clearly positively correlated with each other. Similar covariations were also found in the study of Lindgren et al. (2000). Our results are consistent with those of van den Burg (1983), who concluded that, at least under conditions of low N availability, N seems to stimulate Cu uptake. In a nutrient optimisation experiment in young Norway spruce stands in northern Sweden, the Cu concentrations and Cu/N ratios in the needles were found to remain relatively constant over time and between treatments, despite large differences in biomass production (Linder 1995). This observation, which indicates that Cu is taken up in relation to the demand rather than to the supply, fits well with our results. However, in comparison with the optimum value of 0.02 (Linder 1995), the Cu/N ratios found in our study were relatively low, varying in the range of 0.0062 – 0.0173. In addition to low concentrations in the parent material, Cu availability may be reduced as a result of the complexation of Cu with organic compounds (Stevenson & Fitch 1981). Moreover, a low temperature has been shown to affect strongly the desorption of Cu (McLaren et al. 1990). Low needle Cu in spruce stands has been also observed in other parts of Finland, both on peatlands (Silfverberg 1980) and on mineral soils (Raitio 1994). However, the visible Cu deficiency symptoms described by van Goor & Henkens (1966) and van Goor (1968) have so far not been reported in Finland.

4.5. Soil microbial dynamics along the primary successional transect

4.5.1. Net N mineralisation

Net N mineralisation decreased along the primary succession transect (alder/rowan, birch, birch/spruce, spruce I and II; III) in both the field and laboratory incubations. These results confirm the results obtained in successional floodplain soils along the Tanana River, in interior Alaska. In this area, net ammonification and nitrification were at their highest in the middle successional poplar-alder forest floor, while in the late successional white spruce forests they were at their lowest or even undetectable level (Klingensmith & Van Cleve 1993). A decrease in net ammonification and nitrification during the course of succession has also been reported in a number of other studies, as reviewed by Robertson (1982). The transect studied here – alder/rowan, birch, birch/spruce, spruce I and spruce II – is clearly a sequence ranging from a N-rich ecosystem characterised by easily degradable litter and low canopy interception, to a N-poor ecosystem with highly recalcitrant litter and high canopy interception. Our estimates for the net N mineralisation on an areal basis (2.8 – 7.4 g m^{-2}) are fairly consistent with those reported in Norway spruce stands in Sweden and Denmark (1.7-6.8 g m^{-2} yr^{-1} in the LFH layer; Persson & Wirén (1995)).

The N mineralisation coefficient (Weier & MacRae 1993), i.e. net N mineralisation as a proportion of the total N concentration of the organic layer, tentatively declined in the spruce sites compared to the sites representing earlier successional stages. This is assumed to be an indication of the more recalcitrant nature of soil organic matter, generally expressed as a higher lignin content and C/N ratio (Berg 1986) in late successional spruce forests than in the preceding deciduous stands (Pastor et al. 1987, Priha & Smolander 1999, Côte et al. 2000). Initial concentrations of NH_4-N and DON in the samples seemed to predict well the actual net N mineralisation rate, since these variables accounted for the differences in net N mineralisation between the forest sites, as well as between the incubation periods (alder/rowan site excluded). The initial DON concentration evidently depicts the easily mineralisable N pool in the samples and, together with NH_4-N, also indicates the recent activity of soil microbes.

4.5.2. Net nitrification in the alder/rowan site

Net nitrification only occurred in the alder/rowan site. This result is consistent with the findings of Van Cleve et al. (1993) and Hart & Gunther (1989). The latter authors found net nitrification in the soil only in the alder site when four different subarctic vegetation types (alder, dry tundra, moist tundra and white spruce sites) were compared. However, a lack of net nitrification does not necessarily indicate the absence of nitrifiers, because the nitrate formed may be rapidly immobilised by soil micro-organisms (Stark & Hart 1997, Stottlemyer & Toczydlowski 1999). Dinitrogen-fixing alder influences mineral soil N transformations both by increasing the size of the total N pool in the soil, and by supplying higher quality litter inputs to the forest floor than non-dinitrogen-fixing plants (Hart & Gunther 1989). In our study the organic layer of the alder/rowan site differed from that of later successional sites in having a higher pH and greater N availability. Plant secondary compounds may also have played a role in the cessation of net nitrification after the transition from a dominance of alder and rowan to birch, and further to spruce. In Alaskan river floodplains, for instance, the rapid decrease in N_2 fixation and nitrification during the transition from alder to balsam poplar has been attributed to the effects of secondary compounds in balsam poplar on microbial activity (Schimel et al. 1996, Schimel et al. 1998, Fierer et al. 2001).

Net nitrification in the alder/rowan site was found to correlate positively with pH($CaCl_2$) in the range of 3.32–4.84, which is in accordance with the results of other studies (Smolander et al. 1998, Ste-Marie & Paré 1999). Net nitrification was also positively correlated with the initial concentrations of TDN, mineral N and (NO_2 + NO_3)-N, but not with that of NH_4-N. Although NH_4-N is the substrate for autotrophic nitrifying bacteria, the initial concentration of (NO_2 + NO_3)-N, which is the net product of recent nitrification activity, showed a better correlation with the rate of net nitrification than the initial concentration of NH_4-N. This indicates that, in conditions favourable for nitrification activity, the NH_4-N produced in ammonification is rapidly consumed by nitrifying bacteria.

4.5.3. Gross N mineralisation and microbial biomass N

In contrast to decreasing net N mineralisation rates, the gross mineralisation of N showed a tentative increase along the transect, although the differences between the forest sites were non-significant. Similarly, in a study on net and gross N mineralisation below birch (*Betula papyrifera* Marsh.), spruce (*Picea glauca* (Moench) A. Voss) and alder (*Alnus incana* (L.) Moench) in Isle Royale, Michigan, the alder forest showed the highest net N mineralisation rate, but gross mineralisation was the highest beneath spruce and birch (Stottlemyer & Toczydlowski 1999). The authors concluded that the higher net N mineralisation rates beneath alder in comparison to birch and spruce resulted from lower microbial immobilisation rather than greater gross N mineralisation. In our study, microbial biomass N was not followed during the incubation, but the increasing microbial biomass N (measured in Jul-98) along the transect from alder/rowan to spruce I, in part supports this interpretation. However, greater immobilisation of N in the late successional spruce sites is probably an inadequate explanation for the stable or even increasing gross N mineralisation rate and decreasing net N mineralisation rate along the transect, since we cannot assume that the microbial N pool will continuously increase. This contradiction in the results could be due to the $^{15}NH_4^+$ pool dilution method used, as discussed in the recent paper of Fierer et al. (2001). The proportion of microbial biomass N out of total N in the organic layer increased along the transect, and hence the rate of gross N mineralisation per unit of microbial biomass N remained relatively stable (data not shown). Thus, the gross mineralisation rates observed would appear plausible if pool dilution measured the microbial cycling and recycling of small pools of highly labile, N-rich compounds rather than the overall decomposition of soil organic matter and microbial growth, as suggested by Fierer et al. (2001). Further, it may be hypothesized that, in the late successional spruce sites, the higher proportion of N in the microbial pool, compared to the earlier sites, will be transformed into the more stabile N pool, i.e. to humic substances, resulting in a decreasing net N mineralisation along the transect.

Microbial biomass N tended to increase along the transect from the alder/rowan site to spruce I, but was lower again in spruce II. Correspondingly, since the C/N ratio increased along the transect, the response of microbial biomass N to the C/N ratio was concavely curvilinear rather than linear. This may indicate that the microbes in the N-rich alder/rowan site are relatively C limited, as reported earlier for an early successional alder stage by Clein & Schimel (1995). During the succession, increasing C availability creates conditions in which the microbial biomass can increase, but a reducing N pool leads to N limitation of the microbial community (Ohtonen et al. 1992, Aikio et al. 2000). In the spruce II site, microbial growth may again become limited by factors other than nitrogen, e.g. by the presence of more recalcitrant C sources.

4.5.4. Microbial respiration, biomass and the carbon use efficiency

Along the primary successional transect studied (alder/rowan, birch, birch/spruce, spruce I, spruce II) we hypothesized a concavely curvilinear response of basal respiration (BASAL) and microbial biomass (SIR) to changing organic matter quality, which was primarily indicated by an increasing C/N ratio and decreasing pH and net N mineralisation (III).

In contrast to our hypothesis, BASAL and SIR were relatively stable along the transect. This result can be interpreted to indicate that the decomposition of aged soil organic matter occurs over a wide range of substrates at a relatively stable rate, or that the labile C pool was able to maintain microbial activity irrespective of the size and decomposability of the recalcitrant C pool. Similarly, BASAL and SIR remained unchanged along a fertility gradient studied by Pennanen et al. (1999). However, Nohrstedt (1985), who investigated microbial activity in forest floors using bulked samples of three samplings during one growing season, found a curvilinear response between respiration and the C/N ratio in the organic layer, and concluded that optimum conditions for decomposition were within the C/N ratio range 20–30. In our study, the samples taken during the most favourable temperature and moisture conditions in the field (BASAL in Jul –97 and BASAL and SIR in Jul –98) tended to show this pattern, i.e. BASAL and SIR increased slightly along the transect from alder/rowan to spruce I, but were again lower in spruce II, and thus partly supported our hypothesis. Consistent support for the hypothesis that N limitation or more recalcitrant C sources would reduce microbial biomass and activity in the late successional spruce site was not, however, obtained.

In the alder/rowan site, microbial activity may be affected by the influence of a high N concentration on the degradation or degradability of lignified organic substances. N-rich litter degrades relatively rapidly in the early stages of decomposition but, during the later stages, negative correlation has been repeatedly reported between the nitrogen concentration and the rate of loss of lignin mass (Berg et al. 1982, Berg & Wessen 1984, McClaugherty & Berg 1987, Berg & Ekbohm 1991). A similar relationship has also been found between the basal respiration and N concentration in the humus layer (Berg & Matzner 1997, Persson et al. 2000). Accumulation of soil organic matter in the early stages of primary succession is an important process which, by increasing the water-holding and cation exchange capacities, facilitates the establishment of later successional species. The finding that N-rich litter has a larger recalcitrant fraction than N-poor litter and, consequently, results in higher accumulation of soil organic matter in relation to the amount of litterfall (Berg et al. 2001), thus appears to be very appropriate from the successional point of view.

BASAL and SIR in spruce I site were occasionally surprisingly high. The highest rates were actually observed on stony, and therefore dry, infertile patches with a thin, poorly decomposed organic layer. These patches obviously had a high density of fine roots and associated ectomycorrhizal hyphae. It can be assumed that the mycorrhizal hyphae, still present in the sample after sieving, continued to respire after excision from their host and, together with the root exudates remaining in the sample, also provided a source of substrates for decomposing microbes, resulting in the relatively high BASAL, SIR and FungPLFA measured in spruce I site. Moreover, the high microbial activity and biomass measured in this site may have reflected the favourable temperature and moisture conditions in the field, since poorly decomposed organic material evidently contains easily decomposable C sources for soil microbes. The presence of poorly decomposed organic material may also partly explain the highest FungPLFA concentration in spruce I, because fungal communities have been found to play a dominant role in litter breakdown in the early stages of decomposition (Dilly et al. 2001).

$q\mathrm{CO}_2$ showed no significant differences between the successional sites in three of the five samplings, and the birch/spruce (Jul –97) and birch and birch/spruce (Aug –97) in the other two samplings tended to show higher $q\mathrm{CO}_2$ than the other sites. In a recent paper, Vance & Chapin (2001) suggested that differences in $q\mathrm{CO}_2$ between forest ecosystems may reflect several kind of disparities, such as differences in the proportion of inactive microbial biomass, in the degree of substrate limitation of microbial activity or in the metabolic rates, turnover, and growth efficiency of different microbial functional groups. In our study (I) these factors seemed to counteract each other and few, if any, differences were found between the sites. While qCO_2 undoubtedly indicates microbial efficiency, this quotient appears to be too unspecific to reflect ecosystem development (Wardle & Ghani 1995).

4.5.5. Microbial community structure

As revealed by NMS ordination of the PLFA data, the microbial community structure showed relatively clear differences along the transect, and was closely related to the C/N ratio and pH of the soil. It was possible, on the basis of the similarities in the variation pattern along this transect, to divide the PLFAs into 6 groups, even though the indicative value of most of the single PLFAs is not clear. The most distinctive group in NMS ordination was formed by the samples from the alder/rowan site. The amount of PLFA 16:1w5, which has been reported to be present in higher amounts in soil containing arbuscular mycorrhizal fungi (Olsson et al. 1995), was at its maximum in this site. The result is consistent with the fact that the understorey vegetation in the alder/rowan site was dominated by grasses and herbs (III), which generally form this type of mycorrhizal association.

5. Concluding remarks

In summary, the results suggest that the poor crown condition of the coastal spruce stands is related to natural soil factors such as periodic water-logging and low fertility. These factors are likely to affect the condition of spruce in the region, since infertile, stony and paludified sites are more common on the western coast than in the inland parts at the same latitudes in Finland. Climatic factors such as persistent soil frost caused by the thin snow cover may be an additional stress factor that impairs water and mineral nutrient uptake at the beginning of the growing season.

The case study on the dynamics of C- and N-related soil microbial activities along a successional transect provided evidence of distinctive changes in organic matter quality and decreasing mineral N availability during forest succession. Low N availability may contribute to the poor crown condition and growth of the aged Norway spruce forests on the land-uplift coast in western Finland, although the ability of mycorrhizal roots to utilise organic forms of nitrogen may, in part, compensate for the reduced availability of mineral N. Moreover, it should be borne in mind that N mineralisation rates obtained in incubation experiments are merely indications of the actual N supply, and should not be taken as accurate determinations. Microbial biomass and respiration were relatively stable among the successional forest sites, in spite of the clear differences in the structure of the microbial community along the transect. During the most favourable temperature and moisture conditions in the field, however, these variables tended to increase along the transect from alder/rowan to spruce I and decreased in spruce II site, suggesting that seasonal factors may account for the observed variation. The contribution of abundant mycorrhizal hyphae to microbial respiration and biomass, especially in the spruce sites, cannot be ruled out either.

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Corrections

- Paper I, p. 415, column 1, line 1. LECO analyser used was CHN-600, not TGA-500.
- Paper I, p. 416, column 2, line 1. 4a-c, not 2a-c.
- Paper II, p. 362, column 1, line 4. LECO analyser used was CHN-600, not TGA-500.
- Paper III, p. 378, Table 3. Letter b, denoting the significant differences between the groups, is missing from the initial concentration of NH_4-N (mg kg^{-1} OM) in spruce I site in Jun -97.
- Paper III, p. 382, column 1, line 4-5. The reference Persson et al. 1995 should be replaced with Persson,T. & Wiren, A. 1995. Nitrogen mineralization and potential nitrification at different depths in acid forest soils. Plant and Soil 168-169:55-65.