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THE INFLUENCE OF CHEMICAL SOIL TREATMENT ON NUTRIENT ECONOMY OF SCOTS PINE (*PINUS SILVESTRIS* L.)

ABSTRACT: Study was made of the effect of supplying various elements (N, P, K, Ca, S) to soil on the rates of needle and litter production, translocation of elements and their return to litter in a pine sapling. Fertilization with N, P or K led to a significant increase in the needle production rate, with simultaneous preservation of the ratios among nutrient elements in the foliage. The applied treatments caused small changes in the element retranslocation efficiency, which led, however, to significant alternations of the chemical composition of needlefall.

KEY WORDS: nutrient economy, needle production, litterfall dynamics, uptake, retranslocation efficiency, element return.

1. INTRODUCTION

In studies of element cycling in forest ecosystems it is essential to gain close insight into tree strategy with respect to nutrient economy, i.e. into the processes of uptake, translocation and return of elements to the nutrient cycle. Whereas the second of these processes, i.e. element translocation has been well known for a long time (Olsen 1948, Tamm 1965, Duvigneaud and Denaeyer-De Smet 1970), it became of interest only in recent years. According to Switzer and Nelson (1972), internal translocation of elements within plants represents so-called biochemical cycle. Autumnal retranslocation, reabsorption or withdrawal consists in nutrient transfer from the older to the younger plant tissues for reuse during the next year. Thus, nutrient losses in litterfall are minimized (Stachurski and

Z i m k a 1975b, C h a p i n and K e d r o w s k i 1983). This is of special importance in the case of infertile soils because trees are less affected by availability of soil nutrients (M i l l e r et al. 1979, L i m and C o u s e n s 1986a, 1986b, M i l l e r 1986). Other studies have shown that the element retranslocation efficiency depends on the fertility of soils and type of tree species, and that – moreover – elements are withdrawn selectively (Z i m k a and S t a c h u r s k i 1976, S t a c h u r s k i and Z i m k a 1979, 1981). Oligotrophic species characteristic of nutrient-poor sites retranslocate nutrients at a high rate. It has been calculated that Scots pine withdraws large amounts of nutrients, reaching about 30% of carbon, 75% of nitrogen, 80% of phosphorus and as much as about 90% of potassium (S t a c h u r s k i and Z i m k a 1981). In consequence of this economical strategy, litter with greatly reduced nutrient contents is transferred to the ecosystemic cycle, this being decisive of slowing down of the processes of organic matter decomposition (S t a c h u r s k i and Z i m k a 1975a).

In the light of presented pattern of nutrient economy of trees it was expected that supplying soil with many mineral components may cause changes in the course of the processes decisive of the element cycling rate in young pine stands. The importance of this problem is substantiated by the hazard to forests from intensifying environmental pollution with mineral components, particularly with sulphur and nitrogen.

2. MATERIAL AND METHODS

The experimental plot is situated in the Człuchów Forest (Słupsk voivodeship) in NW Poland, in an 11 years old Scots pine sapling, in a fresh forest habitat. It comprises 12 treatment plots and one control plot, arranged as shown in Figure 1. In the experiment the following agents and doses (calculated per pure component) were applied: (1) N1 – ammonium nitrate (28% N) – ca. 80 kg N $\cdot$ ha^{-1} in 2 portions; (2) N2 – urea (46% N) – ca. 260 kg N $\cdot$ ha^{-1} in 4 portions; (3) N3 – urea (46% N) and sublimed sulphur (100% S) – ca. 260 kg N $\cdot$ ha^{-1} and 100 kg S $\cdot$ ha^{-1} in 4 portions; (4) P – powdered superphosphate (18% P_2O_5) – ca. 90 kg P $\cdot$ ha^{-1} in 2 portions; (5) K – potassium salt (57% KCl) – ca. 110 kg K $\cdot$ ha^{-1} in 2 portions; (6) Ca – magnesia lime (34% CaO, 16% MgO) – ca. 1500 kg CaO $\cdot$ ha^{-1} and ca. 700 kg MgO $\cdot$ ha^{-1} – in a single dose; (7) S1 – sublimed sulphur (100% S) – ca. 50 kg S $\cdot$ ha^{-1} in 4 portions; (8) S2 – sublimed sulphur (100% S) – ca. 100 kg S $\cdot$ ha^{-1} in 4 portions; (9) S3 – pure sulphuric acid (98% H_2SO_4) – 1% solution – ca. 160 kg H_2SO_4 $\cdot$ ha^{-1} in 4 portions; (10) S4 – pure sulphuric acid (98% H_2SO_4) – 2% solution – ca. 300 kg H_2SO_4 $\cdot$ ha^{-1} in 4 portions; (11) (Ca+S)1 – magnesia lime (34% CaO, 16% MgO) and sublimed sulphur (100% S) – ca. 1500 kg CaO $\cdot$ ha^{-1} and 700 kg MgO $\cdot$ ha^{-1} – in a single dose, and ca. 100 kg S $\cdot$ ha^{-1} in 4 portions; (12) (Ca+S)2 – magnesia lime (34% CaO, 16% MgO) and pure sulphuric acid (98% H_2SO_4) – 2%

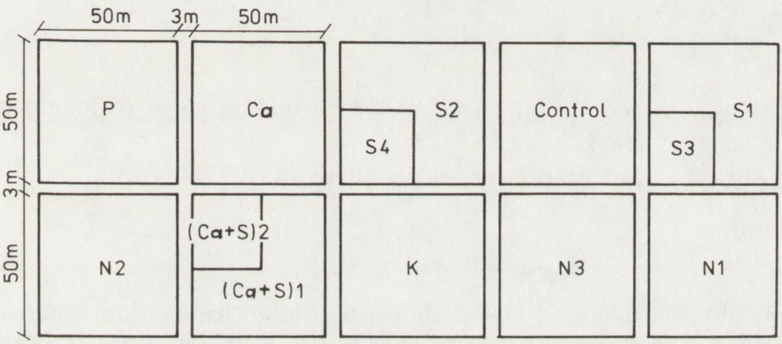

Fig. 1. Scheme of the experimental plot
See text for symbol description

solution – ca. 1500 kg $CaO \cdot ha^{-1}$ and 700 kg $MgO \cdot ha^{-1}$ -- in a single dose, and ca. 300 kg $H_2SO_4 \cdot ha^{-1}$ in 4 portions.

Fertilizer doses were chosen according to soil analyses and pine requirements of mineral components (Kucaba, personal communication). All substances were applied in 1986; soil acidification with sulphur as well as sulphuric acid was repeated in 1987, using identical doses as in 1986.

Samples of green needles were collected on 16 Oct. 1987 from 8 trees in each experimental plot (i.e. in total – from 104 trees), always from the third top whorl. Only 3-year-old needles (the 1985 class), i.e. those usually accounting for the major part of needlefall (according to Larsson and Tenow 1980, ca. 70%), were collected. For the determination of the annual needlefall (W_{fn}), each experimental plot was provided with 4 litter traps with a collection area of 0.5 m^2 from which the falling needles were taken (P. usinkiewicz et al. 1974). Needlefall was collected from the beginning of May 1987 until the end of April 1988 at ca. 3–4 week intervals; this to some extent eliminated the effect of precipitation on the contents of mineral components in needlefall.

Determinations of the length, weight and chemical composition were performed using green needles (*gn*) and needles fallen between 7 Oct. and 16 Oct. 1987 (*fn*); in this period no precipitation was recorded. For each experimental plot samples of 200 undamaged green needles and of 200 fallen needles were taken, dried for 24 h at 65°C, weighted and measured in length classes. Determination was made of:

1. mean weight of 1 needle ($\overline{w}$)

$\overline{w} = \frac{w_n}{n}$, where w_n – weight of sample, n – size of sample (n = 200);

2. mean length of 1 needle ($\bar{l}$)

$$\bar{l} = \frac{1}{n}\sum_{i=1}^{k} x'_i n_i,$$

where k – number of 0.5-cm length classes, x'_i – middle value of length class, n_i – frequency in length classes.

3. weight of 1 cm of needle (green or fallen) ($\overline{w}_{1cm}$)

$$\overline{w}_{1cm} = \frac{\overline{w}}{\bar{l}}$$

Subsequently, on the basis of the annual needlefall, estimation was made of the production assumed to be the weight of 3-year old needles by the end of the vegetation period, taking into consideration weight losses caused by element retranslocation (Stachurski and Zimka 1975b):

$$W_{gn} = W_{fn} \cdot r, \quad \text{where} \quad r = \frac{\overline{w}_{1cm\,gn}}{\overline{w}_{1cm\,fn}}$$

Chemical composition, length and weight of the needles *gn* and needles *fn* were determined for each of 13 experimental plots separately (i.e., in total 26 needle samples). Chemical analyses of total C and N were performed on a gas chromatograph CHN produced by Carlo Erba. After grinding and combustion of samples in a muffle furnace, K, Ca and Mg were determined with atomic absorption spectrophotometer (Varian Techtron). Phosphorus was determined using the vanadium – molybdate method, and sulphur – by nephelometric procedure, using in both cases a Specol spectrophotometer.

Two principal calculations involved comparison of the experimental plots by needlefall intensity and translocation efficiency of various elements. In the comparison of the needlefall rate in different treatments (calculated by simple regression), the t-test was used for comparing the regression coefficients. In the subsequent calculations of the percentile weight losses of falling needles in relation to 3-year old green needles, as well as of the percentile translocation of the investigated elements, use was made of the following general formula:

$$\%R = \frac{W_{gn} \cdot c_{gn} - W_{fn} \cdot c_{fn}}{W_{gn} \cdot c_{gn}} \cdot 100$$

where c_{gn} – concentration of element in green needles, c_{fn} – concentration of element in needlefall.

On the basis of the mean results obtained for all 13 treatments, a general pattern of translocation of mineral components in a young pine stand was proposed. Subsequently, different groups of treatments were compared by the retlanslocation efficiency of various elements. The following groups of treatments were singled out from among the total of 13 treatments: (1) N – plots treated with nitrogen compounds, i.e.

N1, N2 and N3; (2) P – plot fertilized with superphosphate; (3) K – plot fertilized with potassium salt; (4) S – plots acidified with sulphur (S1 and S2) and sulphuric acid (S3 and S4); (5) Ca – lime-treated plot; (6) Ca+S – plots with simultaneous acidification and liming, i.e. (Ca+S)1 and (Ca+S)2; (7) Control – untreated plot.

Treatments were combined on the grounds of application of similarly acting agents (e.g. sulphur and sulphuric acid; nitrogen compounds).

3. RESULTS

3.1. DYNAMICS OF NEEDLE AND LITTER PRODUCTION

It was found that needle abscission in pine stands is a continuous process proceeding with different intensity throughout the year. In autumn, on the turn of September and October, the needlefall rate increases exponentially and is, on the average, 6 times higher than in spring and summer. In this phase, ca. 50–70% of the annual needlefall weight reach the forest floor. After the abscission peak, i.e. in the second half of October, the needlefall rate abruptly drops to attain the level resembling that observed in spring and summer. Figure 2 presents the pattern of this process, exem-

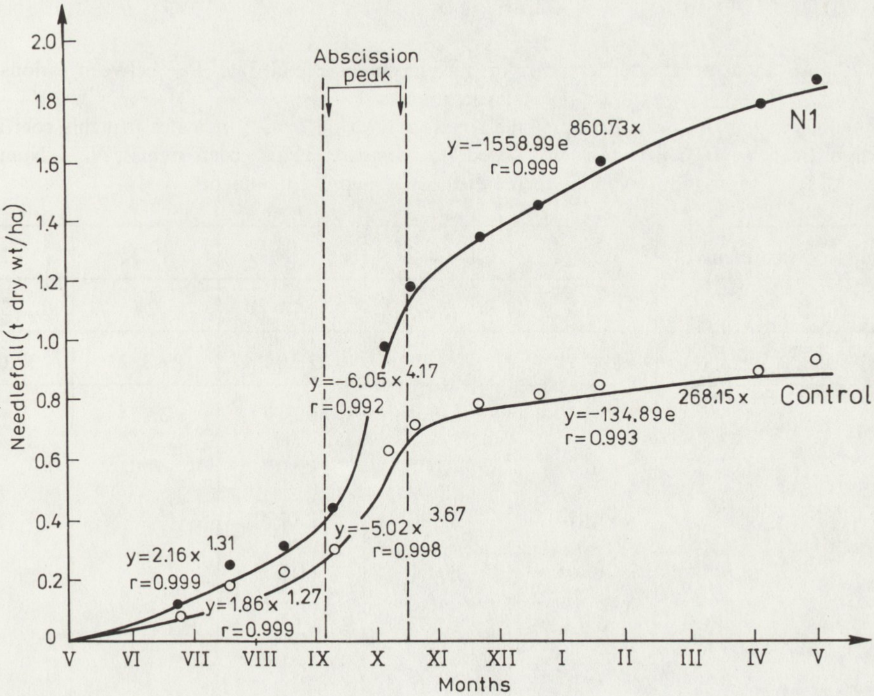

Fig. 2. Pattern of needlefall dynamics in young pine stand
N1 – plot fertilized with ammonium nitrate, control – untreated plot

plified by two treatments: ammonium nitrate fertilization and control. It is evident that fertilizing soil with nitrogen intensifies the needlefall process.

In detailed studies of the effect of soil treatment with chemical substances on the course of the abscission process, for simplification of the calculations we accepted as a criterion the mean weekly needlefall rate, to which the value of simple regression coefficient corresponds. This allowed for demonstrating that although chemical treatment did not influence the character of the process, it caused substantial changes in needlefall intensity. Three groups of significantly different treatments were singled out. The first, most numerous group comprised the following treatments: liming (Ca), liming with acidification (Ca+S), acidification with sulphur or sulphuric acid (S) and control; on the plots of this group the needlefall rate was lowest, amounting to ca. 20 kg · ha^{-1} · week^{-1}. The second group included two treatments: fertilization with phosphorus (P) and with potassium (K) where the needlefall rate was nearly 30 kg · ha^{-1} · week^{-1}. The third group comprised the nitrogen treatments (N) where the needlefall rate was highest, accounting to ca. 40 kg · ha^{-1} · week^{-1} (Table 1).

The increased needlefall rate on the plots fertilized with N, P or K led to a rise of the yearly needlefall values which amounted to 1.7 t · ha^{-1} in the group of nitrogen-treated plots and to 1.2 t · ha^{-1} in the group fertilized with P or K; this represented a ca. 79 and 30%, respectively, increase in this parameter, as compared with control (and with the remaining plots of this group) where the needlefall was ca. 0.9 t · ha^{-1} · yr^{-1} (Table 2).

Table 1. Significance of the differences in the mean needlefall rate (R_{fn}) between various groups of treatments

R_{fn} corresponds to the slope coefficient of the simple regression line; * indicates that this coefficient is highly signifficant (p<0.01); (t–test was used to compare slope coefficients), N_i – Number of observations in the different groups of treatments

Groups of treatments		Control	Ca, Ca + S	S	P, K	N
N_i		12	36	48	24	36
R_{fn} (kg · ha^{-1} · week^{-1})		20.451*	20.109*	22.504*	27.382*	37.031*
N	t	3.796	6.220	5.619	2.914	
	p	<0.01	<0.01	<0.01	<0.01	
P, K	t	2.074	3.128	2.027		
	p	<0.05	<0.01	<0.05		
S	t	0.672	1.203			
	p	>0.05	>0.05			
Ca, Ca + S	t	–0.123				
	p	>0.05				

Table 2. Annual production of needles (W_{gn}) and needle litter (W_{fn}) (in kg · ha^{-1} · yr^{-1}), and needle weight losses (%) in Scots pine growing under different conditions of soil treatment
The percentages of changes in the parameters relative to control are given in brackets. The sign + denotes a relative increase, and the sign – a relative drop in the values of the parameters

Groups of treatments	W_{gn}	W_{fn}	Needle weight losses (%)
Control	1226.64	936.20	23.7
Ca, Ca + S	1344.56 (+9.6)	915.87 (–2.2)	31.9 (+34.6)
S	1373.81 (+12.0)	1028.95 (+9.9)	25.1 (+5.9)
P, K	1524.64 (+24.3)	1213.26 (+29.6)	20.4 (–13.9)
N	2293.30 (+87.0)	1671.75 (+78.6)	27.1 (+14.3)

In the case of annual needle production, calculated on the basis of needlefall and supplemented by a correction for weight loss of needles due to retranslocation process, the situation was similar. Namely, the highest needle production amounting to 2.3 t · ha^{-1} · yr^{-1} was displayed by trees from the nitrogen-fertilized plots (an 87% increase in production in relation to control); lower needle production (1.5 t · ha^{-1} · yr^{-1}) was characteristic of trees of P or K fertilized plots (a 24% increase in production), and the production was the lowest (ca. 1.3 t · ha^{-1}· yr^{-1}) on the limed, acidified or control plots.

These results indicate that soil treatment (particularly with N, P, K) intensifies the production of needles and litter, and thus is a factor monitoring the stream of organic matter introduced every year into ecosystemic cycle.

3.2. UPTAKE OF ELEMENTS

It was found that the variation of the contents of nearly all elements determined in green needles of the investigated stands fluctuated near the value of 26%, this corresponding with the variation coefficient calculated for needle production (Table 3). There were close relationships between the content of the different elements in the foliage and its annual production. These results indicate that nutrient uptake by trees is determined by the magnitude of produced needle biomass. The higher the needle production, the greater the amount of elements taken up (Table 4). Relationships of this type were particularly strong for the uptake of carbon, phosphorus and potassium. The effect of needle production on the uptake of these elements was calculated to exceed 95% (coefficient of determination). Sulphur proved to be a specific element because needle production was decisive of its uptake to be a degree not

Table 3. Contents of elements in ageing green needles before abscission ($\bar{x}_1$) and in dead fallen needles ($\bar{x}_2$) (kg · ha^{-1}), and their variation (V%) in the investigated treatments (N=13)

Parameter	$\bar{x}_1 \pm SD$	V (%)	$\bar{x}_2 \pm SD$	V (%)	$\bar{x}_2/\bar{x}_1$
Biomass	1591.14 ± 415.86	26.1	1172.41 ± 299.58	25.6	0.74
C	722.6 ± 199.8	27.6	527.4 ± 127.2	24.1	0.73
N	16.41 ± 4.90	29.8	5.37 ± 1.50	27.9	0.33
Ca	7.487 ± 1.919	25.7	5.703 ± 1.521	26.7	0.76
K	6.009 ± 1.549	25.8	0.422 ± 0.220	52.1	0.07
P	1.941 ± 0.500	25.2	0.452 ± 0.134	29.5	0.23
S	1.267 ± 0.184	14.5	0.651 ± 0.141	21.7	0.51
Mg	0.575 ± 0.160	27.9	0.299 ± 0.080	26.7	0.52

exceeding 50% (Table 5). The relatively low variation of the sulphur content in living needles, amounting to ca. 14% (Table 3), suggests that its uptake is related rather to its availability in soil than to the plant's requirement.

Since the uptake of most elements greatly depends on the magnitude of needle production, and since in turn the latter is determined by the kind of treatment, it can be stated that soil treatments (mainly with N, P, K) influence the chemical composition of living needles. This is realized via an increase in the absolute contents of elements in the foliage, according to the current requirements of trees. Therefore, the contents of all investigated elements in foliage were the highest in the case of nitrogen fertilization, and the lowest for the foliage of the untreated and limed plots (Table 4). It is particularly noteworthy that the applied treatments only very slightly disturbed the ratios among mineral components in living needles, as compared with control (Table 6), this being essential from the standpoint of normal nutrient balance of trees. The few observed changes in the ratios of nutrient elements in foliage, as compared with control, did not exceed 30%. Only potassium fertilization caused a ca. 60% increase in this element in the assimilatory apparatus and at the same time a drop in magnesium content by ca. 25%, as compared with control. This finding emphasizes the antagonistic relationship between K and Mg cations. However, on all investigated treatments the general principle of relative stability of the ratios of nutrient elements in the produced needles remains in force.

3.3. ELEMENT RETRANSLOCATION

3.3.1. General pattern of element translocation in young pine stand

The results showed that green needles produced per 1 ha during one year contained on the average 16 kg N, whereas the total annual litterfall – only 5 kg N,

Table 4. Contents of mineral components in ageing green needles (*gn*) and in brown fallen needles (*fn*) ($kg \cdot ha^{-1}$)
Ca – limed plot; Ca+S – group of plots with simultaneous acidification (with sulphur compounds) and liming ($N = 2$); S – group of plots acidified with sulphur compounds ($N = 4$); K – plot fertilized with potassium salt; P – plot fertilized with superphosphate; N – group of plots fertilized with nitrogen compounds ($N = 3$) (See also Chapter 2 of this paper)

Treatments		Biomass	C	N	Ca	K	P	S	Mg
Control	*gn*	1226.64	548.3	12.84	6.929	4.012	1.554	0.991	0.460
	fn	936.20	424.5	4.34	4.782	0.206	0.340	0.483	0.189
Ca	*gn*	1317.86	595.7	12.54	6.584	4.367	1.532	1.041	0.485
	fn	917.85	420.9	4.57	4.924	0.202	0.310	0.473	0.367
Ca + S	*gn*	1357.92	610.4	14.63	6.406	5.451	1.726	1.357	0.562
	fn	914.88	418.5	4.52	4.725	0.270	0.390	0.620	0.240
S	*gn*	1373.81	619.2	13.46	5.934	5.358	1.706	1.206	0.482
	fn	1028.95	466.2	4.26	0.349	0.349	0.355	0.588	0.275
K	*gn*	1575.30	699.7	14.33	7.347	7.171	1.793	1.178	0.388
	fn	1238.54	549.2	6.03	5.830	0.964	0.655	0.622	0.251
P	*gn*	1473.98	670.5	16.14	8.906	5.436	1.809	1.425	0.736
	fn	1187.98	546.7	4.97	6.539	0.284	0.499	0.872	0.343
N	*gn*	2293.30	1060.5	24.81	10.298	8.267	2.753	1.432	0.785
	fn	1671.75	737.6	7.92	7.874	0.630	0.632	0.817	0.386

i.e. 3 times less. From the content of K in green needles, calculated at ca. 6 $kg \cdot ha^{-1} \cdot yr^{-1}$, only ca. 0.4 $kg \cdot ha^{-1} \cdot yr^{-1}$ (i.e. nearly 15 times less) reached forest bottom. Out of the 2 $kg\ P \cdot ha^{-1} \cdot yr^{-1}$ contained in green needles, trees returned to litter only ca. 1/4th, i.e. 0.5 $kg \cdot ha^{-1} \cdot yr^{-1}$. Moreover, fallen needles, as compared with green needles, displayed ca. twice smaller contents of Mg and S, and lower ones of C and Ca (by ca. 30 and 25%, respectively) (Table 3). All these differences are significant at $p<0.001$.

The presented data indicate that the investigated elements were intensively retranslocated from needles prior to their falling, and that various elements differed in the retranslocation rate. This confirms the statement of selective nature of the retranslocation process. It was calculated that pine retranslocates 93% K, 77% P, 67% N, 49% S, 47% Mg, 26% C and 23% Ca (Table 7, Fig. 3).

3.3.2. The effect of soil treatment on the element retranslocation process

Since the 13 plots studied differed in the kind of soil treatment, the mean element retranslocation level could be expected to display high variation. It was found, how-

Table 5. Coefficients of correlation, determination and indetermination, characterizing the relationships between the uptake (1) and return (2) of elements, on one hand, and needle biomass and other factors (N = 13)

Element	Effect of needle biomass				Effect of other factors	
	correlation		determination		indetermination	
	r_1	r_2	$100\ R_1^2\%$	$100\ R_2^2\%$	$100\ (1-R_1^2)\%$	$100\ (1-R_2^2)\%$
C	0.999	0.997	99.7	99.5	0.3	0.5
P	0.986	0.856	97.2	74.9	2.8	25.1
N	0.977	0.939	95.4	88.1	4.6	11.9
K	0.945	0.671	89.3	45.1	10.7	54.9
Ca	0.914	0.823	83.6	67.8	16.4	32.2
Mg	0.835	0.682	69.7	46.5	30.3	24.5
S	0.685	0.736	47.0	54.1	53.0	45.9

Table 6. Chemical composition of ageing needles of pine expressed by the ratios of elements relative to nitrogen (See Table 4 for symbol description)
The percentages of changes in these ratios in relation to control are given in brackets. The sign + denotes a relative increase, and the sign – relative drop in the content of a given element in needles. Changes in ratios relative to control, exceeding ±20%, are printed in bold-face type

Groups of treatments	C	N	P	K	Ca	Mg	S
Control	42.7	1	0.121	0.312	0.540	0.036	0.077
Ca	47.5 (+11.2)	1	0.122 (+0.8)	0.348 (+11.5)	0.525 (–2.8)	0.039 (+8.3)	0.083 (+7.8)
Ca + S	41.6 (–2.6)	1	0.118 (–2.5)	0.372 (+19.2)	0.436 (–19.3)	0.038 (+5.6)	0.092 (+19.5)
S	46.1 (+8.0)	1	0.127 (+5.0)	**0.399** (+27.9)	0.441 (–18.3)	0.036 (0)	0.090 (+16.9)
K	48.8 (+14.3)	1	0.125 (+3.3)	**0.500** (+60.3)	0.513 (–5.0)	**0.027** (–25.0)	0.082 (+6.5)
P	41.5 (–2.8)	1	0.112 (–7.4)	0.337 (+8.0)	0.552 (+2.2)	**0.046** (+27.8)	0.088 (+14.3)
N	42.7 (0)	1	0.111 (–8.3)	0.332 (+6.4)	**0.414** (–23.3)	0.031 (–13.9)	**0.058** (–24.7)

Table 7. Needle weight losses (%) and efficiency of element retranslocation (R%) from pine needles, and variation of these parameters (V%) among the treatments (N=13)
All calculated values are significantly different from zero at p <0.001

Parameter	$R \pm SD$	V (%)
K	93.3 ± 2.5	2.7
P	76.5 ± 5.0	6.5
N	66.9 ± 3.8	5.7
S	48.6 ± 7.0	14.4
Mg	47.0 ± 12.0	25.5
C	26.4 ± 4.8	18.2
Biomass	26.2 ± 4.2	16.0
Ca	23.2 ± 9.7	41.8

ever, that this variation fluctuated from several to 10–20%, and amounted to ca. 42% only in the case of Ca (Table 7). In spite of low variation of the element retranslocation efficiency, the latter was shown to be related to the needlefall rate. There were two opposite types of relationships. The first of them, characteristic of most treatments, consisted in a gradual drop in retranslocation efficiency with an increase in annual needlefall. Treatments listed in order of decreasing retranslocation efficiency assumed the following sequence: Ca, Ca+S, control, S, K, P. In the case of both last treatments (K and P), the needlefall rate (and the needle production rate) was relatively the highest, whereas the retranslocation efficiency of all elements studied was relatively low.

The group of nitrogen-treated plots showed an opposite tendency. Namely, the greater the annual needlefall in the consecutive plots of this group, the higher the calculated element retranslocation efficiency (Fig. 4). Apart from both extreme types of relationship, it is noteworthy that the group of plots acidified with sulphur compounds assumed an intermediate position in the earlier mentioned sequence of decreasing retranslocation efficiency. This leads to the conclusion that in the initial phase the effect of soil acidification on translocation efficiency is only slight.

For closer determination of the effect of different agents applied to soil on the course of the element retranslocation process, the retranslocation calculated for the singled out groups of treatments was compared with the retranslocation in untreated plot (Table 8, Fig. 5). The trees from all groups of treatments exhibited a drop in the Mg and Ca retranslocation efficiency relative to that calculated for control. This may testify to a relative improvement of the conditions of utilization of both these elements, as a result of action of the external stimulus, i.e. of soil enrichment with the nutrient elements. It was found, moreover, that the trees affected by K or P fertilization retranslocated nutrients less efficiently than did the trees growing on the other

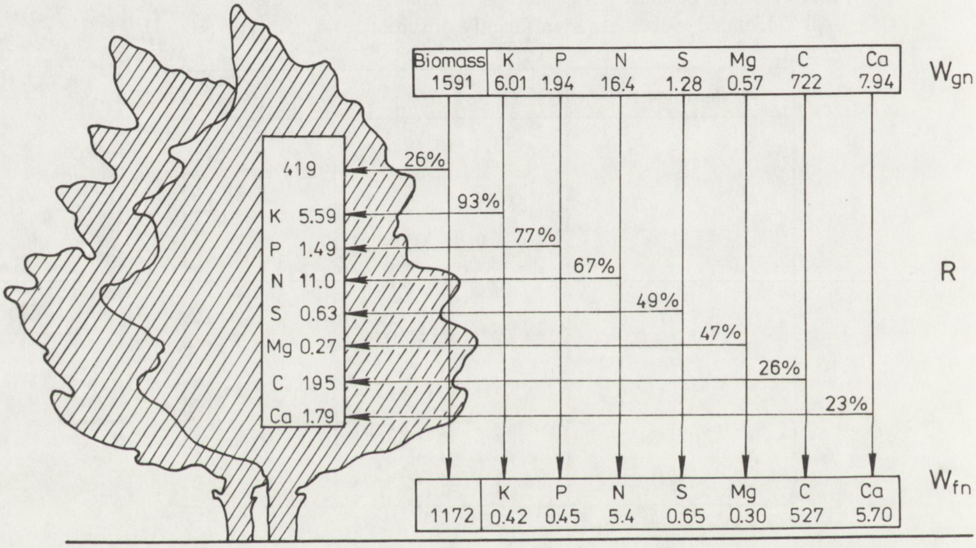

Fig. 3. General pattern of autumnal element translocation in young Scots pine stand
W_{gn} – element contents in ageing green needles ($kg \cdot ha^{-1}$), R – retranslocation efficiency, W_{fn} – element contents in falling brown needles ($kg \cdot ha^{-1}$). Mean values for 13 treatments studied were used

plots. This may indicate relatively greatest improvement of the trophic conditions in both K and P-fertilized plots. Tree response to the other treatments, as compared with control, comprised mainly an increase in the carbon retranslocation (or depletion) intensity. The increase in carbon retranslocation (exceeding 37%, as compared with control) was the most significant in the case of the simultaneous acidification and liming (Ca+S), whereas this increase was smaller (ca. 10%) in the group of plots acidified with sulphur compounds (S).

An analysis of the range of fluctuations of the retranslocation level on different treatments showed that nutrients were retranslocated the most intensively after simultaneous acidification and liming (Ca+S), liming (Ca) as well as on the untreated plot (Table 9). This may indicate that in these plots the trophic conditions were relatively the least favourable.

3.4. RETURN OF ELEMENTS TO LITTER

The present results showed that the rate of element return to litter is determined by the magnitude of needlefall, but at the same time it is modified by varying intensity of element retranslocation. Therefore, the relationships between the magnitude of yearly needlefall and contents of various elements in needlefall were in most cases weaker than the analogous relationships between needle production and nutrient uptake (Table 5). The effect of needlefall magnitude proved to be the weakest in the

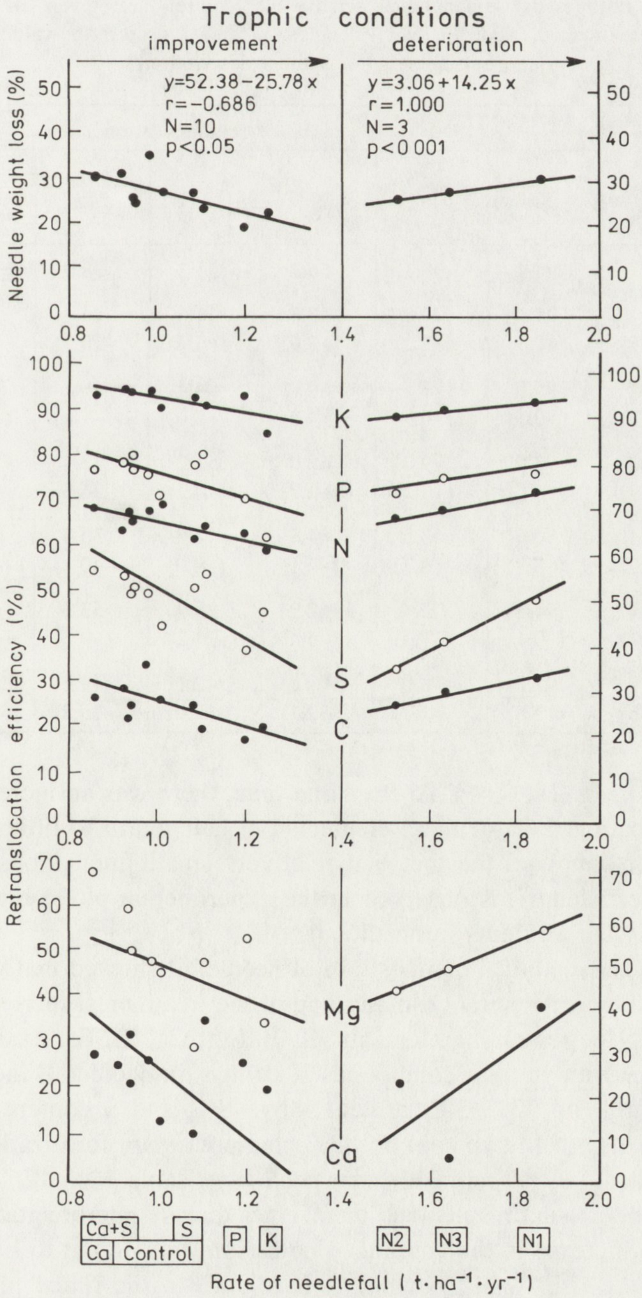

Fig. 4. Trends of changes in needle weight losses and in retranslocation efficiency in relation to the annual rate of needlefall (and to alterations of trophic conditions)
See text for details

Table 8. Needle weight losses before abscission (%) and element retranslocation efficiency (%) in Scots pine sapling
The percentages of changes in the parameters relative to control are given in brackets. The sign + denotes a relative increase, and the sign – denotes a relative drop in the values of the parameters (See Table 4 for symbol description)

Treatments	% of needle weight losses	% of retranslocation						
		K	P	N	S	Mg	Ca	C
Control	23.7	94.9	78.1	66.2	51.3	58.9	31.0	22.6
Ca	30.4 (+28.3)	95.4 (+0.5)	79.8 (+2.2)	63.6 (–3.9)	54.6 (+6.4)	24.3 (–58.7)	25.2 (–18.7)	29.3 (+29.6)
Ca + S	32.4 (+36.7)	95.0 (+0.1)	77.5 (–0.8)	69.0 (+4.2)	54.4 (+6.0)	58.1 (–1.4)	26.4 (–14.8)	31.0 (+37.2)
S	25.1 (+5.9)	93.5 (–1.5)	79.0 (+1.2)	68.0 (+2.7)	51.2 (–0.2)	43.4 (–26.3)	19.5 (–37.1)	24.8 (+9.7)
K	21.4 (–9.7)	86.6 (–8.7)	63.5 (–18.7)	64.8 (–2.1)	47.2 (–8.0)	35.3 (–40.1)	20.6 (–33.1)	21.5 (–4.9)
P	19.4 (–18.1)	94.8 (–0.1)	72.4 (–7.3)	62.2 (–5.4)	38.9 (–24.2)	53.3 (–9.5)	26.6 (–14.2)	18.5 (–18.0)
N	26.9 (+13.5)	92.2 (–2.8)	76.8 (–1.7)	67.6 (+2.1)	42.1 (–17.9)	49.6 (–15.8)	22.6 (–27.1)	30.1 (+33.2)

case of K, S and Mg (ca. 50%). At the same time, there was an increase in the effect of the retranslocation level of these elements on their return to litter. The essence of this phenomenon involved the fact that relatively small fluctuations of the element retranslocation efficiency (as observed in the experimental plots) created changes in the ratios among the nutrients in needlefall.

Analysis of the chemical composition of needlefall showed that whereas the C:N ratio did not change substantially in any one of the treatments, there were changes in the ratios among the remaining elements (K, P, Mg, Ca, S). For example, as a result of supplying soil with sulphur compounds K content in needlefall increased, as compared with control, by 73%, Mg content – by 48%, and S content – by 25%; soil liming caused a rise of Mg content by 82%, and potassium fertilization – an increase in P and K contents by 69 and 313%, respectively (Table 10).

Not all of the present results lend themselves to easy interpretation. Some results, e.g. the relative increase in the amount of potassium transferred to litter in the K-fertilized plot, or the rise of Mg content in needlefall in the limed plot (the fertilizer contained some Mg), can be interpreted in terms of a direct reaction of trees to soil enrichment with the given element. This reaction involves, of course, a decrease in the element retranslocation efficiency, with resulting acceleration of the rate of element return to litter. On the other hand, our attempts at elucidation of the increase in

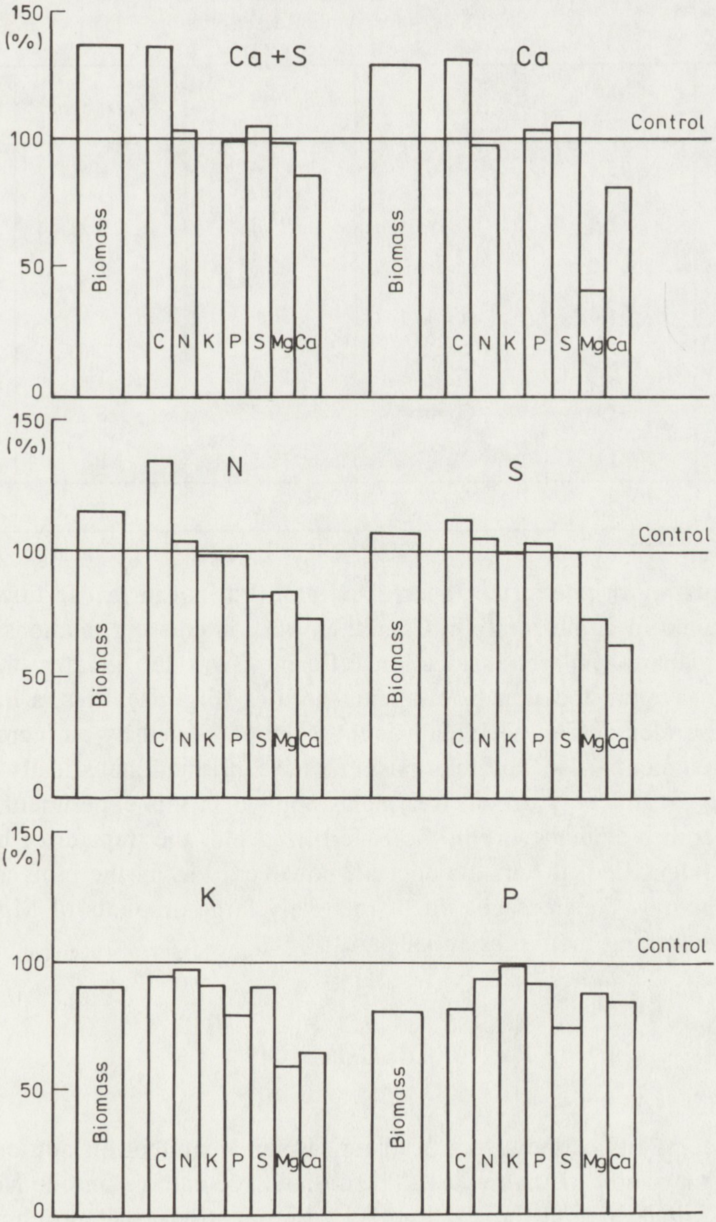

Fig. 5. Neddle weight losses before shedding and retranslocation efficiencies for different treatments related to control

Ca+S – group of plots simultaneously limed and acidified with sulphur compounds (N = 2), Ca – lime-treated plot, N – group of plots fertilized with nitrogen compounds (N = 3), S – group of plots acidified with sulphur compounds (N = 4), K – plot fertilized with potassium salt, P – plot fertilized with superphosphate

Table 9. Fluctuation range of the percentile needle weight losses before needle abscission and element retranslocation efficiency in Scots pine sapling
See Table 4 for symbol description

Parameter	Max (%)	Treatment	Min (%)	Treatment	Difference (%)
K	95.4	Ca	86.6	K	8.8
P	79.8	Ca	63.5	K	16.3
N	69.0	Ca + S	62.6	P	6.4
S	54.6	Ca	38.9	P	15.7
Mg	58.9	Control	24.3	Ca	34.6
Ca	31.0	Control	19.5	S	11.5
C	31.0	Ca + S	18.5	P	12.5
Biomass	32.4	Ca + S	19.4	P	13.0

the phosphorus return rate in the K-fertilized plot (but not in that fertilized with phosphorus) resulted in demonstration of another, very interesting relationship. Namely, it was shown that the P retranslocation efficiency was the greater, the higher the efficiency of K retranslocation from ageing needles (Fig. 6a); thus, a higher content of one of these elements in needlefall ought to be paralleled by an increased content of the other element. Also this relationship was confirmed statistically (Fig. 6b), in spite of the great diversity of soil treatments applied in this experiment. In this connection it becomes evident why in the K-fertilized plot the transfer of both K and P to litter was intensified. It remains unclear, however, why in the plots acidified with sulphur compounds the trees got rid of relatively large amounts of Mg and K (and not only S), returning their substantial part to litter.

4. DISCUSSION

In considerations of the effect of chemical soil treatment on nutrient balance of pine, the notion of soil treatment has to be defined accurately. On one hand, we often deal with so-called mineral fertilization, i.e. with intentional soil enrichment with nutrients limiting to forest growth. On the other hand, forest soils are reached by many elements and chemical substances, being adverse or harmful even in relatively small amounts. However, irrespective of the origin of mineral components and the advisability of their application, in ecological studies it is most essential to determine the effects of definite elements on the processes directly related to the nutrient economy of trees, as well as to estimate the possible consequences for cycling of matter and of different elements in whole ecosystems.

Table 10. Chemical composition of needlefall expressed by the ratios of elements relative to nitrogen The percentages of changes in these ratios in relation to control are given in brackets. The sign + denotes a relative increase, and the sign – denotes relative drop in the content of a given element in needles. Changes in ratios relative to control, exceeding ±20%, are printed in bold-face type

Groups of treatments	C	N	P	K	Ca	Mg	S
Control	98.0	1	0.078	0.047	1.102	0.044	0.111
Ca	92.1 (–6.0)	1	0.068 (–12.8)	0.044 (–6.4)	1.077 (–2.3)	**0.080 (+81.8)**	0.104 (–6.3)
Ca + S	92.5 (–5.6)	1	0.086 (+10.3)	**0.060 (+27.7)**	1.040 (–5.6)	0.052 (+18.2)	**0.137 (+23.4)**
S	110.2 (+12.4)	1	0.084 (+7.7)	**0.081 (+72.3)**	1.123 (+1.9)	**0.065 (+47.7)**	**0.139 (+25.2)**
K	110.5 (+12.8)	1	**0.132 (+69.2)**	**0.194 (+312.8)**	1.173 (+6.4)	0.050 (+13.5)	0.125 (+12.6)
P	90.7 (–7.4)	1	0.083 (+6.4)	0.047 (0)	1.084 (–1.6)	**0.057 (+29.5)**	**0.145 (+30.6)**
N	93.0 (–5.1)	1	0.080 (+2.6)	**0.079 (+68.1)**	0.990 (–10.2)	0.049 (+11.4)	0.098 (–11.7)

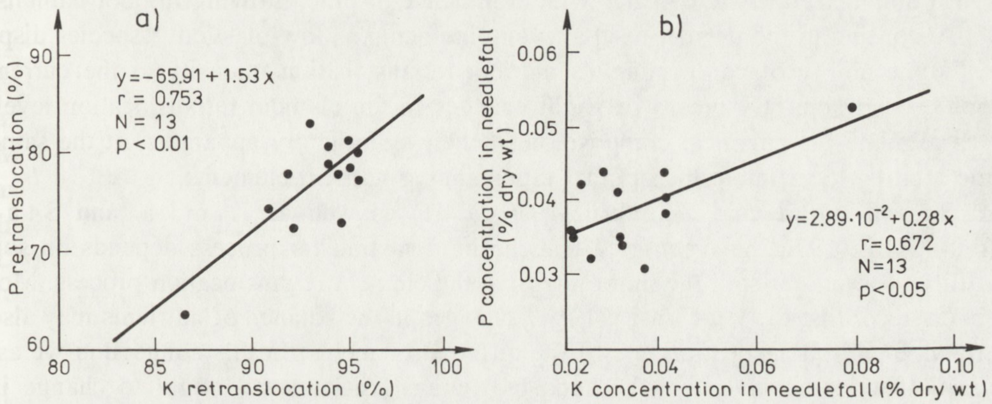

Fig. 6. Positive interrelations between potassium and phosphorus in: (a) retranslocation efficiency, (b) element return to litter

The effect of various elements added to soil on the rates of needle and litter production in pine stands is the first problem to be discussed. According to the literature, needle production may be an indicator of the production of the whole tree biomass (M a d g w i c k 1970). Thus, an estimation of the needle production rate in stands influenced by various chemical substances may afford an approximate picture of the attained growth effects. In the present experiment, this effect was the strongest in the case of nitrogen fertilization (an 87% increase in the needle production rate, as compared with control); the effect was somewhat weaker, but still clear-cut, in the phosphorus – fertilized plot and in that fertilized with potassium (a 24% increase in the needle production rate) (Table 2). On the other hand, there were no marked changes in the needle production rate in the plots with acidification or liming.

Intensification of needle production in the case of N, P or K fertilization was followed by acceleration of the rate of uptake of all nutrients (Table 4), whereas it did not disturb – apart from a few exceptions – the ratios of nutrient elements accumulated in the foliage (Table 6). This fact is of extreme importance for normal nutrient balance of trees (I n g e s t a d 1979, 1982; W a r i n g 1984). Moreover, the greater the needle biomass produced yearly by the stand, the higher the annual needlefall in the stand (Table 2). Thus, in the N-fertilized plots the needlefall rate was relatively the highest (a 79% increase, as compared with control), and in the plots fertilized with P or K the needlefall rate exceeded by 30% that found for untreated plot (Tables 1 and 2). Irrespective of the kind of soil treatment, in all plots the abscission peak took place on the turn of September and October (Fig. 2). At this time ca. 50–70% of the yearly needlefall got to litter. It is known, however, that before abscission the trees retranslocate many nutrients from ageing needles. In the case of Scots pine we found the following mean efficiencies of autumnal retranslocation: 93% K, 77% P, 67% N, 49% S, 47% Mg, 26% C and 23% Ca (Table 7, Fig. 3). These values correspond with the results of S t a c h u r s k i and Z i m k a (1981) obtained for mature stands with dominance of pine, growing in poor habitats.

According to the present results, even pine being a "low-plasticity" species displays some ability of conforming its nutrient retranslocation intensity to the current trophic conditions. By means of slight changes in the element retranslocation level, trees regulate the chemical composition of their assimilatory apparatus, at the same time tending to maintain the optimal ratios among nutrient elements.

S t a c h u r s k i and Z i m k a (1979, 1981) as well as Z i m k a and S t a c h u r s k i (1976) have reported that the nutrient transfer process depends on soil fertility. The poorer soil, the more intensive the element retranslocation process. Moreover, according to W a r i n g (1984), changes in the balance of nutrients may also influence the retranslocation rate of the different elements. In this connection we assumed that in the investigated stands the retranslocation level ought to change in compliance with alterations of the rates of needle and litter production, since these parameters are some kind of a measure of the trophic conditions (the better the trophic conditions, the higher the rates of needle and litter production). It was found, however, that the changes in the retranslocation level proceeded in the gradient of annual needlefall in two opposite directions (Fig. 4). The first trend concerning the major part of the investigated treatments was consistent with expectations, i.e. the greater the yearly needlefall, the lower the retranslocation efficiency of all elements studied (left part of Fig. 4). It may thus be concluded that in these plots the trophic conditions in fact gradually improved, and that they were relatively the best in the case of fertilization with K or P.

A different tendency was characteristic of the plots fertilized with nitrogen compounds (right side of Fig. 4). In this case the higher was the yearly rate of needlefall, the higher – the retranslocation efficiency. In the interpretation of this phenomenon it has to be born in mind that single element fertilization (in this case – supplying soil with, only, nitrogen) causes not only an increase in the needle production rate, but also leads to an abrupt rise of the requirements of other nutrients. In the initial phase the trees utilize the reserves of elements available in soil. The further increase in production "forced" by the stimulus, i.e. element added to soil, may result in deficiency of the other soil nutrients. Thus, the rising nutrient requirements of the trees may not be satisfactory fulfilled. Probably, the change in nutrient balance may release a mechanism which enhances the intensity of element retranslocation from needles. This mechanism acts as an "emergency brake" which, in the case of disturbances in the nutrient balance protects the plant from losses of the elements taken up earlier. It may thus be suggested that retranslocation process is – owing to the possibilities of its regulation (adjusting of retranslocation rate to trophic conditions) – a homeostatic process on the level of an individual organism (in this case – a tree). The above considerations are summarized in Scheme 1.

Scheme 1. Pattern of changes caused by soil fertilization in Scots pine sapling

PINE SAPLING

P or K fertilization	N fertilization
Moderate increase in needle and litter production	Substantial increase in needle and litter production
Maintained balance between available nutrients in soil	Disturbed balance between available nutrients in soil
Improvement of trophic conditions	Deterioration of trophic conditions
Decrease in element retranslocation efficiency	Increase in element retranslocation efficiency

It is noteworthy that despite the clear-cut directional changes in the retranslocation rate in the first year after soil treatment with N, Ca, Ca+S and S only carbon retranslocation was evidently increased in relation to control (Table 8, Fig. 5). This may indicate that under adverse trophic conditions the retranslocation (or depletion) of carbohydrates was the first to be intensified. As opposed to the above-mentioned treatments, fertilization with K or P limited the retranslocation of virtually all elements studied, as compared with control.

Although Scots pine may to some extent adjust the element retranslocation intensity to the current requirements of trees (related to the current trophic conditions), the range of these changes is incomparably more narrow than that characteristic of the species representing the oak-hornbeam forest type of nutrient economy (Z i m k a and S t a c h u r s k i 1976). It seems that in critical situations, e.g. in the case of excessive fertilization of soil with some element, when it comes to a strong "dilution effect" (S t e e n b j e r g 1954), the increase in the intensity of nutrient retranslocation within pine may prove to be insufficient for maintaining constant ratios among elements in the foliage. In extreme cases this may led to reduction and even to a breakdown of tree biomass production.

Since the processes of element retranslocation from foliage modify the chemical composition of litterfall (Z i m k a and S t a c h u r s k i 1976), it could be expected that in the investigated treatments the chemical composition of needlefall may differ from that of living needles. Moreover, since the element retranslocation intensity was adjusted to the current requirements of trees consistently with the changes in trophic conditions (in the present experiment – caused by supplying the soil with different elements), the chemical composition of needlefall ought to display high variation among the treatments. The present results confirmed these assumptions. In some cases small fluctuations (from several to 10–20%) of the retranslocation level led to disproportionately large changes in the ratios among nutrient elements in needlefall. Although there were no significant differences in the C:N ratio among the treatments, the proportion of some elements in litter relative to N content was often very increased (Table 10). Whereas we did not succeed in elucidation of all observed relationships between application of a definite element to soil and the rate of element return to litter, we found the characteristic (often drastic) increase in the participation of K, Mg and S, resulting from application of different agents to soil. It seems that e.g. the increase in K content in litter of the stand fertilized with this element, exceeding 300% relative to control, exerts some effect on the losses of this valuable and clearly mobile nutrient from the ecosystem. It may thus be assumed that even rational mineral fertilization of soil, improving the trophic conditions of trees and allowing to reduce the retranslocation intensity, may cause losses of some elements from the ecosystem. This is of importance, particularly in the case of loose sandy soils (P r u s i n k i e w i c z et al. 1974). The presented problems call for initiation of relevant detailed studies.

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5. SUMMARY

It was attempted to determine the response of Scots pine (*Pinus silvestris* L.) to the action of various mineral components added to soil (N, P, K, Ca, S, H_2SO_4). The study was made of the processes of needle and litter production, retranslocation of different elements (C, N, P, K, Ca, Mg, S) and their return to litter.

It was shown that a significant increase in the production of needles and needle litter was associated with soil fertilization with nitrogen (an 87% rise in needle production), and to a less extent – with P or K fertilization (a 24% rise in needle production) (Table 2). Intensification of needle production resulted in an increase in the rates of uptake of all elements studied (Table 4) in amounts which allowed to maintain the ratios among nutrient elements in the foliage on the unchanged level (Table 6). A direct consequence of the increase in needle production in the plots fertilized with N, P or K consisted in an acceleration of the needlefall rate (Table 2, Fig. 2), and thus of the return of larger amounts of elements to ecosystemic cycle, as compared with control (Table 4).

It was confirmed that, irrespective of the kind of the substance supplied to soil, dead fallen needles are much poorer in nutrients than living needles, because of intensive element retranslocation from ageing needles before abscission. It was calculated that in autumn pine retranslocates ca. 93% K, 77% P, 67% N, 49% S, 47% Mg, 26% C and 23% Ca (Fig. 3, Table 7). In the presence of various chemical substances added to soil, the retranslocation efficiency displays some fluctuations (Tables 8, 9). We observed, among others, a tendency for a drop in the retranslocation level of all investigated elements together with an increase in the rate of organic matter input to soil, expressed most clearly in the P-fertilized and K-fertilized plots. Moreover, the plots fertilized with N compounds displayed an opposite tendency involving an increase in the element retranslocation efficiency in parallel with a rise of the needlefall rate (Fig. 4). It was found that in the case of K or P fertilization the element retranslocation efficiency did not exceed that found for control. On the other hand, a significant increase in carbon retranslocation efficiency, as compared with control, was characteristic of the trees affected by all remaining treatments (N-fertilized, Ca-limed, Ca+S-limed and acidified, S-acidified) (Table 8, Fig. 5).

Whereas the variation of the element retranslocation efficiency in pine being influenced by different mineral substances supplied to soil was rather slight (from several to 10–20%) (Table 7), it resulted in substantial changes (amounting to several dozen of %) in the ratios among nutrient elements in needlefall. Quantitative changes were the largest in the case of K, Mg and S; as a rule, in needle litter their participation relative to nitrogen increased. The applied treatments did not cause any significant changes in N:C ratio of needle litter (Table 10).

Some of the observed responses were explained in terms of strong positive interrelations between elements, being the strongest between phosphorus and potassium. It was found that an increase in the retranslocation efficiency of one of these elements was accompanied with an increase of the same parameter calculated for the other element of this pair (Fig. 6a). As a result, also the return of these elements to litter was closely interrelated (Fig. 6b).

The types of pine responses to soil treatments were discussed. Element retranslocation within pine was defined as a homeostatic mechanism on the level of an individual organism, with – however – a relatively narrow regulation range. Moreover, discussion was made of the effects of soil treatment with various nutrients on element cycling in a young pine stand. It was suggested that in some cases even proper fertilization may result in nutrient losses from the ecosystem.

6. POLISH SUMMARY

W badaniach podjęto próbę określenia reakcji sosny pospolitej (*Pinus silvestris* L.) na działanie rozmaitych składników mineralnych wprowadzonych do gleby (N, P, K, Ca, S, H_2SO_4). Zbadano jak

kształtują się w tych wariantach procesy produkcji i opadu igieł, retranslokacji różnych pierwiastków (C, N, P, K, Ca, Mg, S) oraz proces przekazywania tych elementów do ściółki.

Metodą regresji liniowej wykazano, że istotny wzrost produkcji i opadu igliwia związany jest z nawożeniem gleby azotem (87% wzrost produkcji), a w mniejszym stopniu również z nawożeniem P lub K (24% wzrost produkcji) (tab. 2). Nasilenie produkcji igieł pociąga za sobą wzrost tempa pobierania wszystkich składników pokarmowych (tab. 4), w ilościach zabezpieczających trwałość proporcji pomiędzy nimi w żywym aparacie asymilacyjnym (tab. 6). Bezpośrednim następstwem zwiększonej produkcji igliwia w środowiskach nawożonych N, P lub K jest przyspieszenie tempa opadu ściółki (tab. 2, rys. 2), a tym samym przekazywanie do obiegu ekosystemalnego większych ilości pierwiastków niż to ma miejsce w warunkach kontrolnych (tab. 4).

Potwierdzono, że ściółka sosnowa, niezależnie od rodzaju wprowadzanej do gleby substancji, jest silnie zubożona w składniki pokarmowe względem igliwia zielonego, powodem czego są intensywne procesy retranslokacji pierwiastków z igieł przed ich opadnięciem. Obliczono, że sosna wycofuje jesienią ok. 93% K, 77% P, 67% N, 49% S, 47% Mg, 26% C i 23% Ca (rys. 3, tab. 7). Pod wpływem różnych substancji chemicznych wprowadzanych do gleby efektywność wycofywania ulega pewnym wahaniom (tab. 8, 9). Między innymi zaobserwowano tendencję do spadku poziomu retranslokacji wszystkich badanych pierwiastków wraz ze wzrostem tempa dopływu materii organicznej do gleby, najsilniej zarysowującą się w wariancie nawożonym P i w wariancie nawożonym K, oraz charakterystyczną dla środowisk nawożonych związkami N, tendencję przeciwną, wyrażającą się wzrostem efektywności wycofywania pierwiastków w miarę wzrostu tempa opadu igieł (rys. 4). Określono przy tym, że efektywność wycofywania pierwiastków w wariantach z potasem oraz z fosforem nigdy nie przewyższa tejże na powierzchni kontrolnej, natomiast we wszystkich pozostałych badanych środowiskach (nawożonych N, wapnowanych Ca, wapnowanych i jednocześnie zakwaszanych Ca+S oraz zakwaszanych S) dał się zauważyć przede wszystkim znaczący wzrost poziomu retranslokacji węgla (względem kontroli) (tab. 8, rys. 5).

Aczkolwiek zmienność efektywności retranslokacji pierwiastków u sosny będącej pod wpływem działania rozmaitych substancji mineralnych wprowadzanych do gleby jest na ogół niewielka (kilka, kilkanaście %) (tab. 7), to jak wykazano, jest ona źródłem powstawania znacznych (kilkudziesięcio- i więcej %) zmian w proporcjach pomiędzy składnikami mineralnymi w opadającym igliwiu. Największe zmiany ilościowe zaobserwowano w przypadku trzech pierwiastków, a mianowicie K, Mg i S, przy czym regułą jest wzrost ich udziału w stosunku do ilości zawartego w ściółce azotu. Jednocześnie nie stwierdzono istotnych przesunięć w stosunku C:N w ściółce jakiegokolwiek spośród badanych wariantów (tab. 10).

Niektóre spośród zaobserwowanych reakcji wyjaśniono istnieniem silnych dodatnich sprzężeń pomiędzy różnymi elementami, wśród których najsilniejsze dotyczą fosforu i potasu. Stwierdzono, że wzrost efektywności retransolacji jednego z tych pierwiastków pociąga za sobą nasilenie wycofywania drugiego elementu tej pary (rys. 6a). Skutkiem tego również przekazywanie tych pierwiastków do ściółki jest ze sobą ściśle związane (rys. 6b), nawet w zróżnicowanych warunkach chemizacji gleby.

W dyskusji omówiono typy reakcji sosny na traktowanie gleby różnymi związkami. Retranslokację pierwiastków u sosny określono jako mechanizm homeostatyczny na poziomie pojedynczego organizmu, jednakże o stosunkowo niewielkim zakresie regulacji. Dyskutowano ponadto nad konsekwencjami chemizacji gleby dla obiegu pierwiastków w młodniku sosnowym, które mogą w niektórych wypadkach polegać na wymywaniu składników pokarmowych poza ekosystem.

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