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SEASONAL CHANGES IN FOLIAGE BIOMASS AND AGE COMPOSITION OF LIVE AND FALLING NEEDLES IN SCOTS PINE SAPLINGS TREATED WITH SULPHURIC ACID, UREA, OR LIME

ABSTRACT: Using destructive sampling, seasonal dynamics of needle biomass and age composition of foliage and needle fall were studied in a Scots pine forest under conditions of various chemical soil treatments. Foliage mass was primarily affected by needle age and season, while treatment effect was relatively minor. Overall mean foliage mass per tree increased from 734 g in April to 870 g in August, and then decreased to 595 g in November. In general, proportion of current needles to the foliage grew from zero in April to more than 50% in late November. Proportion of one-year-old (c+1) needles decreased relatively slightly (from 55 to 41%), while that of two-year-old ($\geq c+2$) needles declined from 45% in spring to less than 6% of the total foliage in autumn. Significant treatment effects comprised reduced total mass of needles, particularly current ones (Acid), increased mass of $\geq c+2$ needles (Lime), and a clear dominance (absolute and relative) of c+1 over $\geq c+2$ needles (Urea), when compare with the untreated stand (Control). Within- and between-treatment variations were generally lower in the case of relative proportions than absolute values of cohort biomass. In most plots, more than half of needles shed over the entire study period were $\geq c+2$, while current needles contributed about

10% to the needle fall. In contrast to other plots, composition of needle fall at the Urea treatment was shifted toward a greater contribution of younger needles.

KEY WORDS: soil treatment, foliage biomass dynamics, needle proportions, needle losses

1. INTRODUCTION

As majority of evergreen coniferous tree species, Scots pine (*Pinus sylvestris* L.) retains more than one generation of needles at the same time. Depending on genetic and environmental factors, pine needles may live for two up to ten or more years (Evers and Schmid 1981). Extended leaf life span is usually considered as an adaptation to high stress environments (Grime 1977, Evers and Schmid 1981, Chabot and Hicks 1982, Aerts 1995), although it can be environmentally controlled (Aerts 1989, Reich *et al.* 1996). Species with long-lived leaves typically support a greater mass of foliage by

overlapping leaf cohorts (Gower *et al.* 1993, Aerts 1995). Prolonged leaf longevity is believed to increase retention time of nutrients and nutrient use efficiency (Chapin 1980, Chabot and Hicks 1982, Escudero *et al.* 1992).

Foliage biomass in evergreen conifers changes seasonally, primarily as a result of two processes: production and abscission of needles. Both can be modified by external factors, such as inadvertent or experimental addition of chemical substances to an ecosystem. Recently, much attention has been paid to adverse effects of sulphur or nitrogen compounds (e.g. Hällgren and Näsholm 1988, Oren *et al.* 1988a, b, Reich *et al.* 1992, Ling 1995), as well as to soil liming, which is a common mitigation tool in declining forest stands, as it usually affects positively longevity and vitality of conifer needles (e.g. Huetll 1989, Katzensteiner *et al.* 1992).

It has been hypothesised that Scots pine trees would adjust not only foliage mass, but also proportions of particular needle cohorts in response to altered soil conditions. The response was examined in a Scots pine stand

treated experimentally with sulphuric acid, urea-nitrogen, or lime.

Because dry matter and content of nutrients may decline in conifers, by as much as half, for each older class of needles (van den Driessche 1984), it is essential to consider foliage of different age separately. This is important for proper assessment of elemental pools and fluxes, for instance element storage in foliage or nutrient resorption from senescing needles (van den Driessche 1984, Flower-Ellis and Yang Mao-Sheng 1987).

The objective of this work was to estimate the effects of needle age, season, and different soil treatments on biomass and proportions of needle cohorts to total foliage and needle fall in a Scots pine sapling stand. Seasonal changes in mass relations of needle cohorts are to be used as a calculation tool in further studies on element cycling within the chemically treated pine stands.

2. STUDY SITE

The studies were conducted in a man-planted Scots pine sapling stand in north-west Poland (53°55' N, 17°10' E) (Fig. 1). The study region is situated in temperate climatic zone. Annual mean air temperature is 6.3°C and precipitation sum is 640 mm. Soils are podsollic and brown podsollic formed on loose sands of fluvio-glacial origin. Most of the sites are covered with fresh pine forests classified as *Leucobryo-Pinetum* (Szujecki *et al.* 1983).

The experimental stand was established in 1986 in order to study effects of various chemical soil treatments (Tarabuła-Szmyga 1992). Within the existing treatments, four smaller subplots

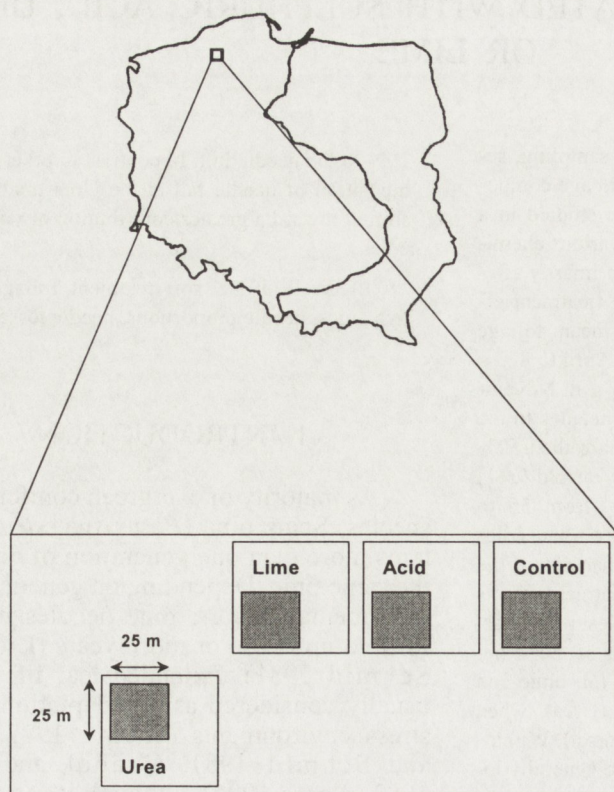


Fig. 1. Locality of the study site and arrangement of treatment plots

were delimited, each of 25×25 m, for the present study (Fig. 1). These included an untreated plot (Control), a plot treated with pure sulphuric acid diluted with well water to 2% solution (Acid), urea-treated plot (Urea), and a plot treated with Supromag II, i.e. burned magnesium lime enriched with copper (Lime). Urea and lime applied to the soil were commercial fertilisers commonly used in agricultural practice. The soil was first treated in 1986, when the stand was 10-year old. Acid addition continued over 1987 and 1988. In 1991, all the substances were applied again, but the application rates were much higher. Timing and yearly application rates recalculated for pure elements were following:

(1) Control – no treatment,

(2) Acid – about 100 kg of pure S per hectare per year in 1986–1988, and about 400 kg S ha⁻¹ in 1991. Each year the soil was sprinkled with the acid solution on 4 occasions during the growing season,

(3) Urea – 120 kg and 480 kg N ha⁻¹ yr⁻¹, in 1986 and 1991, respectively. The granulated fertiliser was sowed over the plot on 4 occasions during the two growing seasons,

(4) Lime – 1000 kg Ca, 400 kg Mg ha⁻¹ in 1986, and 5000 kg Ca, 2000 kg Mg, and almost 500 kg Cu ha⁻¹ in 1991. The fertiliser was sowed over the plot once a year.

Materials for the present studies were collected three years after last application of the chemical substances, i.e. in 1994, when the stand was at canopy closure. Because the area was plain and the experimental stand was initially fairly homogenous, no replications were made of the treatments, and particular plots selected in this study were treated as separate stands. The untreated plot (Control) served as a reference area.

3. MATERIAL AND METHODS

The material consisted of live pine needles. Sampling was made three times during the growing season of 1994: on 10th April – before expansion of current needles, on 11th August – after completion of current needles' growth, and on 25th November – after cessation of massive needle fall.

Branches with live needles were taken from ten so-called average trees per plot. The term "average tree" means the tree having diameter and height equal to the mean values

estimated for particular plots (Tarabuła and Żero 1997). Three sample branches per tree were cut off. Each branch represented different crown position: upper, middle and lower, and was further cut into particular age classes: current (c), one-year-old (c+1), two-year-old (c+2) and three-year-old (c+3). The branches with attached needles were labelled and transported to the lab, then dried at room temperature until the needles could be easily separated from the branches. The needle samples were oven-dried at 65°C over 24 hours and weighed.

At the first step, needle biomass data derived from sample branches were recalculated per crown zone basis, taking into account the total number of branches in successive whorls of a given zone (Tarabuła and Żero 1997). However, as the top whorls did not carry older needle generations, needle biomass of the upper crown positions was estimated taking into account the number of branches in each whorl, separately. Thereafter, the biomass values were summed for each tree, by needle age, treatment and sampling date. Because proportions of the oldest needles were very small (about 1% of total foliage), c+3 and c+2 needles were pooled into one class ($\geq c+2$). During preliminary exploration of the data, evident "outliers" (one tree per plot) were excluded from the data set. In this way, 9 trees per plot were left for further calculations.

Prior to statistical analyses, all the data were corrected for stocking differences to eliminate the density effect (Czarnowski 1989). Because the differences in tree densities between particular treatments and the Control were not high (CV = 19%) and reflected exactly those in mean foliage mass per tree (Tarabuła and Żero 1997), stem density at the Control plot was taken as a base of the calculations. Needle mass estimated for individual trees in particular plots were thus corrected by the factor of D_T/D_C , where D_T denotes tree density in a given plot, and D_C is tree density at the Control plot. The data obtained in this way relate to needle biomass of individual trees, as if they have been growing in stands of density equal to 6650 stems per hectare. Additionally, it has been assumed that biomass of current needles at the beginning of August represents yearly needle production.

Three-way analysis of variance was employed to examine the effects of sampling date, needle age and soil treatment on the to-

tal biomass of needles per tree. Prior to the analysis, the data were log-transformed using formula $\ln(y+1)$ to make the variances independent of the means. The data were back-transformed for presentation.

Sampling dates were compared among each other using paired t-test, needle age classes – using simple t-test, whereas the treatment effect was studied with use of two-sided Dunnett's test, where the untreated plot served as a reference. When necessary, log-transformation of data was applied prior to the detailed analyses. The statistical procedures were performed with the General Linear Model (GLM) (SPSS 8.0 for Windows).

4. RESULTS

Needle biomass was significantly influenced by age of the needles, season and treatment. The effect of needle age was modified by season and by soil treatment, whereas no statistically significant interaction was found between the two latter variables. The third order interaction was not statistically significant, either. The greatest significant effect, expressed by the highest values of F-ratio and eta-squared characteristics, was found for the season \times age interaction, whereas the smallest significant effect comprised the influence of soil treatments (Table 1).

The overall pattern of foliage dynamics was following. Total foliage biomass in-

creased from 734 g tree⁻¹ in April to 870 g tree⁻¹ in August (18% increase). The positive net change resulted from approximately 56% dominance of needle production over needle losses in that period. Later in the season, foliage biomass significantly decreased reaching, on the average, 595 g tree⁻¹ in November. It is by 32% less than summer foliage maximum (Aug), and by 19% less than spring minimum (Apr) (Table 2). The substantially greater foliage biomass found in April than in November reflects most likely an effect of the very hot and dry summer 1994.

The interaction age \times season from Table 1 represents different patterns of seasonal biomass dynamics for particular needle generations. Mass of current needles grew substantially till August, and then it decreased slightly, yet significantly. Biomass of older needles decreased continuously and significantly throughout the growing season (Table 2). When expressed in relative terms, current needles increased their contribution from zero (Apr) to 53% (Nov), while older needles decreased it from spring to autumn – from 55 to 41% (c+1) and from 45 to 6% (\geq c+2) (Fig. 2).

None of the treatments influenced the general trend of seasonal dynamics of foliage mass (insignificant interaction of treatment \times season from Table 1). However, treatment effect was noticeable in the case of total foliage and mass of particular needle generations. Total foliage mass was affected by acid treatment only. Despite correction for tree densities, it was, on the average, by 31% lower than found for the reference stand. Tree foliage in the other treatments differed insignificantly from the Control (Table 3).

A detailed analysis of the treatment effect showed that acid addition led primarily to a significant reduction of current needle biomass. Although older needle generations at this plot had also smaller biomass, this was statistically confirmed for April sampling only (Table 3). The trees fertilised with nitrogen compounds tended to have a greater mass of c and c+1 needles, and smaller mass of needles \geq c+2, when compare with the untreated saplings. The differences between the two plots were statistically confirmed in a few cases (Table 3). When compare with the Control plot, trees growing on the limed soil tended to have greater biomass of \geq c+2 needles on every sampling occasion. However, significance of the differences was proved only for November sampling (Table 3).

Table 1. Summary 3-way ANOVA for needle biomass by season, needle age-class and treatment showing degrees of freedom (df), variance ratios (F), significance levels (*P*) and effect size statistics (eta-squared). The analysis was performed after correction for tree density effect on biomass and $\ln(y+1)$ transformation of the data set

Source of variation	df	F	<i>P</i>	Eta-squared
Season	2	256.9	0.000	0.641
Needle age	2	369.2	0.000	0.719
Treatment	3	14.4	0.000	0.130
Season \times Age	4	734.8	0.000	0.911
Treatment \times Age	6	14.6	0.000	0.233
Treatment \times Season	6	0.4	0.853	0.009
Season \times Age \times Treatment	12	0.8	0.616	0.034

Table 2. General pattern of foliage mass dynamics (in g tree⁻¹). The values are grand means \pm SD ($n = 36$). Prior to the analysis, the data for particular plots were corrected for tree density effect (see text). Different letters denote significant differences among sampling dates ($P < 0.05$) according to paired t-test

Sampling date	Needle generation ¹			Total
	c	c+1	$\geq c+2$	
April		405 \pm 159 a	329 \pm 184 a	734 \pm 283 a
August	379 \pm 169 a	361 \pm 122 b	130 \pm 78 b	870 \pm 276 b
November	316 \pm 206 b	245 \pm 104 c	34 \pm 27 c	595 \pm 199 c

¹c – current, c+1 – one-year-old, $\geq c+2$ – two-year-old and older.

Table 3. The effect of treatment on mean biomass of needles (\pm SD) of different age classes (in g tree⁻¹) ($n = 9$ trees per plot). Prior to the analysis, the values were corrected for tree density effect (see: Methods). Values typed in bold are significantly different from the Control at $P < 0.05$ according to two-sided Dunnett's test

Season	Treatment	Needle generation ¹			Total
		current	c+1	$\geq c+2$	
Apr	Control	0	435 \pm 181	402 \pm 179	837 \pm 342
	Acid	0	277 \pm 51	256 \pm 107	533 \pm 129
	Urea	0	474 \pm 169	173 \pm 106	647 \pm 217
	Lime	0	434 \pm 144	487 \pm 160	921 \pm 251
Aug	Control	418 \pm 146	348 \pm 80	148 \pm 70	915 \pm 196
	Acid	261 \pm 77	263 \pm 80	122 \pm 72	646 \pm 156
	Urea	463 \pm 226	456 \pm 98	69 \pm 51	988 \pm 304
	Lime	374 \pm 148	376 \pm 144	181 \pm 81	930 \pm 314
Nov	Control	355 \pm 129	207 \pm 91	29 \pm 18	592 \pm 192
	Acid	223 \pm 95	197 \pm 80	26 \pm 19	445 \pm 142
	Urea	391 \pm 154	341 \pm 99	22 \pm 26	754 \pm 215
	Lime	296 \pm 62	236 \pm 89	58 \pm 30	590 \pm 128

¹ See Table 2.

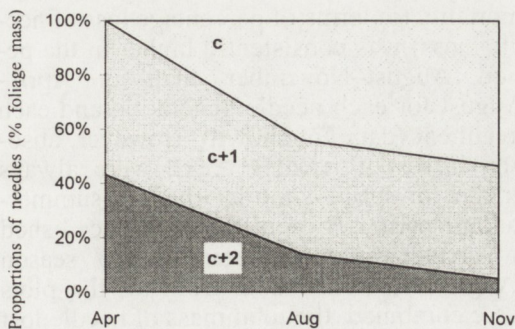


Fig. 2. Seasonal changes in contribution of needle cohorts to the pine foliage (c – current, c+1 – one-year-old, c+2 – two-year-old needles)

When percentage proportions were used instead of absolute values, a different picture emerged. First of all, within- and between-

treatment variation was generally lower than found previously for absolute biomass values, at least for younger needle generations (cf. Table 3 and 4). It turned out that the treatment effect was negligible in the case of soil acidification and liming. Regardless of sampling date, proportions of needle age-classes to the total tree foliage in both plots resembled those of the untreated plot (Table 4). In general, proportions of young and old needles outside the growing season were almost equal. Before expansion of current needles, total foliage biomass was partitioned by halves between c+1 and $\geq c+2$ needles, and after the peak of autumnal litter fall – between c and $\geq c+1$ needles (Table 4). In mid-summer (August), at the actual foliage maximum, average proportions of current and c+1 needles were almost equal (about 40%) and significantly greater than the oldest needle

Table 4. Mean percentage proportions (\pm SD) of particular needle age classes to total foliage of sample trees ($n = 9$ trees per plot). Values typed in bold are significantly different from the Control at $p < 0.05$ according to two-sided Dunnett's test

Season	Treatment	Needle generation ¹		
		current	c+1	$\geq c+2$
Apr	Control		52.0 \pm 6.9	48.0 \pm 6.9
	Acid		52.0 \pm 11.4	48.0 \pm 11.4
	Urea		73.3 \pm 13.2	26.7 \pm 13.2
	Lime		47.1 \pm 10.4	52.9 \pm 10.4
Aug	Control	45.7 \pm 8.6	38.0 \pm 1.9	16.3 \pm 8.5
	Acid	40.4 \pm 7.4	40.7 \pm 5.0	18.9 \pm 9.4
	Urea	46.8 \pm 9.5	46.2 \pm 6.9	7.0 \pm 6.1
	Lime	40.2 \pm 8.0	40.4 \pm 4.4	19.4 \pm 9.0
Nov	Control	59.9 \pm 12.0	35.0 \pm 11.1	5.1 \pm 3.4
	Acid	50.1 \pm 8.8	44.3 \pm 11.2	5.6 \pm 7.6
	Urea	51.9 \pm 9.5	45.2 \pm 6.3	2.9 \pm 5.0
	Lime	50.2 \pm 9.3	40.0 \pm 9.3	9.8 \pm 6.2

¹ See Table 2.

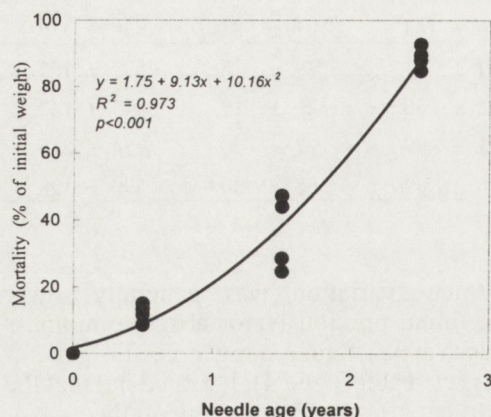


Fig. 3. The influence of needle age on percentage losses of needle mass from sample branches

fraction (about 20%). By contrast to the three plots, proportions of c+1 needles in the nitrogen-fertilised trees were substantially greater, and those of $\geq c+2$ needles – much smaller than corresponding proportions at the Control, at least in April and August (Table 4). The dominance of c+1 over $\geq c+2$ needles can be expressed as mass ratios of (c+1)/($\geq c+2$). The ratios approximated 3, 7 and 16 in the Urea plot, and only 1, 2 and 7 in

the Control plot, for the three consecutive sampling dates, respectively.

On the basis of data from Table 3, a crude estimation of needle losses was made. Losses of needles relative to their initial mass, representing here needle mortality, increased curvilinearly with needle age, irrespective of treatment. This highly significant relationship was best described by a second-order polynomial, as shown in Fig. 3. Needle mortality (in terms of percentage loss of needle mass) was consistently higher in the period August–November than in April–August for each needle generation and each treatment (data not shown). However, absolute losses of needles $\geq c+2$ were always greater in spring-summer than in summer-autumn period. By contrast, needles c+1 shed in greater amounts later in the season (Aug–Nov). When data from all the plots were combined, the total mass of needle lost over the two analysed periods appeared to be fairly similar (Fig. 4). This shows that drought causes needle abscission to begin relatively early in the growing season. Needles $\geq c+2$ made up about 82% of the needle fall in April–August (assuming no losses of current needles in this period). Later in the season, the dominant fraction became c+1 needles (42%), needles $\geq c+2$ constituted

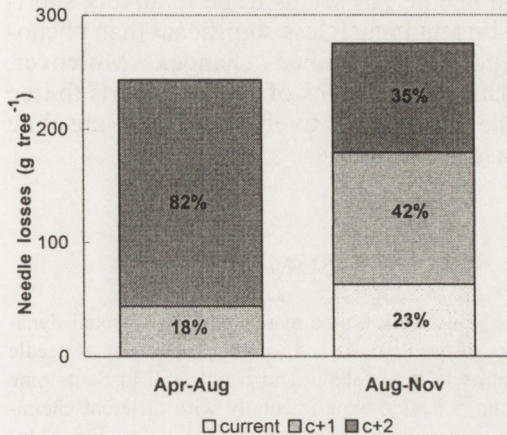


Fig. 4. Age composition of needle fall in two consecutive sampling periods (see Fig. 2 for symbol description)

slightly less (35%), while current needles – the least part of the needle fall (23%) (Fig. 4). Taking into account the entire study period, more than half of the total needle fall consisted of needles $\geq c+2$. The only exception was the urea-fertilised plot where the oldest class of needles made up relatively a minor fraction of the needle fall, because the needles were scarce already in April. Consequently, proportions of younger needle generations to the needle fall were greater here, when compared with the remaining plots (Table 5).

Table 5. Age composition of needle fall over the period Apr–Nov 1994, calculated from the data given in Table 3

Treatment	Needle generation ¹		
	current	c+1	$\geq c+2$
Control	9.6	34.3	56.1
Acid	10.8	23.0	66.3
Urea	20.1	37.4	42.5
Lime	11.0	28.1	60.9
Mean \pm SD	12.9 \pm 4.9	30.7 \pm 6.4	56.4 \pm 10.2

¹ See Table 2.

5. DISCUSSION

Foliage biomass in coniferous tree canopies, as shown in this work, changes seasonally as a result of two opposite processes: growth of current needles and fall of older

generations. Although the processes may coincide, the former one dominates in spring, while the latter one – in autumn. As an effect, net changes in foliage biomass tend to be positive earlier, and negative – later in the season. The changes in foliage mass are more evident in the case of particular needle generations, the youngest generation increasing its contribution, while the oldest one – decreasing it clearly from spring to autumn.

One of the main objectives of this work was to find to what extent needle mass relations could be affected by chemical soil treatments. When compared to such factors as season or needle age, the treatment effect was relatively minor, despite high application rates of the chemical substances. In the acid-treated plot, the effect consisted in reduction of foliage biomass, particularly that of current needles, which may suggest generally impoverished growth conditions and reduced ability of the trees to produce new biomass. Such phenomena have been widely described in the ecological literature and often attributed to base cation deficiency (Hauhs and Wright 1986, Oren *et al.* 1988a, Schultze 1989). In contrast, the oldest needles at the limed plot tended to have greater biomass than corresponding age-class at the control. This may reflect slightly prolonged leaf longevity. Such a response could be an effect of improved magnesium supply due to the fertiliser application. Improved vitality of older needles is fairly well documented in the literature from experimentally limed and Mg-fertilised forests (Huettl 1989, Bonneau *et al.* 1990/91). Despite the differences in absolute values of needle mass, differences in age composition of foliage between any of the two plots (Acid, Lime) and the Control were practically negligible.

The most striking treatment effect comprised a significant shift in dominance of needles c+1 over those $\geq c+2$ in the urea-treated plot, with no effect on current needles (i.e. needle production) or total foliage. Because the stands were at canopy closure, total foliage would be unlikely to show any positive response to fertilisation due to self-shading of needles. On the other hand, particular needle generations could probably do so. However, it would be possible only at the expense of other needle cohorts. Based on literature opinions, this could include enhanced production of new needles and/or shortened longevity of needles.

Enhanced biomass production following N addition to N-limited sites is presumably one of the best-documented phenomenon in the literature. The increase is generally proportional to the N concentration in the foliage (Hällgren and Näsholm 1988). On the other hand, increased tissue N concentration is known to decrease leaf life span (Reich *et al.* 1992). Discoloration and premature shedding of needles in stands with enhanced N loads have often been attributed to nutrient deficiencies and/or nutrient imbalances, especially to increased ratios between N and basic cations (Oren *et al.* 1988b, van Dijk and Roelofs 1988, Kölling *et al.* 1997). Other possibilities include a greater sensitivity of N-enriched plants to fungal pathogens (van Breemen and van Dijk 1988), insect attacks (Fox and Macauley 1977), and physical factors, such as frost, drought, wind, and snow (Linder *et al.* 1987, Hällgren and Näsholm 1988, Dueck *et al.* 1990/91).

Although needle production reported for the Urea plot did not differ significantly from that of control in the study year, it does not exclude increased production in previous seasons. This would be supported by a greater mass and proportion of c+1 needles when compare with the untreated trees. A similar conclusion can be drawn with regard to needle shedding. Although needles $\geq c+2$ had clearly smaller mass and proportion to the total foliage than observed in the Control, needle fall in the N-fertilised stand did not differ from that in the Control in the study year. However, it exhibited much year-to-year variability, increasing a year or two after N application and decreasing thereafter (Tarabula and Žero 1997). The above observations would suggest that response of the trees to N-fertilisation was short-lasting and confined to first two years following application of the fertiliser. According to some authors, the effect of N addition can last between 5 and 17 years (Kenk and Fischer 1988) or even longer (Miller and Miller 1988). Other experiments show typically only transitory response with a peak 2–4 years after fertiliser application followed by a growth decline to a level of unfertilised stands (Ballard 1984). The results of this work would rather support the latter opinion, at least for production and senescence of needles in trees exposed to enhanced N load.

To summarise, despite high application rates of the chemical substances, their modifying effect on age composition of foliage

and needle fall seems to be relatively short-lasting and much less significant than phenologically determined changes. Moreover, relative proportions of needle cohorts to tree foliage vary relatively less than absolute mass of the needles.

6. SUMMARY

This work aimed at recognising seasonal dynamics of needle mass and weight proportions of needle cohorts to total foliage and needle fall in Scots pine saplings treated experimentally with different chemical compounds (sulphuric acid, urea, lime+Mg) (Fig. 1). Destructive sampling was made on three dates (April, August, November 1994) representing different phenological phases. Three-factor analysis of variance revealed that the needle biomass was primarily affected by needle age and season, and much less by soil treatments (Table 1). Overall mean needle mass per tree grew from 734 g in April to 870 g in August and then declined reaching, on the average, 595 g in late November (Table 2). Contribution of current needles increased continuously from zero in April to more than 50% in November. Proportion of needles c+1 changed relatively little over the growing season (from 55 to 41 per cent), whereas that of $\geq c+2$ – declined significantly from 45% in April to 6% in November (Fig. 2). Although soil treatments did not affect the general trends in foliage dynamics, there were some differences in masses and proportions of needle cohorts to total foliage between particular treatments and the Control. Acid addition resulted in smaller total foliage and mass of current needles, whereas soil liming tended to increase mass of oldest needles (Table 3). However, the two treatments hardly modified age composition of the foliage (Table 4). Urea fertilisation led to a substantial shift in dominance of c+1 over $\geq c+2$ needles, when compare with the Control (Tables 3 and 4). This was attributed to stimulated needle production and premature shedding of older needles following N application. Lack of differences in needle production and fall between Urea and Control in the study year suggested only a short-lasting response.

Percentage losses of needle mass increased curvilinearly with the needle age, irrespective of the treatment (Fig. 3). Absolute losses of needles were comparable in the two analysed periods (Fig. 4), suggesting early start of needle abscission during drought. Needles $\geq c+2$ were major contributor of the needle fall earlier, while needles c+1 – later in the season (Fig. 4). In most plots, more than half of needles shed over the entire study period were $\geq c+2$, while current needles contributed about 10% to the needle fall. Composition of needle fall at the Urea was shifted toward a greater contribution of younger needles (Table 5).

In general, relative proportions of needle cohorts to tree foliage changed less than their absolute biomass in response to altered soil conditions in both within- and between-treatment comparisons.

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