

Decomposition of Four Tree Species Leaf Litters in Headwater Riparian Forest

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Abstract

Litterbag studies on decomposition of Black alder, European beech, Norway maple and Red oak leaves were conducted in headwater riparian forest in northern Poland. Alder litter represent material produced *in situ*, whereas the remaining litters materials originating from external sources, supplied by wind. The highest intensity of decomposition was observed in rich in nitrogen alder leaves ($k = 2.77 \text{ year}^{-1}$) and lower in maple ($k = 1.02 \text{ year}^{-1}$), oak ($k = 0.49 \text{ year}^{-1}$) and beech ($k = 0.49 \text{ year}^{-1}$). In alder leaves, accumulation of N in the first phase of decomposition, and decrease in its concentration and stocks in the second phase were indicated. However, in leaves of remaining species accumulation of N over the whole experiment time was observed. Concentration of phosphorus in poor in the element alder leaves for all the time increased, and in richer maple, oak and beech leaves leaching in the first and accumulation in the second phase were observed. Potassium and magnesium were intensively leached during the first two months of decomposition from each litter, and in the next months their concentration was relatively stable, or increased. Release of calcium was related to weight loss of leaves, and its concentration was relatively stable over time. An intensive accumulation of iron and aluminium was observed in alder, maple and oak leaves, and much smaller in beech leaves. The observed differences among the litters in decomposition rate and nutrients release dynamics was strongly affected by chemical composition of initial materials. Especially large differences were observed among alder litter, as produced *in situ*, and the remaining litters originating from external sources. Based on the data obtained, we can conclude that beech, oak and maple litterfall influx from external sources can influence the intensity of accumulation, stocks and quality of soil organic matter in the investigated ecosystem.

Key words: litterfall decomposition, Black alder, European beech, Norway maple, Red oak, headwater areas

Introduction

The importance of litterfall decomposition, as a stage of matter and energy balance in natural and some modified ecosystems, is confirmed by results of many studies. In forest ecosystems decomposition is a critical process in nutrient cycling, which often determine their bioavailability. Chemical composition of initial material, soil properties, including biological activity, species composition of plant communities, and climatic conditions (especially temperature and humidity) are the most important factors affecting intensity of the process (e.g., Stachurski and Zimka 1975, Kotowski 1979, Herlitzius 1983, Cortez 1998, Pereira et al. 1998, Moore et al. 1999, Albers et al. 2004, Drewnik 2006, Preston et al. 2009). Sometimes it is also observed a significant impact of human activity (Cortufo et al.

1995, Emmaerling and Eisenbeis 1998, Gunapala et al. 1998, Li et al. 2009, Smith et al. 2009).

Quantitative proportions between annual production of litterfall and its decomposition rate in a longer time determine forms and stocks of soil organic matter. Tree species associated with riparian areas (like alder, poplar and willow) produce rich in nutrients, soft, susceptible to decomposition litterfall, which is almost completely decomposed within the first year (Jonczak 2009). However, headwater riparian forests are usually located in land depressions and can be supplied with different litters from neighbouring areas. Litterfall influx from external sources can influence soil properties and plant species composition. Humid microclimate and high availability of nutrients in the soils of headwater areas are factors, which can accelerate decomposition of resistant to decomposition “external” lit-

ters, like oak or beech (Dziadowiec 1990, Cortez 1998, Heim and Frey 2004, Lorenz et al. 2004, Ritter 2005, Annunzio et al. 2008). On the other hand, water surplus, which is typical for riparian areas, can also reduce intensity of the process (Dziadowiec 1987). Identification of the patterns of different litters (which can supply headwater areas) decomposition can be a basis to determine their potential influence on the ecosystems of headwater areas.

The aim of the study was to evaluate decomposition intensity and nutrients release patterns of four types of leaf litters in headwater riparian forest in northern Poland. Alder litterfall is produced *in situ* and the remaining litters (beech, maple and oak) are materials from external sources, inflowing to the investigated spring niche from neighbouring areas.

Materials and Methods

Stand characteristics

The studies were conducted in northern Poland, in the valley of the Kamienna Creek - almost completely afforested left bank tributary of the Słupia River. Mean annual temperatures for the region is about 7.6°C, and sum of precipitation 770 mm. Average annual temperature measured 1 cm above ground level in the study plot during the experiment period was +7.7°C, with maximum +32°C in July and minimum -13.5°C in February (Figure 1). The valley of the Kamienna Creek is deeply incised in Holocene sands and loams of the headwater valley with riparian area in the bottom. The study plot (40 × 50 m) was located in the

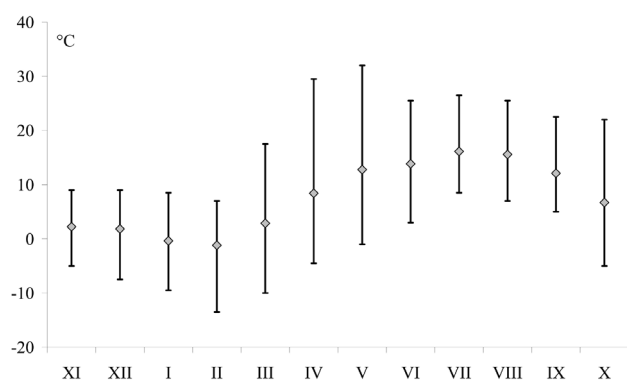


Figure 1. Mean, minimum and maximum monthly temperatures measured 1 cm above ground level during the experiment period (11.2011-10.2012)

upper course of the valley, on the area of headwater peatland [54°19'N; 17°10'E] covered with 40-86-year-old Black alder (*Alnus glutinosa*) in tree layer and very rich in species herb layer (106 species of vascular plants, 17 species of mosses and 8 species of liverworts were noticed in 2012). Norway maple (*Acer platanoides* L.), Red oak (*Quercus rubra* L.) and European beech (*Fagus sylvatica* L.) grow in the vicinity of peatland, along valley slopes, and their litterfall also supply peatland. Thick to 90 cm Histosols formed from alder and alder-sedge peat were noticed in the study plot. The soils were slightly acid, very rich in nitrogen and medium rich in phosphorus. Selected properties of the soils in top 1-10 cm horizon are presented in Table 1.

Litterbag studies

The studies were carried out using litterbags method (1×1 mm mesh, size 20×20 cm). Leaves of alder, maple, oak and beech were collected from autumn maximum of litterfall in the year 2011 and dried in 65°C until the constant weight. Litterbags were filled with 10.00 g dry mass of leaves, and placed in a study plot in three locations on 1st November 2011. Ten litterbags of each type of litter (each tree species) were placed in each location. The litterbags containing particular litter types were separated from each other. One litterbag containing alder, maple, beech and oak litters was taken from three locations every two months. After mechanical removal of roots, fresh parts of plants, and other foreign particles, samples were dried in 65°C until the constant weight, weighted and homogenized for chemical analysis. Temperatures of air 1 cm above ground level, in 1 hour intervals, were recorded during the experiment period using electronic data logger.

Chemical analysis of decaying leaves

The content of C was analyzed with Alten method and N with Kjeldahl method. Concentrations of P, K, Ca, Mg, Fe and Al were analyzed in a solution after samples digestion in a mixture of 30% H₂O₂ and 65% HNO₃. Concentration of P in solution was analyzed colourimetrically with molybdenum blue method and remaining elements with microwave plasma atomic emission spectrometry (Agilent 4100 MP-AES). In initial materials additionally was analyzed pH_{H2O} with potentiometric method, content of ash as residue after ignition at 550°C and content of lignin with gravi-

Location	pH _{H2O}	SOM	C	N	P	K	Ca	Mg	Fe	Al	C/N	C/P
1	6.1	725.0	422.3	33.0	1.21	0.87	22.28	1.10	10.26	2.43	13	349
2	6.5	810.8	437.0	32.9	1.02	0.55	23.55	1.13	2.95	1.31	13	428
3	5.9	805.2	449.4	29.7	1.56	0.51	20.17	1.11	19.76	2.20	15	288

Table 1. Selected properties of topsoil (0-10 cm) in locations of litterbag exposition

metric method after hot extraction of samples in 72% H₂SO₄ (Klason method).

Soil analysis

0-10 cm topsoil samples were collected from every litterbag locations, dried at 40°C until the constant weight, milled and analyzed. The pH was analyzed with potentiometric method in soil: water proportions 1:10, the content of organic carbon with Alten’s method and total nitrogen with Kjeldahl method. The content of P, K, Ca, Mg, Fe and Al was analyzed in a solution after samples digestion in a mixture of 65% HNO₃, 60% HClO₄ and 95% H₂SO₄ in a proportion of 20:5:1 by volume. The concentration of P in solution was analyzed colourimetrically with molybdenum blue method, and the remaining elements with microwave plasma atomic emission spectrometry (Agilent 4100 MP-AES).

Statistical analysis

Mean values (based on three replications) of remaining weight of leaves and concentration of elements were calculated for every tree species and every sampling term. Stocks of elements (as % of initial stocks) were calculated on the basis of their concentration (% of dry mass) and % of remaining weight of decaying leaves. Decomposition rates, *k*, were calculated after Olson model (Olson 1963):

$$X_t = X_o e^{-kt}$$

where: X_o is a weight of initial material, X_t is a weight of decaying material after time *t*, *k* is a rate of decomposition, *e* is a base of natural logarithm

Results

Properties of initial materials

Initial materials used for the experiment differed in chemical composition (Table 2, 3). Maple leaves contained the highest amount of ash (106.11 g·kg⁻¹), and oak leaves the lowest (53.11 g·kg⁻¹). The content of lignin ranged from 305.60 g·kg⁻¹ in alder leaves to 419.97 g·kg⁻¹ in beech. Alder leaves were rich in nitrogen (20.72 g·kg⁻¹) and poor in phosphorus (0.65 g·kg⁻¹). Leaves of remaining species contained 6.29-7.62 g·kg⁻¹ of N and 0.77-1.04 g·kg⁻¹ of P. In each litter low concentration of K (3.11-7.83 g·kg⁻¹), and relatively low concentration of Ca (10.58-23.79 g·kg⁻¹) and Mg (1.35-1.88 g·kg⁻¹) were observed. The concentrations

Table 2. Reaction and content of ash and lignin in initial materials

	Alder	Maple	Oak	Beech
pH	4.30	4.27	4.19	4.90
Ash [g·kg ⁻¹]	59.61	106.11	53.11	74.35
Lignin [g·kg ⁻¹]	305.60	327.40	343.34	419.97

of Fe and Al were very low comparing to other elements and ranged from 0.06 to 0.20 g·kg⁻¹ and 0.03-0.10 g·kg⁻¹, respectively.

Decomposition rates

The highest decomposition rate (*k* = 2.77 year⁻¹) was observed in alder leaves, lower one in maple leaves (*k* = 1.02 year⁻¹), and the lowest one in oak (*k* = 0.49 year⁻¹) and beech leaves (*k* = 0.49 year⁻¹). At the end of experiment it was noticed weight loss of 90%, 64%, 39% and 39%, respectively (Figure 2).

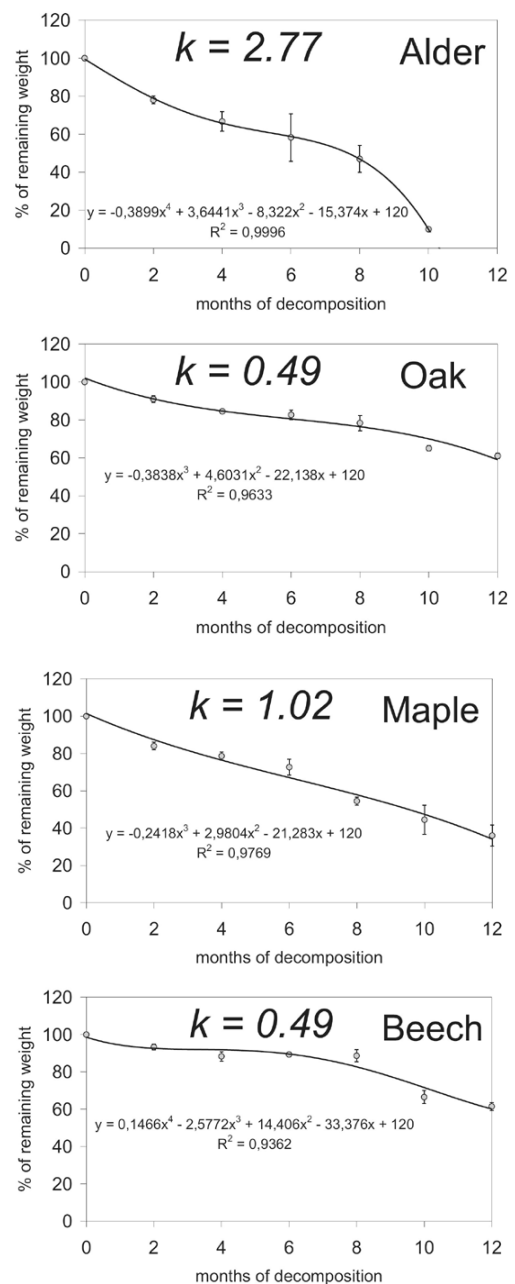


Figure 2. Weight loss and decomposition rate, *k*

Release of elements during decomposition

A continuous increase of N concentration was observed in maple, oak and beech leaves (Table 3). The increase was 233%, 224% and 242% of initial concentration, respectively (Figure 3). Stocks of the element were relatively constant over time for maple and slightly increased for oak and beech. Increase of N concentration (from 20.72 g·kg⁻¹ to 31.65 g·kg⁻¹) during the first six months and decrease in the second phase of decomposition (to 27.32 g·kg⁻¹) was observed in alder leaves. Stocks of N continuously decreased. C/N ratios decreased over time in each litter – from 23:1 to 14:1 in

alder, from 57:1 to 24:1 in maple, from 76:1 to 33:1 in oak and from 63:1 to 26:1 in beech leaves (Table 3).

Decrease in P concentrations in relation to initial ones on average 8.4% in alder, 20.3% in maple, 47.2% in oak and 44.4% in beech leaves were observed during the first two months of decomposition (Figure 4), following increase in later stages. The observed maximum values were 211.4% for alder and 155.3% for maple. In oak and beech leaves the concentration of P reached only initial value. C/P ratios increased during the first 2-4 months in each litters, and then decreased to 319:1 in alder, 352:1 in maple, 597:1 in oak and 414:1 in beech leaves (Table 3).

Both concentration and stocks of K rapidly decreased during the first two months of decomposition (Table 3, Figure 5), and were constant (in alder and maple), or increased (in oak and beech) later. The concentration of Ca was relatively constant over the experiment time, and was at level 14.94-18.96 g·kg⁻¹ for alder, 18.85-23.90 g·kg⁻¹ for maple, 12.35-16.15 g·kg⁻¹ for oak and 10.58-12.92 g·kg⁻¹ for beech. Stocks of the element decreased according to weight losses (Figure 6). Similar schemes of release and comparable concentrations of Mg were observed in each litter. Relatively rapid decrease in concentration of the element was noticed in the first two months of decomposition (loss of 18.1-35.6% of initial concentration), and slower in the remaining time (Figure 7). Finally, the concentra-

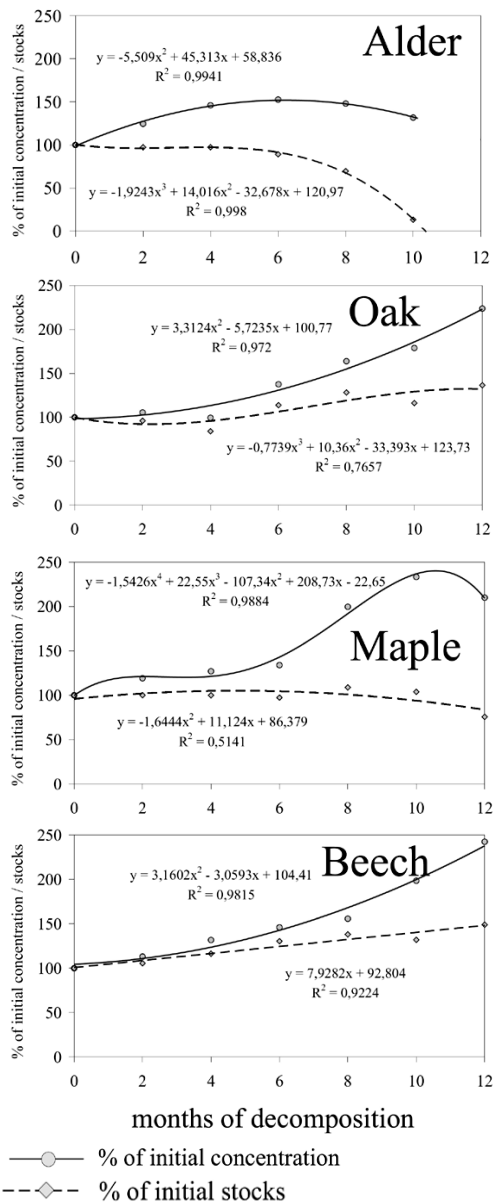


Figure 3. Changes in the concentration and stocks of nitrogen as percentage of initial ones during leaves decomposition

Table 3. Chemical composition of leaves during their decomposition

Months	g·kg ⁻¹								C/N	C/P
	C	N	P	K	Ca	Mg	Fe	Al		
Black alder										
0	471.29	20.72	0.65	6.90	14.94	1.57	0.15	0.03	23	721
2	482.54	25.82	0.60	1.31	16.40	1.14	0.40	0.07	19	832
4	487.04	30.26	0.71	0.95	16.12	1.09	0.34	0.10	16	690
6	464.89	31.65	0.79	1.17	17.11	1.05	0.56	0.10	15	593
8	433.18	30.69	0.84	1.13	16.33	1.08	0.43	0.19	14	516
10	440.44	27.32	1.38	1.42	18.96	1.01	0.60	0.25	16	319
12	-	-	-	-	-	-	-	-	-	-
Norway maple										
0	436.93	7.62	0.77	7.83	23.79	1.88	0.18	0.08	57	568
2	438.35	9.09	0.61	1.36	22.05	1.21	0.23	0.08	48	725
4	428.47	9.69	0.61	1.01	23.63	1.20	0.25	0.09	45	700
6	440.98	10.22	0.78	1.26	23.90	1.04	0.44	0.14	43	580
8	424.78	15.23	1.08	1.70	23.04	1.24	0.60	0.34	28	403
10	419.72	17.79	1.19	1.66	23.35	1.50	0.68	0.31	24	352
12	422.85	16.01	0.97	2.11	18.85	1.26	0.51	0.24	27	443
Red oak										
0	478.22	6.29	0.84	3.80	12.39	1.35	0.06	0.04	76	572
2	459.05	6.63	0.44	1.71	12.35	1.11	0.07	0.03	70	1043
4	476.30	6.26	0.45	0.98	12.93	1.10	0.07	0.04	76	1063
6	471.56	8.65	0.57	1.11	12.75	1.07	0.20	0.08	55	825
8	460.81	10.29	0.69	1.30	16.15	1.14	0.23	0.22	45	668
10	473.63	11.24	0.80	1.56	14.76	1.15	0.35	0.17	42	597
12	459.39	14.06	0.73	1.97	14.04	1.12	0.33	0.20	33	633
European beech										
0	436.73	6.94	1.04	3.11	10.58	1.46	0.20	0.10	63	418
2	436.97	7.85	0.58	0.79	10.98	1.07	0.24	0.10	56	756
4	446.42	9.15	0.58	0.67	11.42	0.92	0.26	0.12	49	765
6	445.10	10.14	0.65	0.94	11.24	1.08	0.21	0.12	44	700
8	435.63	10.81	0.85	1.17	12.69	0.97	0.24	0.14	40	511
10	436.87	13.78	1.06	1.55	12.34	1.14	0.48	0.20	32	414
12	442.11	16.83	1.06	2.09	12.92	1.15	0.49	0.23	26	418

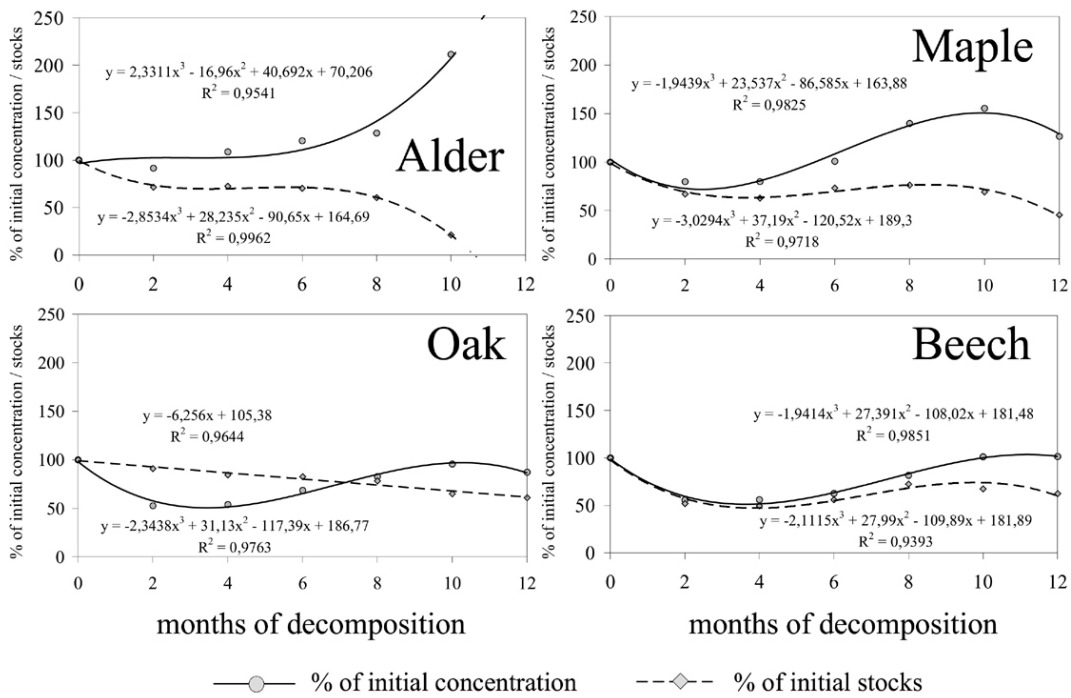


Figure 4. Changes in the concentration and stocks of phosphorus as percentage of initial ones during leaves decomposition

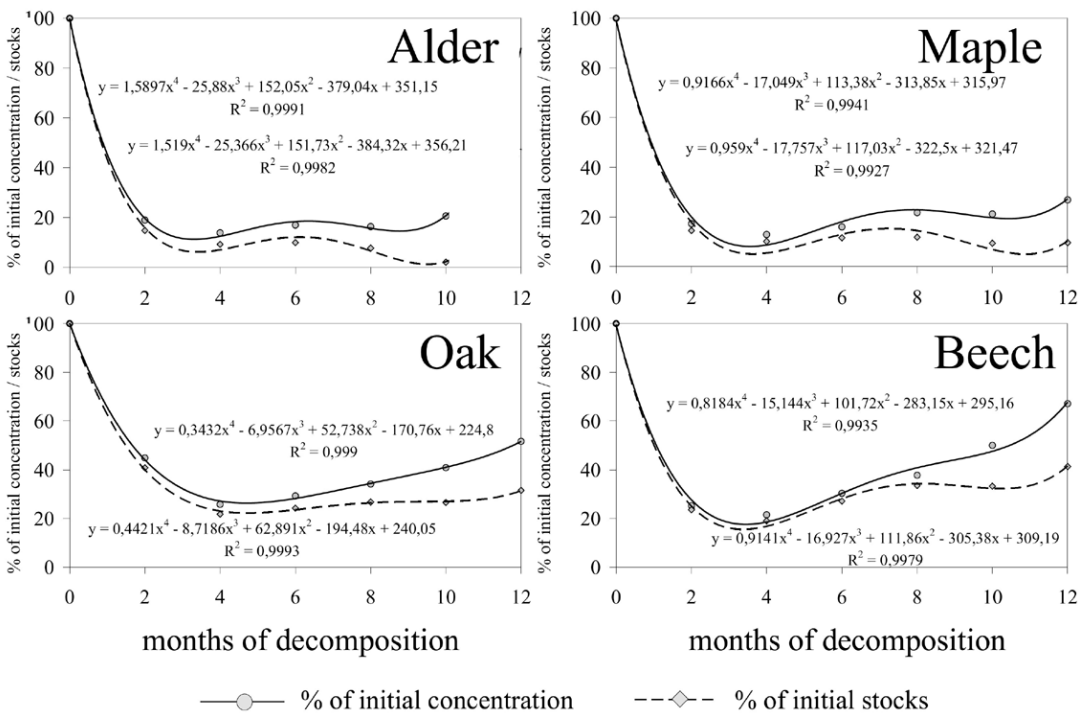


Figure 5. Changes in the concentration and stocks of potassium as percentage of initial ones during leaves decomposition

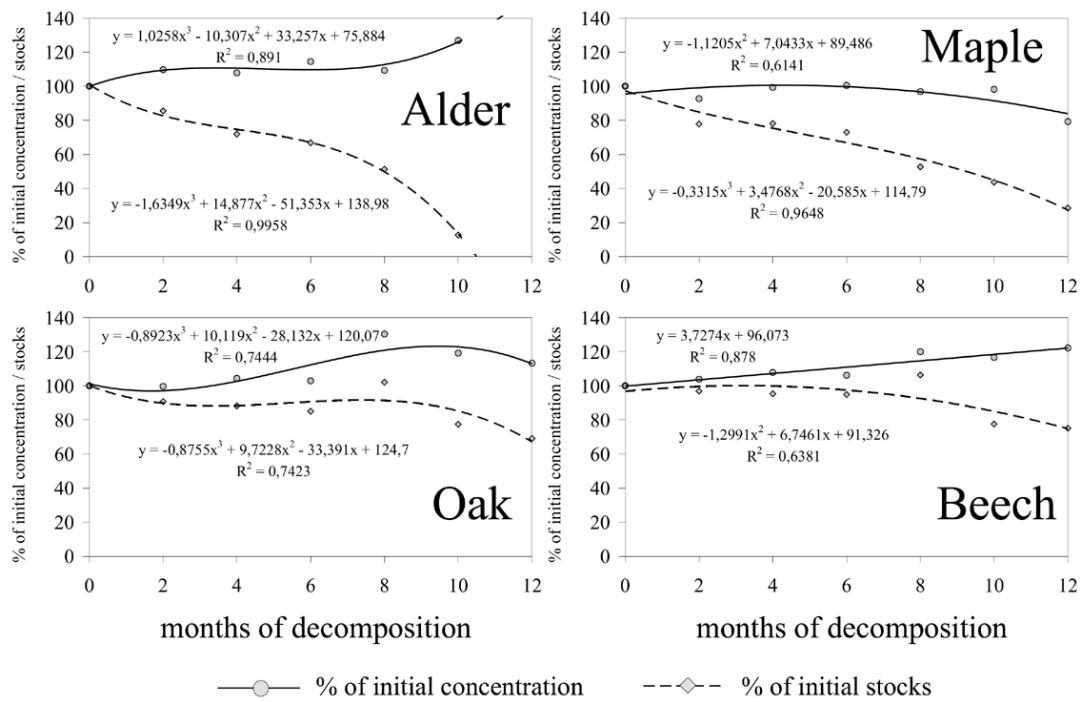


Figure 6. Changes in the concentration and stocks of calcium as percentage of initial ones during leaves decomposition

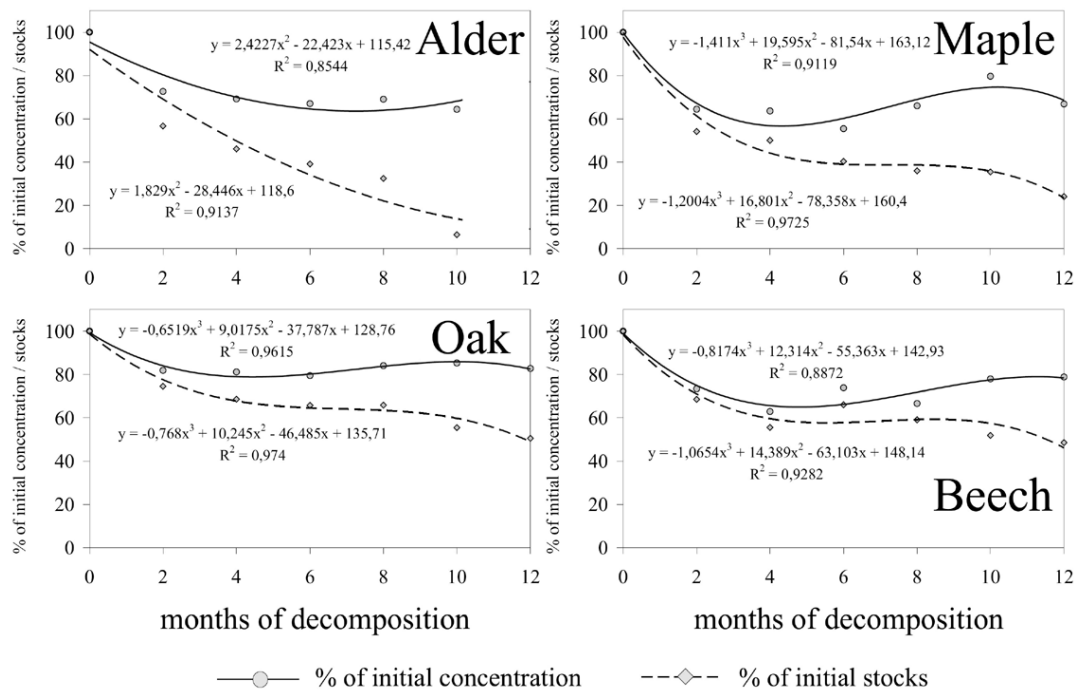


Figure 7. Changes in the concentration and stocks of magnesium as percentage of initial ones during leaves decomposition

tion of Mg was 64.4% of initial in alder, 66.8% in maple, 82.8% in oak and 78.8% in beech leaves.

Typical for leaf litters low initial concentration of Fe (0.06-0.20 g·kg⁻¹) and Al (0.03-0.10 g·kg⁻¹), and accumulation of the elements during decomposition was observed in the investigated materials (Table 3, Fig-

ures 8, 9). The observed maximum increase of Fe concentrations were 391.8% of initial ones for alder, 373.0% for maple, 535.3% for oak and 238.9% for beech. As to Al, the increases were 838.5%, 450.8%, 551.6% and 227.2%, respectively.

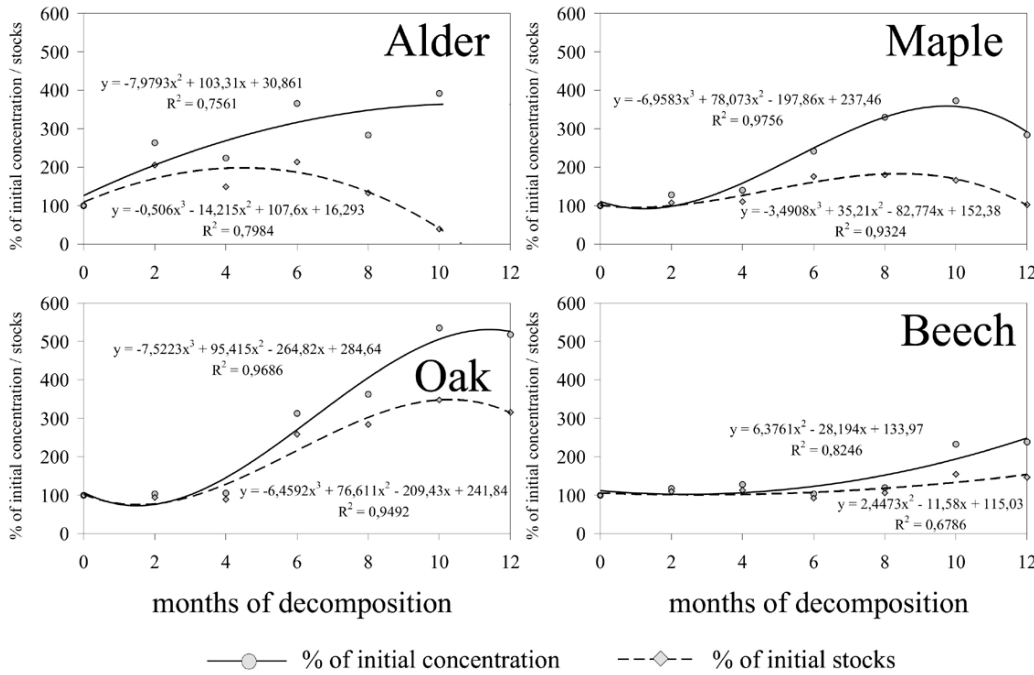


Figure 8. Changes in the concentration and stocks of iron as percentage of initial ones during leaves decomposition

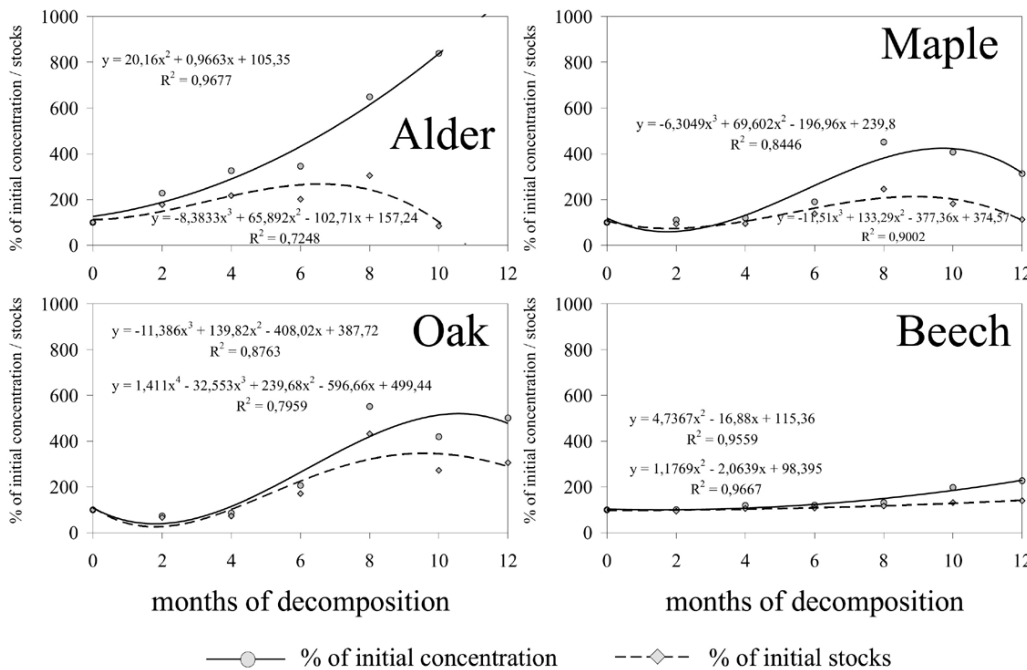


Figure 9. Changes in the concentration and stocks of aluminum as percentage of initial ones during leaves decomposition

Discussion

Litterfall, as a source of various chemical compounds and elements, can strongly influence properties of forest soils and direction of soil-forming processes (Norden 1994, Jonczak 2012), and in a consequence soil microbiological activity and also species composition of plant communities in the herb layer. It can be assumed, that especially large effect of litterfall may occur in sensitive sites, like headwater areas. Spring niches, as integral components of headwater areas, are usually small objects, located in land depressions along river valleys. They are often supplied with litters from neighbouring areas. The recognition of properties and decomposition patterns of the litters can help us to assess their potential effect on the functioning of these ecosystems.

Humid microclimate and high availability of nutrients in soils undoubtedly are factors accelerating litterfall decomposition in headwater areas. Both favourable site conditions in the investigated stand and properties of initial material have contributed to very fast decomposition of alder leaves. Their rate of decomposition, $k = 2.77 \text{ year}^{-1}$, was higher than reported by Wedderburn and Carter (1999), $k = 2.13 \text{ year}^{-1}$, and much higher than that reported by Pereira et al. (1998), $k = 0.908 \text{ year}^{-1}$. The rate of decomposition of maple leaves (1.02 year^{-1}) was comparable to literature data (Adams and Angradi 1996). Oak leaves decomposed relatively slow ($k = 0.49 \text{ year}^{-1}$), comparing to data of Dziadowiec (1987) ($k = 0.76 \text{ year}^{-1}$), or Lorenz et al. (2004) ($k = 0.69 \text{ year}^{-1}$). The observed rate of decomposition in beech leaves ($k = 0.49 \text{ year}^{-1}$) is within the range of high values reported by other authors (Cortez 1998, Heim and Frey 2004, Lorenz et al. 2004, Ritter 2005, Annunzio et al. 2008). High intensity of beech leaves decay is probably an effect of relatively mild and wet coastal climate and the influence of high availability of external nitrogen (as component of soils and alder leaf litterfall). The influence of coastal climate conditions on fast decomposition of beech leaves was also confirmed by Jonczak (2014) in 120-years beech stand located about 1 km from the investigated headwater area. Also the effect of external nitrogen on litterfall decomposition intensity is confirmed by many results of field and laboratory experiments (e.g., Rustad and Cronan 1988, Taylor et al. 1989, Dziadowiec 1990, Prescott 1996, Robinson et al. 1999, Gartner and Cardon 2004). Decomposition of litterfall is at least two-phase process. Climate conditions and quality of initial material strongly affect its intensity in the first phase (e.g. Berg et al. 1987, Limpens and Berendse 2003), and the content and chemistry of lignin play an important role in the second phase (e.g. Gill and Lav-

ender 1983, Berg et al. 1984, Tablot et al. 2012). We observed relatively slow decomposition of leaves during the first phase of the experiment, which is a result of cumulative effect of reduced by low temperature soil biological activity during autumn and winter periods and deficit of nitrogen in initial materials, as indicated by high values of C/N ratios in maple, oak and beech leaves. Faster decomposition in the second half of the year was affected by increase in temperature, influx of external nitrogen and litterfall colonization by microorganisms.

Changes in chemical composition of litters observed during their decomposition are a result of varied over time intensity of different processes, like leaching, mineralization, humification, colonization by microorganisms, supplying and binding of foreign substances (especially mineral particles of soil and ions). Dziadowiec (1990) divided elements into three groups: elements which are released faster than weight loss (Na, K), elements released at rate similar to weight loss (P, Mg, Ca), and elements releasing slower than weight loss (N, Al, Fe).

Dynamics of N concentration and stocks during decomposition varied between rich in the element alder leaves and poor external litters. We can identify two phases in N release from alder leaves. During the first phase it was observed increase of the element concentration, and relatively constant its stocks, despite weight loss. During this phase leaching of nitrogen was compensated by influx of external nitrogen. In the second phase we observed decrease both in concentrations and stocks of N. In poor in nitrogen leaves of maple, oak and beech intense accumulation of N was observed over the whole time of experiment. These data confirm, that nature of N release from decaying litters is complicated, which is also confirmed by many models of the process (e.g., Berg and Staaf 1980, Bosatta and Staaf 1982, Melillo et al. 1982, McLaugherty et al. 1985, Aber et al. 1990, Berg and Cortina 1995). Initial concentration of N is very important factor in the most of them.

Phosphorus can be released via different patterns, depending especially on its concentration in initial material and site conditions. During the first phase of decomposition usually it is observed its leaching. In next stages intensity of P release is strongly affected by its bioavailability. Low availability resulted in intensive uptake of P by plant roots (sometimes with applying of enzymatic mechanisms) (McGill and Cole 1981). Accumulation of P during litterfall decomposition indicates high bioavailability of the element in soils (Dziadowiec 1990, Jonczak 2009). However, the observed accumulation can be a result of penetration of decaying material by rich in P fungal hyphae (Dziadowiec and Hołownia

1979). The concentration of P in alder leaves increased slowly during the first eight months of decomposition, and very fast during the last two months, whereas its stocks were closely related to weight loss. In richer in P maple, oak and beech leaves it was observed its leaching during the first two months, accumulation in the second phase (to the tenth month), and decrease again during last two months.

Potassium is present in plants only as ionic form, so it can be easily leached, even from alive plant organs. Fast release of K just in the first phase of decomposition is observed in every types of litter, irrespective of climatic zone, and it was also observed in the investigated stand. Leaching is also an important mechanism in release of Mg, and was observed in every litter in the investigated stand in the first phase of their decomposition. After the first two months we observed 18.1-35.6% lower concentration, and 25.5-45.9% lower stocks of this element. Then the concentration of Mg remained constant or increased. The observed dynamics is typical for this element (Edmonds 1984, Dziadowiec 1990).

Concentration of Ca during litterfall decomposition is usually constant or show upward trend (Dziadowiec 1990, Jonczak 2009), which is a result of the presence of the most of this element in resistant to decomposition cellular structures (calcium pectinates of middle lamella). Only a small part of Ca is present in easy soluble components. Dziadowiec (1987) reported that Ca release is strongly related to the concentration of N. In the investigated litters release of Ca was related to weight loss.

Increasing trends of iron and aluminium concentrations are usually observed during leaf litters decomposition. Binding of Fe and Al ions by newly formed humic acids (Dziadowiec 1990), and pollution of decaying material with rich in the elements mineral particles of soil (especially clay) are pointed as a reason of the process. The observed increase in Fe concentration in our experiment was from 238.9% in beech to 535.3% in oak leaves, and in Al from 227.2% in beech leaves to 838.5% in alder leaves. These values are within the range of data reported by many authors (e.g. Staaf 1980, Dziadowiec 1987).

Conclusions

Results of our studies show different rates of decomposition and patterns of elements release during the process in alder, as material produced in situ, and maple, oak and beech litters, as materials originating from external sources. The highest decomposition rate ($k = 2.77 \text{ year}^{-1}$) was noticed for alder, lower one for maple ($k = 1.02 \text{ year}^{-1}$) and the lowest one for beech and oak

leaves ($k = 0.49 \text{ year}^{-1}$). A large intensity of alder leaves decomposition, comparable with maple and relatively slow with oak was observed in the investigated stand, compare to the data of other authors. The observed decomposition rate of beech leaves was within the highest values reported by other authors, which is an effect of relatively mild climate of the investigated stand and high availability of nitrogen in the soils. Chemical composition of initial materials and high abundance of nitrogen and some other elements in the soils also were factors strongly affecting nutrients release dynamics from the investigated litters. An accumulation of nitrogen was observed in the first phase of decomposition of every litter, and decrease of its concentration and stocks in the second phase in alder leaves, whereas in leaves of the remaining species it was observed accumulation of N over the whole experiment time. In phosphorus-poor alder litter it was noticed increase of the concentration of this element, whereas in richer remaining litters leaching in the first phase and accumulation in the second phase. A typical form of potassium and magnesium release patterns (intensive leaching) was observed in each litter. Release of calcium was related to weight loss of leaves, and its concentration was relatively stable over time. An intensive accumulation of iron and aluminium was observed in alder, maple and oak leaves, and much smaller in beech leaves. Our data show that influx of litters from external sources is undoubtedly factor disturbing functioning of headwater ecosystems. Differences in chemical composition, decomposition rates and nutrients release dynamics during decomposition of produced *in situ* and external litters can influence nutrient balance, soil organic matter accumulation and its quality, soil chemistry and water quality in these ecosystems. Knowledge about the influence of various tree species litters on the functioning of headwater areas can be useful for their protection, which can be contributed by suitable shaping of tree species composition in adjacent to headwaters production forests.

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