Forest Ecosystems in Industrial Regions

Studies on the Cycling of Energy
Nutrients and Pollutants in the Niepołomice Forest
Southern Poland

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Chapter 7

Energy, Nutrient, and Pollutant Budgets of the Forest Ecosystems

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7.1 Introduction

It is now time to piece together the final energy and nutrient budgets for the coniferous and deciduous forests of Niepołomice. The budgets will be principally of the input-output type but with insights into the intrasystem flows and cycles presented whenever possible. The input from precipitation is based on data from Chapters 2 and 5, whereas the output of water from the woodland watershed is taken from Chapter 6. The estimates of biomass or standing crop at the producer trophic level are derived mainly from Chapter 3, those for consumers from Chapter 4, and those for the litter subsystem are taken from Chapter 6. Despite the careful planning of research, it was necessary to supplement estimates from data from various sources.

The approach to construct energy, nutrient, and pollutant budgets followed the classic examples for watershed studies of forest ecosystems (e.g., Likens et al. 1977, Bormann and Likens 1979, Sollins et al. 1980, Swank and Waide 1980). A graphical presentation of budgets has also been used (see Appendix Figs. 7.9–7.20) and similar terminology, with the exception of two terms: retention and accumulation. The term "retention" is used here as the net difference between total output and input, while "accumulation" is calculated as the sum of dry mass, energy or nutrient storage in all components of the ecosystem.

This chapter involves energy budgets and such nutrients as N, P, K, Ca, and S and the following pollutants (S, Fe, Ni, Cu, Zn, Cd, and Pb). When compared with other attempts, our budgets undoubtedly have many shortcomings, but at the same time represent a broader perspective provided by the emphasis placed on the consumer subsystem and on pollutant cycles.

Any study of energy flow and nutrient cycles in an ecosystem with all its complicated trophic relationships represents a formidable task, but attempts to determine an integrated budget of all elements makes the problem still more difficult. Such a bold design requires not only a concerted effort on the part of many researchers concentrated on one specific area, but also implies that a broad range of required information can be obtained only at the expense of precision.

The numerous and diverse data obtained in the Niepołomice Forest by various working groups have been organized in two ways: by constructing flow diagrams to balance matter and energy budgets, and by attempts to balance total matter inputs from outside the system with total outflow from the watershed.

The first approach allows insight into paths of energy flow and matter cycling through all the living components of the system and provides some information on where the accumulation of specific elements takes place. This has been the only way to outline a complete energy flow diagram, but it nevertheless has provided an opportunity to follow at least some pathways of elemental flow and accumulation sites. However, if applied to all the important parts of the system, such a procedure becomes meticulous. Thus some parameters have been roughly estimated while others were simply omitted.

The second approach gives a clear presentation of the total budget of chemical elements in the system, but fails to explain the details of transfer and accumulation mechanisms within the ecosystem. Not all the potentially important elements could have been included. For example, no information about the release of elements from parent rock was available. Balancing the nutrient flows in a system by means of watershed studies presumes its tightness, a condition which is not fulfilled in most lowland forests. The experimental data used in constructing elemental budgets err considerably due to variability usual in studies at the ecosystem level. In complicated systems many measurements cannot be repeated under conditions similar enough to facilitate statistical assessment of the reliability of the results. Thus using the utmost caution in drawing conclusions about processes taking place within complex ecological systems is the only way of avoiding serious errors.

The Niepołomice Forest, comprising two principally different parts, provides an interesting testing ground for comparisons of flow and accumulation of energy, nutrients, and pollutants in coniferous and deciduous forests growing under similar geographical and climatic conditions and exposed to the same level of air pollution. Yet the two forest complexes grow on sites which differ in respect to soil type and water availability – factors important in deciding their pecularities – but are undoubtedly two parts of the same forest complex. The interdisciplinary studies carried out by a single large group of researchers in both sections guarantee that the results obtained will be comparable (Grodziński 1978).

7.2 Biomass Production, Nutrient Uptake and Pollutant Accumulation by Plants

7.2.1 Data Sources

Estimates of biomass standing crop and annual biomass, energy, and nutrient increment, have been based on the data presented in Chapter 3. These eco-physiological and dendrometric data pertain, however, only to the aboveground parts of trees. Moreover, determining the amounts of elements by chemical analyses in specific parts of plants required more categories than have already been distinguished in Chapter 3.

Biomass of tree roots, bark, small twigs ("browse"), and seeds were among these categories. Both published and unpublished data obtained from the Niepołomice Forest were used. The volume of small twigs was estimated from twig/leaf ratios as given by Szulakowska (1974). Data on the proportions of roots and bark to total tree biomass were applied from literature dealing with relevant tree species in other European forests (Sukachev and Dylis 1964, Rodin and

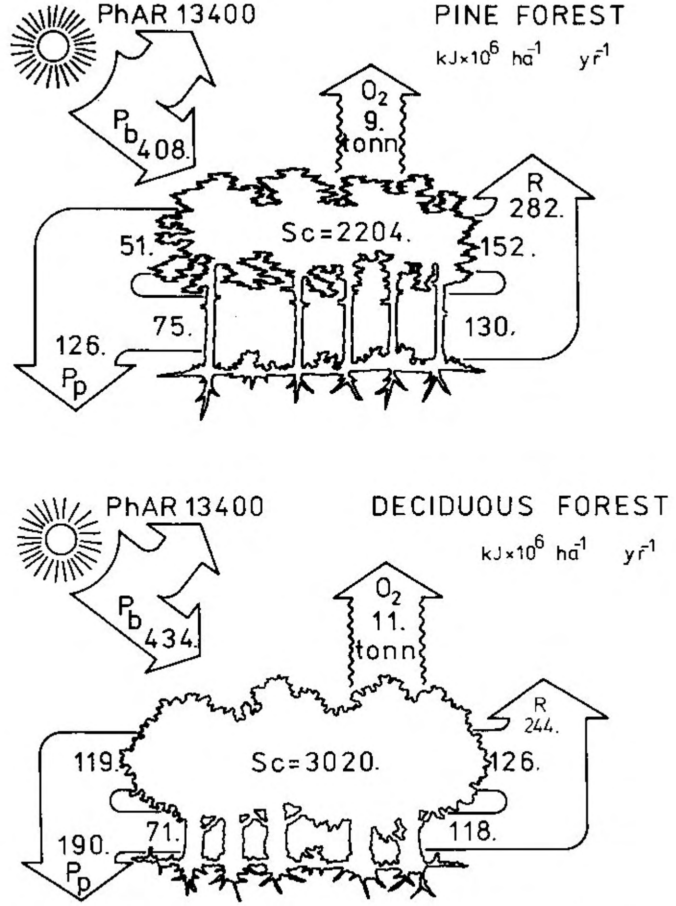

Fig. 7.1. Aboveground primary production of trees in the Niepołomice Forest. P_p net primary production; *PhAR* photosynthetically active radiation; *R* respiration; P_b gross primary production (assimilation); *Sc* aboveground biomass standing crop, in kJ 10^6 ha^{-1} yr^{-1}. O_2 production of oxygen (t ha^{-1} yr^{-1})

Bazilevich 1967, Molchanov 1971, Yurkievich and Yaroshevich 1974), taking into consideration the age structure of stands. It was thus assumed that the bark constituted 10% of the dry mass of boles and roots and from 11% to 16% of the total tree biomass.

Caloric values of the dry mass of specific parts of plants have been taken from various works, mostly from those concerning materials from the Niepołomice Forest (Molchanov 1971, Bobek et al. 1972, Bobek unpubl. data, Bandoła-Ciołczyk 1974, Sawicka-Kapusta et al. 1981).

Data were also available on the chemical composition of plant materials from the Niepołomice Forest (Szulakowska 1974, Grodzińska 1980, Grodzińska et al. 1983, Bobek unpubl., and others). Seed production in the deciduous section has been taken from Bandoła-Ciołczyk (1974) and pine seed production was estimated from values given by Molchanov (1971) supplemented by caloric values of seeds provided by Grodziński and Sawicka-Kapusta (1970).

The chemical composition of the forest herb layer and meadow vegetation was based on unpublished data of B. Bobek and on Rams (1978) after calculating, in both cases, weighted averages for more than ten dominant species. Heavy metal and sulfur content in tree leaves, small branches (twigs), bark and wood and also in forest herbaceous and meadow vegetation was taken from unpublished data of K. Grodzińska and B. Bobek, and from Grodzińska (1980) and Grodzińska et al. (1983) The chemical composition of roots has been assumed to be similar to that of wood.

7.2.2 Energy Budget of Primary Production

Figure 7.1 presents an outline of the energy budget for both parts of the forest. Gross primary production is slightly higher in the deciduous forest (434×10^6 kJ ha^{-1} yr^{-1}) than in the pine (408×10^6 kJ ha^{-1} yr^{-1}) which constitute 3.2 and 3.0% of PhAR, respectively. However, the net production of deciduous forest exceeds that of coniferous by as much as 50% (Fig. 7.1), while the efficiency of net primary production reaches 43.8 and 30.9% of gross primary production in deciduous and coniferous forests, respectively. These values constitute 1.42 and 0.94% of PhAR. In both forests about 10 t ha^{-1} of oxygen is released into the atmosphere.

7.2.3 Standing Crop of Biomass, Energy, and Chemical Elements

Tables 7.1 and 7.2 present values for the standing crop of dry mass, energy and specific nutrients in both types of forest stands. There is a noteworthy high

Table 7.1. Average standing crop of dry mass, energy, nutrients, and pollutants in woody plants in pine forests, Niepołomice, Poland

Item		Needles	Twigs	Wood		Bark	Total above-ground	Roots	Total
				Boughs	Boles				
Dry mass $g \times 10^6$ ha^{-1}		3.58	1.32	13.93	82.10	8.95	109.88	17.72	127.60
Energy kJ $\times 10^6$ ha^{-1}		75.20	27.46	278.60	1,642.00	180.80	2,204.00	354.00	2,558.00
$g \times 10^3$ ha^{-1}	N	54.40	15.84	2.37	13.96	0.09	86.66	9.04	95.70
	P	4.33	1.32	4.18	24.63	–	34.46	5.32	39.78
	K	8.66	11.88	2.37	13.96	0.18	37.05	6.73	43.78
	Ca	7.84	5.15	5.29	31.20	24.52	74.00	7.09	81.09
	Mg	3.33	1.45	3.20	18.88	0.89	27.76	8.15	35.91
	S	6.34	0.80	2.93	17.24	11.81	37.12	3.72	40.84
	Fe	2.17	4.55	0.31	1.81	15.57	20.31	0.39	20.70
g ha^{-1}	Zn	205.34	198.10	136.80	606.22	316.83	1,463.30	174.02	1,637.30
	Pb	82.73	70.00	36.22	213.46	489.92	892.30	46.07	938.37
	Cu	18.19	7.40	19.08	112.48	102.93	260.10	24.27	284.37
	Ni	33.47	1.90	39.84	234.81	49.49	354.50	50.68	410.18
	Cd	6.30	1.45	16.57	97.70	11.27	133.30	21.08	154.38

Table 7.2. Average standing crop of dry mass, energy, nutrients, and pollutants in woody plants in oak-hornbeam forest, Niepołomice, Poland

Item		Leaves	Twigs	Wood		Bark	Total above ground	Roots	Total
				Boughs	Boles				
Dry mass $g \times 10^6 ha^{-1}$		4.00	1.88	15.26	116.50	12.96	150.5	30.55	181.1
Energy $kJ \times 10^6 ha^{-1}$		82.40	36.38	305.20	2,330.0	265.2	3,019.0	611.0	3,630.0
$g \times 10^3 ha^{-1}$	N	81.60	19.93	15.56	118.88	87.33	323.3	93.48	416.7
	P	6.93	1.32	0.61	4.66	2.45	15.97	6.11	22.1
	K	12.88	2.93	1.53	11.65	5.03	34.02	3.06	37.1
	Ca	21.68	4.61	4.12	31.46	173.12	235.0	8.25	243.3
	Mg	4.72	2.82	2.44	18.64	4.39	33.01	9.78	42.8
	S	8.12	1.37	3.97	30.29	44.12	87.87	7.94	95.81
	Fe	13.19	0.54	0.23	1.75	24.81	40.52	0.46	40.97
$g ha^{-1}$	Zn	639.11	112.80	21.06	160.8	891.4	1,830.0	42.16	1,872.16
	Pb	199,61	21.81	67.45	514.9	1,057.8	1,860.0	135.03	1,995.03
	Cu	157.41	24.65	25.63	195.7	251.2	655.0	51.31	706.31
	Ni	72.02	6.77	27.93	213.2	110.0	430.0	55.91	485.91
	Cd	16.58	1.56	12.67	96.7	26.7	154.2	25.36	179.6

correlation between dry mass and energy content within the biomass categories. This is in sharp contrast to a lack of correlation between dry mass and content of chemical nutrients due to the variability in chemical composition between various parts of the plant.

In general, the standing crop of biomass maintained on a single hectare is higher in deciduous forest than in coniferous (151×10^6 and 111×10^6 g ha^{-1}, respectively). Similarly, the total content of nutrient elements (nitrogen, potassium, calcium, and magnesium) is higher in the deciduous part than in the coniferous, with the sole exception of phosphorus (Tables 7.1 and 7.2).

An uneven allocation of nutrient elements between categories of plant and animal biomass becomes more evident when presented as percentages (Table 7.3). During the vegetative season foliage retains most of the nutrients (nitrogen, phosphorus, and potassium) although leaves constitute a relatively small portion of total biomass. There is a characteristic difference in the site of calcium. In pine forest most of the calcium is stored in wood, whereas in deciduous it is in oak bark with large quantities of nitrogen (Table 7.3). The quantities of biomass and energy contained in the bodies of animals are minute, but it is worth noting the relative content of nutrients is larger by an order of magnitude than the content of energy or dry mass.

7.2.4 Nutrient Uptake by Forest Vegetation

The annual production of various categories of plant biomass (Chap. 3) combined with their chemical composition permits an estimate on the annual nutrient uptake from the soil. Data presented in Tables 7.4 and 7.5 indicate that deciduous

Table 7.3. Partitioning of dry mass, energy, nutrients, and pollutants in above-ground biomass of forests, Niepołomice, Poland. All values in per cent

Item	Coniferous					Deciduous				
	Leaves	Wood	Bark	Herbs	Consumers	Leaves	Wood	Bark	Herbs	Consumers[a]
Dry mass	3.3	88.0	8.1	0.6	0.008	2.6	88.5	8.5	0.3	0.007 (0.059)
Energy	3.4	87.9	8.2	0.5	0.004	2.7	88.2	8.8	0.3	0.009 (0.074)
N	56.1	33.2	0.1	9.5	1.11	24.2	5.9	26.0	3.6	0.56 (3.13)
P	12.1	83.9	0.0	2.6	1.25	38.2	36.3	13.5	8.8	3.25 (9.20)
K	21.9	71.5	0.5	5.9	0.15	25.7	32.1	10.0	31.9	0.19 (0.89)
Ca	10.5	55.8	32.8	0.9	0.04	9.0	16.7	71.9	2.1	0.26 (0.28)
Mg	11.7	82.6	3.1	2.6	0.0	14.2	71.8	13.2	3.9	0.0 (0.0)
Fe	9.5	11.3	68.3	1.9	9.1	30.1	5.8	56.6	0.2	7.28 (34.92)
Zn	13.5	61.8	20.8	3.7	0.1	33.3	15.4	46.5	4.5	0.09 (0.86)
Pb	9.2	35.4	54.3	1.2	0.0	10.7	32.5	56.9	0.02	0.004 (0.02)
Cu	6.9	52.5	38.9	1.8	0.1	23.9	37.3	38.1	0.7	0.003
Ni	9.1	75.6	13.5	1.7	0.08	16.6	57.2	25.4	0.74	0.004
Cd	4.7	85.9	8.4	0.9	0.1	10.7	71.5	17.2	0.51	0.11 (0.27)

[a] Values in parentheses calculated for an outbreak of *Tortrix viridana*

Table 7.4. Mean annual dry mass production, nutrient uptake and pollutant accumulation of trees in pine forests, Niepołomice, Poland

Item		Needles	Twigs	Wood		Bark	Total above-ground	Roots	Total
				Boughs	Boles				
Dry mass $g \times 10^6$ ha^{-1} yr^{-1}		1.79	0.66	0.64	2.95	0.15	6.19	0.69	6.88
Energy $kJ \times 10^6$ ha^{-1} yr^{-1}		37.59	13.73	12.74	59.0	3.03	126.09	13.8	139.9
$g \times 10^3$ ha^{-1} yr^{-1}	N	27.11	7.92	0.11	0.50	–	35.74	0.35	36.09
	P	2.16	0.66	0.19	0.86	–	3.90	0.21	4.11
	K	4.33	5.94	0.11	0.50	–	10.88	0.12	11.0
	Ca	3.92	2.57	0.24	1.12	0.41	8.26	0.28	8.54
	Mg	1.66	0.73	0.15	0.68	0.01	3.23	0.32	3.55
	S	3.17	0.40	0.13	0.62	0.20	4.52	0.14	4.60
	Fe	1.09	0.23	0.01	0.06	0.26	1.65	0.02	1.67
g ha^{-1} yr^{-1}	Zn	102.67	99.1	6.26	28.97	5.31	242.31	6.78	249.1
	Pb	41.37	35.0	1.66	7.67	8.21	93.91	1.80	95.71
	Cu	9.09	3.7	0.87	4.04	1.73	19.43	0.95	20.38
	Ni	16.74	0.92	1.82	8.44	0.83	28.75	1.97	30.72
	Cd	3.15	0.73	0.76	3.51	0.19	8.34	0.82	9.16

forest takes up larger quantities of principal nutrients than does pine forest. This difference is striking in the case of nitrogen and phosphorus, although the standing crop of the latter is higher in pine than in deciduous forest.

When compared with relevant data obtained in other forest ecosystems which can be found in the literature, those for pine forests at Niepołomice fall within

Table 7.5. Mean annual dry mass production, nutrient uptake and pollutant accumulation of trees in deciduous forests, Niepołomice, Poland

Item		Leaves	Twigs	Wood		Bark	Total above-ground	Roots	Total
				Boughs	Boles				
Dry mass $g \times 10^6$ ha^{-1} yr^{-1}		4.00	1.88	0.36	3.04	0.16	9.44	0.83	10.27
Energy $kJ \times 10^6$ ha^{-1} yr^{-1}		82.40	36.38	7.20	60.80	3.29	190.07	16.60	206.70
$g \times 10^3$ ha^{-1} yr^{-1}	N	81.60	19.93	0.37	3.10	1.08	106.10	2.54	108.60
	P	6.93	1.32	0.01	0.12	0.03	8.42	0.17	8.58
	K	12.88	2.93	0.04	0.30	0.06	16.21	0.08	16.30
	Ca	21.68	4.61	0.10	0.82	2.15	29.36	0.22	29.58
	Mg	4.72	2.82	0.06	0.49	0.05	8.14	0.27	8.40
	S	8.12	1.37	0.09	0.79	0.55	10.92	0.22	11.15
	Fe	13.19	0.54	0.01	0.05	0.31	14.09	0.01	14.10
g ha^{-1} yr^{-1}	Zn	639.11	112.80	0.50	4.19	11.06	767.70	1.19	768.90
	Pb	199.61	21.81	1.59	13.44	13.12	249.57	3.18	252.75
	Cu	157.41	24.65	0.60	5.10	3.11	190.87	1.43	192.30
	Ni	72.02	6.77	0.66	5.56	1.36	86.37	1.58	87.95
	Cd	16.58	1.56	0.30	2.52	0.33	21.29	0.71	22.00

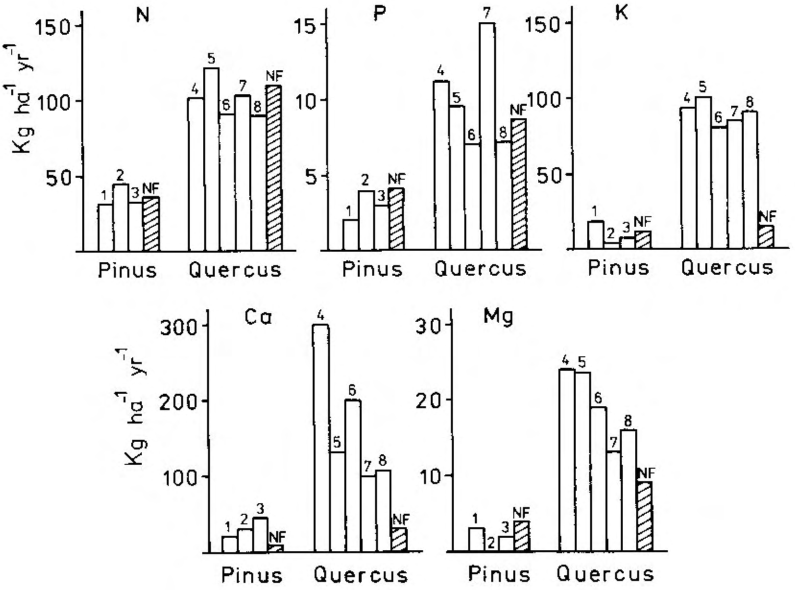

Fig. 7.2. A review of nutrient uptake estimates in various coniferous and deciduous forests of the temperate zone. *1 Pinus banksiana*, Foster and Morrison 1976; *2 Pinus silvestris*, Dengler 1930; *3 Pinus silvestris*, Ehwald 1957; *NF Pinus silvestris*, this study; *4 Quercus stellata/Q. marilandica*, Johnson and Risser 1974; *5, 6 Quercus robur/Fraxinus excelsior*, Duvigneaud and Denaeyer-de Smet 1970: *7, 8 Quercus aegopodialis*, Duvigneaud and Denaeyer-de Smet 1970; *NF Quercus robur*, this study

the range for such forests. Only calcium uptake appears to be slightly lower (Fig. 7.2; Rodin and Bazilevich 1967, Duvigneaud and Denaeyer-De Smet 1970). Oak forests at Niepołomice take up nitrogen and phosphorus in quantities similar to other known forests of the type, but significantly less calcium and potassium (Fig. 7.2).

The differences in the nutrient uptake by deciduous and coniferous trees at Niepołomice result from different levels of biomass production as well as from differences in average chemical composition of biomass produced. In deciduous forest the uptake of all nutrients, except potassium per unit of biomass produced always exceeds, sometimes even twofold, the corresponding values found in pine forest (Table 7.6).

A reverse relationship can be noted in biomass production and nutrient uptake in the herb layers of the two types of forest. Herbaceous vegetation in the

Table 7.6. Quantities of nutrients to synthetize 1 tonn of plant biomass in coniferous and deciduous forests, Niepołomice, Poland

Element	Nutrient uptake – kg t^{-1} biomass	
	Coniferous forest	Deciduous forest
N	5.15	10.5
P	0.59	0.83
K	1.57	1.58
Ca	1.21	2.90
Mg	0.51	0.82

Table 7.7. Average standing crop (= annual accumulation) of dry mass, energy, nutrients and pollutants in the herb layer of forests, Niepołomice, Poland

		Pine forests			Deciduous forests		
		Above-ground	Below-ground	Total	Above-ground	Below-ground	Total
Dry mass $g \times 10^6\ ha^{-1}$		663.00	259.70	922.70	487.50	629.40	1,116.90
Energy $kJ \times 10^6\ ha^{-1}$		11.90	4.66	16.56	8.75	11.30	20.10
$g \times 10^3\ ha^{-1}$	N	9.22	3.32	12.54	12.09	14.35	26.44
	P	0.95	0.25	1.20	1.63	1.92	3.55
	K	2.31	0.44	2.75	16.01	9.94	25.95
	Ca	0.66	0.29	0.95	5.07	7.49	12.56
	Mg	0.73	0.14	0.87	1.27	0.82	2.09
	S	1.83	0.71	2.54	0.98	1.26	2.23
	Fe	0.43	0.17	0.59	0.08	0.10	0.18
$g\ ha^{-1}$	Zn	56.6	22.1	78.7	87.2	112.6	199.8
	Pb	10.8	4.2	15.0	0.44	0.56	1.00
	Cu	4.8	1.9	6.7	4.78	6.17	10.95
	Ni	6.3	2.5	8.8	3.22	4.15	7.37
	Cd	1.2	0.47	1.37	0.79	1.03	1.82

coniferous forest produces more biomass and retains more nutrients than the corresponding layer in deciduous forest (Table 7.7). Herbs constitute less than 1% of biomass and energy standing crop in both types of forest, but participation of this part of vegetation in the total nutrient standing crop and uptake is higher by one order of magnitude (Table 7.3). Unlike trees, the herb layer of pine forest plays a larger role in energy flow and matter cycling than does its counterpart in deciduous forest (Table 7.7).

7.2.5 Heavy Metal Accumulation

The concentrations of heavy metals and sulfur in specific parts of plants and in the bodies of animals, the standing crop of these elements and the annual biomass increment provide a basis for an estimate of the biotic pool and the annual rate of accumulation. Yet the data available do not permit distinction between that fraction of these elements which constitutes the physiological component of plant and animal bodies and that fraction which entered the organisms via mechanical and biomechanical processes caused by an enormous surplus of airborne compounds of these elements in the polluted environment. Moreover, there are no data pertaining to the normal physiological requirements of essential trace elements (micronutrients) in specific plant and animal species. However, since standing crop had been known, it was possible to follow their pathways and allocation in the forest ecosystem. Tables 7.1 and 7.2 give details of the distribution of elements in woody plants, and Table 7.7 provides corresponding information for herbaceous vegetation. Chapter 5 deals with heavy metal concentration in the litter layer of the pine forest. The partitioning of heavy metals among aboveground biomass components is given in Table 7.3.

In both sections of the Niepołomice Forest most of the heavy metal pool is concentrated in tree bark, less in leaves and wood. This indicates the mechanical deposition of elements originating from industrial pollution. The fact that a relatively large part of the pool is located in the bodies of consumers, in greater proportion than their share of total biomass, would indicate that some heavy metals are essential as micronutrients to many animals.

Estimates of the amounts of heavy metals contained in the aboveground vegetation indicate how small a fraction of these elements is actually stored there, in comparison to the pool stored in the litter (Chap. 5, Table 5.7). The litter pool of cadmium amounts to twice as much, and that of lead is as much as 35 times the corresponding values accumulated in the aboveground biomass in pine forest. Unfortunately, no relevant data from the deciduous forests are available. The amounts of nutrients in the litter there also exceed or at least equal those in the standing biomass.

7.2.6 Standing Crop, Production, and Turnover Rates of Biomass, Energy, Nutrients, and Pollutants

The ratio of annual production (annual accumulation of biomass, energy, and nutrients) to actual standing crop, i.e, turnover rate (Θ) characterizes the relative

Table 7.8. Standing crop, production and turnover rates of dry mass, energy and chemical elements in plants, Niepołomice Forest, Poland

		Coniferous			Deciduous		
		Production P	Standing crop Sc	Turnover rate Θ	Production P	Standing crop Sc	Turnover rate Θ
Dry mass $g \times 10^6$ ha^{-1} (yr^{-1})		7.80	128.52	0.061	11.39	182.21	0.0625
Energy $kJ \times 10^6$ ha^{-1} (yr^{-1})		142.65	2,574.56	0.055	226.75	3,650.05	0.0621
$g \times 10^3$ ha^{-1} yr^{-1} (P)	N	48.28	108.24	0.446	135.04	443.17	0.305
$g \times 10^3$ ha^{-1} (Sc)	P	5.31	40.78	0.130	12.13	25.63	0.473
	K	13.75	46.53	0.296	42.25	63.03	0.670
	Ca	9.49	82.04	0.116	42.14	255.81	0.165
	Mg	2.96	36.78	0.080	10.49	44.88	0.234
	S	7.21	43.38	0.166	3.38	98.04	0.136
	Fe	2.26	21.29	0.106	14.28	41.15	0.347
g ha^{-1} yr^{-1} (P)	Zn	327.8	1,716.0	0.191	968.7	2,071.96	0.468
g ha^{-1} (Sc)	Pb	110.71	953.37	0.116	253.75	1,996.03	0.127
	Cu	27.08	291.07	0.093	203.25	717.26	0.283
	Ni	39.52	418.98	0.094	95.32	493.28	0.193
	Cd	10.53	155.75	0.068	23.82	181.42	0.131

rate of processes in ecosystems. Turnover rates calculated for gross biomass and energy are slightly higher in the deciduous forest than the coniferous (0.0625 and 0.0621 as compared to 0.061 and 0.055). Similar, but more significant differences occur in the turnover rates of phosphorus, potassium, magnesium, and all heavy metals in deciduous forests, where the rates are twice as high as in the pine forests (Table 7.8).

7.3 Energy and Matter Flow Through Consumer Populations

7.3.1 Energy and Nutrient Intake by Consumers

Ecological studies on energy flow through terrestrial ecosystems thus far have led to the unequivocal conclusion that the participation of the consumer food chain is quite small, actually no more than a few percent of the total flow. The only exceptions noted have been special cases, intensively grazed grasslands, or outbreaks of some pests (Petrusewicz and Grodziński 1973, 1975).

Data on food intake in major groups of consumers obtained in both parts of the Niepołomice Forest was useful not only for the estimation of energy intake, but also for that of several principal nutrients. The total consumption removed from the producer level by all groups of consumers is provided in Table 7.9. In the course of the calculations several assumptions have been made; for example,

Table 7.9. Quantities of energy and chemical elements entering the consumers' trophic chain annually

Item		Coniferous			Deciduous		
		Annual production P	1st order consumption C	% C/p	Annual production P	1st order consumption C[a]	% C/p[a]
Energy kJ × 10^6 ha^{-1} yr^{-1}		142.65	3.16	2.2	226.75	9.7 (30.9)	4.3 (13.6)
g × 10^3 ha^{-1} yr^{-1}	N	48.28	10.18	21.1	135.04	18.6 (59.9)	13.7 (44.4)
	P	5.31	1.13	21.3	12.13	2.5 (8.9)	20.6 (73.4)
	K	13.75	3.88	28.2	42.25	2.3 (8.1)	5.4 (19.2)
	Ca	9.49	4.47	47.1	42.14	14.5 (53.6)	34.4 (127.2)
	S	7.21	0.234	3.2	13.38	0.70 (2.76)	5.2 (20.6)
	Fe	2.26	0.036	1.6	14.28	0.34 (1.33)	2.4 (9.3)
g ha^{-1} yr^{-1}	Zn	327.80	9.37	2.9	968.70	28.77 (75.36)	3.0 (7.8)
	Pb	110.71	1.12	1.0	253.75	5.46 (20.02)	2.2 (7.9)
	Cu	27.08	0.96	3.5	203.25	3.85 (15.33)	1.9 (7.54)
	Ni	39.52	1.14	2.9	95.32	1.83 (7.09)	1.9 (7.44)
	Cd	10.53	0.11	1.0	23.82	0.53 (1.74)	2.2 (7.30)

[a] Values in parentheses calculated for an outbreak of *Tortrix viridana*

plant material makes up about 25% of the diet of birds, 78% of the diet of rodents from the deciduous forest, whereas in rodents from pine forest it constitutes over 90% (Chap. 4).

In both forest types the energy intake by consumers has not exceeded 4.5% of annual production, the only exception being during oubreaks of the oak leafroller (*Tortrix viridana*) when as much as 13% of the energy of annual production may be consumed (Table 7.9).

There is quite the reverse situation when it comes to a consideration of matter flux in consumer populations. The combined effects of preferences for foods with higher nutrient content and an uneven distribution of nutrients within various parts of plants (Tables 7.1–7.3) contributes to a wide range of values of nutrient flow through the consumer food chain, the variation is from 4.5% to as much as 45% of all nutrients retained annually in plant biomass production.

In coniferous forests consumers take in more than 21% of the nitrogen and phosphorus, 28% of the the potassium and nearly half of the calcium accumulated in plant production. Though consumers have the larger share of total energy flow in the deciduous forest, they participate to a lesser degree in the nutrient flux (more than 13% of nitrogen, 21% of phosphorus, only 5% potassium, and 34% of calcium) (Table 7.9).

During leafroller outbreaks annual consumption may even exceed annual accumulation in total primary production. This paradox may be attributed to an acceleration of nutrient turnover rates due to intensive grazing and subsequent regrowth of leaves, although possible errors cannot be excluded.

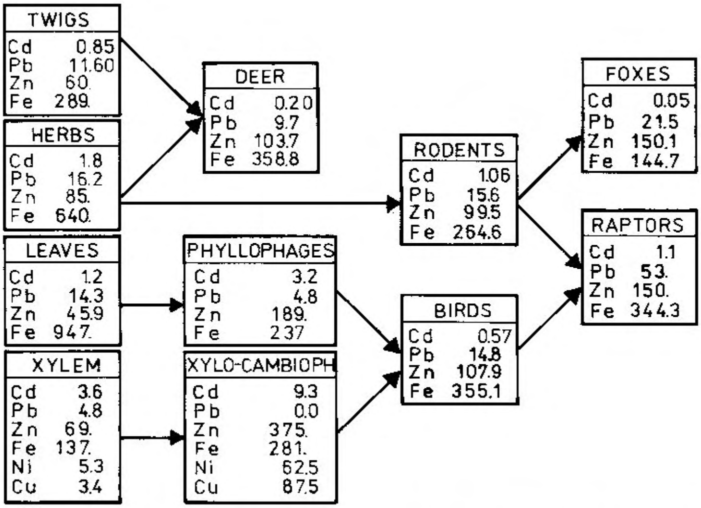

Fig. 7.3. Concentration of selected heavy metals (ppm) in various links of the trophic web of the Niepołomice Forest

The nutrients taken in by herbivores are returned almost completely to the system in excreta and to some extent as dead bodies. The amount of biomass transported out of the ecosystems studied by emigration of insects, birds, and deer, is considered negligible. Thus in a relatively short period nutrient elements are re-cycled in the form of compounds that are easily decomposable and suitable for uptake by plants (see also nutrient consumption as a percent of primary production, Table 7.9). The quantities of nutrients made available in this way correspond roughly to those applied in aerial fertilization (Grodziński and Lesiński 1978).

7.3.2 Intake and Accumulation of Pollutants by Consumers

Intake of heavy metals has been calculated from the chemical composition of biomass consumed (Chap. 4), then converted to percent of total heavy metal burden in plants consumed by animals. These percentages do not differ from the percentage of consumed total biomass and from the percentage of energy consumed (Table 7.9). This suggests that the intake of heavy metals in food is indiscriminate.

Pathways of pollutants (heavy metals, sulfur, fluorides, pesticides, etc.) in ecosystems have traditionally attracted the interest of ecologists, since these elements and compounds were shown to accumulate in trophic chains and finally reach levels dangerous to organisms. Such accumulation has been reported in respect to mercury and other heavy metals in aquatic ecosystems but has not yet been confirmed for forest ecosystems, this study included.

Figure 7.3 depicts part of the food web of forest ecosystems and the concentrations of heavy metals in specific organisms. A marked increase in heavy metal concentration can be noted in the case of herbivorous insects, particularly for zinc, nickel, and copper concentrations which may be attributed to normal physiological factors. In other groups of consumers even a decrease in heavy metal concentration has been observed (cadmium in mammals and birds). The explanation for such diferences may be that the food chain shown in Fig. 7.3 consists of mainly homeothermic consumers in whom the excretion of toxic elements may be more efficient than that in invertebrates and heterothermic vertebrates. Similar changes in heavy metal concentrations have been found in detritus food chains in these forests (Grodzińska unpubl.).

7.4 Chemical Budgets in the Forested Ecosystems

The data collected do not include the transfer of elements from parental rock via weathering and also lack information on atmospheric nitrogen fixation and nitrogen volatilization. Nevertheless precise data on elemental input in dusts and gases (Chap. 2, see also Manecki et al. 1981) and an estimation of nutrient export in watershed outflow (Chap. 6) allow determination of an approximate overall budget of nutrients and pollutants.

The data on total elemental influx (Chap. 2) do not include nutrients. The atmospheric inflow in precipitation was, however, studied by Zieliński in coniferous forests to facilitate the study of elemental budgets in forest litter (Chap. 5). Because some methods applied to pollutants have given results similar to those obtained by Manecki and others (Chap. 2), it appeared acceptable to apply the results of Zieliński on nutrients only to overall budgets.

The net difference between the amount of an element going into the system and that leaving it in watershed outflow or retention may be compared with the accumulation of the element in organic matter or the biotic pool, calculated as the sum of levels of this element in the annual biomass increment of plant and animals. Obviously, no quantitative conclusions can be drawn from such a comparison, due to differences in calculation procedures and errors involved. It may, however, suffice for the formulation of quantitative hypotheses on pathways and accumulation sites of chemical elements.

The outflow was measured from two woodland watersheds considered the most representative for the two respective forest types. They were used for an estimate of total outflow from the two forest complexes (Chap. 6).

Overall budgets, retention, and accumulation of nutrients as well as pollutants in both sections of the Niepołomice Forest are in Table 7.10. Two nutrients, calcium and magnesium, demonstrate marked negative net differences in both deciduous and coniferous forests. This is undoubtedly associated with the levels of these elements in the soil where they are leached by water. The same holds for manganese, which is present in high levels in the soils of the northern section of the forest (Chap. 1) so that more is exported from the ecosystem than has entered by industrial dusts (Table 7.10). All other elements studied have positive net differences. For example there is approximately 20 kg of nitrogen retained annually, 16–30 kg of sulfur and 23-26 kg of iron ha^{-1} in both forest types (Table 7.10). Amounts of most nutrients, as well as sulfur and iron retained do not show any

Table 7.10. Budgets of chemical elements in forest ecosystems, Niepołomice, Poland

Element		Input[a]	Coniferous			Deciduous		
			Output[b]	Retention	Accumulation[d]	Output[a]	Retention[c]	Accumulation[d]
$g \times 10^3$ ha^{-1} yr^{-1}	N	20.08	3.64	17.16	48.28	1.76	19.04	135.04
	P	1.83	0.165	1.665	5.31	0.46	1.37	12.13
	K	8.59	2.70	5.89	13.75	2.14	6.45	42.25
	Ca	26.27	40.9	−14.63	9.49	75.48	−49.21	42.14
	Mg	2.54	9.5	− 6.96	4.42	15.74	−13.20	10.49
	S	60.3	33.3	27.0	7.21	44.36	15.94	13.38
	Fe	30.3	12.15	18.15	2.26	5.16	25.14	1.59
	Zn	1.231	0.532	0.699	0.328	0.221	1.010	0.969
	Pb	0.315	0.023	0.292	0.111	0.018	0.297	0.254
	Cu	0.187	0.020	0.167	0.027	0.016	0.171	0.203
	Ni	0.066	0.024	0.042	0.040	0.026	0.040	0.095
	Cd	0.015	0.003	0.012	0.011	0.002	0.013	0.024
	Mn	0.721	0.413	0.308		0.806	− 0.085	

[a] N, P, K, Ca, Mg after Zieliński (Chap. 5); others after Manecki et al. (Chap. 2)

[b] After Reczyńska-Dutka et al. (Chap. 6)

[c] Retention = input − output

[d] Accumulation in biotic pool (after Chap. 3 and 4; cf. Table 7.4, 7.5, 7.7, and 7.9)

significant differences in the two ecosystems. Of the heavy metals deposited in dust only zinc displays a tendency for higher retention in deciduous areas, while other metals are retained in almost equal quantities in deciduous and coniferous sections.

Accumulation in the biotic pool is somewhat higher in deciduous forests. This holds true for all metals, particularly copper, but with the exception of iron. All nutrients are taken in by producers in considerably larger quantities than actually retained. This implies that the intrasystem cycling is much more intensive than transfers in and out.

In coniferous forest cadmium and nickel accumulation actually equal retention. This indicates that these two metals are concentrated in living organisms and are later transferred to litter (Chap. 5). In the deciduous forests cadmium and nickel as well as copper and iron accumulate in the biotic pool at even higher rates than they enter the system (Table 7.10). This may indicate that they cycle within the system much more intensively than in the coniferous forests.

Lead, cadmium, and copper retention are equal and almost complete in both types of forest. Nickel is similarly accumulated in both forests but only to 60% (Fig. 7.4). Iron and zinc are retained in larger quantities in deciduous forests, while sulfur is retained in greater amounts in coniferous forest.

Relative accumulation in the biotic pool is always higher in deciduous forest, except for iron (Fig. 7.4). Accumulation of copper, nickel, and particularly cadmium exceeds the current input, which indicates that remarkable quantities of these metals are taken up from deposits previously stored in litter and soil.

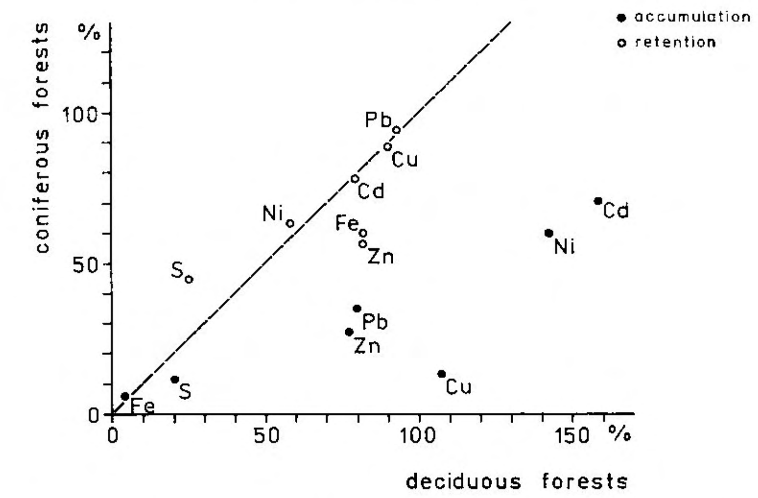

Fig. 7.4. Corresponding values of retention in the whole ecosystem (*open circles*) and accumulation in the biotic pool (*solid circles*) of heavy metals in coniferous and deciduous forests at Niepołomice, Poland

7.5 Discussion

7.5.1 Primary Production

Net primary production in the oak-hornbeam forest at Niepołomice has been studied by Medwecka-Kornaś et al. (1974), Bandoła-Ciołczyk (1974) and also by Banasik (1978 a). All these studies were undertaken on the same 1-ha plot of 70–100-year-old Tilio-Carpinetum forest. The total aboveground net primary production recalculated from data given in these papers reaches 197×10^6 kJ ha^{-1}, yr^{-1}, which is equivalent to 9.77 metric tons dry weight ha^{-1} yr^{-1}. In this chapter net primary production of deciduous forest has been estimated to be 190×10^6 kJ yr^{-1}, i.e. 9.44 t ha^{-1} yr^{-1} (Fig. 7.1, 7.9), which agrees well (3.5% difference) with the previous estimates (Medwecka-Kornaś et al. 1974). In addition, the estimates presented here involved more precise determinations of the biomass standing crop of trees and growth rates for various age classes and habitats throughout the whole deciduous complex. The stand chosen by Medwecka-Kornaś and others was apparently quite representative of the entire deciduous section.

The primary production for pine forest given here (see also Chap. 3) constitutes the first estimate for this forest. Average primary production for the entire pine forest is 126×10^6 kJ ha^{-1} yr^{-1}, which is equivalent to 6.19 metric tons of dry weight of annual increment (Fig. 7.1). Estimates of production and standing crop for both types of forest fall within the range of values determined for European temperate lowland forests (for comparison see Rodin and Bazilevich 1967, Cannell 1982, Reichle 1981). Actually the Niepołomice Forest has lower than average net production of deciduous stands and definitely a lower value than average production of pine forests. Long-term affects of air-borne pollution and changes in water regime (lowering of the water table) may explain this lower productivity.

7.5.2 Nutrient Budgets

A better understanding of biogeochemical cycling in forest ecosystems has been achieved by determining input–output balances in woodland watersheds (e.g., Bormann and Likens 1967, Likens et al. 1977, Swank and Waide 1980). Such an experimental approach to the whole ecosystem enabled ecologists to discover many of the functions of forest ecosystems including elemental budgets. Nutrient and water budget estimates can be determined more precisely in mountainous watersheds (Swank 1981) than in those of the lowlands. This technique has been employed in both sections of the Niepołomice Forest despite many inaccuracies of measurement in water budget of this lowland watershed (Chap. 6). Thirteen nutrients and pollutants whose pathways have been studied quantitatively (Fig. 7.10–7.20 in Appendix) may be compared with those in four long-studied forest ecosystems in the USA. These represent various geographical and climatological conditions but have been studied using methods similar enough to enable comparisons (Swank and Waide 1980).

The four watershed ecosystems include oak-hickory forest in the Coweeta basin, Southern Appalachian Mts, NC (Johnson and Swank 1973, Swank and Douglass 1977), oak-hickory forest in Walker Branch, Eastern Tennessee, TN (Van Hook et al. 1977, Henderson et al. 1978), northern hardwoods in the Hubbard Brook Experimental Forest, White Mts, NH (Likens et al. 1977, Bormann and Likens 1979), and Douglas-fir forest in the Western Cascade Mts, OR (Grier et al. 1974, Sollins et al. 1980). In European forests early elemental budgets were determined by Duvigneaud and Denaeyer-De Smet (1970) in mixed oak forest in Belgium. This study, however, did not follow the input–output design.

Each watershed study is unique, representing specific features of vegetation with a local history, hence no comparisons of elemental pools in biomass of various ecosystem components can easily be made. It is possible to attempt to compare input–output budgets for several nutrients (Ca, K, and N) which are common to those studies.

Precipitation is considered the way in, while streamflow from the watershed is the way out of the system. In the North-American watersheds the calcium budgets (= retentions) are always negative. Output is higher than input by 3–136 kg ha^{-1} yr^{-1}, whereas in the Niepołomice watersheds in the pine and deciduous sections of the forest this value is correspondingly -15 and -49 kg ha^{-1} yr^{-1}. Such an agreement of results (Table 7.11) indicates a universal phenomenon in that calcium is almost always surplus in the soil from which large quantities are leached (Likens et al. 1967, 1977).

It is more difficult to compare nitrogen budgets because they involve both organic and inorganic nitrogen. Inorganic nitrogen budgets were always positive in the North-American watersheds (0.5–7.8 kg of N ha^{-1} yr^{-1}), while at Niepołomice nitrogen retention is even higher, reaching 17–19 kg of N ha^{-1} yr^{-1}. This seems to be a reliable result because of known high input of atmospherically derived nitrogen compounds (Table 7.11).

Table 7.11. Nutrient budgets kg ha^{-1} yr^{-1} – calcium, potassium and nitrogen in the Niepołomice Forest and a comparison with selected North American forest ecosystems. Budgets computed for various forest watersheds. Inputs in precipitation, outputs in streamflow, Niepołomice Forest, Southern Poland from Table 7.10 and Figs. 7.10, 7.12, 7.13 (see Appendix). Coweeta, NC, and Walker Branch, TN, from an outline in Swank and Waide (1980), Hubbard Brook, NH, from Bormann and Likens (1979), whereas for H. J. Andrews, OR from Sollins et al. (1980)

Nutrient Site and forest type	N$_{(inorganic)}$			K			Ca		
	Input	Output	Retention	Input	Output	Retention	Input	Output	Retention
Niepołomice S. Poland oak-hornbeam	20.8	1.8	+19.0	8.6	2.1	+6.5	26.3	75.5	−49.2
Niepołomice S. Poland pine	20.8	3.6	+17.2	8.6	2.7	+5.9	26.3	40.9	−14.6
Coweeta, NC oak-hickory	4.5	0.1	+ 4.4	2.1	5.6	−3.5	4.8	7.7	− 2.9
Walker Branch, TN, oak-hickory	9.3	1.5	+ 7.8	3.0	7.0	−4.0	12.0	148.0	−136.0
Hubbard Brook, NH, Northern hardwoods	6.5	4.0	+ 2.5	0.9	1.9	−1.0	2.2	13.7	− 11.5
H.J. Andrews, OR, Douglas-fir	2.0	1.5	+ 0.5	0.9	9.5	−8.6	3.6	123.1	−119.5

Budgets for potassium are usually negative (Table 22 in Likens et al. 1977). In the four North-American watersheds discussed here the loss of potassium ranged from 1 to 9 kg ha^{-1} yr^{-1} (Table 7.11). In both deciduous and coniferous sections of the Niepołomice Forest the net difference in potassium budgets are conclusively positive (5.9 and 6.5 kg). This may be due to unusually heavy deposition in precipitation (8.6 kg ha^{-1} yr^{-1}) and is in sharp contrast to values summarized by Likens et al. (1977) from as low as 0.8 to 3.2 kg of K ha^{-1} yr^{-1}.

Only three nutrient elements (N, K, Ca) have been discussed here. Data for three others (P, Mg, and S) are presented in Table 7.10 and Figs 7.10, 7.12. It is worth noting that net budgets for all nutrients except potassium conform well to the common pattern in various forest ecosystems summarized by Likens and others (1977, their Table 22).

These comparisons could have been extended to intrasystem cycles of these nutrients including standing crop and transfers but, for the sake of brevity, the reader should refer to comprehensive works by Likens et al. (1967), Sollins et al. (1980), and Swank and Waide (1980).

7.5.3 Pollutant Budgets

Of the North-American watersheds discussed, the one most similar to the Niepołomice Forest is undoubtedly the Walker Branch forest. Located near coal-

Table 7.12. Pollutant budgets of zinc, lead and cadmium in forest ecosysystems, Niepołomice, Southern Poland, and in Walker Branch, TE. Atmospheric inputs and stream outputs from those watersheds in g ha^{-1} yr^{-1}

Pollutant Site and forest type	Zn			Pb			Cd		
	Input	Output	Retention	Input	Output	Retention	Input	Output	Retention
Niepołomice[a] S. Poland oak-hornbeam	1,231	221	+1,010	315	18	+297	15	3	+13
Niepołomice[a] S. Poland pine	1,231	532	+ 699	315	23	+292	15	3	+12
Walker Branch, TN[b] oak-hickory	538	140	+ 398	286	6	+280	21	7	+14

[a] This Chapter, cf. Table 7.10 and Figs. 7.18–7.20 in Appendix

[b] Van Hook et al. (1977), for similar atmospheric deposition see Lindberg and Harriss (1981)

fuelled power plants, this site is characterized by heavy atmospheric deposition including 286 g of Pb, 21 g of Cd, and 538 g of Zn (Van Hook et al. 1977) and 6.3 kg of S ha^{-1} yr^{-1} (Lindberg and Harris 1981). Lead and calcium depositions are quite similar to those at Niepołomice but there is only half the zinc and one tenth the sulfur.

Budgets summarized by Van Hook and others (1977) closely resemble those obtained for the same pollutants at Niepołomice (Figs. 7.18–7.20, Table 7.10). This relates not only to accumulations in the litter layer but also to the retention of large amounts of toxic heavy metals and sulfur in the forest. Unfortunately the budgets for heavy metals are ominously positive. The accumulation of the most toxic element, cadmium, in the pine and deciduous forests at Niepołomice is 80% and 87%, respectively, whereas in Walker Branch the relevant figure was 67%. Similar comparisons of lead and zinc accumulations show that the Niepołomice Forest retains 93% and 94% of lead and 57% and 82% of zinc in the deciduous and coniferous sections respectively while in Walker Branch 98% of lead and 74% of the zinc is retained (Table 7.12). Sulfur has very high net retention in both parts (27 and 16 kg ha^{-1} yr^{-1}, Table 7.10, Fig. 7.10), whereas in slightly polluted watersheds of Hubbard Brook its input in bulk precipitation was always smaller than hydrologic output (Eaton et al. 1980). Fluorine compounds which are extremely harmful to forests (Amundson and Weinstein 1980) have not been included in these studies. Tentative estimates of their fall are 4.4 kg ha^{-1} yr^{-1} for 1978 (Bik and Zajac 1980). Fluorine accumulation in the bones of large herbivorous mammals such as roe deer (*Capreolus capreolus L.*) reached over 2,000 ppm (Grodzińska et al. 1983, Grodziński unpubl.). The fluorine danger has gradually decreased since 1981 when the electrolytic production of aluminum in an aluminum plant near Cracow was discontinued.

7.5.4 The General Pattern of Energy, Nutrient, and Pollutant Behavior in Forest Ecosystems

The patterns of matter, nutrient, and pollutant cycling discussed for the Niepołomice Forest and other forest watersheds permit one to attempt to describe the general behavior of these elements in forest ecosystems (Fig. 7.5). The simplest diagram of a forest ecosystem, including only producers, consumers, and decomposers shown with the soil and a pool of plant biomass has been used. Energy entirely from outside flows mainly via producers and decomposers and leaves the system in the form of dissipated heat. In forests, a large portion of this energy is temporarily stored in wood and is often exported from the system as timber (Fig. 7.5 a).

Quantities of nutrients transferred in and out are minute when compared with internal streams, particularly those between producers and decomposers. It can be concluded from our studies that consumers have a much larger share in nutrient cycling than can be inferred from their share in the energy flow. Nutrient accumulation in wood is negligible (Fig. 7.5 b).

The heavy metal cycles represent quite reverse characteristics. Heavy metals in ecosystems are mainly allochtonous. They do not leave the systems, but accumulate mainly in the litter and soil. They also cycle in the grazing food chain but only to a slight degree (Fig. 7.5 c).

Sulfur, which is actually a nutrient and becomes a pollutant ($SO_4^=$) only when present in excessive amounts, does not conform to the general pattern outlined here (Fig. 7.10 in Appendix).

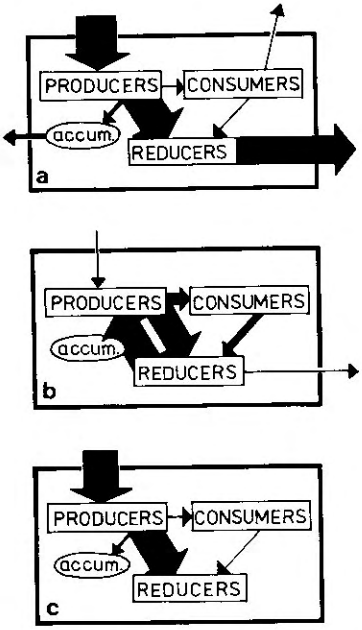

Fig. 7.5 a–c. A general scheme for the dynamics of energy (*a*), nutrients (*b*), and pollutants (*c*) in the forest ecosystems. *Thickness of arrows* indicates the intensity of flux