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# The decomposition of plant litter fall in an oak-linden-hornbeam forest and an oak-pine mixed forest of the Białowieża National Park

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Abstract

The decomposition of hornbeam, linden and oak leaves in an oak-linden-hornbeam (*Tilio-Carpinetum*) forst and of pine and spruce needles in an oak-pine mixed forest (*Pino-Quercetum typicum*) of the Białowieża National Park were studied. The decay of the hornbeam and linden leaves progressed at the same rates, while that of oak leaves was slower. During the first year in the oak-pine mixed forest, the decay of pine needles was more intense than that of spruce needles, then during later periods, the rate of decomposition of spruce needles exceeded that of pine. The initial rates of decomposition were determined by the C/N ratio and the content of easily soluble components in the starting materials. The decomposition rate coefficients were: 1.06 for hornbeam leaves, 0.91 for linden leaves, 0.63 for oak leaves, 0.21 for pine needles and 0.30 for spruce needles; the time necessary for 95% of the initial material to decay was from 3 to 5 years for the oak-linden-hornbeam forest and from 10 to 14 years in the oak-pine mixed forest. Elements can be arranged in the following orders on the basis of their rates of release: K > Mg > P > > Ca > N or K > Mg > Ca > P > N. A decisive role is played by microbiological processes in the release of nitrogen, phosphorus and calcium, while potassium and magnesium are released mainly by leaching.

*Key words*: *plant litter fall, decomposition, hornbeam, linden, oak, pine, spruce, Białowieża National Park*

## INTRODUCTION

The annual plant litter fall in forest communities is a very important stage in the cycle of elements. Studies done previously in the "Las Piwnicki" forest reserve near Toruń have shown, for example, that in the *Pino-Quercetum* community, growing on poor sandy soil, the following amounts of elements were released yerly into the soil with the plant debris: c. 51 kg ha $^{-1}$ nitrogen, 32 kg ha $^{-1}$ calcium, 11 kg ha $^{-1}$ postassium, 10 kg ha $^{-1}$ magnesium and 4 kg ha $^{-1}$ phosphorus (Prusinkiewicz et al. 1974).

The nutrients contained in plant litter are gradually released in the process of mineralization and can be reused by plants, and so re-enter the biological cycle.

There have been numerous studies done in Poland on the decomposition of plant litter fall and the release of nutrients from decaying plant remains (Karkanis 1975, Stachurski and Zimka 1976, Dziadowiec 1979, Dziadowiec and Kwiatkowska 1980, Zieliński 1980, 1984, Badura and Pacha 1983, 1984). These studies were mainly done, however, in ecosystems significantly changed by the economic activities of man, whereas there is a lack of data on the decomposition of plant debris in the best conserved virgin forest ecosystems of the Białowieża National Park. These types of studies are necessary for the better understanding of the functioning of natural forest communities. They can also be used as valuable comparative material for transformed or degraded ecosystems.

## MATERIAL AND METHODS

Two sites (Fig. 1) in the Białowieża National Park (BNP) were studied: 1) a typical oak-linden-hornbeam forest (*Tilio-Carpinetum*, Traczyk 1962) with droso-mull type of forest humus, site 342, plot E 40, and 2) an oak-pine mixed forest (*Pino-Quercetum typicum*, Kozłowska 1925) with moder-mor type of forest humus, site 374, plot E 53. More detailed information on the studied sites is contained in the book edited by Faliński (1968).

On both sites, the decay of the main litter fractions was studied:

Table 1

The number and weight of the samples used in field studies in the Białowieża National Park

| Material | Number of samples | Weight of one sample, g |
|---|---|---|
| Hornbeam leaves | 20 | 6 |
| Linden leaves | 20 | 4 |
| Oak leaves | 30 | 5 |
| Pine needles | 25 | 10 |
| Spruce needles | 25 | 10 |

hornbeam (*Carpinus betulus*), linden (*Tilia cordata*) and oak (*Quercus robur*) leaves in the *Tilio-Carpinetum* and of pine (*Pinus silvestris*) and spruce (*Picea excelsa*) needles in the *Pino-Quercetum*. The leaves came from the autumn shedding. the pine and spruce needles were green, collected from the trees directly preceding their placement in the terrain.

The leaves and pine needles were packed in nylon net bags with a mesh-size of 2 mm. Spruce needles were packed in bags made from nylon hose. The samples were placed in the study sites on 1981.11.19 (Table 1). In addition, 5 samples from 2–5 g each were collected in order to determine their moisture contents and chemical compositions.

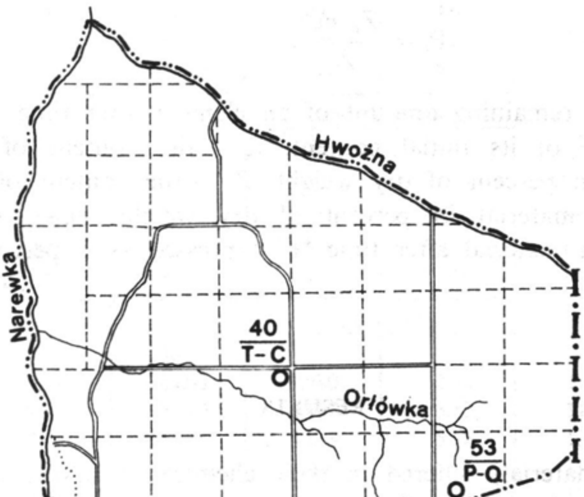


Fig. 1. The distribution of the experimental sites in the Białowieża National Park. 40, 53 — permanent plots of the Białowieża Geobotanical Station; T–C — *Tilio-Carpinetum*; P–Q — *Pino-Quercetum*

After the specified number of days, 5 samples were taken, dried at 65°C and weighed. In the *Tilio-Carpinetum*, samples were taken every 120 or 80 days. The decay of hornbeam and linden leaves was studied during one year, since they decompose quickly; oak leaves, which take longer to decay, were studied for 1.5 years. In the oak-pine forest, samples were taken every 200 or 160 days and the experiment was run for 2.5 years.

The humification degree was determined according to Springer by comparing the absorption of an extract of the studied sample in a mixture of sodium hydroxide and sodium oxalate with the absorption of the same type of extract of Merck's humic acids.

Loss on ignition was determined by incineration in a muffle furnace at 550°C, carbon was assayed accoding to Alten, nitrogen according to Kieldahl, potassium, phosphorous, calcium and magnesium, after mineralization of the material in a mixture of nitric, sulphuric and perchloric acids, were assayed according to the methods described in the IMUZ methodological materials (Metody ... 1979).

On the basis of losses of weight and changes in the chemical composition, a budget of the elements was made up, using the formula:

$$P_t = \frac{Z_t \cdot m_t}{Z_o},$$

where: $P_t$ — the remaining amount of an element after time "t" expressed as a percentage of its initial content, $Z_t$ — the content of an element after time "t" in percent of dry weight, $Z_o$ — the content of an element in the starting material in percent of dry weight, $m_t$ — the weight of the decomposing material after time "t" expressed as a percentage of the initial amount.

## RESULTS

The initial materials differed in their chemical compositions (Table 4). Linden leaves and pine needles contained the most nitrogen, while oak leaves contained the least. Linden leaves were also the richest in calcium. The concentration of calcium in these leaves was about twice that in hornbeam and oak leaves. three times greater than in spruce needles and six times greater than in pine needles. In addition, leaves contained almost twice the amount of magnesium found in needles.

These differences influenced both the course of decomposition of organic material and the release of elements from the decomposing matter.

### RATE OF DECOMPOSITION

In the oak-linden-hornbeam forest, the decomposition of the hornbeam and linden leaves took place at the same rate (Table 2). The recorded differences were statistically insignificant. The losses of weight of these two materials were the most intense during the autumn-winter period (the first 120 days of decomposition), but even later, the rate of this

Table 2

Changes in the weight of decomposing materials in an oak-linden--hornbeam forest given in percentages of initial weight ($\bar{x}$), standard deviation ($\sigma$), and variation coefficiant (V) and degree of humification

| Duration of decay, days | $\bar{x}$ | $\sigma$ | V | Degree of humification |
|---|---|---|---|---|
| | hornbeam leaves | | | |
| 0 | 100 | – | – | – |
| 120 | 74.40 | 0.788 | 1.06 | 13.8 |
| 200 | 61.16 | 2.491 | 4.07 | 13.3 |
| 280 | 45.06 | 2.359 | 5.24 | 13.9 |
| 360 | 34.80 | 2.090 | 6.01 | 17.5 |
| | linden leaves | | | |
| 0 | 100 | – | – | – |
| 120 | 71.07 | 1.091 | 1.53 | n.d.* |
| 200 | 59.63 | 4.650 | 7.80 | n.d.* |
| 280 | 47.60 | 4.956 | 10.33 | n.d.* |
| 360 | 40.44 | 7.151 | 17.68 | n.d.* |
| | oak leaves | | | |
| 0 | 100 | – | – | – |
| 120 | 84.03 | 1.970 | 2.34 | 13.0 |
| 200 | 75.85 | 4.187 | 5.52 | 12.1 |
| 280 | 68.41 | 3.888 | 5.68 | 15.0 |
| 360 | 63.49 | 3.640 | 5.75 | 19.3 |
| 480 | 45.00 | 4.500 | 10.00 | 17.6 |
| 560 | 37.46 | 5.172 | 13.81 | 17.4 |

* No determined

process was considerable. The 1st-year weight loss for hornbeam leaves was 65% of linden leaves, 60% of their initial weight. The remainder of both types of leaves were dark in color, highly disintegrated and visually amorphous. If they had not been isolated in bags, it would have been difficult to discern them from the amorphous soil organic matter.

The decomposition of oak leaves took place more slowly (Table 2), and differed in a significant manner from the rate of decomposition of hornbeam and linden leaves (P — 95 and 99%). After a year, the oak leaf weight loss equalled 36.5%. A certain acceleration of this process took place in the third half-year of the study (between the 360th and 560th days), when the weight losses equalled 26% and were even greater than in the first half-year. The remains of the oak leaves were very crumbled, but had not lost their tissue structure. These remains were only slightly darker than the initial material.

At the oak-pine mixed forest site, the decomposition of both studied materials proceeded differently (Table 3). The decomposition of pine needles was initially very intense. The weight losses during the first half-year amounted to 44%. In the subsequent half-years. this process was almost twice as slow each time. In the last half-year, the weight losses were below 2%. In all, during the 2.5 years, the weight losses amounted to 71% of the material, of this, 60.6% during the first year, and only 11% during the subsequent 1.5 years. The remaining needles were dark grey and very brittle.

The decomposition of spruce needles was slower in the first year, then quicker than the of pine needles (Table 3). During the first half-year the weight losses amounted to 25% then in the following half-year periods from 6 to 11%. During the whole period of study (920 days), 58% of the material decomposed. The remainder retained the structure and color of the initial material to a large extent. The rate of decomposition of spruce needles in comparable periods of time differed decidedly from that of the other studied materials.

Table 3

Changes in the weight of decomposing materials in an oak-pine forest given in percentages of initial weight ($\bar{x}$), standard deviation ($\sigma$) and variation coefficient (V) and degree of humification

| Duration of decay, days | $\bar{x}$ | $\sigma$ | V | Degree of humification |
|---|---|---|---|---|
| | pine needles | | | |
| 0 | 100 | – | – | – |
| 200 | 55.51 | 3.371 | 6.07 | 7.7 |
| 360 | 39.40 | 2.700 | 6.85 | 10.1 |
| 560 | 33.26 | 1.548 | 4.65 | 16.4 |
| 720 | 30.23 | 1.544 | 5.11 | 15.8 |
| 920 | 28.54 | 2.425 | 8.49 | 18.4 |
| | spruce needles | | | |
| 0 | 100 | – | – | – |
| 200 | 74.72 | 2.267 | 3.03 | 16.6 |
| 360 | 66.30 | 2.455 | 3.70 | 16.6 |
| 560 | 59.02 | 3.070 | 5.20 | 19.4 |
| 720 | 47.57 | 7.678 | 16.14 | 20.7 |
| 920 | 41.62 | 5.753 | 13.82 | 16.6 |

Table 4

Changes in the chemical composition of decomposing materials in the Białowieża National Park given in percentages of dry weight ($x \pm \varepsilon t_s$; n = 5; P = 95%)

| Duration of decay, days | Loss on ignition | C | N | P | K | Ca | Mg |
|---|---|---|---|---|---|---|---|
| | hornbeam leaves | | | | | | |
| 0 | 93.23 | 41.88 | 1.218 | 0.166 | 0.652 | 1.283 | 0.132 |
| 120 | 91.67±0.44 | 46.05±0.41 | 1.963±0.082 | 0.175±0.002 | 0.207±0.006 | 1.804±0.103 | 0.126±0.002 |
| 200 | 91.20±0.39 | 45.42±0.90 | 2.328±0.053 | 0.201±0.007 | 0.293±0.036 | 2.014±0.186 | 0.129±0.005 |
| 280 | 88.31±0.80 | 45.30±0.72 | 2.649±0.136 | 0.217±0.015 | 0.227±0.024 | 2.233±0.165 | 0.146±0.005 |
| 360 | 85.67±0.92 | 40.78±0.35 | 2.299±0.121 | 0.171±0.011 | 0.135±0.027 | 2.100±0.141 | 0.131±0.004 |
| | linden leaves | | | | | | |
| 0 | 91.01 | 45.74 | 1.470 | 0.155 | 0.436 | 2.550 | 0.154 |
| 120 | 90.29±1.38 | 48.84±0.89 | 2.255±0.118 | 0.208±0.011 | 0.195±0.015 | 2.994±0.289 | 0.136±0.003 |
| 200 | 89.45±0.64 | 46.58±0.67 | 2.665±0.071 | 0.231±0.005 | 0.333±0.053 | 3.060±0.018 | 0.126±0.003 |
| 280 | 88.09±0.65 | 45.77±0.68 | 2.810±0.083 | 0.246±0.009 | 0.244±0.024 | 2.950±0.143 | 0.139±0.017 |
| 360 | 87.14±0.98 | 40.89±0.92 | 2.633±0.105 | 0.214±0.010 | 0.170±0.039 | 2.690±0.156 | 0.144±0.008 |
| | oak leaves | | | | | | |
| 0 | 95.11 | 46.86 | 1.120 | 0.122 | 0.182 | 1.098 | 0.132 |
| 120 | 94.58±0.36 | 50.81±0.44 | 1.445±0.068 | 0.118±0.001 | 0.135±0.001 | 1.405±0.079 | 0.130±0.002 |
| 200 | 93.76±0.55 | 49.45±0.82 | 1.781±0.038 | 0.142±0.001 | 0.233±0.023 | 1.642±0.024 | 0.128±0.002 |
| 280 | 91.51±0.25 | 46.09±1.02 | 2.223±0.050 | 0.183±0.010 | 0.240±0.008 | 2.015±0.044 | 0.158±0.004 |
| 360 | 89.74±0.99 | 42.62±1.09 | 2.162±0.120 | 0.151±0.017 | 0.174±0.005 | 2.000±0.138 | 0.164±0.003 |
| 480 | 86.89±3.64 | 42.43±1.07 | 2.046±0.057 | 0.108±0.008 | 0.073±0.005 | 2.107±0.119 | 0.140±0.006 |
| 560 | 87.68±1.57 | 40.90±0.78 | 2.155±0.098 | 0.118±0.014 | 0.074±0.014 | 2.210±0.121 | 0.107±0.006 |
| | pine needles | | | | | | |
| 0 | 97.73 | 50.51 | 1.452 | 0.145 | 0.581 | 0.415 | 0.065 |
| 200 | 95.73±0.89 | 55.91±0.81 | 2.613±0.059 | 0.207±0.003 | 0.267±0.020 | 0.668±0.096 | 0.071±0.003 |
| 360 | 94.27±0.86 | 51.28±0.63 | 3.065±0.209 | 0.194±0.023 | 0.202±0.014 | 0.602±0.012 | 0.054±0.005 |
| 560 | 94.24±1.90 | 50.94±1.52 | 2.837±0.273 | 0.144±0.016 | 0.095±0.003 | 0.819±0.167 | 0.043±0.003 |
| 720 | 94.02±1.53 | 50.96±0.75 | 2.582±0.298 | 0.131±0.010 | 0.088±0.004 | 0.917±0.072 | 0.036±0.002 |
| 920 | 93.09±1.03 | 49.24±0.69 | 2.527±0.142 | 0.128±0.015 | 0.096±0.011 | 0.943±0.084 | 0.042±0.006 |
| | spruce needles | | | | | | |
| 0 | 95.78 | 49.15 | 1.219 | 0.138 | 0.508 | 0.739 | 0.059 |
| 200 | 94.70±0.22 | 52.38±0.50 | 1.735±0.052 | 0.162±0.004 | 0.298±0.012 | 1.037±0.025 | 0.066±0.000 |
| 360 | 92.35±1.44 | 50.34±0.65 | 1.984±0.049 | 0.153±0.002 | 0.209±0.021 | 1.276±0.054 | 0.075±0.004 |
| 560 | 93.45±0.50 | 50.93±0.70 | 2.074±0.060 | 0.128±0.003 | 0.102±0.008 | 1.141±0.039 | 0.056±0.002 |
| 720 | 90.52±1.78 | 49.06±1.47 | 2.165±0.113 | 0.125±0.015 | 0.098±0.021 | 1.184±0.067 | 0.052±0.007 |
| 920 | 90.72±1.21 | 47.36±0.83 | 2.396±0.121 | 0.146±0.015 | 0.107±0.020 | 1.059±0.102 | 0.051±0.006 |

CHANGES IN CHEMICAL COMPOSITION AND RELEASE OF NUTRIENTS

Losses of weight were accompanied by changes in the chemical composition of the decomposing materials (Table 4). The ash content in decomposing linden leaves rose by 4%, by 5% in decomposing pine and spruce needles

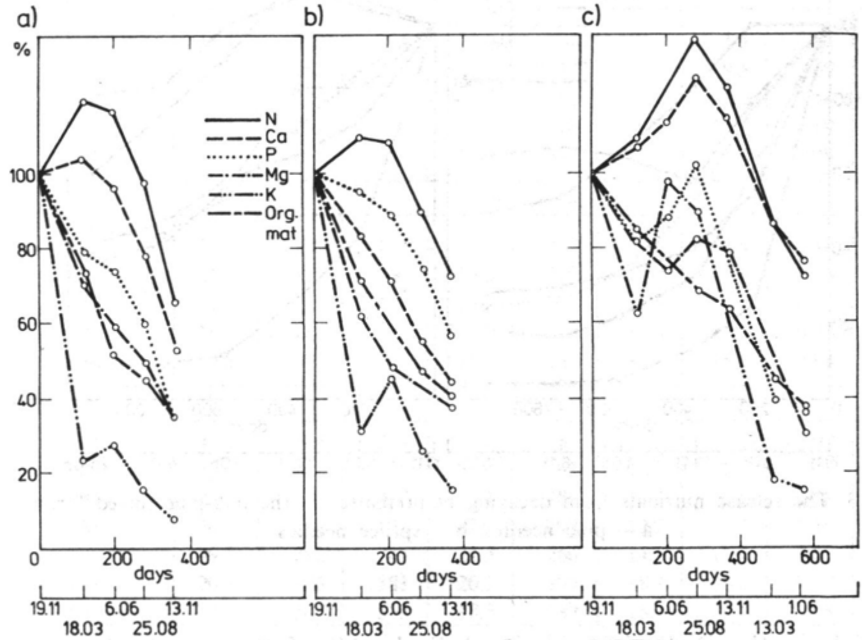


Fig. 2. The release of nutrients from decaying plant matter in the oak-linden-hornbeam forest. a — hornbeam leaves, b — linden leaves, c — oak leaves

and by 8% in decomposing hornbeam and oak leaves. In the initial stage of decomposition, the percentages of carbon and nitrogen also increased.

The changes in the content of the studied ash elements in the decaying plant material was different (Table 4). The potassium content (in percent) already clearly fell in the first phase of decomposition and remained to the end of the study on a decidedly lower than in the initial material. Calcium concentration in all of the studied materials rose and remained higher than in the initial materials throughout the duration of the experiment. The percentages of phosphorus and magnesium exhibited variable tendencies.

The proportions between the elements also changes (Table 5). The ratio of carbon to nitrogen and calcium fell. while its ratio to potassium widened, as did the ratio of nitrogen to phosphorous, potassium and magnesium. A change in the ratio of two elements can be the result of absolute accumulation of one of the elements due to its influx from the outside, or of relative accumulation brought about by the unequal release of the studied elements. The budget of the elements (Figs. 2, 3) showed that both of these processes took place in the decomposing plant

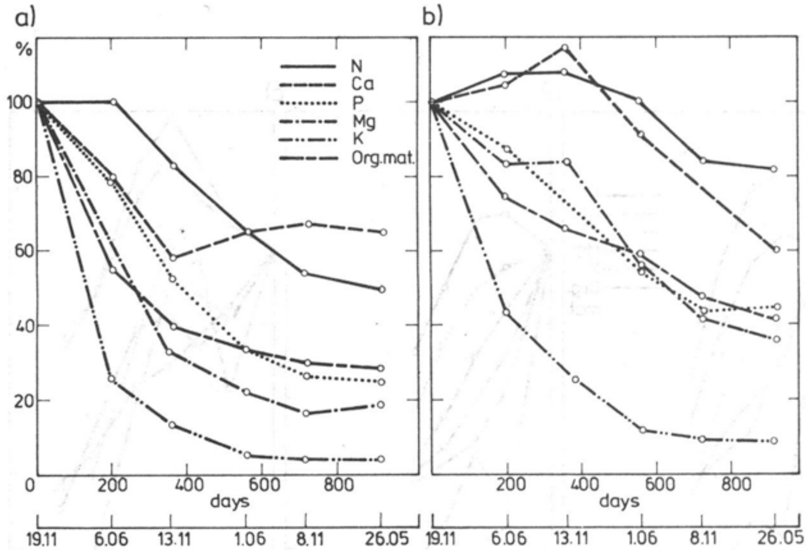


Fig. 3. The release nutrients from decaying plant matter in the oak-pine mixed forest. a — pine needles, b — spruce needles

materials in the Białowieża National Park. All of the examined elements underwent absolute accumulation at one time or another, even so mobile an element as potassium.

The elements can be arranged in the following orders on the basis of their release rates (Figs. 2, 3): K > Mg > P > Ca > N or K > Mg > Ca > > P > N.

Nitrogen was the slowest to be released from the decomposing materials. In the initial stages of decomposition, either no losses of this element were noted (pine Fig. 3a) or, more often, its absolute accumulation (the remaining materials) was observed. The period of accumulation lasted from 120 to 360 days, and the amount of stored nitrogen equalled from 7 to 35% of the initial amount. During the later stages of decomposition, this element was released but its losses were always less than that of weight.

Phosphorous was released from all of the studied materials from the BNP from the beginning of their decomposition. However, its initial rates of release were less than weight losses. In the later stages, this process was accelerated, and near the end of the study, the phosphorous

Table 5

Changes in the ratios of carbon and nitrogen to other elements in decomposing plant matter in the Białowieża National Park

| Duration of decay, days | C/N | C/P | C/K | C/Ca | C/Mg | N/P | N/K | N/Ca | N/Mg |
|---|---|---|---|---|---|---|---|---|---|
| | hornbeam leaves | | | | | | | | |
| 0 | 34.4 | 252 | 64 | 32.6 | 317 | 7.3 | 1.9 | 0.95 | 9.2 |
| 120 | 23.5 | 263 | 222 | 25.5 | 365 | 11.2 | 9.5 | 1.09 | 15.6 |
| 200 | 19.5 | 226 | 155 | 22.6 | 352 | 11.6 | 8.0 | 1.16 | 18.1 |
| 280 | 17.1 | 209 | 200 | 20.3 | 310 | 12.2 | 11.7 | 1.19 | 18.1 |
| 360 | 17.7 | 238 | 302 | 19.4 | 311 | 13.4 | 17.0 | 1.09 | 17.6 |
| | linden leaves | | | | | | | | |
| 0 | 31.1 | 295 | 105 | 17.9 | 297 | 9.5 | 3.4 | 0.58 | 9.6 |
| 120 | 21.7 | 235 | 250 | 16.3 | 359 | 10.8 | 11.6 | 0.75 | 16.6 |
| 200 | 17.5 | 202 | 140 | 15.2 | 370 | 11.5 | 8.0 | 0.87 | 21.2 |
| 280 | 16.3 | 186 | 188 | 15.5 | 329 | 11.4 | 11.5 | 0.95 | 20.2 |
| 360 | 15.5 | 191 | 241 | 15.2 | 284 | 12.3 | 15.5 | 0.98 | 18.3 |
| | oak leaves | | | | | | | | |
| 0 | 41.8 | 384 | 257 | 42.7 | 355 | 9.2 | 6.2 | 1.02 | 8.5 |
| 120 | 35.2 | 431 | 376 | 36.2 | 391 | 12.3 | 10.7 | 1.03 | 11.1 |
| 200 | 27.8 | 348 | 212 | 30.1 | 386 | 12.5 | 7.6 | 1.08 | 13.9 |
| 280 | 20.7 | 252 | 192 | 22.9 | 292 | 12.2 | 9.3 | 1.10 | 14.1 |
| 360 | 19.7 | 282 | 245 | 21.3 | 260 | 14.3 | 12.4 | 1.08 | 13.2 |
| 480 | 20.7 | 393 | 581 | 20.1 | 303 | 18.9 | 28.0 | 0.97 | 14.6 |
| 560 | 19.0 | 347 | 553 | 18.5 | 382 | 18.3 | 29.1 | 0.98 | 20.1 |
| | pine needles | | | | | | | | |
| 0 | 34.8 | 348 | 87 | 121.7 | 777 | 10.0 | 2.5 | 3.5 | 22.3 |
| 200 | 21.4 | 270 | 209 | 83.7 | 787 | 12.6 | 9.8 | 3.9 | 36.8 |
| 360 | 16.7 | 264 | 254 | 85.2 | 950 | 15.8 | 15.2 | 5.1 | 56.8 |
| 560 | 18.0 | 354 | 536 | 62.2 | 1185 | 19.7 | 29.9 | 3.5 | 66.0 |
| 720 | 19.7 | 389 | 579 | 55.6 | 1416 | 19.7 | 29.3 | 2.8 | 71.7 |
| 920 | 19.5 | 385 | 513 | 52.2 | 1172 | 19.7 | 26.3 | 2.7 | 60.2 |
| | spruce needles | | | | | | | | |
| 0 | 40.3 | 356 | 97 | 66.5 | 833 | 8.8 | 2.4 | 1.7 | 20.7 |
| 200 | 30.2 | 323 | 176 | 50.5 | 794 | 10.7 | 5.8 | 1.7 | 26.3 |
| 360 | 25.4 | 329 | 241 | 39.5 | 671 | 13.0 | 9.5 | 1.6 | 26.5 |
| 560 | 24.6 | 398 | 499 | 44.6 | 909 | 16.2 | 20.3 | 1.8 | 37.0 |
| 720 | 22.7 | 392 | 501 | 41.4 | 943 | 17.3 | 22.1 | 1.8 | 41.6 |
| 920 | 19.8 | 324 | 443 | 44.7 | 929 | 16.4 | 22.4 | 2.3 | 47.0 |

losses were usually equal to the weight losses. Only in oak leaves was it noticed that after the initial period of slow release, a period of absolute accumulation of phosphorous took place until levels close to initial values

Table 6

Coefficients of decomposition (k) and time necessary for the decay of 95% of the material ($T_{95}$) given in years

| Material | k | $T_{95}$ |
|---|---|---|
| Hornbeam leaves | 1.06 | 2.83 |
| Linden leaves | 0.91 | 3.30 |
| Oak leaves | 0.63 | 4.76 |
| Pine needles | 0.21* | 14.29* |
| Spruce needles | 0.30* | 10.00* |

* Values for the second and third years of the experiment.

were reached. Further decomposition of oak leaves was connected with intense phosphorous loss, the result of which was that at the end of the year and a half long experiment, the percentage of remaining phosphorous was very close to the percentage of retained weight.

The beginning stages of decomposition of hornbeam and oak leaves and spruce needles were characterized by absolute accumulation of calcium (Figs. 2a, 2c, 3b). This period lasted from 120 to 360 days and the amount of accumulated calcium equalled from 4 to 25% of the initial values.

The decomposition of linden leaves was accompanied from the beginning by the release of calcium (Fig. 3a). This process continued rather uniformly throughout the whole year (Fig. 2b). It seems that this is related to the high initial calcium content in the initial material.

The decomposition of pine needles was also accompanied from the start by the release of calcium (Fig. 3a), although this material was very poor in this element (C: Ca — 120: 1). It seems that this phenomenon can be explained by the very intense process of decay which causes the destruction of tissue structures and the release of the calcium contained in them. A certain degree of accumulation of calcium took place only after a year when the rate of pine needle decay clearly fell.

As usual, potassium was the quickest to be removed from the decaying plant material. Its losses were much greater than that of weight. At the end of the study, only 5 to 15% of the initial amount of this element remained in the decaying material, while 29 to 42% of the organic matter was left. The small increase in the absolute content of this element in the *Tilio-Carpinetum* after 200 days was probably due to the translocation of this element from newly fallen bracts, buds and flowers.

Magnesium was released more slowly than potassium. Initially, this process was similar to weight losses, later it generally proceeded quicker.

### THE PROCESS OF HUMIFICATION

In decaying plant materials, humification occurs simultaneously with mineralization. In each of the studied materials, the value of the humification index rose by several units (Table 2, 3). In spite of this, at the end of the study, the degree of humification turned out to be not very large and did not exceede the values characteristic of the AoL horizon of forest floor.

It was noted that the slower course of mineralization favored the accumulation of humic substances, which is shown by the rise in the humification index (Table 2 — oak leaves between the 260th and 360th days of decomposition. Table 3 — spruce needles between the 360th and 560th days of decomposition). Conversly, increasing the rate of decay caused the lowering of the effectivity of the process of humification.

## DISCUSSION

### RATE OF DECOMPOSITION

It can be seen from the data presented in this paper that the initial phase of decomposition of plant matter in the Białowieża National Park was determined by the morphological and chemical properties of the decaying material. The rate of decomposition of pine needles during the first year of the study was comparable to that of hornbeam and linden leaves, although their decomposition took place under different forest habitat conditions. Although the decomposition of oak leaves took place under the same conditions as did that of hornbeam and linden leaves, it differed significantly from the dynamics of this process for both of the above-mentioned species.

In the opinion of many authors, the most important determining factor of the process of decay in its initial stage is the ratio of carbon to nitrogen in the starting material (Bocock 1963, Wittich, cit. Baule and Fricker 1971, Jensen 1974, Zieliński 1980). The data gathered in the BNP support this thesis (compare the data from Tables 2, 3 and 5).

Not less important for the losses of weight in the initial stage of decomposition is the content of well soluble substances in the starting material. It was found that during one hour of extraction by shaking powdered material with water, 17% of the weight of hornbeam leaves, 18% of linden leaves, 10% of oak leaves, 12% of pine needles and 8% of the weight of spruce needles was extracted by the water. Comparison of these values with the data in Tables 2 and 3 indicates that a considerable part of the weight loss in the initial phase of decomposition was due to leaching.

Both the C/N ratio and the content of well soluble components were decisive factors in the very rapid decomposition of pine needles in the first year, since green needles with a relatively high nitrogen content were used in the study. It is known from literature (Baule and Fricker 1971) that the decomposition rates noted in the second and third years of the experiment are more typical for this type of material.

The course of decomposition is described by many authors, following Jenny et al. (1949) by a first order rate equation:

$$y_t = y_o\, e^{-kt},$$

where: $y_o$ — initial weight of the decomposing material, $y_t$ — weight of the material after time "t", $e$ — the base of natural logarithm, $k$ — coefficient of decomposition rate.

This equation was also used to describe the decomposition in the BNP, although with a certain reservation. It is known (Prusinkiewicz 1980) that the decomposition of plant matter does not proceed with a constant intensity at all times. The older the material, the slower its mineralization. In the five-year long studies on the decomposition of pine needles in the Bory Tucholskie (*Cladonio-Pinetum* forest), it was found that the results of especially the first year deviate from the theoretical curve drawn on the basis of the above equation, since the true reaction rate is much higher than the calculated one. The results of the subsequent years of the experiment showed better agreement with the theoretical values, and for this reason it was proposed that the indexes which are important for understanding the functioning of ecosystems, such as the coefficient of decomposition rate "k" and the time necessary for the disappearance of 95% of slowly decomposing material ($T_{95}$), be calculated omitting the first year data (Dziadowiec 1985). This proposition was followed when calculating the parameters of decay in the oak-pine mixed forest of the BNP (Table 6).

## RELEASE OF NUTRIENTS

The rate of release of nutrients from decaying plant matter depends only to a small degree on the rate of decomposition of the plant material. The deciding factors in the dynamics and course of this process are the form in which the element occurs in the plant material and the requirements of microorganisms for a given element. Elements which occur in plants mainly in ionized form (potassium, magnesium) are released from decaying plant matter much more quickly than would be expected from the weight losses occurring at this time. A decisive role in releasing these components is played by the process of leaching, which is indicated by the very intense widening of the ratio of carbon to these elements (Table 5).

The elements necessary for the building of the bodies of microorganisms (nitrogen, phosphorous) and those which are a part of persistent cellular structures of plants (calcium) are released during the decomposition of plant matter more slowly than would seem to result from the losses of weight. In the initial phase of decomposition, they can be completely retained by microorganisms, or even accumulated. In the literature on this subject, the opinion can be come across that the dynamics of the release of nitrogen and phosphorous is determined by the ratio of carbon to these elements. According to Block (cit. by Staaf 1980), there are certain critical values of these ratios, above which the entire amount of the released element will be retained and used by a microorganism for building of its own protein, and the mineralization of an element can only take place below these values. According to the author cited above, the critical C/N value lies between 15:1 and 33:1. Lutz and Chandler (cit. by Gosz et al. 1973) report narrower limits of this value — from 20:1 to 30:1.

The critical C/P values given in literature range from 200:1 to 480:1 (Gosz et al. 1973, Casgrove, cit. Staaf 1980). In our own studies in the "Las Piwnicki" Reserve near Toruń and in the Bory Tucholskie, it was found that the critical values of the carbon to phosphorus ratio ranged from 200:1 to 300:1 for decomposing leaves and around 400:1 for decomposing pine needles (Dziadowiec — in press).

The critical values hypothesis can be applied almost entirely to explain the course of releasing nitrogen and phosphorus from decaying plant matter in the BNP. The only exception is the release of phosphorus from decomposing oak leaves.

The composition of the initial materials was characterized by a rather low nitrogen content. The carbon to nitrogen ratio was 31:1 (linden) to 42:1 (oak), and for this reason, accumulation of this element took place in the initial phase of decomposition. Nitrogen release from the studied material began only when the C/N ratio fell to 18:1 (linden) and 25:1 (spruce) (Table 5, Figs. 2, 3).

In respect to phosphorous, the materials undergoing decomposition in the BNP (with the exception of oak) were characterized by lower than critical C/P values, and therefore no stoppages were noted in the release of this element. In respect to oak leaves, the initial losses of phosphorous should be attributed to leaching processes and not to microbiological ones. The release of phosphorous due to microbiological processes occurred only after 280 days of decomposition, when due to accumulation, the C/P ratio fell to 250:1.

The release of calcium is usually explained by the fact that in plants, most of this element occurs in the form of calcium pectinates forming the middle lamella of cell walls, and that calcium in this form can be released only when the cell walls have desintegrated. Because of this, the process of releasing calcium usually begins in the following year during late summer and autumn along with the intense development of basidium fungi myceliums, which are capable of decomposing cell walls (Wachowska-Serwatka 1966, Burges cit. Attiwill 1968).

The above facts only partially explain the course of calcium release in the BNP. In my opinion, a considerable influence on this process is exerted by the interrelations of calcium with other elements: carbon, nitrogen and phosphorus. The mutual interdependence of the release of calcium and nitrogen in the decaying materials is indicated by the constant, in some of the materials, N/Ca ratio, the C/Ca ratio which is very similar to the C/N ratio (Table 5) and also the positive correlation between the concentrations (expressed as percentages) of both elements. The correlation coefficients are: for linden leaves — 0.993, oak leaves — 0.968, spruce needles — 0.71. This is probably connected with the role of calcium in the metabolism of microorganisms, mainly in nitrogen assimilation, in fixation of free nitrogen, in nitrification and other processes (Marszewska-Ziemięcka 1974).

The transient accumulation of all of the studied elements needs to be discussed. In earlier publications on this subject (Dziadowiec and Kwiatkowska 1980, Dziadowiec — in press), and in the works of other authors (Attiwill 1968, Arvisto 1970, Gosz et al. 1973, Staaf 1980), attention was pointed to the fact of enrichment of decaying plant matter in nitrogen, iron and aluminum. Absolute accumulation can come about only due to the influx of an element from the outside. In the case of nitrogen, these outside sources can be: fixation of free nitrogen or its supply by precipitated water and the excrements and bodies of soil animals. The source of iron and aluminum, as has been found, is the soil environment of the decaying material, and their accumulation is the result of the high affinity of the humic compounds formed in the process of humification to both of these elements.

The soil around decaying plant matter can also be the source of other elements. In our unpublished studies, we have found that synthetic resin aliquots (Amberlite IR-120, $H^+$ form, exchange capacity 420 mv per 100 g resin) placed in the oak-linden hornbeam forest of the "Las Piwnicki" Reserve, absorbed 10–13 g Ca, 20–29 g Mg and 9–16 g K per 100 g of resin.

Decaying plant matter is also characterized by high ion-exchange capabilities, and the absorption capacity of the humic compounds formed in the process of humification is similar to that of the resin used in the experiment.

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## REFERENCES

Arvisto E., 1970. Razlozheniye i prevrashcheniye organicheskogo veshchestva v dernovo--karbonatnykh i burykh pochvakh. Sbornik Nauchnykh Trudov Estonskoy s-kh Akad. 65: 106–142.

Attiwill P. M., 1968. The loss of elements from decomposing litter. Ecology 49: 142–145.

Badura L., Pacha J., 1983. Porównawcze badania nad procesem rozkładu igieł w wybranych siedliskach leśnych. Acta Biol., Katowice 11: 101–110.

Badura L., Pacha J., 1984. Szybkość rozkładu igieł w borach otaczających Hutę Cynku w Miasteczku Śląskim. Acta Biol., Katowice 15: 102–103.

Baule H., Fricker C., 1971. Nawożenie drzew leśnych. PWRiL, Warszawa.

Bocock K. L., 1963. Changes in the amounts of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. J. Ecol. 52: 273–284.

Dziadowiec H., 1979. Szybkość rozkładu różnych ściółek leśnych w świetle badań stacjonarnych Pr. Kom. Nauk. V/37. Mat. Konf. Nauk. nt. "Próchnica gleb leśnych: akumulacja, rozkład, właściwości, klasyfikacja". Pol. Tow. Glebozn., Warszawa-Toruń, pp. 201–210.

Dziadowiec H., 1985. Razlozheniye sosnovoy khvoi v lishaynikovom sosniake (*Cladonio--Pinetum*). Studies about humus. Transactions of the VIIIth International Symposium. Praque 28th August-3rd September 1983. Vol. II, pp. 265–271.

Dziadowiec H., (in press). Uwalnianie składników pokarmowych w rozkładających się ściółkach leśnych. Acta Univ. N. Copernici.

Dziadowiec H., Kwiatkowska A., 1980. Mineralization and humification of plant fall in mixed forest stand of the reserve "Las Piwnicki" near Toruń. Ecol. Pol. 28: 111–128.

Faliński J. B., (ed.), 1968. Park Narodowy w Puszczy Białowieskiej. PWRiL, Warszawa.

Gosz J. R., Likens G. E., Bormann F. H., 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hempshire. Ecol. Monogr. 43: 173–191.

Jenny H., Gessel S. P., Bingham F. T., 1949. Comparative study of decomposition rates of organic matter in temperature and tropical regions. Soil Sci. 68: 419–432.

Jensen V.,. 1974. Decomposition of angiosperme tree leaf litter. In: Biology of plant litter decomposition. Dickinson C. H., Pugh G. J. R. (eds.). Acad. Press, London-New York, pp. 66–104.

Karkanis M., 1975. Decomposition of litter of various species of decidous trees and its effect on soil environment. Fragm. Flor. Geobot. 20: 477–496.

Marszewska-Ziemięcka J. (ed.), 1974. Mikrobiologia gleby i nawozów organicznych. PWRiL, Warszawa.

Metody analizy chemicznej roślinności łąkowej, gleby i wody. Cz. 1. Analiza chemiczna roślinności łąkowej. 1979. IMUZ, Falenty.

Prusinkiewicz Z., 1980. A mathematical model of energy budgets of forest humus of mull, moder and mor types in Poland. Geoderma 23: 79–93.

Prusinkiewicz Z., Dziadowiec H., Jakubusek M., 1974. Zwrot do gleby pierwiastków biogenów z opadem roślinnym w lesie liściastym i mieszanym na luźnych glebach piaskowych. Rocz. Glebozn. 25: 237–245.

Staaf H., 1980. Release of plant nutrients from decomposing leaf litter in a South Swedish beach forest. Holarctic Ecol. 3: 128–136.

Stachurski A., Zimka J. R., 1976. Methods of studying forest ecosystems nutrient release from the decomposing litter. Ecol. Pol. 24: 253–262.

Wachowska-Serwatka K., 1966. Sezonowe zmiany azotu i składników mineralnych w ściółce, glebie i w roślinach lasu mieszanego rezerwatu Lubsza. Acta Univ. Wratislav. 48, Pr. Bot. 8: 72–130.

Zieliński J., 1980. The effect of nitrogen content on the rate of organic matter decomposition. Pol. Ecol. Study 2: 167–182.

Zieliński J., 1984. Decomposition in the pine forest of Niepołomice. In: Ecological studies. 49, Grodziński W., Weisner J., Maycock P. F. (eds.), Forest ecosystems in industrial regions. Springer, Berlin-Heidelberg-New York-Tokyo, pp. 149–166.

## *Rozkład opadu roślinnego w grądzie i borze Białowieskiego Parku Narodowego*

### Streszczenie

W pracy przedstawiono wyniki badań nad rozkładem liści grabu, lipy i dębu w grądzie oraz igieł sosny i świerka w borze Białowieskiego Parku Narodowego. W grądzie liście grabu i lipy rozkładały się z podobną szybkością. Współczynniki rozkładu (k) wynosiły odpowiednio 1,06 i 0,91, a czas potrzebny do rozkładu 95% materiału ($T_{95}$) — 3 i 4 lata. Liście dębu rozkładały się wolniej: k — 0,63, $T_{95}$ — 5 lat. W borze rozkład igieł sosny był w pierwszym roku intensywniejszy niż igieł świerka, a w późniejszym okresie szybkość rozkładu igieł świerka była większa niż sosny. Parametry rozkładu dla drugiego i trzeciego roku badań wynosiły dla sosny k — 0,21 i $T_{95}$ — 14 lat, a dla świerka k — 0,30 i $T_{95}$ — 10 lat. Początkowe etapy rozkładu były determinowane przez stosunek węgla do azotu (C/N) i zawartość łatwo rozpuszczalnych składników w materiałach wyjściowych. Szybkość uwalniania składników pokarmowych nie zależy wyłącznie od szybkości rozkładu materiału organicznego. Czynnikami decydującymi są: forma występowania pierwiastka w roślinie i zapotrzebowanie mikroorganizmów na dany biogen. Na podstawie szybkości uwalniania pierwiastki można uporządkować w następujący szereg: $K > Mg > P > Ca > N$ lub $K > Mg > Ca > P > N$. W uwalnianiu azotu, fosforu i wapnia decydującą rolę odgrywają procesy mikrobiologiczne, natomiast potas i magnez uwalniane są głównie przez wymywanie.

Stopień zaawansowania procesu humifikacji w materiałach rozkładających się w BPN nie przekraczał wartości charakterystycznych dla poziomu AoL próchnic nadkładowych. Wolniejszy przebieg procesu mineralizacji sprzyja nagromadzeniu się substancji humusowych i odwrotnie, przyspieszenie tempa mineralizacji zmniejsza efektywność procesu humifikacji.