

**SCOTS PINE NEEDLE  
LONGEVITY AND OTHER  
SHOOT CHARACTERISTICS  
ALONG POLLUTION  
GRADIENTS**

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Department of Biology,  
University of Oulu

OULU 2002





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# Lamppu, Jukka, Scots pine needle longevity and other shoot characteristics along pollution gradients

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## *Abstract*

Branches of adult Scots pine (*Pinus sylvestris* L.) trees were sampled from boreal dry pine forests to study needle longevity, its variation and its relation to other shoot characteristics. The stands studied were located along transects from two smelters and one city, e.g. along gradients of pollution impact. Constant needle age structures were assumed and static life-tables generated.

Mean needle longevity was calculated as the sum of the proportions of living needle fascicles on the successive annual shoots. It fully incorporated the information of the static life-tables and was preferred to median or maximum ages because of its significantly lower variation. The first half of the shedding span, the duration of the period when the needle survival gradually dropped from 90 to 50 %, proved to validly reflect the changes in the needle age structure.

Needle longevity decreased 15-40 % towards the pollution sources along the transects studied. Near the smelters, needle longevity decreased with the increasing needle Fe, or Fe, Ni and Cu concentration that represented the main constituents of the airborne particle emissions. Near the city, needle longevity decreased with the increasing needle N and P concentrations, annual needle mass and needle mass packing and decreasing needle area packing.

In the urban forests, needle Mg, P and K concentrations decreased linearly with the decreasing needle survival from the second to the fourth needle age class. Concentrations in the living needles of the fourth age class stayed over 80 % of the average for all the age classes, though needle survival dropped below 50 %. A decreasing needle Mn concentration was detected towards all the emission sources. Leaching, especially from the soil, as a possible cause was discussed.

Needle longevity had the lowest variation among the shoot characteristics, which increases its value as a tool in ecological monitoring. Low plasticity in needle longevity could be an acclimation to the ambient environmental conditions and length of the growing season and to maximise the carbon gain per time. Needle longevity decreased and annual needle mass and leaf mass per area increased upwards in the crowns of mature Scots pines, reflecting the acclimation to irradiance.

*Keywords:* acclimation, air pollution, life-span, monitoring, plasticity



## Acknowledgements

The idea to start working with needle longevity was raised a couple of years after I had graduated in 1989. In the same year, I took part in a study designed to monitor the effects of an oil refinery on Scots pine forests in Southern Finland. As part of that study, crown transparency was assessed. During the field work already, and especially after the critical comments regarding our results, I started to look for a more objective method. The number of needle age classes had been counted to observe the changes in needle longevity. Classification of needle survival on annual shoots with 25% and, after that, with 10% classes was a more precise method. In 1993, I discovered a method to count the scars of needle fascicles. At that time, I realised I had found a suitable topic for my doctoral dissertation.

I thank you, Professor Satu Huttunen, my first supervisor, for the time I have spent working as a researcher in your group, and especially for the time when the idea to study needle longevity arose and developed. Branches from the surroundings of Oulu were first sampled in 1994, and the more intensive phase of the doctoral research started in the autumn 1995, after I had finished my licentiate thesis (on another topic). Since 1995, I have worked mostly as a teacher or assistant at the Department of Biology, but I have also made elemental analyses and one survey. All these works have been rewarding but have taken a lot of time.

The first manuscript on needle longevity was submitted for the first time to a journal in 1998. Writing one's first research paper is probably the most instructive phase of a person's career. During that process, my second supervisor Docent Risto Jalkanen guided me without sparing his energies. Many thanks for that. I think I have learnt much about scientific writing, especially about writing to possible readers. Satu and Risto have frequently guided me with their comments. Collegiate thanks for such comments also go to PhD Pasi Rautio. My sincere thanks to Professor Markku Rahiala. Co-operation with him has been most instructive. I highly appreciate the warm atmosphere between the members of our research group: it has always been easy to discuss with all of you.

The process of learning to count and calculate, read and write and make some drawings has been time-consuming. It has required days and days of work (sometimes even evenings) at the university. Still, I have had a real life too. My warmest thanks for

that go to my children Pauli, Matti and Marja and my wife Tarja and her sons Jaakko and Antti. Special thanks to Tarja for her patience.

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I thank the reviewers, Professor John Marshall and Professor Peter Reich, for their invaluable comments on this work and Salla Finnilä, Robert Gear, Keith Kosola and Sirkka-Liisa Leinonen who corrected the English. The work was partly financed by the Kone Foundation and a grant from the University of Oulu.

Oulu, November 2002      Jukka Lamppu



## **List of original papers**

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

Lamppu J & Huttunen S (2001) Scots pine needle longevity and gradation of needle shedding along pollution gradients. *Can J For Res* 31: 261-267.

Lamppu J & Huttunen S (2002) Relations between Scots pine needle element concentrations and decreased needle longevity along pollution gradients. (*Environmental Pollution*, in press).

Lamppu J, Huttunen S & Rahiala M (2002) Scots pine needle longevity affected by crown position and needle nitrogen concentration along a gradient from an industrial urban area. Manuscript (submitted).

Lamppu J (2002) Variation and fluctuations in needle longevity related to other shoot characteristics of Scots pine. Manuscript (submitted).



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# 1 Introduction

Studies clearly focusing on needle longevity, especially that of evergreen conifers, have been published already in the 19th and in the beginning of the 20th century (Wiesner 1871, Wiesner 1905, Pease 1917) and the studies have included successful and vindicated conclusions. Some early works have concentrated on the regional variations of a number of phenotypic traits, including needle longevity (Sylvén 1916, Schotte 1923, Pravdin 1967). In the late 1970's and the early 1980's, the extended leaf life-span was considered an adaptational mechanism in infertile or generally stressful environments (Grime 1977, Chapin 1980, Ewers & Schmid 1981) and an ecophysiological trait influencing the costs and benefits of carbon gain (Chabot & Hicks 1982, Field 1983). Improved nutrient availability has been connected to the shortened life-spans (Shaver 1981). In the late 1980's and in 1990's, the leaf life-span was related to other basic physiological parameters in leaf functioning (Reich *et al.* 1992), differences in the construction costs and anti-herbivory defence (Coley 1988, Williams *et al.* 1989), other shoot characteristics and self-shading (Schoettle 1990, Schoettle & Smith 1991, Ackerly & Bazzaz 1995, Balster & Marshall 2000), and variation in the conditions of the growing season (Schoettle 1990, Kudo 1992, Jalkanen *et al.* 1995). Models describing costs and benefits in relation to longevity have been developed (Kikuzawa 1991, Thornley 1991, Kikuzawa & Kudo 1995, Ackerly 1999). The models show that in order to sufficiently increase carbon gain per time, e.g. conifer needles with a relatively low photosynthetic rate and high construction costs must have relatively long life-spans. However, as the net assimilation rate declines with leaf ageing, the optimal life-span is usually reached well before the net assimilation ceases.

Scots pine (*Pinus sylvestris* L.) is one of the dominating coniferous trees in the dry and nutrient-poor forests of the temperate and boreal vegetation zones (Monk 1966, Mirov 1967). Scots pine has sclerophyllous features and the stress tolerant strategy of an evergreen (Grime 1977) that has been explained by nutrient conservation (Monk 1966, Chapin 1980, Moore 1980), or improved nutrient use efficiency (Vitousek 1982, Escudero *et al.* 1992), improved carbon balance (Chabot & Hicks 1982, Sprugel 1989, Kikuzawa 1991), and adaptation to environmental stress (Chabot & Hicks 1982).

The rates of leaf burst and senescence determine the leaf life-span. Species-specific and genetically controlled initiation of senescence (Thomas & Stoddart 1980) is affected

by latitude (Sylvén 1916, Karlsson 1992, Kudo 1995), altitude (Ewers & Schmid 1981, Schoettle 1990), the length of the growing season (Kudo 1992, Jalkanen *et al.* 1995), light (Nilsen 1986, Schoettle & Smith 1991), water and nutrient relations (Shaver 1981, Gover *et al.* 1993, Balster & Marshall 2000), pathogens and insects (Jalkanen 1986, Jutinen & Varama 1986), weather conditions (Hadley & Smith 1986, Grier 1988, Jalkanen 1998), and air pollutants (Boltneva 1982, Gluch 1988, Yarmishko 1993, Jalkanen 1996).

The annual leaf production is influenced by weather conditions (Junttila & Heide 1981), altitude (Schoettle 1990), latitude (Kudo 1995) and light (Ilonen *et al.* 1979, Schoettle & Smith 1991). Leaf longevity seems to decrease with increasing annual leaf production (Shaver 1981, Schoettle 1990, Kudo 1995, Balster & Marshall 2000). It has been suggested that the increased leaf longevity could be an adaptation mechanism maximising nutrient use efficiency in conditions of low nutrient availability (Vitousek 1982, Escudero *et al.* 1992).

Scots pine is adapted to grow on dry infertile soils (Mirov 1967). In urban forests, the nutrition of forest trees is affected by the increased nitrogen deposition (Rennenberg & Gessler 1999). Added nitrogen has improved the shoot growth of Scots pine (Valinger 1993), and the greatest increases in growth have occurred in the least productive forest sites (Mälkönen *et al.* 1990). Therefore, the changes in shoot characteristics, including the increased annual needle production and decreased needle longevity, could be expected in relation to the effects of the nitrogen deposition from urban sources.

The negative effects of the major point sources of air pollutants on forest health are generally well known (Smith 1981, Innes 1993) as well as the negative effects around the sources in the present study (Lumme *et al.* 1997, Tikkanen & Niemelä 1995, Oulu City Council 1989, 1994). These two types of environment, the surroundings of two big point sources and urban forests, have offered an opportunity to study needle longevity as an ecological indicator, as a trait showing plasticity along gradients in light and nutrient availability and to define the relations to the other shoot characteristics.

The assessment of crown transparency has been widely used as a method of forest condition monitoring (Stolte *et al.* 1992, Lorenz *et al.* 2001) since the "new kind of forest decline" has been a concern to the scientists (Blank 1985, Schütt & Cowling 1985). However, transparency is a subjective measure, and thus the observer's experience and even factors like the weather influence the quality of the data (Innes 1988, Innes 1993). Needle longevity of conifers has been used as a more objective tool (Wachter 1985, Fraude 1988, Gluch 1988, Skuhravy 1990, Stolte *et al.* 1992, Jalkanen 1996).

Most conifers are typical evergreens having a long-living foliage in more than one cohort (age class). The observations of the age structures are commonly used to determine leaf longevity of this kind of plants (Kimura 1963, Shaver 1981, Maillette 1982, Gluch 1988). This method includes an assumption of the constant age distributions, and yields static life-tables (Krebs 1994).

## **2 Aims of the study**

Scots pine needle longevity, its variation and relation to other shoot characteristics have been studied in environments with clear air pollution impacts. This has been done to describe the changes in needle life-span and age structure and to define needle longevity as a factor coupled to the acclimation process. Needle longevity was expected to decrease towards the pollution sources. The variation in needle age parameters and their character were compared in order to select the most feasible one to be used in monitoring studies. One aim was to show the possible changes in needle age structure that affect the duration of the gradual needle shedding. Increased duration of gradual shedding was expected to be coupled to decreased needle longevity.

It was hypothesised that the decreasing patterns in the concentrations of mobile nutrients (magnesium, phosphorus, and potassium) in needles on the successive annual shoots could be similar as the decreasing pattern in needle survival. Common characters in needle element concentrations in the three polluted areas, related to general environmental changes, were expected. One hypothesis was that needle longevity would decrease in urban forests with increasing needle mobile nutrient concentrations and increasing size of annual shoots and near the two smelters with increasing needle heavy metal concentrations.

The impact of crown position and nitrogen availability on different shoot traits, including needle longevity, and the relations between them was studied in urban pine forests. Needle longevity was hypothesised to decrease with increasing size of annual shoots towards upper crown. The variation in needle longevity and other shoot characteristics were of special interest. The differences in variation were expected to indicate differences in phenotypic plasticity between different shoot traits. Seasonal and annual fluctuations in needle longevity and its relations to other shoot characteristics were determined to describe the feasibility of needle longevity in ecological monitoring. Low variation and relatively small fluctuation in needle longevity was expected.

## 3 Materials and methods

### 3.1 Study areas

Scots pine branches were sampled in dry, pine-dominated natural forests near Monchegorsk (Kola Peninsula, Russia), Kostomuksha (Karelia, Russia) and Oulu (Finland). Near Monchegorsk, the forest stands were located along a transect running south-west from a copper-nickel smelter ( $67^{\circ} 55'N$ ,  $32^{\circ} 50'E$ ); near Kostomuksha, to the north and north-northwest from the iron mining and processing complex ( $64^{\circ} 40'N$ ,  $30^{\circ} 45'E$ ); and near Oulu, along three transects running north, north-northeast and northeast from the city centre ( $65^{\circ} 01'N$   $25^{\circ} 28'E$ ). The distances to the nearest and to the most remote stands were 12 and 113 km from the smelter in Monchegorsk, 2 and 64 km from the smelter in Kostomuksha, and 3 and 17 km from the city centre of Oulu (Fig. 1). Monchegorsk is located in the northern boreal, Kostomuksha on the boundary between the middle and the northern boreal, and Oulu in the northern part of the middle boreal vegetation zone (Ahti *et al.* 1968).



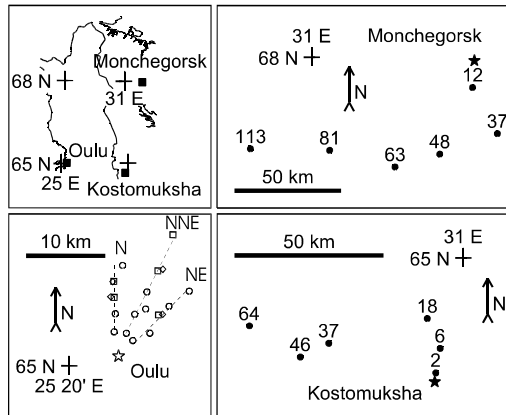


Fig. 1. Location of the study areas and the forest stands. The numbers above the dots refer to the distance from the smelters in kilometres, and the stars refer to the smelters near Kostomuksha and Monchegorsk and the city centre of Oulu. The open squares refer to the stands (near Oulu) sampled in August 1995 and before and open diamonds to those sampled in August 1995 and thereafter. Open circles refer to the stand included in all samplings.

### 3.2 Emissions and deposition

The annual emissions and deposition (Tables 1 and 2) were rather stable during the study period. In Oulu, the emissions of sulphur and sulphur deposition have decreased considerably from the 1980's to the 1990's.

Table 1. The annual  $SO_2$ -,  $NO_2$ - dust, Ni and Cu emissions (tons) in Monchegorsk 1991-96, Kostomuksha 1986-92, and Oulu 1991-96 and 1969-88 (Provincial State Office of Lapland 1992, Kryuchkov 1993, Baklanov and Rodjushkina 1993, Poikolainen and Lippo 1995, Lumme et al. 1997, Oulu City Council 1997, Karelkomizdata 1998, Miljaeva and Feschenko 1998).

Emissions	$SO_2$	$NO_2$	Dust	Ni	Cu
Monchegorsk	200000-250000	1200-5100	12300-17400	3100-3150	2100-2200
Kostomuksha	50000-60000	1200-1500 <sub>a</sub>	5000 <sub>b</sub>		
Oulu (1969-88)	5800-12060	5000-6000	2400-4040		
Oulu (1991-96)	3400-4200	4200-4300	600-950		

<sub>a</sub>  $NO_x$  in 1996-97

<sub>b</sub> Mainly iron

Table 2. The distance from the source and annual deposition ( $\text{mg m}^{-2} \text{a}^{-1}$ ) of  $\text{SO}_4\text{-S}$  and  $\text{NO}_3\text{-N}$  near Monchegorsk (1986-88), Kostomuksha (1992-94) and Oulu (mid 1990's and early 1980's) (Jevtjugina 1991, Poikolainen and Lippo 1995, Oulun kaupunki 1997).

Deposition	distance (km)	$\text{SO}_4\text{-S}$	$\text{NO}_3\text{-N}$
Monchegorsk	7 SW	1700	
Monchegorsk	80 SE	400	
Kostomuksha	10 E	300	90-95
Oulu (early 1980's)	3 NNE	1000-1700	100-250
Oulu (mid 1990's)	3 NNE	150-400	100-150

### 3.3 Forest stands

Near Monchegorsk, branches of ten trees from each of the three stands were sampled in February 1993. Six stands were chosen and branches of five trees from each stand were sampled in August 1993. The stands near Monchegorsk were selected for the Lapland Forest Damage Project (Tikkanen & Mikkola 1990), and the samples were taken by the staff of the Finnish Forest Research Institute. Near Kostomuksha, branches of ten trees from each of the six stands were sampled. Near Oulu, five stands were selected along each of the three transects (facing N, NNE and NE) in October 1994. Branches of nine trees per stand were sampled. In October 1994, and in March and August 1995, branches were sampled along the NNE transect, also in a sixth stand (17 km from the city centre, Fig. 1). Middle crown branches were sampled near Monchegorsk, Kostomuksha and Oulu. In August 1995 near Oulu, branches were also sampled from the lower and upper crown thirds (III). For additional information see Table 1 in I.

### 3.4 Sample preparation

Fresh samples were stored for one week at the most in a cold room at 4°C until prepared. The sample shoots were selected and their lateral twigs were removed in laboratory. Each sample shoot was composed of successive foliated annual shoots along the same axis and at least one annual shoot that was older than the oldest foliated one. The sample shoots had healthy looking growth and buds.

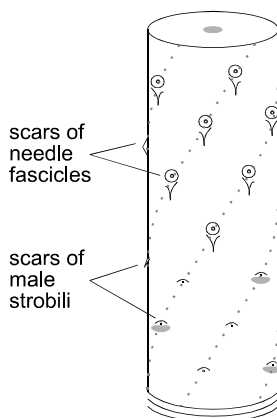
### 3.5 Measurements and analyses

The successive annual shoots were separated cutting along the bud scale scars. All the measurements were made of annual shoots. Needle longevity analysis was based on

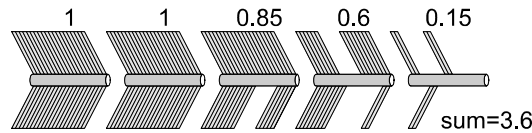
either evaluated or calculated needle proportion values. The static life-tables were generated assuming the needle age structures to be constant. Values were evaluated for the shoots sampled near Kostomuksha and for those sampled near Monchegorsk in February 1993. The evaluation (classification) was made with the needle proportions of 10, 20, ..., 90% as class midpoints; the proportions under 5% were considered as 0%, and the proportions of 95% and above as 100%. The needle proportion values were divided by 100 in order to calculate needle longevity.

For other materials the needle proportions were calculated. The shoots were first left to dry at room temperature. The living intact needle fascicles were then removed and counted. After that, all the scars of both needle fascicles (annual number of needle fascicles) and male strobili were counted following their spiral arrangement (Fig. 2). The needle proportion was the ratio of the living needle fascicles to all scars of them. Needle longevity was the sum of the needle proportions of the successive annual shoots (Fig. 3).

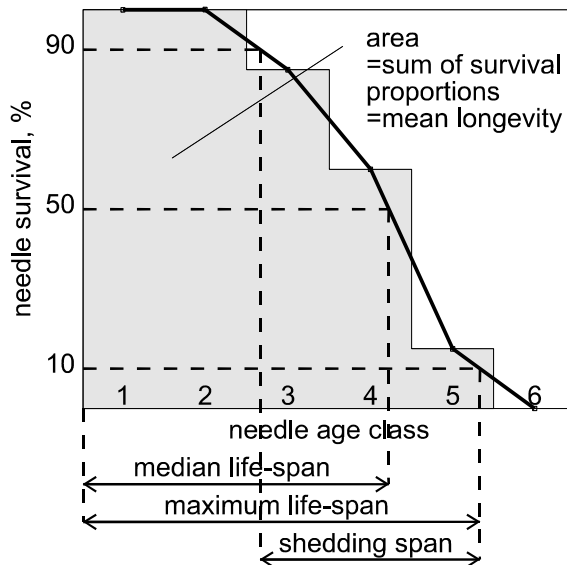
The maximum needle age was the time span up to 10%, and the median needle age up to 50% needle survival (Fig. 4). To study the changes in the needle age structure, parameters describing the gradation of needle shedding were calculated. The total gradual shedding was the time span between 90 and 10%, the first half between 90 and 50%, and the latter half between 50 and 10% needle survival. The analyses and measurements made in each study are collected in Table 3.



**Fig. 2. A piece of a young annual shoot without short shoots. The dashed lines show the spirals of scars of male strobili and scars of needle fascicles.**



**Fig. 3.** The successive annual shoots of a sample shoot. The needle survival proportions are indicated above the shoot. Mean longevity is the sum of the successive survival proportions.



**Fig. 4.** The needle survival proportions of the successive annual shoots (see Fig. 3) as bars and a survival curve. Mean longevity, median and maximum needle life-spans and the duration of the gradual shedding are illustrated.

Dry weights were obtained with an electrical balance after drying the annual shoots for 24 hours at 40°C in a forced-ventilation drying oven. Needle length and dry weight were measured from a sample of ten needle pairs. The total needle area was calculated from needle length using the equation,  $\text{area} = 4.2235 * \text{length} + 15.6835$ , introduced by Flower-Ellis & Olsson (1993), and used to calculate leaf mass per area (LMA) and needle area packing. Annual shoot stem mass and the present needle mass were weighted to an accuracy of one milligram. Foliated shoot stem mass was the sum of annual stem mass weighted by the respective needle proportions. Annual needle mass was calculated dividing the present annual needle mass by the respective needle proportion. Shoot needle mass was the sum of the present annual needle mass of the successive annual shoots. Annual shoot length was measured to an accuracy of one millimetre. Stem unit length was the ratio of annual shoot length to the sum of the scars of male strobili and the scars of needle fascicles. Foliated shoot length was the sum of annual shoot lengths weighted by the respective needle proportions (Table 3).

Needles used for the elemental analyses were left unwashed, dried 48 hours at 40°C and ground. The needle samples for N analyses were ground with a Cyclotec 1093 sample mill (Foss Tecator, 1.0 mm mesh), and for the other elemental analyses with a Type 120 SAKO mill (Koneteollisuus Oy, 0.8 mm mesh). Total needle nitrogen (N) was analysed using the dynamic flash combustion method (Elemental Analyser EA1110 CHSN-O, Fisons Instruments S.p.A., CE Instruments). The total amounts of magnesium (Mg), phosphorus (P), potassium (K), manganese (Mn), iron (Fe), nickel (Ni) and copper (Cu) were analysed with an X-ray fluorescence spectrometer (Siemens SRS 303 AS) calibrated with commercial reference materials. The total amounts of the elements were calculated multiplying the concentrations by the weight of the present needle mass.

*Table 3. Shoot characteristics measured in different studies (I-IV).*

Needle longevity (growing seasons)	I	II	III	IV
Maximum needle age (growing seasons)	I			
Median needle age (growing seasons)	I			
Total gradual shedding (growing seasons)	I			
First and latter halves of gradual shedding (growing seasons)	I			
Needle concentration of Mg, P, K, Mn, Ni, and Cu ( $\mu\text{g g}^{-1}$ dw)		II		
Shoot needle amounts of Mg, P, K (mg)		II		
Needle concentration of N ( $\text{mg g}^{-1}$ dw)		II	III	
Leaf mass per area (LMA, $\text{mg dw cm}^{-2}$ )			III	
Needle area packing ( $\text{cm}^2 \text{mm}^{-1}$ )			III	
Needle mass packing ( $\text{mg dw mm}^{-1}$ )			III	
Annual needle mass (g dw)		II	III	IV
Shoot needle mass (g dw)		II		IV
Stem unit length ( $\text{mm pcs}^{-1}$ )			III	IV
Annual shoot length (mm)			III	IV
Annual number of needle fascicles (pcs)				IV
Weight of one needle (mg dw)				IV
Foliated shoot length (mm)				IV
Foliated shoot stem mass (g dw)				IV

### 3.6 Statistical analyses

The effects of different needle, shoot, tree and stand parameters on needle longevity, annual needle mass and LMA were studied composing mixed linear models. The tree effects were treated as random, whereas all other effects were treated as fixed. Estimated coefficients, Wald test statistics and p-values for each effect were computed. SAS (8.2, Mixed-procedure) and SPSS (8.0 Pearson and Spearman correlation, Paired samples t-test, Wilcoxon-test, one-way ANOVA, Repeated Measures Anova) software were used in the data analyses.

## **4 Results**

### **4.1 Needle longevity along the transects**

Needle longevity in the mid-crown branches of adult Scots pines decreased as the different pollution sources were approached (I,II,III). Reduction of 40%, 15% and 15% were observed near Monchegorsk, Kostomuksha and Oulu, respectively (I). This was the only shoot characteristic that had a clear trend in each crown position when an urban source was approached (III). Needle longevity in the most slightly polluted stands also decreased considerably towards the south with the increasing thermal sum of the growing season (I, Figures 1 and 2a, Table 1).

### **4.2 Features of mean needle longevity**

Compared to median and maximum needle ages, mean longevity values had the lowest variation (I). Among all the shoot parameters studied (Table 3), needle longevity had the lowest variation in the middle crown (IV). Also, the fluctuations in needle longevity were small compared to the structural shoot parameters (IV).

### **4.3 Gradation of needle shedding**

Sample shoots usually had 2-3 annual shoots with 10-90% needle survival. The first half of the gradual shedding (the span from 90 to 50% needle survival) had relatively larger variation than the total gradual shedding but was strongly positively correlated with it. It was noted that the length of the first half of the gradual shedding did not correlate with median needle age, but the variation increased near the smelters (I).

#### **4.4 Changes in the shoot characteristics within the crown**

Leaf mass per area (LMA) and annual needle mass increased towards the upper crown (III). Needle longevity decreased upwards in the crown and the needle nitrogen concentration showed no differences between the crown positions (III). In the models describing the variation in needle longevity, annual needle mass and LMA most of the explanatory variables interacted with crown position (III). In the model of needle longevity these interacting variables were annual needle mass and needle mass packing, in the model of annual needle mass these were LMA, needle nitrogen concentration and basal area and in the model of LMA needle nitrogen concentration and basal area.

#### **4.5 Needle longevity and the other shoot characteristics**

Near the smelters, needle longevity decreased with the increasing needle concentrations of some of the main elements that were present in airborne particle emissions: Fe near Kostomuksha, and Fe, Ni and Cu near Monchegorsk (II). A significant decrease in needle longevity related to the increasing annual needle mass was found in the urban forests (II) especially in the lower crown (III), but the correlation coefficients were small (II). A little bit stronger correlation was detected for all samplings (IV). Needle longevity decreased with the increasing P and N concentrations of the youngest needles along the two transects showing increasing needle N concentrations towards the city centre (II, III). The increased needle nutrient concentrations and annual needle biomass were quite equally related to the decreased needle longevity (II). Decreasing needle longevity near Oulu was also related to the increasing needle mass packing in upper and middle crown and decreasing needle area packing throughout the crown (III).

In the urban forests near Oulu, the needle wintertime Mg, P and K concentrations linearly decreased with the decreasing survival from the second to the fourth age class when the mean wintertime needle longevity was 2.4-3.9 years (II). The concentrations stayed over 80% of the average still in the fourth needle age class, although needle survival dropped below 50%. Shoot needle mass or the total amounts of nutrients in all the successive age classes did not show any correlation with needle longevity (II).

Needle Mn concentrations decreased with the decreasing distance to all pollution sources. Needle Mn concentrations increased with needle age, and the range of needle Mn concentrations along the transects climaxed in the oldest age classes (II).

## **5 Discussion**

### **5.1 Decreased needle longevity**

#### ***5.1.1 The degree of reductions***

The reductions in needle longevity from 15 to 40% observed (I) along the transects of the present studies were of about the same magnitude as those found by Gluch (1988) in strongly and very strongly polluted areas compared to the slightly polluted areas in East Germany. Near Monchegorsk, where the reductions were the highest, similar results have been obtained by Jalkanen (1996) using the needle trace method, and by Yarmishko (1993) analysing the biomass of 35-40 years old Scots pines. The number of the lost needle age classes was the highest near Monchegorsk as a result of both the highest relative losses of needle biomass and an increase in the number of needle age classes towards the north.

#### ***5.1.2 Near the two smelters***

The decrease in needle longevity near the smelters in Monchegorsk and Kostomuksha was closely related with an increase in needle concentrations that describe the high pollution load around these areas (II). An increase in needle Ni, Cu and S and a decrease in Mn and Zn concentrations have been found to be related to the decrease in the number of needle age classes and the increase in needle tip necrosis near Monchegorsk (Rautio *et al.* 1998a). Kukkola *et al.* (1997) have detected visible and ultrastructural changes in the same area (up to 40 km SSW of the smelter in Monchegorsk) where the greatest reductions in needle longevity were observed in the present studies (I). Near Kostomuksha the frequency of cytological injury in Scots pine needles of the two youngest age classes and crown defoliation estimates were the highest in the nearest



stand to the smelter (Poikolainen & Fedorets 1997). Poikolainen & Fedorets (1997) have connected the increase in defoliation of Scots pine to the increased iron and sulphur deposition near Kostomuksha.

### 5.1.3 *In urban forests*

Needle nutrient concentrations and annual shoot needle mass in the urban forests near Oulu were not as closely correlated with needle longevity as were the needle heavy metal concentrations near the smelters (II). This could be a consequence of smaller differences in needle longevity in less polluted urban forests. According to the model of needle longevity (III) needle nitrogen concentration had the strongest (negative) effect on needle longevity and most of the other explanatory variables reflected the changes in shoot structure and interacted with crown position. In dry pine forests, the supply of N is usually suboptimal (Mälkönen *et al.* 1990) and branch biomass increases with N additions (Valinger 1993).

The negative relation of needle longevity to the size of annual shoots (II, III) may have been caused by self-shading which has been suggested to serve as a trigger to needle senescence and abscission (Schoettle & Smith 1991, Schoettle & Fahey 1994, Ackerly 1999). One possible mechanism leading to the increased self-shading could be an increase in annual needle mass caused by a higher photosynthetic rate due to the increased needle N concentration (Field & Mooney 1986, Schoettle & Smith 1999). However, clear associations between needle nitrogen concentrations and photosynthetic rate have not been shown in Scots pine (Vapaavuori *et al.* 1995, Laitinen *et al.* 2000). Our results were consistent with the conceptual model of the environmental and physiological controls of shoot growth and needle longevity introduced by Schoettle & Fahey (1994). According to the model, needle longevity is a consequence of resource availability, crown position, annual shoot increment, and needle physiology. In the urban forests the balance between biomass production and needle longevity was changed probably due to the increased nitrogen availability.

According to Rennenberg & Gessler (1999), high nitrogen deposition could serve as an important nitrogen source. Further, Shaver (1981) and Balster & Marshall (2000) have recorded the shortening of leaf longevity as a consequence of fertilisation. Our results imply, that the heavy nitrogen deposition most likely has significant consequences for the pine shoot needle longevity and structural characteristics, which are connected to shoot function.

Shoot needle mass or the total amounts of nutrients in all the successive needle age classes did not show any correlation with needle longevity (II, IV). Similarly, studying *P. contorta* ssp. *latifolia* at two elevations Schoettle (1990) did not find any difference in shoot foliar biomass or foliated length despite the significantly lesser annual growth and greater needle longevity at the higher elevation. Further, Balster & Marshall (2000) who studied *Pseudotsuga mezesii* var. *clauca* (Beissn.) and *Abies grandis* (Lindl.) showed that needle longevity of fertilised trees decreased but foliated branch length remained unchanged.

## 5.2 The feasibility of mean needle longevity

It has been shown in these studies that needle longevity values obtained sampling a small number of shoots (3-12) from a relatively small number of trees per stand (5-10) clearly detect differences even along relatively weak pollution gradients (I, II, III). Mean longevity values has been considered objective and reliable in describing the vitality of Scots pine in other small-scale studies as well (Fraude 1988, Gluch 1988, Jalkanen & Kurkela 1990). Calculated as the sum of the survival proportions, needle longevity values describe the possible changes in the needle survival of all the age classes, and sometimes even changes in needle biomass.

Other age parameters are often time-spans to single points or values impaired by the highest amount of variation at a mean survival of 50% in a certain needle age class. The variation in the mean needle longevity is small compared to the other age parameters (I) and other shoot characteristics (IV). This feature improves the feasibility of the mean needle longevity as a tool in ecological monitoring and in studies where the leaf life-span of different groups are compared.

## 5.3 The first half of the shedding span

During the gradual shedding process, the senescent needles from one or several needle age classes are mainly shed during the autumnal needle fall. The number of the youngest needle age classes that have lost a considerable proportion (>10%) of needle mass is reflected in the values of the first half of shedding span. Because the latter half of shedding span was relatively constant, the variability and changes in the needle age distribution were expressed in the duration of the first half (I). The shoot may not benefit from the needles retained in the old and sparse cohorts (Kikuzawa & Kudo 1995). The wide range, variability, and strong correlation with the total gradual shedding indicate the high sensitivity of the first half to reflect the changes in the needle age structure. The variation of the first half increased with the median needle age near the smelters in the areas with still a high incidence of acute needle injuries (I). This may be an indication of the acute effects of pollutants on the elongating needles (Shaw *et al.* 1993). Also, long-term stress shortens mean longevity.

## 5.4 The trends within the crown

Significant trends within the crown in needle longevity, annual needle mass and LMA were detected studying the values for the lower, middle and upper crown (III). These crown thirds of the dominant trees, forming a closed canopy, represent a gradient of penetrating light (Beadle *et al.* 1985, Schoettle & Smith 1991). LMA, increasing towards the upper crown (III), may be the trait that is the most clearly related to the increasing

irradiance as has been shown in Scots pine (Kellomäki & Oker-Blom 1981) and in other conifers (Del Rio & Berg 1979, Niinemets 1997). The increase in annual needle mass (III) was most probably related to an increase in the average irradiance also described earlier in pine canopies (Schoettle & Smith 1991). The significant interaction with crown position of most of the explanatory variables in the models of needle longevity, annual needle mass and LMA (III) reflects the plasticity of shoot structure within the canopy and the impact of the gradient of irradiation on pine shoot structural acclimation.

## 5.5 Needle survival and nutrients

The high concentrations of mobile nutrients (Mg, P, K) in the first age class needles (II) is explained by their high physiological activity (Wang *et al.* 1995). These concentrations decreased linearly with the decreasing needle survival from the second to the fourth age class (II). The daily integral of photosynthetically active radiation (PAR) also decreases linearly from the terminal parts of the shoot towards the oldest needles on the same shoot axis in *Pinus contorta* Dougl. ssp. *latifolia* (Engelm.) (Schoettle & Smith 1991). A positive relation between the daily PAR and the needle mobile nutrient concentrations along the shoot seems likely.

## 5.6 Adjusted needle longevity

Phenotypic plasticity was perceptible in the structural characteristics of both needles and shoots (III, IV). In the shoots of the middle crown, plasticity showed mainly as a high variation in annual needle and shoot stem biomass, while needle longevity remained quite stable (IV). Low variation in needle longevity compared to the other shoot characteristics (IV) has also been shown for other conifer species (Schoettle & Smith 1991, Balster & Marshall 2000). Longevity of evergreen leaves has been shown to increase with the decreasing length of the growing season (Kudo 1992), decreasing effective temperature sum (Jalkanen *et al.* 1995), increasing altitude (Ewers & Schmid 1981, Schoettle 1990) and increasing nutrient availability (Shaver 1981, Ackerly & Bazzaz 1995, Balster & Marshall 2000). The relatively low photosynthetic efficiency of conifer needles has to be compensated by a long life-span (Reich *et al.* 1992, Kikuzawa & Kudo 1995). As Troeng & Linder (1982) have shown, a major part of the carbon assimilated by current needles is spent to pay the construction costs of the current shoot. These costs should be in proportion to the benefits in a given climate and light environment, and needle longevity should be adjusted by the mechanisms of adaptation and acclimation to a given length of the growing season and for maximising carbon gain per time (Chabot & Hicks, Williams *et al.* 1989, Kikuzawa & Kudo 1995).

## 5.7 Needle Mn concentrations

The clear trends in the needle Mn concentrations (II) are most probably a result of leaching. Mn in the soil as a hydrated ion has a relatively low binding strength (Schnitzer 1980) and it is released quickly during litter decomposition (StAAF & Berg 1982). Increased deposition of SO<sub>4</sub> and NO<sub>3</sub> close to the pollution sources may have affected elements like Mn, as noted by Norton (1977). The passive uptake of Mn (Romero 1997), following the concentrations in the soil (Gärtner 1985, DeVisser 1992), led to lower concentrations and especially to lower Mn accumulation in the older needles in the stands near the sources (II).

Mn is the cation the most easily leached from the foliage (Helmisaari & Mälkönen 1989). A clear increase in the needle Mn concentration was detected already in the first age class (II). Therefore, the increased foliage leaching may not have been the primary cause for the differences between the stands.

Natural Mn accumulation was diminished due to the decreased accumulation and needle longevity (II). Also, leaching of Mn from the soil could have increased and a negative Mn budget developed. However, the total amounts of Mg, P or K in the needles did not change with needle longevity, implying that the decreased needle longevity may not significantly affect stand Mg, P or K cycling.

## 6 Conclusions

Clear decreasing trends in needle longevity of Scots pine were observed when the two smelters and one urban pollution source were approached. Mean longevity decreased 15 and 40% near the smelters and 15% near the city. The trend towards the city was evident in all the crown positions.

Mean longevity (the sum of leaf proportions of annual shoots) is preferred to maximum or median ages in the studies where the leaf life-spans, especially that of evergreen plants in seasonal climates, are ranked or compared. Mean longevity is based on the total leaf biomass and it had the lowest variation among the age parameters studied. It was also the shoot characteristic with the lowest variation within and between the trees and the lowest seasonal and annual fluctuation.

The first half of the shedding span shows the time span from 90% to 50% needle proportion in an annual shoot. It proved to be a valid indicator of those changes in the needle age structure that were not detected by means of mean longevity.

In the urban forests, needle Mg, P and K concentrations were shown to linearly decrease with the decreasing needle survival from the second to the fourth needle age class. Wintertime needle longevity varied from 2.4 to 3.9, and needle survival had dropped below 50% in the fourth needle age class, but the concentrations of these mobile nutrients still stayed above 80% of the average.

Near Monchegorsk, needle longevity decreased with the increasing Fe, Ni and Cu, and near Kostomuksha, with the increasing Fe concentrations. These elements were the main constituents of the airborne particle emissions. Near Oulu, the decrease in needle longevity towards the city was related to an increase in the needle N and P concentrations of the two youngest needle age classes. Needle longevity also decreased with the increasing annual needle mass (in lower crown) and needle mass packing (in upper and middle crown) and decreasing needle area packing.

A decrease in the needle Mn concentration towards the pollution source was detected along all the transects studied. Mn accumulated in the needles during needle ageing. Therefore, the ranges in needle Mn concentrations along the transects were the highest in the oldest needles. Leaching, especially from soil, as a cause for the decrease was discussed.

Leaf mass per area (LMA) and annual needle mass increased and needle longevity decreased upwards in the crowns of mature trees. These changes were most likely related to the higher irradiance and more intensive production of annual shoot biomass in the upper parts of the crown. Needle nitrogen concentration showed no differences between the crown positions.

Plasticity in needle longevity was low compared to that in the other shoot characteristics. Low plasticity could be a consequence of needle longevity adjusted to a given length of the growing season, to other environmental conditions, and for maximising carbon gain per time.

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