6. Elemental cycling in forest ecosystems

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Introduction

Among the functions regulating activity and evolution of forest ecosystems, mineral cycling is of critical importance. The study of cycling of elements in forest ecosystems has given us insights into the dynamics of these systems, including nutrient needs, rates of nutrient turnover, loss of nutrients by leaching and addition by weathering, fixation, and the atmosphere. The study of mineral cycling has led also to an understanding of the processes regulating the pathways and rates of flow for the various elements within these systems, information essential for the rational management of our forest lands.

Cycling of elements in forest ecosystems is an integrating process that brings together most other functions of the system. These elements are obviously essential in the plant growth processes of photosynthesis, assimilation, and respiration. The dynamics of nutrient uptake and transport within the soil are considered also within the context of cycling studies. Decomposition of organic materials and weathering of mineral materials are vital aspects of the overall cycle, providing the means by which elements

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become available to higher plants. Thus, the study of mineral cycling involves study of the ecosystem as a whole. Since one process functions as the precursor to another (i.e., mineralization precedes nitrogen uptake), the flow of elements in a forest ecosystem is inseparably linked in a set of specific interconnected steps that ultimately lead to a set of cyclic pathways.

It is reasonable to expect that, although the processes will remain, their rates will change drastically from one forest type to another, from one climatic zone to another, and from one soil type to another.

Such patterns in cycling have, in all probability, slowly and systematically evolved as a part of the genetic evolution of species. Adaptability of a particular plant to its environment, thus, depends on entire sets of cycling processes that collectively allow the plant to compete within this environment. There are obviously several ways in which these cycling processes have been collectively arranged to allow a plant to adapt to its ecological niche. For example, the strategy of meeting annual nutrient requirements for growth between low and high elevation forests has been handled by different forests' species in quite different ways. Retention of foliage for a number of years (25 yr in the case of black spruce) allows a coniferous forest to occupy sites where only a marginal nutrient supply is available from the soil. Other species, such as alder, have the specific ability through a symbiotic nitrogen-fixing process of providing their own supply of nitrogen and, thus, effectively can occupy disturbed sites where nitrogen levels are low.

To provide clearer insight into the role that mineral cycling has played in the evolution of forest ecosystems, we have collected and compared IBP data sets concerning production and mineral cycling. We here analyze these data sets and make comparisons among them. Our principal contribution has been to assemble and summarize this information. Many of the ideas that we discuss are not new; they were originally presented by such pioneers in the field as Ehwald, Remezov, and Ovington in articles and books on the subject. In recent years Duvigneaud and Ellenberg have added to this literature with much information and many new ideas. It is due to their influence that part of the IBP effort was focused on this subject.

Data base used for this synthesis

One of the primary purposes of IBP forest studies was to provide a general overview of biological productivity in the forest ecosystems of the world and to establish the basic factors that regulate this productivity. As mentioned above, mineral cycling plays a critical role and provides an integrated view of this important process for a forest ecosystem.

Although IBP studies were conducted around the world, under a wide array of forest and environmental conditions located at 117 different sites, unfortunately for the program and this synthesis effort mineral cycling studies were conducted on a far more limited scale. Even at those sites where mineral cycling was studied, the vast bulk of the research was limited to some narrow aspect of the subject. In a detailed review of the available information provided by the Oak Ridge international synthesis group, reasonably complete data adequate for mineral cycling comparisons were available from only 20 forest stands. Contact with the investigators of the other sites expanded the data base to include 32 forest stands from 14 different sites. Workers at the remaining sites either did not have a sufficient data base or failed to respond to the inquiries. It became evident in reviewing the data base supplied to Oak Ridge that there were many obvious errors and other inconsistencies with published results. We hope these differences have been resolved and the data base used here adequately represents these forest stands.

Table 6.1 summarizes the sites from which our final synthesis was completed. These sites are arranged into climatic zones, vegetative types, species, and site location. The name of the scientist(s) responsible for the specific site and through whom the data were obtained is also listed. A more complete description of each site is included in the Appendix to this chapter. Table 6.1 shows that this program did not result in uniform or systematic coverage of areas or geographic regions. Rather, most sites are located within a relatively small geographic area covering North America and Europe. Important ecological areas such as the Mediterranean zone are poorly represented. There is no comprehensive data set for either tropical or equatorial forest types.

Purpose and scope of this synthesis effort

Our purpose in attempting this synthesis of mineral cycling information was twofold. First, we wanted to provide within one document a summary of the cycling information collected as a result of IBP efforts. Second, we wanted to see if a comparison of such information would add a new dimension to our understanding of ecosystem behavior, an understanding that had not or could not emerge without the more extensive data base that this assemblage provided.

In spite of the limitations of the data sets, we believe these IBP studies represent a wide spectrum of conditions and include a variety of regions, life forms, and environmental settings, as indeed is evident from Table 6.1. However, since the diversity of conditions associated with these sites was not selected as a part of a comprehensive experimental design, some of our initial expectations for the synthesis of these data on elemental cycling could not be met.

The difficulties were further magnified by the many problems and caveats

Table 6.1. *IBP study sites and forest types used in this mineral cycling synthesis*

Stand no.	Forest region and species	Stand age (yr)	Country and site	Investigator
	Boreal Coniferous			
1	*Picea mariana*	51	USA; Alaska	Van Cleve
2	*Picea mariana*	55	USA; Alaska	Van Cleve
3	*Picea mariana*	130	USA; Alaska	Van Cleve
	Boreal Deciduous			
4	*Betula papyrifera*	50	USA; Alaska	Van Cleve
	Temperate Coniferous			
5	*Pseudotsuga menziesii*	42	USA; Cedar River	Cole, Turner
6	*Pseudotsuga menziesii*	73	USA; Cedar River	Turner
7	*Pseudotsuga menziesii*	450	USA; Andrews	Grier
8	*Picea abies*	45	USSR	Kazimirov
9	*Picea abies*	60	Sweden; Kongalund	Nihlgard
10	*Picea abies*	34	W. Germany; Solling	Ulrich
11	*Picea abies*	87	W. Germany; Solling	Ulrich
12	*Picea abies*	115	W. Germany; Solling	Ulrich
13	*Pinus echinata*	30	USA; Oak Ridge	Harris
14	*Pinus strobus*	15	USA; Coweeta	Swank
15	*Abies firma*	97–145	Japan	Ando
16	*Tsuga sieboldii*	120–443	Japan	Ando
17	*Tsuga heterophylla*	121	USA; Cascade Head	Grier
	Temperate Deciduous			
22	*Liriodendron tulipifera*	50	USA; Oak Ridge	Reichle *et al.*
23	*Liriodendron-Quercus*	30–80	USA; Oak Ridge	Harris
24	*Quercus-Carya*	30–80	USA; Oak Ridge	Harris
25	*Quercus prinus*	30–80	USA; Oak Ridge	Harris
26	*Quercus-Carya*	60–200	USA; Coweeta	Swank
27	*Acer-Betula-Fagus*	110	USA; Hubbard Brook	Whittaker, Likens
28	*Quercus*-mixed	mixed	Belgium	Duvigneaud
29	*Quercus*-mixed	80	Belgium	Duvigneaud
30	*Fagus sylvatica*	59	W. Germany; Solling	Ulrich
31	*Fagus sylvatica*	80	W. Germany; Solling	Ulrich
32	*Fagus sylvatica*	122	W. Germany; Solling	Ulrich
33	*Quercus-Betula*	mixed	Great Britain; Merlewood	Satchell
34	*Fagus silvatica*	45–130	Sweden; Kongalund	Nihlgard
35	*Alnus rubra*	30	USA; Cedar River	Turner
	Mediterranean			
36	*Quercus ilex*	150	France; Rouquet	Lossaint, Rapp

associated with comparing data collected by different people in different ways at different times. Because of these limitations our primary emphasis is directed toward more general considerations of elemental cycling and productivity in natural ecosystems.

This discussion is presented in five parts:

1. Systematic changes in elemental cycling associated with stand maturity.
2. Biomass and elemental accumulation and elemental cycling for forest regions and ecosystem types.
3. Differences between deciduous and coniferous species relative to accumulation and cycling.
4. Effect of elemental cycling on forest productivity.
5. Addition and losses of nutrient elements from forest ecosystems.

Methods used in this synthesis

Selection of information

The data used in this synthesis were derived from several sources, IBP data files at Oak Ridge (corrected or modified), correspondence with investigators at the IBP field sites, IBP publications, and unpublished data obtained directly from investigators involved in IBP mineral cycling studies. A basic set of data comprising elemental accumulations, increments, and fluxes was tabulated for each study site. This information included both organic matter and elemental nitrogen, potassium, calcium, magnesium and phosphorus.

Unfortunately, a complete data set comprising all the above parameters was never available from any site. In particular, few sites had information on soil and forest floor leaching rates. Elemental addition by way of atmospheric particulate input was seldom measured. Only one study examined rates of nitrogen fixation. The available information was tabulated on a standard entry form in units of kg/ha or kg/ha/yr. These data sheets are included in the Appendix.

Use of information

This information was used in several comparative ways as the chapter outline makes evident. A part of this comparison involved calculating annual elemental uptake, requirement, and interval recycling from the information base. Since these terms have been defined and calculated in many ways, we had to decide on a standardized means of deriving these values. Although it can be argued that these values can be established in a more sophisticated way than in the procedure we used, it should be remembered that this was not possible with the limited data available from most of the study sites. We defined and calculated these terms as follows:

Uptake – annual elemental increment associated with bole and branch wood plus annual loss through litterfall, leaf wash, and stemflow.

This calculation assumes a steady-state condition for tree foliage and excludes any consideration of root and bark increment.

Requirement – annual elemental increment associated with bole and branch wood plus the current foliage production.

This calculation is dependent on the same assumptions as stated for uptake. An indication of the extent of the internal recycling of elements can be derived by subtracting uptake from requirement.

Recycling – Requirement minus Uptake

This calculation is obviously based on the same assumption associated with uptake and requirement calculations. In addition it also includes the assumption that litterfall is primarily foliage fall and elements derived from throughfall and stemflow were derived from foliage.

There are many assumptions, some of them perhaps unacceptable, built into these calculations, but the major difficulty derives from lack of information regarding below-ground processes. Very few studies included any root information, and none had annual elemental increment information for the root system. Consequently it was not possible to include roots into any flux calculations.

Most of the studies did include organic matter and the elements nitrogen, phosphorus, potassium, calcium and magnesium. Consequently, we have included all of these elements on the stand summary sheets prepared for each site and included in the Appendix to this chapter. However, for our purposes much of the discussion is focused on organic matter (biomass accumulation and production), nitrogen, potassium and calcium. These elements were most extensively studied at the IBP sites. In addition, they provide an excellent contrast in cycling.

Nitrogen is closely tied to the carbon cycle. Consequently transfer of nitrogen from one compartment to another within a forest (Fig. 6.1) is dependent on transfer of carbon or release of nitrogen from carbon through the process of mineralization. In this way nitrogen behaves in a manner similar to phosphorus and sulfur. Nitrogen also is involved in fixation, nitrification, and denitrification, all critical processes in the mineral cycle.

By contrast, potassium is not associated with organic structures and is transferred from compartment to compartment through the ecosystem and is basically independent of the carbon cycle. Consequently, quantities of potassium found in throughfall are proportionally far higher than those of nitrogen, since transfer of potassium is not dependent on mineralization. The cycling rate of potassium is rapid compared to other elements.

The third element selected was calcium. This element is not a component of protein and, thus, is not dependent on mineralization for its mobility as is nitrogen. However, it is still found as a part of the organic structure of the

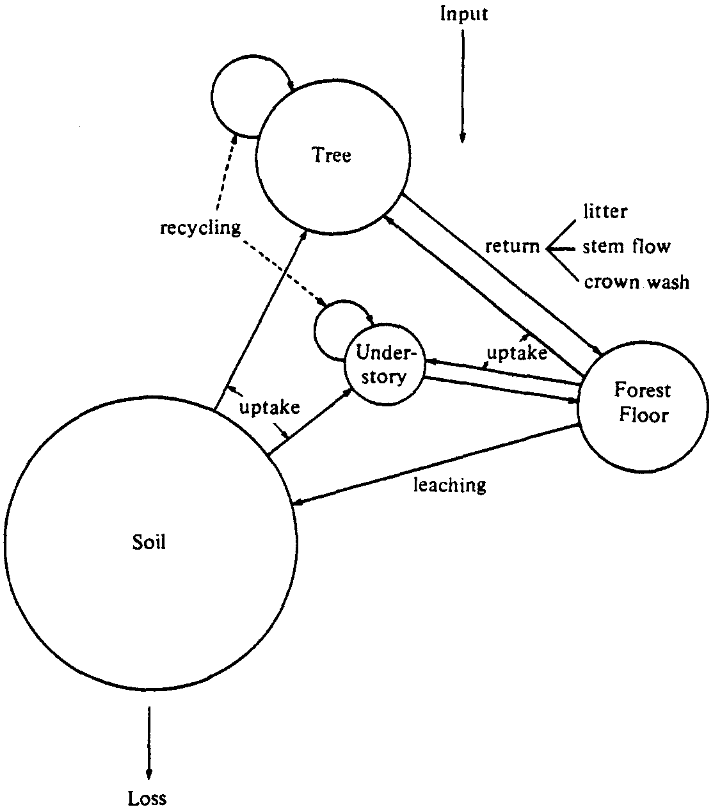

Fig. 6.1. A generalized diagram of nutrient cycling in forest ecosystems. After Turner, 1975.

tree or precipitated as an oxalate or sulfate salt in the plant tissue. Cycling of calcium is, thus, relatively slow within an ecosystem, and recycling within a tree is nearly nonexistant. In this region it behaves in a way similar to magnesium and manganese.

Comparison of these three elements involves in a general way comparison of nearly all of the critical elements associated with mineral cycling of the forest system. We have also included magnesium and phosphorus in many of our tables and some of our discussions when there is an adequate information base for doing so.

Rates of cycling, increments of addition and accumulation of elements within and between ecosystem compartments

The general format in which cycling, increments, and accumulations of elements have been delineated is shown in Fig. 6.1. While this scheme does not provide the detailed resolution desirable in such studies, it does represent the maximum resolution possible with the data base available. Our examination of the ecosystem is presented in the next four subsections.

Systematic changes in elemental cycling associated with stand maturity

It is apparent that a forest ecosystem will change in relationship to its nutrient needs and rates of elemental turnover with the development of the stand, but Ovington (1959) was the first to quantify these changes for *Pinus sylvestris*. He examined a series of plantations varying in age from early stages of development to fully mature, and by establishing the basic parameters of cycling for each stand, he could calculate the changes in nutrient needs as a function of stand development. A similar analysis was done by Switzer & Nelson (1972) for the first 20 yr of a stand of *Pinus taeda*. In this case, however, the investigators used some data that were related only indirectly to the species studied. Recently, Baker & Blackmon (1977) have provided a similar analysis of a cottonwood plantation (*Populus deltoides*) on a monthly basis during the first year after its establishment.

Two such studies were undertaken as a part of the IBP forest studies. In Russia, Kazimirov & Morozova (1973) followed the patterns of cycling in spruce (*Picea abies*) through a series of age classes ranging from 22 to 138 yr. A clear pattern emerged from the examination. The rate of elemental uptake for this spruce forest increased to a maximum of 36.6 kg/ha/yr at age 68 yr and then slowly decreased to less than 17.3 kg/ha at age 138 yr. This decrease in tree uptake corresponded to an increase in the uptake by ground cover vegetation; these uptakes became nearly equal at age 138 yr. Apparently, this reflects changes in cycling associated with the opening of the forest canopy. Up to an age of nearly 70 yr, spruce dominates the site, minimizing the role of the understory flora. Between 70 and 138 yr the understory vegetation assumes a far larger role in the nutrient dynamics of the site until the two are nearly equally important. This relationship for nitrogen is shown in Fig. 6.2.

A similar analysis was undertaken by Turner (1975) for Douglas fir (*Pseudotsuga menziesii*) in Washington State, USA. Turner studied a series of Douglas-fir stands ranging from 9 to 95 yr from which he calculated change in nutrient accumulation and measured transfer with changes in the structure of the forest ecosystem. His analysis makes clear that closure of the forest canopy at about 25 yr played a critical role in the nutrient cycle. Before stand closure, the understory vegetation assumed a prominent position in the structure of this ecosystem. For example, at nine years there was an approximately equal distribution of nitrogen, potassium and cal-

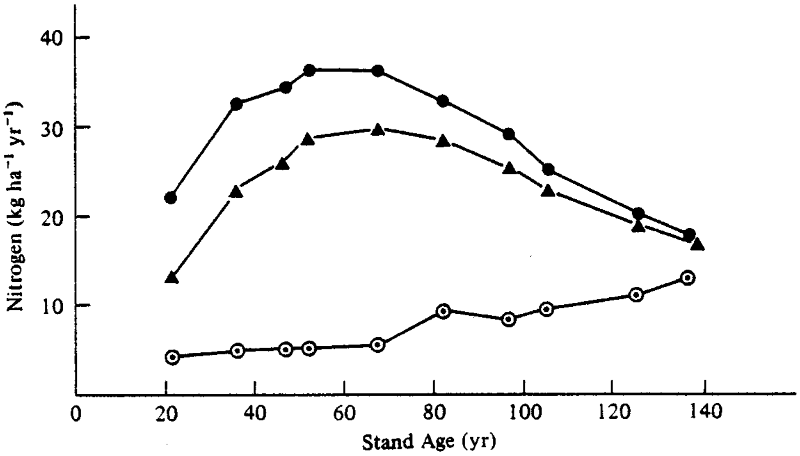

Fig. 6.2. Cycling of nitrogen in spruce (*Picea abies*) from age 22 yr to 138 yr. After Kazimirov & Morozova, 1973. ●—●, tree uptake; ○—○, understory vegetation uptake; ▲—▲, return in litter.

cium between the forest and the understory. This relationship rapidly changed, however, as the crown began to close at age 22 yr. By the age of 30 yr, nutrient accumulation in the understory vegetation declined rapidly (Fig. 6.3).

With closure of the forest canopy at about age 30 yr, there was very little increase in elemental accumulation in the forest foliage (Fig. 6.4). As one would expect, litterfall also remained relatively stable after this period as did a number of other above-ground elemental relationships, such as annual uptake and nutrient requirement by the forest species (Table 6.2). From the summary of stand data in Table 6.2 it is clear that the uptake of both nitrogen and potassium are closely coupled with annual requirements for these two elements. However, in the case of calcium, uptake far exceeded annual requirement for growth, as reflected in the amount of calcium in the current year's growth increment. Excess calcium is stored in older foliage and the woody biomass of the system. It would be speculative, however, to conclude from this that excess calcium is unnecessary to the tree. Its specific role is, however, unclear.

Because litterfall exceeds decomposition in this forest type, the forest floor accumulates biomass with stand age (Fig. 6.5) resulting in a buildup of nutrients in this ecosystem compartment. This accumulation is not uniform between elements. Nitrogen and calcium accumulation closely parallels the accumulation of organic matter. By contrast, potassium is accumulating at a far slower rate because it is not dependent on mineralization for its release (Fig. 6.6).

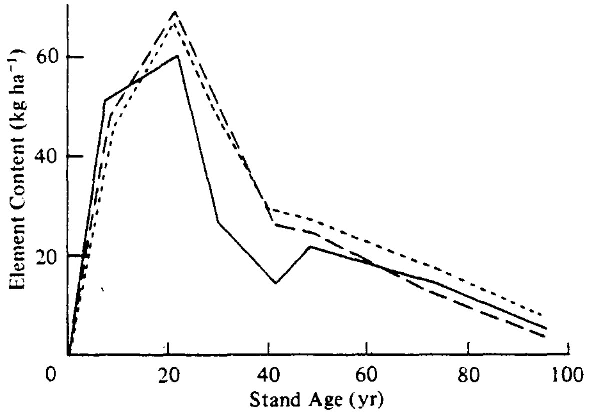

Fig. 6.3. Accumulation of nitrogen (----), potassium (——), and calcium (– – –) in the understory vegetation of various aged stands of Douglas fir. After Turner, 1975.

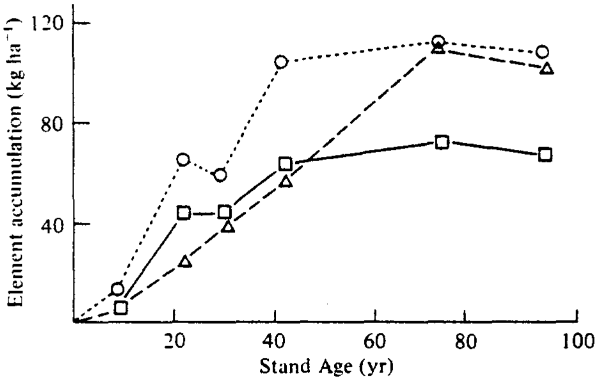

Fig. 6.4. Accumulation of nitrogen (○ . . . .○), potassium (□—□), and calcium (△- - -△) in the foliage of various aged stands of Douglas fir. After Turner, 1975.

Biomass and elemental accumulation and elemental cycling for forest regions and ecosystem types

One of our initial objectives was to make a comparison between the major forest regions for various aspects of accumulation and mineral cycling. The data base developed from the IBP studies was not extensive enough nor adequately distributed between forest regions for regional comparison of types. Significant characteristics were evident, however, in the element accumulation, turnover, and recycling patterns for different forests. Twenty seven of the 32 IBP studies we compared were conducted within the

Table 6.2. *Annual uptake and nutrient requirements of nitrogen, potassium and calcium for Douglas fir between the ages of* 9 *and* 450 *yr (after Turner,* 1975; *Grier et al.,* 1974)

	Nitrogen		Potassium		Calcium	
Age (yr)	Uptake	Requirement	Uptake	Requirement	Uptake	Requirement
9	3.7	5.8	3.6	4.5	4.8	2.2
22	33.7	41.8	26.3	31.0	34.4	13.3
30	32.1	32.8	29.5	27.7	55.7	14.4
42	32.8	36.0	27.4	26.1	40.9	12.9
73	32.5	34.7	21.4	24.5	43.2	14.1
95	37.3	28.7	25.5	25.9	51.4	11.9
450	23.7	34.8	21.2	26.7	53.3	17.9

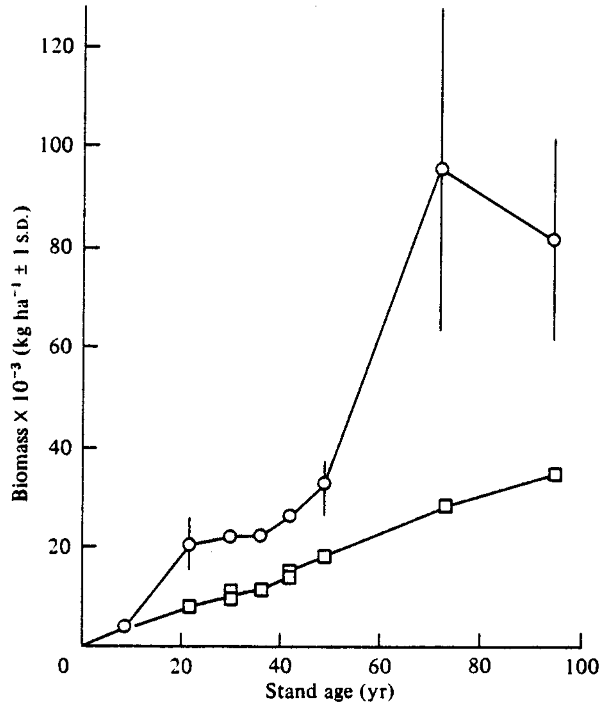

Fig. 6.5. Accumulation of forest floor biomass (○—○, total; □—□, humus) under various aged stands of Douglas fir. After Turner, 1975.

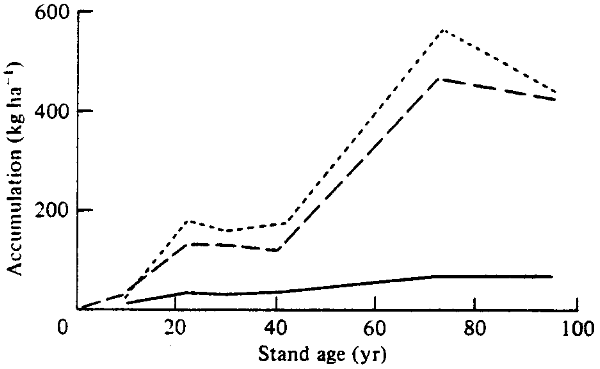

Fig. 6.6. Accumulation of nitrogen (---), calcium (—–—), and potassium (—) in the forest floor of various aged stands of Douglas fir. After Turner, 1975.

temperate forest region. Four of the sites were located in the boreal forest region and one in the Mediterranean region. We were unable to compare any from the tropics. The above-ground forest biomass and nutrient accumulation for the IBP sites, arranged according to forest region are tabulated in Table 6.3. The data do show an apparent greater above-ground accumulation of biomass and nutrients in temperate deciduous and coniferous forests than in those of the boreal region. As one would expect, however, these regional values have a large standard deviation associated with the averages.

The organic matter and nitrogen accumulation in the above-ground tree component can represent a substantial proportion of the total within the ecosystem. This is especially true for organic matter. Average biomass accumulation in the above-ground tree component represents 45% of the total organic matter of these systems (Table 6.4). This value varies strikingly however between regions. In the boreal sites in Alaska only 20% of the organic matter is accumulated in the above-ground tree compartment, probably because of the low production and decomposition rates characteristic of northern latitudes. There seems to be substantially more total and above-ground tree accumulation of organic matter in the temperate coniferous than in the temperate deciduous forests. An analysis of variance for organic matter between these two forest types indicates that these differences are significant at the 0.01 level of confidence. However, the distribution percentage between above-ground and total organic matter is not significantly different for these two forest types. On average, 7% of the total nitrogen is found within the tree compartment, appreciably less than that for organic matter. This lower nitrogen percentage is due to the wide carbon to nitrogen ratio for woody biomass. Again, boreal forests have a far smaller

Table 6.3. *Above-ground organic matter and nutrient accumulation for the IBP study sites arranged according to forest types and regions*

		Accumulation (kg/ha)					
Forest region	Stand no.	Biomass	Nitrogen	Potassium	Calcium	Magnesium	Phosphorus
Boreal coniferous	1	16597	40	24	30	7	6
	2	24018	95	31	120	10	14
	3	113189	215	76	625	60	29
	Average	51268	116	44	258	26	16
	S.D.	±53753	±89	±28	±321	±30	±12
Boreal deciduous	4	97343	221	104	164	38	20
Temperate coniferous	5	126495	227	132	202	29	112
	6	129400	316	205	358	53	54
	7	802310	566	189	687	105	86
	8	78200	282	105	241	31	28
	9	305000	720	406	453	67	80
	10	142700	449	349	291	62	59
	11	244490	729	401	413	56	39
	12	232990	628	342	379	88	65
	13	120600	215	125	307	40	18
	14	69599	224	109	98	—	—
	15	379562	573	1426	1402	130	82
	16	448601	582	441	934	63	25
	17	915480	721	189	478	60	167
	Average	307341	479	340	480	65	68
	S.D.	±271547	±203	±349	±351	±30	±42
Temperate deciduous	22	124700	304	173	456	—	47
	23	109100	267	172	537	59	21
	24	121600	369	220	856	67	24
	25	137300	397	242	852	45	26
	26	137496	405	227	543	—	—
	27	134000	367	154	402	38	33
	28	291850	728	398	1142	92	46
	29	115085	368	200	830	77	28
	30	154658	407	130	324	26	52
	31	158764	404	202	303	26	36
	32	273958	581	273	303	67	20
	33	113065	278	213	480	26	17
	34	104000	1071	456	606	105	85
	35	151020	240	74	170	60	23
	Average	151900	442	224	557	57	35
	S.D.	±58130	±221	±100	±273	±26	±19
Mediterranean	36	269000	745	626	3853	151	224
Overall averages, all stands		207526	429	263	589	60	52
S.D.		±196483	±229	±253	±672	±34	±47

Table 6.4. *Total and above-ground tree accumulation of organic matter and nitrogen for the various forest regions*

		Organic matter (kg/ha)			Nitrogen (kg/ha)		
Forest region	No. of sites	Tree	Total	%[a]	Tree	Total	%[a]
Boreal coniferous	3	51000	226000	19	116	3250	4
Boreal deciduous	1	97000	491000	20	221	3780	6
Temperate coniferous	13	307000	618000	54	479	7300	7
Temperate deciduous	14	152000	389000	40	442	5619	8
Mediterranean	1	269000	326000	83	745	1025	73
Average	32	208000	468000	45	429	5893	7

[a] Percent of total contained in above-ground component.

percentage of nitrogen in the above-ground tree compartment than that found for the other forest regions.

Accumulation of organic matter and the five nutrient elements within the forest floor of the 32 study sites is listed in Table 6.5. In general, the largest forest floor organic accumulations are found in the boreal coniferous forests followed by temperate coniferous, boreal deciduous, temperate deciduous, and Mediterranean in that order. The accumulation of nutrient elements within the forest floor generally follows the same distribution pattern between forest regions noted above for organic matter. These differences between forest regions cannot be statistically substantiated, however, because we lack an adequate number of sites within several of these regions and because of the large standard deviation associated with the data sets.

The rate of organic matter and nutrient return by forest regions is summarized in Table 6.6. As expected, the largest return of organic matter is in the temperate deciduous forest, probably due to the high productivity and deciduous character of this forest type. The high annual rate of organic return is reflected in the return of most of the nutrient elements. On average, over 60 kg/ha of nitrogen is returned each year under a temperate deciduous forest. Only 36 kg/ha of nitrogen is returned annually under a temperate coniferous forest. This contrast is obviously due to the extended period in which coniferous species retain foliage. The duration of foliage retention varied greatly between temperate coniferous forests, ranging from six years for older Douglas-fir stands (stands 6 and 7) to 1.2 years for short leaf pine (stand 13).

It should be recognized that return of the nutrient elements is only in part carried by litterfall. Averaging of all 32 forest stands considered here showed that 83% of nitrogen return was by way of litterfall. Similarly 85% of phosphorus was so returned. By contrast, only 41% of the potassium

Table 6.5. *Forest-floor organic matter and nutrient accumulation for the IBP study sites arranged according to forest types and regions*

		Accumulation (kg/ha)					
Forest type	Stand no.	Biomass	Nitrogen	Potassium	Calcium	Magnesium	Phosphorus
Boreal coniferous	1	88664	486	60	396	96	106
	2	133260	656	145	231	224	152
	3	119235	710	122	452	99	87
	Average	113720	617	109	360	140	115
	S.D.	±22804	±117	±44	±115	±73	±33
Boreal deciduous	4	68772	548	99	489	139	79
Temperate coniferous	5	20540	178	38	114	54	26
	6	26670	223	44	130	54	30
	7	218520	445	80	619	160	62
	8	19200	—	—	—	—	—
	9	18500	245	15	48	8	15
	10	52000	1430	105	72	44	199
	11	49000	960	41	83	20	53
	12	111000	2260	115	258	46	98
	13	27000	290	21	256	23	18
	14	—	—	—	—	—	—
	15	4279	484	113	182	67	32
	16	50780	507	76	159	30	34
	17	301080	474	118	343	83	98
	Average	74881	681	70	206	53	60
	S.D.	±92299	±640	±39	±165	±42	±54
Temperate deciduous	22	6000	78	9	100	—	5
	23	1500	187	14	294	22	11
	24	27000	334	26	517	32	22
	25	25000	298	26	318	22	18
	26	9500	110	29	130	—	—
	27	48016	126	66	372	38	8
	28	5600	—	—	—	—	—
	29	4762	44	17	107	5	2
	30	29000	815	85	86	44	62
	31	39000	1050	123	118	44	72
	32	29700	810	83	91	34	52
	33	6118	74	12	101	8	3
	34	5200	86	104	34	5	6
	35	66350	887	91	391	57	45
	Average	21625	377	53	205	28	25
	S.D.	±19624	±391	±40	±153	±17	±25
Mediterranean	36	11400	125	10	361	20	4
Overall averages, all stands		52343	515	65	236	55	50
	S.D.	±66410	±482	±43	±161	±51	±48

Table 6.6. *Average litterfall and nutrient return by forest regions as determined at the IBP study sites*

			Nutrient return (kg/ha/yr)				
Forest region	No. of sites	Litterfall (kg/ha/yr)	Nitrogen	Potassium	Calcium	Magnesium	Phosphorus
Boreal coniferous	3	322	2.9	1.1	3.8	0.3	0.7
Boreal deciduous	1	2645	20.2	9.8	35.5	9.7	5.2
Temperate coniferous	13	4377	36.6	26.1	37.3	5.6	4.4
Temperate deciduous	14	5399	61.4	41.6	67.7	11.0	4.0
Mediterranean	1	3842	34.5	44.0	95.0	9.0	4.7
All stands	32	4373	43.3	27.9	47.3	7.4	3.7

returned to the forest floor was found in litterfall, the majority returned via throughfall and stemflow, indicating the highly mobile nature of this element. Return of calcium and magnesium seems to be intermediate between that of nitrogen and phosphorus and that of potassium, with 71% of calcium and 60% of magnesium returned via litterfall.

By comparing the rate of nutrient return to total accumulation within the forest floor we can calculate mean residence or turnover times of the forest floor. Such a calculation is based on the assumption that the forest floor and rate of return are both in steady state. Although there is little reason to believe that this is the case, calculation still provides a relative index useful for comparative purposes. Turnover periods have been calculated for each of the forest regions; the influence of latitude and forest type on decomposition is clearly shown in Table 6.7. The more northerly boreal forests have an exceedingly long mean residence time for both organic matter and all five elements. On average, coniferous boreal forests retain nitrogen nearly 100 times longer than the Mediterranean forest, 13 times longer than the temperate coniferous forest, and 42 times longer than the temperate deciduous forest. Similar extremes in turnover periods can be seen for other elements.

Annual elemental uptake and requirement was calculated for each site. These values, including above-ground tree production, are listed in the Appendix to this chapter, and are summarized by forest regions in Table 6.8. We recognize the limitations of the data, but nevertheless, our calculations illustrate some important cycling characteristics of forest ecosystems. It is clear, for example, that forests are relatively modest in removing

Table 6.7. *Mean residence (turnover) time in years for the forest floor and its mineral elements by forest regions as determined at the IBP sites. Values calculated by dividing annual return into total forest floor accumulation. A steady state condition is assumed*

		Mean residence time (yr)					
Forest region	No. of sites	Organic matter	N	K	Ca	Mg	P
Boreal coniferous	3	353	230	94	149	455	324
Boreal deciduous	1	26	27.1	10.0	13.8	14.2	15.2
Temperate coniferous	13	17	17.9	2.2	5.9	12.9	15.3
Temperate deciduous	14	4.0	5.5	1.3	3.0	3.4	5.8
Mediterranean	1	3.0	3.6	0.2	3.8	2.2	0.9
All stands	32	12.0	34.1	13.0	21.8	61.4	46.0

nutrients from the soil. Annual uptake of nitrogen for the 32 sites averaged only 55 kg/ha. Maximum average uptake of 75 kg/ha was found in the temperate deciduous region. The amount of nitrogen required for the growth increment of bole and stem wood and current foliage production is also quite low with the highest value noted again in the temperate deciduous forest.

These values demonstrate that uptake by the temperate deciduous forest for nitrogen is 63% greater than the coniferous forest of the same region and 15 times greater than the spruce in the boreal region. Annual requirement for nitrogen by the temperate deciduous forests is more than twice that of the temperate coniferous forests and 20 times that of the boreal spruce. These differences between sample means are all significant at the 99% confidence level.

Differences in uptake and requirement between forest regions were similar for potassium. Again these differences are significant at the 99% confidence level.

Except for the single evergreen oak site in the Mediterranean region, the temperate deciduous forest also had the highest uptake and requirement for calcium, exceeding the temperate coniferous forest by a factor of 1.9 and 2.4 times, and the boreal coniferous forest by a factor of 14 and 19 times in these two cycling categories. These differences between sample means are significant at the 99% confidence level. The high calcium uptake by the Mediterranean oak is probably related to the calcareous soil from which the forest grows. The uptake and requirement of magnesium and phosphorus follows no consistent pattern between regions except for the consistently low values noted for the black spruce in the boreal region.

Table 6.8. *Annual production and nutrient cycling (uptake and requirement) for the IBP study sites arranged by forest region*

Forest type	Stand no.	Total above-ground production biomass (kg/ha/yr)	Nitrogen (kg/ha/yr)		Potassium (kg/ha/yr)		Calcium (kg/ha/yr)		Phosphorus (kg/ha/yr)		Magnesium (kg/ha/yr)	
			Uptake	Requirement	Uptake	Requirement	Uptake	Requirement	Uptake	Requirement	Uptake	Requirement
Boreal coniferous	1	627	2.6	2.8	1.3	1.7	2.7	2.0	1.6	0.3	0.4	0.3
	2	1402	6.3	8.2	1.9	3.8	8.0	4.3	0.8	1.2	0.6	0.9
	3	1590	6.6	3.3	3.1	1.8	7.8	3.0	0.8	0.4	0.9	0.6
	Average	1206	5.1	4.7	2.1	2.4	6.1	3.1	1.1	0.6	0.6	0.6
	S.D.	±510	±2.2	±3.0	±0.9	±1.2	±3.0	±1.1	±0.5	±0.5	±0.3	±0.3
Boreal deciduous	4	5164	25.0	55.9	12.8	25.7	38.9	18.3	5.7	5.7	10.6	9.0
Temperate coniferous	5	8770	33.7	41.8	26.3	31.0	34.4	13.3	6.3	5.9	9.8	6.8
	6	6570	35.9	36.0	29.7	26.1	49.6	12.9	4.9	5.0	9.2	5.9
	7	6080	23.7	34.8	21.2	26.7	53.3	17.9	5.8	7.1	5.6	3.7
	8	5150	34.4	38.9	15.3	16.6	38.1	25.9	3.7	3.5	5.1	3.5
	9	13800	88.0	67.0	44.4	43.0	45.7	12.7	6.8	9.1	10.2	4.8
	10	8501	53.3	47.1	—	—	—	—	4.8	5.7	3.6	4.5
	11	8864	63.0	49.2	42.9	25.9	44.8	20.2	5.6	4.5	2.8	1.6
	12	6517	55.6	35.6	—	—	—	—	4.9	3.2	2.8	1.6
	13	7878	48.6	49.7	35.0	31.2	73.8	40.2	2.9	3.1	10.8	9.4

	14	13530	50.0	84.4	48.1	30.0	32.8	25.6	—	—	—	—
	15	8365	43.6	44.9	—	—	—	—	—	—	—	—
	16	5069	27.6	34.0	—	—	—	—	—	—	—	—
	17	9510	58.7	41.4	30.2	20.2	28.8	8.6	10.3	6.9	11.4	3.8
	Average	8354	47.4	46.5	32.6	27.9	44.6	19.7	5.6	5.5	7.1	4.6
	S.D.	±2758	±17.3	±14.4	±11.0	±7.5	±13.6	±9.7	±2.0	±1.9	±3.5	±2.4
Temperate deciduous	22	6029	47.9	61.0	55.0	55.6	105.3	44.6	4.2	7.3	—	—
	23	8650	58.1	87.9	40.0	47.5	87.8	82.6	3.4	6.3	12.4	21.7
	24	10400	69.1	87.2	48.2	57.5	97.2	91.0	3.7	6.4	13.8	18.4
	25	10700	68.8	98.1	40.3	58.2	88.8	80.3	3.3	5.5	11.5	13.1
	26	7966	43.0	92.1	48.3	47.1	59.0	50.5	—	—	—	—
	27	7889	74.3	90.0	53.4	37.8	62.3	37.7	6.2	7.4	8.9	6.6
	28	7980	86.4	108.9	51.0	52.0	91.0	59.0	5.4	8.0	19.7	10.0
	29	14775	80.0	96.1	48.8	47.0	169.4	106.3	4.6	6.3	16.4	9.2
	30	11813	91.3	113.9	45.2	32.7	47.7	18.4	7.2	9.1	7.3	4.4
	31	9648	87.6	106.7	46.7	38.1	55.0	28.4	5.7	6.7	6.4	3.4
	32	10352	75.6	88.5	45.0	31.3	50.2	18.8	6.5	6.7	7.0	3.9
	33	6615	78.9	91.9	59.0	43.8	124.1	54.7	3.6	4.9	25.0	10.5
	34	15100	78.3	129.3	42.2	43.3	63.1	49.3	8.6	10.5	10.2	10.9
	35	12780	114.9	119.0	86.1	77.5	91.2	56.0	10.3	8.1	19.5	12.8
	Average	10050	75.4	97.9	50.7	47.8	85.0	55.6	5.6	7.2	13.2	10.4
	S.D.	±2807	±18.2	±16.7	±11.6	±11.9	±33.1	±26.3	±2.1	±1.5	±5.9	±5.6
Mediterranean overall	36	7100	47.7	77.2	52.9	36.9	120.7	63.7	7.3	8.6	11.2	8.2
Averages all stands		8287	55.0	66.3	38.4	35.4	63.3	37.4	5.2	5.9	9.4	7.0
S.D.		±3589	±27.2	±34.6	±19.2	±17.6	±38.2	±28.5	±2.4	±2.6	±6.0	±5.3

Differences between deciduous and coniferous species relative to accumulation and cycling

Because the foliage of deciduous species is replaced each year, unlike that of coniferous species, it is to be expected that many aspects of mineral cycling between these major taxonomic groups will also be different. Recognizing that such differences should exist, we summarized the IBP data sets in a way that would provide direct comparison between two systems relative to mineral cycling parameters. We included all deciduous and coniferous sites in our analysis.

Our comparison clearly shows that the rate of cycling is far more rapid in deciduous than coniferous species for all five elements (Table 6.9). For example, the nitrogen uptake rate of coniferous species is only 56% that of deciduous stands. The potassium, calcium and magnesium uptake rates of coniferous species approximate 50% that of deciduous sites. Only in the case of phosphorus is the difference relatively small (within 80%). Annual requirement and return of these elements showed similar differences when we compared these two forest types.

Deciduous species translocate significantly more nitrogen from old to new tissue than do conifers (Table 9). Average nitrogen uptake for deciduous species is 70.5 ± 21 kg/ha. However, 94 ± 19 kg/ha is needed to meet annual requirements for nitrogen in new tissue. Thus, about 1/3 of annual requirement for nitrogen is met through translocation from older to new tissue. In the case of coniferous species, the data suggest little if any translocation. Essentially identical quantities of nitrogen are taken up (39 ± 22 kg/ha/yr) as are required to produce new tissue (39 ± 21 kg/ha/yr). There is very little apparent translocation of potassium for either deciduous or coniferous species. Calcium uptake, by way of contrast, greatly exceeds annual requirement for both deciduous and coniferous species. In the case of the coniferous species, calcium uptake is about double the requirement. Much of the calcium taken up each year accumulates in older tissue and is not directly incorporated in the growth of new material.

The pattern for magnesium is similar to that for calcium. Uptake greatly exceeds annual requirement for both the deciduous and coniferous species, suggesting, as for calcium, that magnesium accumulates in the older tissue of the tree.

Deciduous and coniferous species were significantly different at the 99% confidence level in the uptake, requirement, and return of all four of these elements. Only for phosphorus did we fail to find a significant difference in the amount of uptake and return. The annual requirement was different at the 99% confidence level.

In contrast, the distribution of these elements within the ecosystems of these same deciduous and coniferous forests was typically not significantly different (Table 6.10). This comparison was made for elemental accumu-

Table 6.9. *Comparison of deciduous and coniferous species relative to element uptake, requirement and return*

Element	Uptake (kg/ha/yr) Deciduous	Uptake (kg/ha/yr) Coniferous	%[a] Sign.	Requirement (kg/ha/yr) Deciduous	Requirement (kg/ha/yr) Coniferous	%[a] Sign.	Return (kg/ha/yr) Deciduous	Return (kg/ha/yr) Coniferous	%[a] Sign.
Nitrogen	70	39	99	94	39	99	57	30	99
Potassium	48	25	99	46	22	99	40	20	99
Calcium	84	35	99	54	16	99	67	29	99
Magnesium	13	6	99	10	4	99	11	4	99
Phosphorus	6	5	79	7	4	99	4	4	60

[a] %significance between means.

Table 6.10. *Comparison between deciduous and coniferous species relative to accumulation of nitrogen, potassium and calcium within certain ecosystem compartments*

	Above-ground accumulation (kg/ha)			Forest floor accumulation (kg/ha)			Soil (kg/ha)		
Element	Deciduous	Coniferous	%[a] Sign.	Deciduous	Coniferous	%[a] Sign.	Deciduous	Coniferous	%[a] Sign.
Nitrogen	447	411	32	368	668	90	5658	6701	30
Potassium	242	284	36	51	78	90	[b]	[b]	[b]
Calcium	737	439	78	223	239	21	[b]	[b]	[b]
Magnesium	63	57	31	35	72	93	[b]	[b]	[b]
Phosphorus	47	38	46	27	72	98	[b]	[b]	[b]

[a] % significance between means.

[b] Soils data for potassium, calcium, magnesium and phosphorus were not compared statistically because of differences in analyses.

Table 6.11. *Comparison of nitrogen accumulation and cycling for deciduous and coniferous species at three IBP study sites*

		Accumulation (kg/ha)			Cycling (kg/ha/yr)		
Site	Species	Above-ground	Forest floor	Soil	Uptake	Requirement	Return
Solling[a]	Beech	464	892	7708	66	106	53
	Spruce	601	1550	6937	57	44	47
Kongalund	Beech	1071	86	7800	78	129	70
	Spruce	720	245	6900	80	67	66
Cedar River	Alder	405	887	5450	115	119	96
	Douglas fir	316	223	2476	36	36	26

[a] Average of three forest stands.

lation above-ground, in the forest floor, and within the soil. Unfortunately, we could compare only nitrogen in the soil compartment because of the many different ways in which the other elements had been analyzed. Only phosphorus accumulation within the forest floor shows a significant difference between a deciduous and a coniferous ecosystem. Since these deciduous and coniferous ecosystems were significantly different in elemental cycling but not in elemental distribution, we inferred that the rate of cycling (Tables 6.9, 6.10) is an inherent property of deciduous and coniferous species and is not significantly regulated by differences in elemental accumulation. However, a better comparison between the elemental composition of the soils of these sites is needed before such a conclusion can be safely drawn.

In several IBP studies, deciduous and coniferous species were directly compared in adjacent plots. The advantage of such a comparison is that soil and climatic conditions should be reasonably similar. The beech (*Fagus silvatica*) and spruce (*Picea abies*) stands of the Kongalund site in southern Sweden (stands No. 9 and 34), the beech and spruce stands at Solling (stands No. 10, 11, 12, 30, 31, 32) and Douglas fir (*Pseudotsuga menziesii*) and red alder (*Alnus rubra*) at the Cedar River site in the USA (stands No. 6 and 35) are examples of this form of comparison. Results form these comparisons have been reported (Nihlgard, 1972; Heinrichs & Mayer, 1977; Cole, Gessel & Turner, 1978). Although we cannot provide a statistical analysis of these studies, as we could for the comparison of all of the plots (as discussed above), there were many of the same differences and similarities (Table 6.11). Except for alder at Cedar River, there is no clear relationship between occurrence of a coniferous or deciduous species and accumulation of nitrogen by the ecosystems. The greater nitrogen accumulation in the alder ecosystem compared to Douglas fir is due to nitrogen fixation. This relationship and the comparison of these two stands relative to nitrogen fixation is discussed later. The spruce forest seems to be accumulating more nitrogen in the forest floor than beech at both the Solling and Kongalund sites. This is probably due to the lower decomposition rates associated with coniferous litterfall.

In general, we can conclude from both this comparison and the one made earlier that the rate of cycling is higher in deciduous stands. Except at the Kongalund site, nitrogen uptake is greater for deciduous species. At all of the deciduous sites nitrogen requirement is substantially higher as is nitrogen return. Productivity of these forests will certainly affect these cycling rates. This interaction is discussed separately.

Effect of elemental cycling on forest productivity

The relationship between elemental cycling and productivity has been addressed in the extensive reviews on this subject by Ovington (1962) and Rodin & Bazilevich (1967). Specific studies have been made comparing elemental cycling, elemental distribution, and forest productivity for individual forest ecosystems and ecosystems that have received fertilization (Heilman & Gessel, 1963; Madgwick, White, Xydias & Leaf, 1970; Fagerstrom & Lohm, 1977). The synthesis of the IBP studies provided another opportunity to examine the general relationship between elemental uptake, requirement, and return as it affects or is affected by forest production.

The coefficients of determination between productivity and elemental cycling in deciduous and coniferous forests are given in Table 6.12. Clearly, production is far more strongly correlated to cycling of nitrogen and potassium than it is to the other three elements. In addition it is equally apparent that production is more strongly correlated to elemental cycling in coniferous ecosystems than in deciduous ones. The highest correlation, $r^2 = 0.92$, was found between coniferous production and nitrogen requirement associated with annual growth of the forest. In contrast, there was little if any correlation between production and cycling of calcium in either coniferous or deciduous forests.

These data suggest several roles for cycling in the production of forest biomass. Uptake and requirement for nitrogen and potassium are far more strongly correlated with production of coniferous than with deciduous species (Table 6.12). The difference in correlation between these two forest types is probably due to the greater amount of nitrogen and potassium that deciduous species translocate before leaffall, thus providing a certain degree of independence from the soil nitrogen supply and a need to supply the annual requirement from uptake. Earlier data (Table 6.3) lent strength to this suggestion. Coniferous species appear to meet all of their annual

Table 6.12. *Coefficients of determination (r^2) of above-ground biomass production and cycling of nitrogen, potassium and calcium in deciduous and coniferous ecosystems*

		Coefficients of determination (r^2)	
Element	Process	Deciduous	Coniferous
Nitrogen	Uptake	0.42	0.78
	Requirement	0.58	0.92
	Return	0.33	0.62
Potassium	Uptake	0.07	0.90
	Requirement	0.07	0.81
	Return	0.00	0.80
Calcium	Uptake	0.02	0.32
	Requirement	0.09	0.22
	Return	0.00	0.21
Magnesium	Uptake	0.01	0.55
	Requirement	0.00	0.34
	Return	0.09	0.48
Phosphorus	Uptake	0.16	0.63
	Requirement	0.17	0.77
	Return	0.04	0.63

requirement for nitrogen through the uptake process (39 kg/ha out of 39 kg/ha), while deciduous species are meeting only 67% of their needs through the uptake process (64 kg/ha out of 95 kg/ha). The rest apparently is derived through translocation from older tissue.

We tested the hypothesis that the lower correlation between production and uptake of nutrients by deciduous species is due to higher soil fertility in areas where deciduous sites are located. Obviously if this was indeed true, a lower correlation would be expected because other factors such as soil moisture conditions or climatic factors could also be involved in regulating production. To some extent, we tested and rejected this hypothesis in the statistical analysis presented in Table 6.10. Deciduous forests of the IBP sites were found to be growing on soils that did not differ statistically in total nitrogen from those supporting the coniferous forest.

Lack of any meaningful correlation between production and cycling of calcium and magnesium for either coniferous or deciduous forests can be attributed to several possible reasons: (1) there are no calcium and magnesium deficiencies at the study sites, (2) calcium and magnesium are accumulated in older as well as new tissue, (3) there is a large variation in soil calcium and magnesium levels between sites, depending on whether they are located on calcareous deposits and the age of the soil. These

Table 6.13. *Above-ground biomass production for deciduous and coniferous forest normalized to the annual uptake, requirement, and return of nitrogen, potassium, calcium, magnesium and phosphorus*

Element	Process	Forest type	Normalized Production (kg/ha/yr)	%[a] Sign.
Nitrogen	Uptake	Deciduous	143 ± 36	99
		Coniferous	194 ± 48	
	Requirement	Deciduous	102 ± 20	99
		Coniferous	201 ± 81	
	Return	Deciduous	180 ± 51	99
		Coniferous	283 ± 126	
Potassium	Uptake	Deciduous	216 ± 85	99
		Coniferous	354 ± 154	
	Requirement	Deciduous	220 ± 78	99
		Coniferous	380 ± 182	
	Return	Deciduous	271 ± 132	98
		Coniferous	521 ± 333	
Calcium	Uptake	Deciduous	130 ± 61	99
		Coniferous	217 ± 95	
	Requirement	Deciduous	232 ± 161	99
		Coniferous	520 ± 303	
	Return	Deciduous	167 ± 86	98
		Coniferous	302 ± 160	
Magnesium	Uptake	Deciduous	915 ± 445	98
		Coniferous	1559 ± 783	
	Requirement	Deciduous	1292 ± 846	96
		Coniferous	2257 ± 1313	
	Return	Deciduous	1151 ± 642	99
		Coniferous	2404 ± 1465	
Phosphorus	Uptake	Deciduous	1859 ± 745	80
		Coniferous	1519 ± 582	
	Requirement	Deciduous	1374 ± 417	90
		Coniferous	1759 ± 732	
	Return	Deciduous	2496 ± 965	37
		Coniferous	2263 ± 1524	

[a] Percent significance between means.

possibilities, either individually or collectively, are undoubtedly influencing calcium and magnesium cycling at the IBP sites.

To compare directly cycling effects between deciduous and coniferous forests we normalized the above-ground production rates to rates of mineral cycling. This comparison (Table 6.13) illustrates that the coniferous forest has a marked advantage over the deciduous in respect to amount of nitrogen needed to produce the same quantity of biomass. Similarly, the

Table 6.14. *Above-ground biomass production for the various forest regions and types normalized to the uptake, requirement, and return of nitrogen*

Forest region	No. of sites	Normalized production (kg/ha/yr) Uptake	Requirement	Return
Boreal coniferous	3	236 ± 12	295 ± 169	425 ± 139
Boreal deciduous	1	207	92	256
Temperate coniferous	13	184 ± 49	179 ± 26	250 ± 102
Temperate deciduous	14	138 ± 34	103 ± 21	173 ± 50
Mediterranean	1	149	92	206
All stands	32	168 ± 49	151 ± 77	232 ± 108

nitrogen requirement for a coniferous forest is only 50% as large as that of a deciduous forest having the same level of production. This apparently greater nitrogen efficiency of a coniferous forest is partly due to needle retention. Since a coniferous forest does not have to replace annually its total foliage, it should not need as much nitrogen to maintain its canopy as does a deciduous forest. The differences between means are all significant at the 99% confidence level.

The relationship between nitrogen uptake (kg/ha/yr) and production (above-ground increment, kg/ha/yr) can be expressed by the regressions:

$$\text{Deciduous forest production} = 4242 + 85 \times \text{uptake},$$
$$\text{Coniferous forest production} = 1201 + 146 \times \text{uptake}.$$

Similarly the relationship between nitrogen requirement and production can be expressed by the regressions:

$$\text{Deciduous forest production} = 1069 + 114 \times \text{requirement},$$
$$\text{Coniferous forest production} = 406 + 170 \times \text{requirement}.$$

Similar differences between deciduous and coniferous forests can also be seen in potassium, calcium and magnesium cycling. These differences between means are nearly all significant at the 98 or 99% confidence level. The deciduous and coniferous forests were statistically similar only for the uptake and return of phosphorus (Table 6.13).

Due to unequal distribution of the number of sites between forest regions, as discussed earlier, we cannot provide a statistical comparison between production and cycling by region. The general relationship that exists between production and cycling of nitrogen is summarized in Table 6.14. As in Table 6.13, production values have been normalized to the various parameters of cycling (uptake, requirement, return). Sufficient information to evaluate the data statistically was available only for the boreal coniferous, temperate coniferous, and temperate deciduous forests. Within this limitation of data, several patterns of production and cycling still emerge. Coniferous forests are consistently more efficient than the deciduous in producing biomass with the same amount of nitrogen. The northern species seem to be more efficient than the more southerly species in producing biomass for a given amount of nitrogen. This could be caused by a greater deficiency of available nitrogen in these boreal sites, resulting in a higher conversion ratio between production and the uptake and utilization of nitrogen.

The requirement of nitrogen shows a similar trend. The coniferous forests within a given region require less nitrogen per unit of production than the deciduous forests. The more northern forests seem to need less than those to the south. Collectively, these data strongly suggest that the production of forest ecosystems is nitrogen-limited, with coniferous forests, especially those in northern latitudes, more limited than are deciduous forests.

Additions and losses of nutrient elements from forest ecosystems

Accumulation of nutrient elements in either an ionic form or incorporated within the organic component of an ecosystem is dependent on the net difference between those processes regulating inputs and those controlling losses. The additions and losses of elements from forested plots and small watersheds have been extensively reported in the literature (Cole, Gessel & Dice, 1967; Duvigneaud & Denaeyer-DeSmet, 1970; Likens *et al.*, 1977; Henderson, Swank, Waide & Grier, 1978). A comprehensive analysis of these processes where the input–output fluxes were isolated and individually assessed as not undertaken at any of the IBP sites. However, some measurements of input–output were made at most of the sites, typically representing the summation or interaction of several processes. For example, few studies isolated precipitation inputs from dry fallout – natural inputs derived through atmospheric processes from inputs associated with atmospheric pollutants. Nutrients losses by soil leaching were not compared to inputs through soil weathering processes. Leaching losses measured from small watersheds were not separated into losses associated with the rooting zone and losses due to mineral weathering below the rooting zone. In addition, only two studies (stands No. 7 and 35) examined the potential input of nitrogen through the process of biological fixation.

We have here limited our discussion of input–output fluxes and processes to those additions resulting from atmospheric precipitation and biological fixation and losses from leaching below the rooting zone. Data are insufficient at the IBP sites to consider comprehensively the other aspects of nutrient additions and losses mentioned above.

Atmospheric nitrogen additions

The amount of elemental addition to forest ecosystems by way of atmospheric precipitation and dryfall varies greatly between study sites. Typically, additions of nutrients by these means are relatively small compared to the amount taken up by forest vegetation. As discussed above, average nitrogen uptake for all sites was 55 ± 27 kg/ha/yr. Average atmospheric addition of nitrogen was 9.8 kg/ha/yr, or about 18% of average annual uptake. However, this value varied greatly between sites ranging from 1.1 kg/ha/yr at the spruce site in the USSR to 22.8 kg/ha/yr at the Solling site in West Germany. This variability in input appears to be highly dependent on the proximity to sources of input such as industrial or population centers, a common observation (e.g., Junge, 1963; Likens & Bormann, 1974). At the Cedar River site in Washington, northwest USA, less than 2 kg/ha of nitrogen is added annually by precipitation, or less than 5% of the annual uptake of second growth Douglas-fir trees at that site. At the Coweeta, Walker Branch and Hubbard Brook sites in the eastern USA, annual nitrogen input is about 8 kg/ha, evidently due to the larger populations and increased industrial activity in that area of the United States. Such an input rate could potentially supply 14% of the uptake needs at these sites. In contrast, at the Solling site in West Germany, atmospheric input is nearly 23 kg/ha/yr, or 32% of the average annual needs.

High rates of nitrogen input should have a positive influence on productivity of such areas, decreasing the potential of a nitrogen deficiency. The possibility that this occurs at the Solling site is shown by our earlier calculations that compared biomass production to nitrogen uptake. Both deciduous and coniferous forests at this site show substantially less production per unit of uptake than that noted for the average deciduous and coniferous stands in the temperate region, indicative of a nitrogen surplus. For example, the spruce stands at Solling produce 135 kg/ha of biomass per kg of nitrogen uptake, while the average for the temperate coniferous forest is 184 kg/ha. The beech stands produce 124 kg/ha of biomass per kg of nitrogen uptake. Average production for temperate deciduous forests is 138 kg/ha. In contrast, nitrogen-deficient Douglas-fir stands on the Cedar River site produce 214 kg/ha of biomass for each kg of nitrogen uptake. The Cedar River site, as we indicated earlier receives only 1.7 kg/ha/yr of nitrogen from the atmosphere.

These results suggest that atmospheric nitrogen inputs can play an important role in minimizing nitrogen deficiencies that occur in many forest stands. In a nitrogen-deficient forest, an increase in atmospheric nitrogen should result in a decrease in the amount of biomass produced per unit of nitrogen uptake. From these data sets, a correlation coefficient (r) of -0.35 exists between production values normalized to nitrogen uptake and the amount of nitrogen added from the atmosphere. Considering only temperate coniferous forests, this correlation coefficient is −0.54. In the temperate deciduous forests where our earlier analysis indicated less likelihood of a nitrogen deficiency (Table 6.12), atmospheric addition of nitrogen has had less effect on changing productivity. In this case the correlation coefficient between normalized production value and atmospheric nitrogen additions is only −0.13.

The atmospheric addition of elements other than nitrogen does not seem to have as important a role in the productivity of these stands. As we discussed earlier, the only other element closely correlated to productivity was potassium (Table 6.12). However atmospheric addition of potassium was seldom reported to be high (maximum of 5 kg/ha/yr) and varied by only 2.3 ± 1.3 kg/ha/yr between sites.

Addition of nitrogen by fixation

In many forest ecosystems nitrogen is also added through the process of biological fixation. The amount of fixation varies, depending on the specific ecosystem, fixation process, and the organism involved. The amount of fixation reported in the literature varies widely, ranging from as little as 1 to 2 kg/ha/yr for free-living fixers to over 200 kg/ha/yr for symbiotic fixation associated with legumes, alder and other higher plants.

In the IBP forest ecosystem program, nitrogen fixation rate and its impact on the elemental cycle was followed at only one site, a red alder ecosystem at the Cedar River site (stand No. 35). This study was designed directly to compare alder and Douglas fir relative to elemental accumulation and cycling rates. The two stands are on comparable soils and located adjacently. The Douglas-fir site was established as a plantation in 1933 after the area was logged. The red alder site was established as natural regeneration adjacent to the Douglas-fir plantation boundaries. We have assumed in comparing these two ecosystems that the differences currently found in elemental accumulation and cycling are caused by the differences in the vegetation of these two sites.

It is evident by comparing distribution of nitrogen within the two ecosystems that alder has yielded an apparent increase of total nitrogen of 3240 kg/ha over a 38-yr period. Although most of this increase can be found in the soil (2180 kg/ha), a substantial amount is also in the forest floor and above-ground vegetation (Table 6.15). These values provide estimates (Cole *et al.*, 1978) that nitrogen accumulates in this alder ecosystem at a rate of 85.3 kg/ha/yr. This value is not markedly different from that reported by other researchers in this field (Tarrant & Miller, 1963; Newton, el Hassan & Zavitkovski, 1968).

These two ecosystems are also very different in nearly every aspect of

Table 6.15. *Estimated nitrogen accumulation and average annual accumulation by 38-yr-old red alder (Alnus rubra)*

	Estimated nitrogen accumulation (kg/ha)		Increase in red alder over Douglas fir (kg/ha)	Average annual accumulation (kg/ha/yr)
	Douglas fir	Red alder		
Overstory	320	590	270	7.1
Understory	10	100	90	2.4
Forest floor	180	880	700	18.4
Soil	3270	5450	2180	57.4
Total	3780	7020	3240	85.3

elemental cycling (Table 6.16). Annual nitrogen uptake by alder is 115 kg/ha, three times higher than the Douglas fir stand. Annual return of nitrogen is 94 kg/ha, six times greater than Douglas fir. In the Douglas fir ecosystem, about 19% of the annual nitrogen requirement is met through recycling from older foliage. In the case of alder only 3% of nitrogen is recycled, apparently due to the high nitrogen levels available to the tree from fixation. Because of this low recycling in alder, the mean residence time of nitrogen in the foliage is only 1.1 yr. By contrast, the mean residence time of nitrogen in the foliage of Douglas fir is 6.5 yr.

These results clearly show that nitrogen fixation by alder results in major nitrogen accretion to these ecosystems. It is also evident that nitrogen cycling is quite different in alder than in the adjacent Douglas fir ecosystem partly because of this added nitrogen. This cycling difference could be attributed in part to differences between a coniferous and a deciduous species, as we have already mentioned. To contrast differences between two deciduous species, of which only one fixes nitrogen, we compared the accumulation and cycling in alder (stand No. 35) with that of a 59-yr-old beech ecosystem (stand No. 30) at Solling, West Germany. The two stands are quite similar in productivity, above-ground nitrogen accumulation, nitrogen content in the forest floor, and annual nitrogen requirement for biomass production (Table 6.16). However, the two ecosystems are strikingly different in nitrogen recycling at the time of senescence. Only 4.1 kg/ha or 3% of the nitrogen required for growth is derived by recycling nitrogen from senescing alder foliage, while 22.6 kg/ha or 20% of the nitrogen is derived from recycling in the beech foliage. As previously indicated (Table 6.8), deciduous stands in the temperate region, on average, recycle 22.9 kg/ha or 23% of the nitrogen for growth.

This lack of nitrogen recycling in alder could explain the longer period of

Table 6.16. *Effect of nitrogen fixation on accumulation and cycling. A comparison between fixing (alder) and non-fixing (beech) deciduous species*

Process	Red alder Stand no. 35	Douglas fir Stand no. 5	Beech Stand no. 30
Accumulation (kg/ha)			
Total tree	416	227	407
Foliage	100	65	97
Forest floor	887	178	815
Cycling (kg/ha/yr)			
Uptake	115	34	91
Requirement	119	42	114
Returned	94	22	75
Recycled	4	8	23
% Recycled	3	19	20

autumnal foliage retention. Since this species does not need to conserve nitrogen through a recycling process it can afford to retain its leaves well into the winter months when they finally freeze. Alder thus has a significantly longer season for photosynthesis than is typically available to deciduous species.

Elemental losses by leaching

Elemental losses through the leaching process were studied at a limited number of IBP sites. Two quite different procedures were used: (1) Soil leachates were collected with lysimeters placed below the rooting zone (stands No. 6, 8, 11, 22, 32, 35), and (2) stream drainage waters were collected from a defined small watershed unit in which the stand is located (stands No. 7, 13, 14, 23, 24, 25). These two techniques for assessing losses are not directly comparable. The lysimeter technique will collect only soil solutions that reach the assigned depth in which the lysimeters have been placed. Stream collections from the small watershed will collect not only solutions leached beyond the rooting zone, but also those elements added to these solutions by bedrock weathering and surface erosional processes. Consequently, stream collections will typically have higher elemental concentrations than those collected by lysimeters (Table 6.17). This is especially true for most of the base elements that are involved in soil and geologic weathering such as calcium, magnesium, iron, manganese and potassium. Since nitrogen is not readily involved in mineralogical weathering processes, concentrations found below the rooting zone are not appreciably different

Table 6.17. *Elemental losses through leaching and stream runoff at the IBP sites*

		Elements (kg/ha/yr)				
Sites	Stand no.	Nitrogen	Potassium	Calcium	Phosphorus	Magnesium
		Deep leaching				
Douglas fir (100 cm)[a]	6	0.6	1.0	4.5	0.02	—
Picea abies (100 cm)	8	0.9	2.2	2.3	0.06	0.45
Spruce (50 cm)	11	14.9	2.1	13.5	0.02	3.7
Yellow poplar (60 cm)	22	3.5	8.9	44.5	0.05	—
Beech (50 cm)	32	6.0	2.9	12.7	0.10	3.7
Oak–Birch	33	12.6	8.3	59.8	0.2	6.0
Red alder (100 cm)	35	1.7		2.2		
		Watershed runoff				
H. J. Andrews	7	1.7	9.7	121.8	0.6	10.7
Coweeta	14	0.2	4.5	5.9	—	—
Hubbard Brook	27	3.9	1.9	13.7	0.01	3.1
Walker Branch	13, 23, 24, 25	1.8	6.8	147.5	0.02	77.1

[a] Depth of leachate collection.

from those in a drainage stream. If anything, there seems to be a tendency for nitrogen concentrations to be lower in runoff waters because of nitrogen immobilization by aquatic biological processes.

These results indicate that most ecosystems receive more nitrogen from atmospheric addition (average of 8.8 kg/ha/yr) than is lost through soil leaching (4.3 kg/ha/yr). This net balance of nitrogen (4.5 kg/ha/yr) is perhaps misleading due to the high nitrogen inputs experienced at a few of the sites. However, only one site (stand No. 33, Merlewood in Great Britain) showed a net deficit. At all other sites where both input and losses were measured, there was a positive net balance of nitrogen. This was true even at those sites where only very small increments of nitrogen were being added each year, such as the USSR site, and the Cedar River and H. J. Andrews sites in the USA. Losses were correspondingly smaller, leaving a net positive accumulation.

Mechanisms by which nitrogen and other ions are conserved in forest ecosystems have been discussed frequently. The important role played by vegetative uptake cannot be minimized (Vitousek *et al.*, 1979). In addition, the soil also has a critical role in retaining this element as long as it remains in the form of ammonium ions (Cole, Crane & Grier, 1975). Transformation of ammonia to nitrate will, however, release nitrogen from the soil exchange sites and increase its potential for leaching. Without active uptake, nitrate will readily leach through the soil such as was reported for the Hubbard Brook watershed (Bormann *et al.*, 1974).

Leaching losses of the base elements occur as one would expect (Table 6.17). At those sites where the bedrock material is high in calcium, leaching of calcium is also high. This is seen in both the Coweeta and Walker Branch watershed studies. The leaching losses of phosphorus are nearly always low, both within the soil and drainage waters. This is probably due to the high phosphorus sorption capacity associated with nearly all soils.

Conclusions

We have attempted here to tabulate, compare, and summarize the elemental studies conducted under IBP sponsorship. Thirty-two forest stands from 14 sites are included. Since the sites are not uniformly distributed, they do not cover the major regions and forest ecosystems in a systematic manner. This has, of course, limited the possibilities of synthesizing the data collected.

At the beginning of this chapter we stated that the most significant aspect of our contribution would be the collection and summarization of the information on elemental cycling that resulted from the IBP. In addition, we also analyzed this information to see whether new insights would emerge to help us better to understand ecosystem behavior. From the synthesis of these data we were also able to test, modify, clarify, and expand some ideas previously developed and discussed in the literature. Some of the more significant observations of our synthesis follow.

1. The cycling of elements is not stable over the life of an ecosystem, rather it changes dramatically during this period. Thus, it is critical to know the development stage of an ecosystem before reaching conclusions about its cycling properties.
2. The cycling of different elements within an ecosystem is markedly different. Apparently those elements present in deficient amounts are cycled far more efficiently than those present in excess. Ecosystems seem to have evolved strategies for efficiently recycling or using those elements that are in short supply. In most of the sites studied, nitrogen appears to be present at deficiency levels.
3. On average, 45% of organic matter and 7% of nitrogen is held in the above-ground tree components of an ecosystem. These percentages tend to decrease at higher latitudes and increase at lower latitudes.

4. The mean residence time of elements in the forest floor varies widely between regions. Turnover periods are longer in the boreal region and significantly shorter in the temperate and Mediterranean regions. Coniferous forest floors have longer turnover periods than deciduous forest floors.
5. The rate of uptake and requirement is significantly higher in deciduous forests than in coniferous forests for all elements except phosphorus.
6. Deciduous species translocate significantly more nitrogen from older foliage before litterfall than do conifers. Very little potassium is translocated for either coniferous or deciduous species. Neither calcium nor magnesium is translocated, rather the uptake of these two elements greatly exceeds annual requirement for both coniferous and deciduous species.
7. In coniferous species, uptake and requirement of nitrogen and potassium are strongly correlated with biomass production. The correlation is somewhat weaker for deciduous species in regards to nitrogen uptake and requirement. There is little, if any, correlation between production, cycling, and the other elements studied for either deciduous or coniferous species.
8. Coniferous species are consistently more efficient than deciduous species in producing biomass with equal amounts of nitrogen uptake. Similarly, species in the boreal sites are more efficient than those in the temperate region. Apparently, the efficiency of production per unit of nitrogen uptake increases as nitrogen becomes more limiting.
9. The atmospheric addition of nitrogen to forest ecosystems varies greatly between sites. In many areas it represents as little as 5% of the average annual uptake by the vegetation. However, at sites adjacent to industrial and population centers this value may be as much as 32% of the average annual uptake. Nitrogen deficiencies seem to be minimized in those areas that receive large quantities of atmospheric nitrogen.
10. The fixation of nitrogen by alder causes a significant increase in nitrogen accumulation. It also results in other changes in the elemental cycle, including an increase in nitrogen uptake and a decrease in amount of nitrogen recycled by foliage.
11. In general, more nitrogen is added annually by way of precipitation than is lost in drainage waters from the forest ecosystems considered in our synthesis. On average, atmospheric additions are twice as large as losses.

Appendix. Elemental cycling data for 32 IBP stands

Stand No. 1
Site. Black Spruce Muskeg, Site 1, Alaska, USA
Investigator(s): Van Cleve
Forest type: Black spruce forest (*Picea mariana*) Muskeg
Geology: Parent material is loess: alkaline in reaction
Soil type: Pergelic cryaquept
Stand age: 51 years
Annual precipitation: 268.8 mm
Mean annual temperature: −3.4°C
Length growing season: 60–80 days
Altitude: 166.7 m
Latitude: 64° N
Institution: Univ. Alaska, USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	5012.0	21.0	9.8	3.5	2.8	2.9
Overstory branches	3590.0	7.4	3.9	1.8	1.1	1.8
Overstory boles	7995.0	11.5	10.3	24.2	1.6	2.2
Overstory roots	12457.0	18.5	13.7	21.4	2.9	3.1
Understory vegetation	8639.0	66.7	20.0	31.7	7.6	11.3
Forest litter layer	88664.0	486.0	59.7	395.6	105.6	95.7
Soil-rooting zone	3951.0	689.0	124.0	1691.6	2.0	853.8
Increments (kg/ha/yr)						
Overstory foliage	233	2.1	1.2	0.6	0.2	0.2
Overstory branches	109	0.22	0.11	0.58	0.03	0.05
Overstory boles	285	0.45	0.38	0.83	0.05	0.08
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation						
Atmosphere particulates						
Overstory litterfall	143	1.1	0.03	0.11	1.4	0.09
Leaf wash (approx)		0.8	0.83	1.14	0.1	0.14
Stem flow						
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 2
Site: Black Spruce Muskeg, Site 2, Alaska, USA
Investigator(s): Van Cleve
Forest type: Black spruce forest (*Picea mariana*) Muskeg
Geology: Bedrock: Birch Creek schist: Loessic soil
Soil type: Pergelic cryaquept
Stand age: 55 yr
Annual precipitation: 286.8 mm
Mean annual temperature: −3.4°C
Length growing season: 60–80 days
Altitude: 469.7 m
Latitude: 64°N
Institution: Univ. Alaska, USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	5310.0	26.4	13.7	53.3	3.6	2.6
Overstory branches	4691.0	19.2	5.4	17.9	1.7	3.1
Overstory boles	14017.0	49.0	12.2	48.7	8.9	4.8
Overstory roots	10401.0	39.5	41.2	88.7	5.1	10.4
Understory vegetation	6283.0	50.8	15.3	22.0	5.2	6.4
Forest litter layer	133260.0	656.5	145.4	231.3	152.1	224.5
Soil-rooting zone	35350.0	2198.0	169.0	609.0	5.4	121.0
Increments (kg/ha/yr)						
Overstory foliage	484	4.3	3.0	1.4	0.6	0.6
Overstory branches	220	0.6	0.2	0.7	0.1	0.1
Overstory boles	698	3.3	0.6	2.2	0.5	0.2
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation						
Atmosphere particulates						
Overstory litterfall	290	1.6	0.26	4.0	0.12	0.17
Leaf wash (approx)		0.8	0.83	1.1	0.09	0.14
Stem flow						
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 3
Site: Black Spruce–Feather Moss Site, Alaska, USA
Investigator(s): Van Cleve
Forest type: Black spruce forest, (*Picea mariana*) Feather moss
Geology: Bedrock: Birth Creek schist, basic in reaction
Soil type: Pergelic cryaquept
Stand Age: 130 yr
Annual precipitation: 268 mm
Mean annual temperature: −3.4°C
Length growing season: 60–80 days
Altitude:
Latitude: 64° N
Institution: Univ. Alaska, USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	14196.0	70.8	17.6	163.3	8.5	15.9
Overstory branches	12947.0	49.0	6.2	71.0	6.1	10.7
Overstory boles	86046.0	95.1	51.8	390.7	14.3	33.4
Overstory roots	51697.0	70.8	24.5	97.5	7.6	11.4
Understory vegetation	7598.4	46.7	24.4	28.4	6.9	7.4
Forest litter layer	119235.0	709.7	122.1	452.2	87.4	99.3
Soil-rooting zone	47490.0	2362.0	286.0	5052.0	4.4	912.0
Increments (kg/ha/yr)						
Overstory foliage	147.0	1.10	0.24	0.44	0.17	0.13
Overstory branches	259.0	0.64	0.80	0.85	0.09	0.12
Overstory boles	1184.0	1.52	0.72	1.69	0.18	0.35
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation						
Atmosphere particulates						
Overstory litterfall	534.3	3.6	0.7	4.1	0.4	0.3
Leaf wash		0.8	0.83	1.14	0.09	0.14
Stem flow						
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 4
Site: Birch Site, Alaska, USA
Investigator(s): Van Cleve
Forest type: Paper birch (*Betula papyrifera*)
Geology: Bedrock: Birch Creek schist
Soil type: Pergelic cryaquept, silt loam
Stand Age: 50 yr
Annual precipitation: 268 mm
Mean annual temperature: −3.4°C
Length growing season: 60–80 days
Altitude:
Latitude: 64° N
Institution: Univ. Alaska, USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	2362.8	51.1	22.8	14.9	5.2	8.2
Overstory branches	11025.2	39.8	17.1	37.9	4.9	5.7
Overstory boles	83954.9	130.0	64.3	110.9	9.4	24.2
Overstory roots	44297.0	131.1	43.3	99.3	15.4	20.6
Understory vegetation	95.0	1.0	44.8	134.2	15.5	23.5
Forest litter layer	68772.0	548.0	99.0	489.0	79.0	139.0
Soil-rooting zone	280100.0	2879.0	186.0	7545.7	26.2	2317.1
Increments (kg/ha/yr)						
Overstory foliage	2362.8	51.1	22.8	14.9	5.2	8.2
Overstory branches	386.9	1.3	0.7	1.2	0.2	0.2
Overstory boles	2414.0	3.5	2.2	2.2	0.3	0.6
Overstory roots	2375.3	25.7	11.8	8.4	2.6	4.1
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation	37.21	2.1	0.16	0.98	0.09	0.06
Atmosphere particulates						
Overstory litterfall	2645.7	18.0	8.3	34.5	5.0	9.2
Leaf wash	30.33	2.1	1.46	1.01	0.20	0.55
Stem flow	3.42	0.1	0.11	0.03	0.006	0.01
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 5
Site: Thompson Research Center, Washington, USA
Investigator(s): Turner
Forest type: Douglas-fir plantation (*Pseudotsuga menziesii*)
Geology: River terraces, glacial outwash
Soil type: Typic haplorthod, Everett gravelly sandy loam
Stand age: 22 yr
Annual precipitation: 1360 mm
Mean annual temperature: 9.8°C
Length growing season: 214 days
Altitude: 210 m
Latitude: 47° 23′N
Institution: Univ. Washington, USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	4995	65.1	42.6	27.0	12.5	5.8
Overstory branches	8162	17.6	40.3	34.7	7.1	7.9
Overstory boles	113338	144.6	49.0	140.6	92.6	15.3
Overstory roots						
Understory vegetation	7638	66.6	59.4	68.7	8.7	18.5
Forest litter layer	20540	177.7	37.8	114.0	25.6	54.0
Soil-rooting zone						
Increments (kg/ha/yr)						
Overstory foliage	2100	29.8	21.4	7.0	4.6	2.9
Overstory branches	540	2.2	3.0	3.4	0.5	0.6
Overstory boles	6130	9.8	6.6	2.9	0.8	3.3
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		1.7	2.2	2.2	2.3	0.5
Atmosphere particulates						
Overstory litterfall	2836	18.8	9.7	22.9	3.2	4.4
Leaf wash	Data included in stem flow					
Stem flow		2.9	7.0	5.2	1.8	1.5
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 6
Size: Thompson Research Center, Washington, USA
Investigator(s): Turner, Cole
Forest type: Douglas-fir plantation (*Pseudotsuga menziesii*)
Geology: River terraces, glacial outwash
Soil type: Typic haplorthod, Everett gravelly sandy loam
Stand age: 42 yr
Annual precipitation: 1360 mm
Mean annual temperature: 9.8°C
Length growing season: 214 days
Altitude: 210 m
Latitude: 47° 23′N
Institution: Univ. Washington, USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	9440	98	66.7	73.1	21.1	14.6
Overstory branches	13720	49	28.7	70.5	9.3	7.4
Overstory boles	106240	169	110.0	214.5	24.1	31.1
Overstory roots						
Understory vegetation	3390	21	24.1	25.1	2.7	5.7
Forest litter layer	26670	223	44.1	129.5	30.3	53.7
Soil-rooting zone		2476	209.5	661.0		97.8
Increments (kg/ha/yr)						
Overstory foliage	2440	26	19.4	9.2	5.2	3.0
Overstory branches	480	4	2.7	1.9	0.3	0.7
Overstory boles	3650	6	4.0	1.8	0.5	2.2
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		1.7	2.5	0.3	2.3	0.5
Atmosphere particulates						
Overstory litterfall	5607	25.4	12.5	40.5	3.3	6.0
Leaf wash		0.5	10.3	5.2	0.8	0.3
Stem flow		0.03	0.25	0.18	0.01	0.03
Leaching–forest floor		7.3	14.6	24.0	2.2	3.6
Leaching–rooting depth (100 cm)		0.6	1.0	4.5	0.02	
Leaching–watershed						

Stand No. 7
Site: Andrews Experimental Forest, Watershed 10, Oregon, USA
Investigator(s): Grier
Forest type: Douglas-fir forest (*Pseudotsuga menziesii*)
Geology: Miocene tuffs and breccias
Soil type: Inceptosol
Stand age: 450 yr
Annual precipitation: 2250 mm
Mean annual temperature: 8.5°C
Length growing season: 150 days
Altitude: 430–670 m
Latitude: 44° 15′N
Institution: Univ. Oregon, USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	14120	147	81	102	33	16
Overstory branches	54220	70	60	184	17	15
Overstory boles	733970	349	48	401	36	74
Overstory roots	172800	140	50	225	12	52
Understory vegetation	5600	14	10	2	2	
Forest litter layer	218520	445	80	619	62	160
Soil-rooting zone	120000	4560	660	2040	34	560
Increments (kg/ha/yr)						
Overstory foliage	3090	33.1	26	12	6.8	3.4
Overstory branches	410	0.5	0.5	1.4	0.1	0.1
Overstory boles	2580	1.2	0.2	4.5	0.2	0.2
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		2.0	1.2	3.1	0.3	1.2
Atmosphere particulates						
Overstory litterfall	6138	18.8	7.3	40.4	4.5	3.3
Leaf wash		3.2	13.2	7.0	1.0	2.0
Stem flow			Negligible			
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed		1.7	9.7	121.8	0.6	10.7

Stand No. 8
Site: Southern Karelian Spruce, Site 10, Karelia, USSR
Investigator(s): Kazimirov, Morozova
Forest type: Spruce forest (*Picea abies*)
Geology: Sand moraine
Soil type: Humus iron podsol
Stand age: 45 yr
Annual precipitation: 650 mm
Mean annual temperature: 2.2°C
Length growing season: 150 days
Altitude: 140 m
Latitude: 62° N
Institution: Karelian Branch of the
Academy of Sciences
Petrozavodsk USSR

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	9800	101.9	50.0	95.1	11.8	13.7
Overstory branches	12100	55.7	15.7	44.8	4.8	6.0
Overstory boles	56300	123.9	39.4	101.3	11.2	11.2
Overstory roots	15800	63.2	23.7	44.2	7.9	6.3
Understory vegetation	1600	22.1	12.0	10.5	3.1	2.0
Forest litter layer	19200					
Soil-rooting zone						
Increments (kg/ha/yr)						
Overstory foliage	2900	29.9	13.8	18.6	2.7	2.6
Overstory branches	190	2.7	0.8	2.2	0.2	0.3
Overstory boles	2060	6.3	2.0	5.1	0.6	0.6
Overstory roots	520	4.2	1.6	2.9	0.5	0.4
Understory vegetation	20	5.4	3.0	2.6	0.7	0.5
Fluxes (kg/ha/yr)						
Atmosphere precipitation		1.1	1.0	2.3		0.9
Atmosphere particulates						
Overstory litterfall	3700	23.8	10.6	28.3	2.6	4.2
Leaf wash		Data included in stem flow				
Stem flow		1.6	1.9	2.5	0.3	
Leaching-forest floor						
Leaching-rooting depth		0.87	2.2	2.3	0.06	0.45
Leaching-watershed						

Stand No. 9
Site: Kongalund Spruce Site, Sweden
Investigator(s): Nihlgard
Forest type: Spruce plantation (*Picea abies*)
Geology: Cambria shales and sandstone, stony-sandy moraine
Soil type: Brown forest soil (acid)
Stand age: 60 yr
Annual precipitation: 800 mm
Mean annual temperature: 7°C
Length growing season: 230 days
Altitude: 120 m
Latitude: 55° 59′N
Institution: Univ. Lund
Sweden

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	1800	220	122	84	21.8	9.6
Overstory branches	25000	230	112	86	30.2	18.2
Overstory boles	262000	270	172	283	28.5	38.9
Overstory roots	59000	90	65	45	5.7	10.5
Understory vegetation	10	0.001	0.02	0.1	0.01	0.02
Forest litter layer	18500	245	15	47.9	15.4	7.5
Soil-rooting zone	207000	6900	65	150	146	31
Increments (kg/ha/yr)						
Overstory foliage	3900	53	34.5	0.7	7.5	2.9
Overstory branches						
Overstory boles	9900	14	8.5	12.0	1.6	1.9
Overstory roots						
Understory vegetation	10					
Fluxes (kg/ha/yr)						
Atmosphere precipitation		8.2	1.9	3.5	0.1	0.9
Atmosphere particulates						
Overstory litterfall	5720	58	10.7	19.8	4.8	3.1
Leaf wash		Data included in stem flow				
Stem flow		16	25.2	13.9	0.4	5.2
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 10
Site: Solling Project, Site F 3, Federal Republic of Germany
Investigator(s): Ulrich, Ellenberg
Forest type: Spruce plantation (*Picea abies*)
Geology: Buntsandstein
Soil type: Brown forest soil (acid)
Stand age: 34 yr
Annual precipitation: 1063 mm
Mean annual temperature: 5.9°C
Length growing season: 132 days
Altitude: 390 m
Latitude: 51° 45′N
Institution: Univ. Göttingen, Fed. Repbl
Germany

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	18870	247.8	132.2	60.5	29.6	17.9
Overstory branches	18730	99.4	111.9	35.3	22.8	21.2
Overstory boles	105100	102.2	105.1	195.4	6.3	22.5
Overstory roots	34560					
Understory vegetation						
Forest litter layer	52000	1430	105	72	199	44
Soil-rooting zone	190000	6650	340	170	2660	36
Increments (kg/ha/yr)						
Overstory foliage	2979	39.0	19.4	9.5	4.6	2.8
Overstory branches	627	3.3	3.8	1.2	0.8	0.7
Overstory boles	4895	4.8	4.9	9.1	0.3	1.0
Overstory roots	1593					
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		21.8	3.7	12.6	0.5	2.6
Atmosphere particulates						
Overstory litterfall	2924	41.5	1.2	14.9	3.5	1.7
Leaf wash	Data included in stem flow					
Stem flow		3.7			0.2	
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 11
Site: Solling Project, Site F 1, Federal Republic of Germany
Investigator(s): Ulrich, Ellenberg
Forest type: Spruce plantation (*Picea abies*)
Geology: Buntsandstein
Soil type: Brown forest soil (acid)
Stand age: 87 yr
Annual precipitation: 1063 mm
Mean annual temperature: 5.9°C
Length growing season: 132 days
Altitude: 505 m
Latitude: 51° 49′ N
Institution: Univ. Göttingen, Fed. Repbl. Germany

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	17880	228.0	118.8	70.3	13.8	5.6
Overstory branches	28210	242.7	183.1	74.8	17.3	19.7
Overstory boles	198400	258.4	99.3	267.6	7.9	30.7
Overstory roots	71720					
Understory vegetation						
Forest litter layer	49000	960	41	83.0	53.0	20.0
Soil-rooting zone	190000	7100	546	283	2630	35
Increments (kg/ha/yr)						
Overstory foliage	2901	37.0	19.3	11.4	3.1	0.9
Overstory branches	603	5.2	3.9	1.6	0.4	0.4
Overstory boles	5360	7.0	2.7	7.2	1.0	0.3
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		21.8	3.7	12.6	0.51	2.6
Atmosphere particulates						
Overstory litterfall	3393	47.1	12.7	17.0	4.0	1.9
Leaf wash		3.7	23.6	19.0	0.2	0.2
Stem flow	Data included in leaf wash					
Leaching–forest floor						
Leaching–rooting depth (50 cm)		14.9	2.1	13.5	0.02	3.7
Leaching–watershed						

Stand No. 12
Site: Solling Project, Site F 2, Federal Republic of Germany
Investigator(s): Ulrich, Ellenberg
Forest type: Spruce plantation (*Picea abies*)
Geology: Buntsandstein
Soil type: Brown forest soil (acid)
Stand age: 115 yr
Annual precipitation: 1063 mm
Mean annual temperature: 5.9°C
Length growing season: 132 days
Altitude: 440 m
Latitude: 51° 44′ N
Institution: Univ. Göttingen, Fed. Repbl. Germany

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	12660	161.4	84.1	49.7	13.3	40.0
Overstory branches	24630	212	160.0	65.3	15.1	17.2
Overstory boles	195700	255	98.0	264.1	36.9	30.3
Overstory roots	74930					
Understory vegetation						
Forest litter layer	111000	2260	115	258	98	46
Soil-rooting zone	251000	7060	342	160	1530	38
Increments (kg/ha/yr)						
Overstory foliage	2123	27.0	14.1	8.3	2.2	0.7
Overstory branches	390	3.4	2.5	1.0	0.2	0.3
Overstory boles	4004	5.2	2.0	5.4	0.8	0.6
Overstory roots	853					
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		21.8	3.7	12.6	0.5	2.6
Atmosphere particulates						
Overstory litterfall	3076	43.3	1.2	15.6	3.7	1.7
Leaf wash		3.7			0.2	
Stem flow	Data included in leaf wash					
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 13
Site: Walker Branch Site 2, Oak Ridge, Tennessee, USA
Investigator(s): Harris
Forest type: Short leaf pine forest (*Pinus echinata*)
Geology: Knox dolomite
Soil type: Typic paleudults derived from dolomitic residuum
Stand age: 30 yr
Annual precipitation: 1400 mm
Mean annual temperature: 13.3°C
Length growing season: 180 days
Altitude: 265–360 m
Latitude: 35° 58′ N
Institution: Oak Ridge National Laboratory, USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	4600	51	36	43	4	12
Overstory branches	27000	64	29	100	7	11
Overstory boles	89000	100	60	164	7	17
Overstory roots	34000	117	128	187	21	17
Understory vegetation						
Forest litter layer	27000	290	21	256	18	23
Soil-rooting zone	116000	4100	38000	3600	1200	10900
Increments (kg/ha/yr)						
Overstory foliage	3728	41.5	29.3	34.8	3	9
Overstory branches						
Overstory boles	4150	8.2	1.9	5.4	0.1	0.4
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		8.7	1.0	9.1	0.06	1.0
Atmosphere particulates			2.2	5.3	0.48	1.1
Overstory litterfall	4130	37.5	14.4	51.0	2.5	7.6
Leaf wash		2.9	18.7	17.4	0.3	2.8
Stem flow	Data included in leaf wash					
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed		1.8	6.8	147.5	0.02	77.1

Stand No. 14
Site: Watershed 1, Coweeta, North Carolina, USA
Investigator(s): Swank
Forest type: White pine plantation (*Pinus strobus*)
Geology: Granite, mica schists, and gneisses (bedrock)
Soil type: Saluda stony loam (typic hapludult, loamy, mixed, mesic, shallow family)
Stand age: 15 yr
Annual precipitation: 1628 mm
Mean annual temperature: 13.6°C
Length growing season: 150 days
Altitude: 706–988 m
Latitude: 35° 04′ N
Institution: Coweeta Hydrologic Laboratory,
USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	4664	72.80	22.7	17.6		
Overstory branches	22825	78.80	45.4	47.5		
Overstory boles	42110	72.40	40.9	32.6		
Overstory roots	60300	422.10	163.2	203.6		
Understory vegetation						
Forest litter layer						
Soil-rooting zone						
Increments (kg/ha/yr)						
Overstory foliage	3630	60.90	15.4	14.0		
Overstory branches	3050	10.80	6.6	6.1		
Overstory boles	6850	12.70	8.0	5.5		
Overstory roots	6900	48.30	18.6	23.5		
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		5.50	2.0	4.1		
Atmosphere particulates		3.30				
Overstory litterfall	3184	26.50	5.5	19.2		
Leaf wash			28.0	2.0		
Stem flow	Data included in leaf wash					
Leaching–forest floor			41.9	31.2		
Leaching–rooting depth						
Leaching–watershed		0.19	4.5	5.9		

Stand No. 15
Site: JPTF–71 Yusuhara Takatoriyama, Japan
Investigator(s): Ando
Forest type: True fir forest (*Abies firma*)
Geology: Cretaceous/Mudstone
Soil type: Brown forest soil (moderately wet)
Stand age: 97–145 yr
Annual precipitation: 2748 mm
Mean annual temperature: 13.6°C
Length growing season:
Altitude: 420 m
Latitude: 33° 20′ N
Institution: Shikoku Branch, Government Forest Experiment Station, Kochi, Japan

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	15134	145.7	157.4	125.6	12.3	14.4
Overstory branches	57760	173.7	255.8	315.5	22.5	33.8
Overstory boles	306668	254.0	1012.3	961.0	46.9	81.7
Overstory roots	145647					
Understory vegetation	121957	363.4	436.9	851.6	40.0	52.4
Forest litter layer	4279	484	113	182	32	67
Soil-rooting zone		3389	368	278	5	143
Increments (kg/ha/yr)						
Overstory foliage	3156	32.9	55.5	20.4	3.4	4.1
Overstory branches	1300	9.4	20.3	9.6	1.6	2.7
Overstory boles	3909	2.6	12.4	10.9	0.6	1.0
Overstory roots						
Understory vegetation	3309	2.9	32.6	30.3	2.4	4.4
Fluxes (kg/ha/yr)						
Atmosphere precipitation						
Atmosphere particulates						
Overstory litterfall	5376	31.6	11.4	37.0	1.9	4.7
Leaf wash						
Stem flow						
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 16
Site: JPTF–70 Yusuhara Kubotaniyama, Japan
Investigator(s): Ando
Forest type: Hemlock forest (*Tsuga sieboldii*)
Geology: Cretaceous/Sandstone
Soil type: Brown forest soil (moderately wet)
Stand age: 120–443 yr
Annual precipitation: 2748 mm
Mean annual temperature: 13.6°C
Length growing season:
Altitude: 720 m
Latitude: 33° 20′ N
Institution: Shikoku Branch, Government Forest Experiment Station, Kochi, Japan

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	7846	84.7	46.7	39.7	5.3	11.7
Overstory branches	92345	205.7	105.4	430.7	13.4	5.1
Overstory boles	348410	291.8	289.1	463.4	6.0	45.8
Overstory roots	165565					
Understory vegetation	118318	281.1	220.5	283.1	14.7	46.6
Forest litter layer	50780	506.8	76.3	159.0	34.1	30.0
Soil-rooting zone		2732	62	49	1.3	21
Increments (kg/ha/yr)						
Overstory foliage	2390	26.6	14.9	8.7	1.8	3.5
Overstory branches	767	6.0	5.6	3.3	0.6	0.7
Overstory boles	1912	1.4	1.5	1.5	0.03	0.2
Overstory roots						
Understory vegetation	2968	25.0	18.8	15.6	1.5	5.1
Fluxes (kg/ha/yr)						
Atmosphere precipitation						
Atmosphere particulates						
Overstory litterfall	4686	20.2	6.8	24.8	1.5	3.6
Leaf wash						
Stem flow						
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 17
Site: Cascade Head, Oregon, USA
Investigator(s): Grier
Forest type: Western hemlock forest (*Tsuga heterophylla*)
Geology: Tyee formation marine siltstone
Soil type: Utisol
Stand age: 121 yr
Annual precipitation: 2500 mm
Mean annual temperature: 10.1°C
Length growing season: 130–140 days
Altitude: 200 m
Latitude: 45° N
Institution: Cascade Head Experimental Forest, US Forest Service
Oregon, USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	8030	85	31	19	11	8
Overstory branches	50580	52	20	26	7	5
Overstory boles	856870	584	138	433	149	47
Overstory roots	189200	179	61	153	44	34
Understory vegetation	4320	16	10	8	3	2
Forest litter layer	301080	474	118	347	98	83
Soil-rooting zone	776000	34900	720	1600	70	1600
Increments (kg/ha/yr)						
Overstory foliage	2870	28.9	13.5	4.7	3.9	2.4
Overstory branches	1880	9.4	6.2	2.4	2.0	1.1
Overstory boles	4760	3.1	0.5	1.5	1.0	0.3
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		5.7	2.7	5.3	0.9	13.0
Atmosphere particulates						
Overstory litterfall	6140	44.0	12.9	21.3	6.9	7.8
Leaf wash		2.0	8.0	3.3	0.3	2.1
Stem flow		0.2	2.6	0.3	0.1	0.1
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 22
Site: Liriodendron Site, Oak Ridge, Tennessee, USA
Investigators(s): Reichle, Harris, Edwards
Forest type: Yellow popular forest, mesic (*Liriodendron tulipifera*)
Geology: Knox dolomite limestone
Soil type: Deep alluvial emory silt loam
Stand age: 50 yr
Annual precipitation: 1400 mm
Mean annual temperature: 13.3°C
Length growing season: 180 days
Altitude: 225 m
Latitude: 35° 55′ N
Institution: Oak Ridge National Laboratory,
USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	3200	53.9	52.3	35.2	6.3	
Overstory branches	27100	78.6	46.1	143.7	30.6	
Overstory boles	94400	172.0	74.8	276.8	9.7	
Overstory roots	36000	122.7	111.5	150.8	18.5	
Understory vegetation	8800	23.8	32.4	115.2	5.7	
Forest litter layer	6000	77.9	9.2	99.6	5.3	
Soil-rooting zone	159000	7650	38960	8130	2840	
Increments (kg/ha/yr)						
Overstory foliage	3200	53.9	52.3	35.2	6.3	
Overstory branches	575	1.7	1.0	3.1	0.7	
Overstory boles	2254	5.4	2.3	6.3	0.3	
Overstory roots	513	1.8	1.2	2.2	0.2	
Understory vegetation	81	0.3	0.2	0.6	0.1	
Fluxes (kg/ha/yr)						
Atmosphere precipitation		7.7	0.73	6.1	0.06	
Atmosphere particulates			2.56	4.5	0.7	
Overstory litterfall	4290	31.3	19.0	77.7	2.8	
Leaf wash		9.4	31.7	17.8	0.4	
Stem flow		0.1	1.0	0.4	0.002	
Leaching-forest floor						
Leaching-rooting depth (60 cm)		3.5	8.9	44.5	0.05	
Leaching-watershed						

Stand No. 23
Site: Walker Branch Site 4, Oak Ridge, Tennessee, USA
Investigator(s): Harris, Henderson
Forest type: Yellow poplar – mixed hardwoods forest (*Liriodendron tulipifera, Quercus*)
Geology: Knox dolomite
Soil type: Typic paleudults derived from dolomitic residuum
Stand age: 30–80 yr
Annual precipitation: 1400 mm
Mean annual temperature: 13.3°C
Length growing season: 180 days
Altitude: 265–360 m
Latitude: 35° 58′ N
Institution: Oak Ridge National Laboratory,
USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	5100	78	45	75	6	21
Overstory branches	21000	54	37	155	7	13
Overstory boles	83000	135	90	307	8	25
Overstory roots	31000	122	132	211	22	19
Understory vegetation						
Forest litter layer	1500	187	14	294	11	22
Soil-rooting zone	189000	7300	36000	6300	1400	8700
Increments (kg/ha/yr)						
Overstory foliage	5100	78	45	75	6	21
Overstory branches						
Overstory boles	3550	9.9	2.5	7.6	0.3	0.7
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		8.7	1.0	9.1	0.06	1.0
Atmosphere particulates			2.2	5.3	0.48	1.1
Overstory litterfall	4330	36.2	19.1	58.3	2.7	8.3
Leaf wash		12.0	18.4	21.9	0.4	3.4
Stem flow	Data included in leaf wash					
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed		1.8	6.8	147.5	0.02	77.1

Stand No. 24
Site: Walker Branch Site 1, Oak Ridge, Tennessee, USA
Investigator(s): Harris, Henderson
Forest type: Oak–Hickory forest (*Quercus–Carya)*
Geology: Knox dolomite
Soil type: Typic paleudults derived from dolomitic residuum
Stand age: 30–80 yr
Annual precipitation: 1400 mm
Mean annual temperature: 13.3°C
Length growing season: 180 days
Altitude: 265–360 m
Latitude: 35° 58′ N
Institution: Oak Ridge National Laboratory,
USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	5600	67	53	70	6	17
Overstory branches	26000	131	53	288	9	19
Overstory boles	90000	171	114	498	9	31
Overstory roots	33000	128	136	244	22	19
Understory vegetation						
Forest litter layer	27000	334	26	517	22	32
Soil-rooting zone	116000	4500	38000	3600	1200	10900
Increments (kg/ha/yr)						
Overstory foliage	5600	67	53	70	6	17
Overstory branches						
Overstory boles	4800	20.2	4.5	21.0	0.4	1.4
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		8.7	1.0	9.1	0.06	1.0
Atmosphere particulates			2.2	5.3	0.48	1.1
Overstory litterfall	4800	36.5	19.8	49.1	2.7	8.7
Leaf wash		12.4	23.9	24.1	0.6	3.7
Stem flow	Data included in leaf wash					
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed		1.8	6.8	147.5	0.02	77.1

Stand No. 25
Site: Walker Branch Site 3, Oak Ridge, Tennessee, USA
Investigator(s): Harris, Henderson
Forest type: Chestnut oak forest (*Quercus prinus*)
Geology: Knox dolomite
Soil type: Typic paleudults derived from dolomitic residuum
Stand age: 30–80 yr
Annual precipitation: 1400 mm
Mean annual temperature: 13.3°C
Length growing season: 180 days
Altitude: 265–360 m
Latitude: 35° 58′ N
Institution: Oak Ridge National Laboratory,
USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	5300	75	52	58	5	12
Overstory branches	30000	139	61	294	10	13
Overstory boles	102000	183	129	500	11	20
Overstory roots	36000	132	140	249	22	18
Understory vegetation						
Forest litter layer	25000	298	26	318	18	22
Soil-rooting zone	116000	4700	38000	3600	1200	10900
Increments (kg/ha/yr)						
Overstory foliage	5300	75	52	58	5	12
Overstory branches						
Overstory boles	5400	23.1	6.2	22.3	0.5	1.1
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		8.7	1.0	9.1	0.06	1.0
Atmosphere particulates			2.2	5.3	0.48	1.1
Overstory litterfall	4450	34.1	16.4	45.0	2.4	7.5
Leaf wash		11.6	17.7	21.5	0.4	2.9
Stem flow	Data included in leaf wash					
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed		1.8	6.8	147.5	0.02	77.1

Stand No. 26
Site: Watershed 1, Coweeta, North Carolina, USA
Investigator(s): Swank
Forest type: Oak–Hickory forest (*Quercus-Carya*)
Geology: Granite, mica schist, and gneisses (bedrock)
Soil type: Saluda stony loam (typic hapludult, loamy, mixed, mesic, shallow family)
Stand age: 60–200 yr
Annual precipitation: 1628 mm
Mean annual temperature: 13.6°C
Length growing season: 150 days
Altitude: 706–988 m
Latitude: 35° 04′ N
Institution: Coweeta Hydrologic Laboratory, USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	5584	95.00	46.0	49.0		
Overstory branches	25599	116.00	46.0	133.0		
Overstory boles	106313	194.00	135.0	361.0		
Overstory roots	52525	434.00	167.0	278.0		
Understory vegetation						
Forest litter layer	9500	110.00	29.0	130.0		
Soil-rooting zone						
Increments (kg/ha/yr)						
Overstory foliage	4195	83.00	41.0	36.0		
Overstory branches	901	3.40	2.1	4.7		
Overstory boles	2870	5.70	4.0	9.8		
Overstory roots	6000	43.20	16.8	27.6		
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		4.90	2.1	4.8		
Atmosphere particulates		3.30				
Overstory litterfall	4369	33.90	18.1	44.5		
Leaf wash			24.1			
Stem flow	Data included in leaf wash					
Leaching–forest floor			31.7	23.4		
Leaching–rooting depth			2.1	1.9		
Leaching–watershed		3.17	5.6	7.7		

Stand No. 27
Site: Hubbard Brook, New Hampshire, USA
Investigator(s): Whittaker, Likens
Forest type: Northern hardwoods forest (*Acer*, *Betula*, *Fagus*)
Geology: Littleton gneiss
Soil type: Boulders, glacial till, podzolic-haplorthod
Stand age: 60 yr
Annual precipitation: 1250 mm
Mean annual temperature:
Length growing season: 110 days
Altitude: 550–710 m
Latitude: 44° 00′ N
Institution: Cornell University,
USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	3180	70.1	30.0	19.5	5.5	4.8
Overstory branches	38980	162.5	52.9	189.3	16.2	13.8
Overstory boles	91840	134.6	70.8	193.2	11.0	18.9
Overstory roots (+crowns)	28560	181	63.2	101	52.7	13.5
Understory vegetation	54	9.0	2.2	3.4	0.8	1.6
Forest litter layer	48016	125.6	66	372	7.8	38.0
Soil-rooting zone	174900					
Increments (kg/ha/yr)						
Overstory foliage	3211	74.8	32.2	21.5	5.9	5.2
Overstory branches	2249	11.3	3.8	11.0	1.2	0.9
Overstory boles	2429	3.6	1.8	5.2	0.3	0.5
Overstory roots	1644	10.5	3.7	6.0	3.1	0.8
Understory vegetation	232	4.7	3.5	1.3	0.4	0.8
Fluxes (kg/ha/yr)						
Atmosphere precipitation[a]		6.5	0.9	2.2	0.04	0.6
Atmosphere particulates						
Overstory litterfall	5860	54.2	18.3	40.7	4.0	5.9
Leaf wash	104	4.7	26.1	5.0	0.6	1.5
Stem flow	11.5	0.5	3.4	0.4	0.1	0.1
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed[a]		3.9	1.9	13.7	0.01	3.1

[a] Long-term averages 1963–1974

Stand No. 28
Site: Virelles, Belgium
Investigator(s): Duvigneaud, Denaeyer-DeSmet
Forest type: Mixed oak forest (*Quercus*-mixed)
Geology: Devon chalk
Soil type: Calcareous brown soil
Stand age: 115–160 yr
Annual precipitation: 951.6 mm
Mean annual temperature: 8.5°C
Length growing season: 155 days
Altitude: 245 m
Latitude: 50° 4′ N
Institution: Univ. Libre de Brussels,
Belgium

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Overstory foliage total	3500	83	40	34	6	7
Overstory branches	78300	259	139	339	23	27
Overstory boles	210050	386	219	769	17	58
Overstory roots	35300	297	112	301.7	29.3	27.7
Understory vegetation	30580	166	112	172	14	32
Forest litter layer	5600					
Soil-rooting zone	300000	13800	767	13865	2100	1007
Increments (kg/ha/yr)						
Overstory foliage	3500	83	40	34	6	7
Overstory branches	4480	25	12	25	2	3
Overstory boles						
Overstory roots	1000	5	6	9	1	1
Understory vegetation	1100	10	3	8	1	1
Fluxes (kg/ha/yr)						
Atmosphere precipitation		8.7	4	15		
Atmosphere particulates						
Overstory litterfall	5600	59	28	66	3.4	9.7
Leaf wash		2.2	9			7
Stem flow		0.2	2			
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 29
Site: Virelles, Belgium
Investigator(s): Duvigneaud, Denaeyer-De Smet
Forest type: Mixed oak forest (*Quercus*-mixed)
Geology: Devon chalk
Soil type: Calcareous brown soil
Stand age: 80 yr
Annual precipitation: 951.6 mm
Mean annual temperature: 8.5°C
Length growing season: 155 days
Altitude: 245 m
Latitude: 50° 4′ N
Institution: Univ. Brussels,
Belgium

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	3458	73	36	54	4.7	4.6
Overstory branches	36425	295	164	776	23	72
Overstory boles	75202					
Overstory roots	34600	121	92	372	10	19
Understory vegetation	4700	46	46	70	4.6	6
Forest litter layer	4762	44	17	107	2	5
Soil-rooting zone	220000	4480	157	13600	920	151
Increments (kg/ha/yr)						
Overstory foliage	3458	73	36	54	4.7	4.6
Overstory branches	5263	23.1	11	52.3	1.6	4.6
Overstory boles	6054					
Overstory roots	2000	7	5.4	22	0.6	1.1
Understory vegetation	874					
Fluxes (kg/ha/yr)						
Atmosphere precipitation	1	13	5	19		5.8
Atmosphere particulates						
Overstory litterfall	5287	50	21	110	2.4	5.6
Leaf wash		0.9	16	6.2	0.6	5.6
Stem flow		6	0.8	0.9	0	0.6
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 30
Site: Solling Project, Site B4, Federal Republic of Germany
Investigator(s): Ulrich, Ellenberg
Forest type: Beech forest (*Fagus silvatica*)
Geology: Buntsandstein
Soil type: Brown forest soil (acid)
Stand age: 59 yr
Annual precipitation: 1063 mm
Mean annual temperature: 6.3°C
Length growing season: 145 days
Altitude: 430 m
Latitude: 51° 45′ N
Institution: Univ. Göttingen, Federal Repbl. Germany

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	3158	97.2	26.9	14.3	6.5	2.5
Overstory branches	41500	105	30.5	118.1	13.7	5.7
Overstory boles	110000	205	72.7	191.1	31.8	17.9
Overstory roots	23950	62.4	34.6	27.8	11.9	5.9
Understory vegetation						
Forest litter layer	29000	815	85.0	86.0	62	44
Soil-rooting zone	186000	6332	500	245	3150	45
Increments (kg/ha/yr)						
Overstory foliage	3158	97.2	26.9	14.3	6.5	2.5
Overstory branches	989	2.5	0.7	28	0.3	0.2
Overstory boles	7666	14.2	5.1	1.3	2.3	1.7
Overstory roots	1263	3.3	1.8	1.5	0.6	0.3
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		21.8	3.7	12.6	0.5	2.6
Atmosphere particulates						
Overstory litterfall	3418	52.5	16.9	17.3	4.2	1.5
Leaf wash		19.6	15.9	22.0	0.4	3.3
Stem flow		2.5	6.6	4.3		0.6
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 31
Site: Solling Project, Site B3, Federal Republic of Germany
Investigator(s): Ulrich, Ellenberg
Forest type: Beech forest (*Fagus silvatica*)
Geology: Buntsandstein
Soil type: Brown forest soil (acid)
Stand age: 80 yr
Annual precipitation: 1063 mm
Mean annual temperature: 6.1°C
Length growing season: 144 days
Altitude: 470 m
Latitude: 51° 45′ N
Institution: Univ. Göttingen, Federal Repbl. Germany

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	3294	95.5	31.4	17.5	5.7	2.5
Overstory branches	25870	97.1	37.4	68.9	11.6	5.7
Overstory boles	129600	211.5	133.7	216.3	18.7	17.9
Overstory roots	22080	57.5	31.9	25.7	10.9	5.9
Understory vegetation						
Forest litter layer	39000	1050	123	118	72	44
Soil-rooting zone	212000	9452	550	280	2310	45
Increments (kg/ha/yr)						
Overstory foliage	3294	95.5	31.4	17.5	5.7	2.5
Overstory branches	447	1.6	0.6	1.2	0.2	0.1
Overstory boles	5907	9.6	6.1	9.7	0.8	0.8
Overstory roots	633	1.6	0.9	0.7	0.3	0.2
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		21.8	3.7	12.6	6.5	2.6
Atmosphere particulates						
Overstory litterfall	4046	54.3	17.5	17.8	4.3	1.6
Leaf wash		19.6	15.9	22.0	0.4	3.3
Stem flow		2.5	6.6	4.3		0.6
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 32
Site: Solling Project, Site B2, Federal Republic of Germany
Investigator(s): Ulrich, Ellenberg
Forest type: Beech forest (*Fagus silvatica*)
Geology: Buntsandstein
Soil type: Brown forest soil (acid)
Stand age: 122 yr
Annual precipitation: 1063 mm
Mean annual temperature: 6.1°C
Length growing season: 144 days
Altitude: 470 m
Latitude: 51° 45′ N
Institution: Univ. Göttingen, Federal Repbl. Germany

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	3078	84.4	24.6	11.1	4.6	2.2
Overstory branches	32480	128.7	42.7	76.7	9.8	8.0
Overstory boles	238400	367.9	205.5	215.2	5.5	56.7
Overstory roots	30040	107	55.5	46	19.0	11.6
Understory vegetation	13					
Forest litter layer	29700	810	83	91	52	34
Soil-rooting zone	190000	7340	387	268	2870	40
Increments (kg/ha/yr)						
Overstory foliage	3078	84.4	24.6	11.1	4.6	2.2
Overstory branches	784	3.1	1.0	1.9	0.6	0.2
Overstory boles	6490	1.0	5.6	5.8	1.5	1.5
Overstory roots	660	2.3	1.3	1.0	0.4	0.2
Understory vegetation	13					
Fluxes (kg/ha/yr)						
Atmosphere precipitation		21.8	3.7	12.6	0.5	2.6
Atmosphere particulates						
Overstory litterfall	3783	49.4	15.9	16.2	4.0	1.4
Leaf wash		19.6	15.9	22	0.4	3.3
Stem flow		2.5	6.6	4.3		0.6
Leaching–forest floor						
Leaching–rooting depth (50 cm)		4.4	2.6	8.4	0.01	2.1
Leaching–watershed						

Stand No. 33
Site: Meathop Wood, United Kingdom
Investigator(s): Satchell
Forest type: Mixed deciduous (*Quercus–Betula*)
Geology: Carboniferous limestone
Soil type: Glacial drift and brown earths
Stand age: 80 yr
Annual precipitation: 1115 mm
Mean annual temperature: 7.8°C
Length growing season: 244 days
Altitude: 45 m
Latitude: 54° 12.5′ N
Institution: The Nature Conservancy, Merlewood, Research Station
Great Britain

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	3505	85.7	38.9	41.9	4.6	9.5
Overstory branches	33640	58.8	61.1	137.4	3.7	8.0
Overstory boles	75920	133.6	113.1	301	8.4	8.5
Overstory roots	242181	223.0	112.8	235.3	11.9	30.8
Understory vegetation	15529	8.1	42.9	66.9	5.4	9.7
Forest litter layer	6118	74.4	12	101	3.3	8.1
Soil-rooting zone	138000		1543	1766.4	1512	81.5
Increments (kg/ha/yr)						
Overstory foliage	3505	85.7	38.9	41.9	4.6	9.5
Overstory branches	948	2.1	1.5	3.9	0.1	0.3
Overstory boles	2162	4.1	3.4	8.9	0.2	0.7
Overstory roots	1978	13.2	6.6	14.3	0.6	1.7
Understory vegetation	343	3.3	2.4	2.2	0.2	0.5
Fluxes (kg/ha/yr)						
Atmosphere precipitation		5.8	3.3	6.9	0.2	5.4
Atmosphere particulates						
Overstory litterfall	3697	63.5	19	83.3	2.6	9.7
Leaf wash		8.8	30.3	22.8	0.7	11.9
Stem flow		0.4	4.8	5.2	0.03	2.4
Leaching–forest floor						
Leaching–rooting depth		12.6	8.3	59.8	0.2	6.0
Leaching–watershed						

Stand No. 34
Site: Kongalund Beech Site, Sweden
Investigator(s): Nihlgard
Forest type: Beech forest (*Fagus silvatica*)
Geology: Cambrian shales and sandstone, stony-sandy moraine
Soil type: Brown forest soil (acid)
Stand age: 45–130 yr
Annual precipitation: 880 mm
Mean annual temperature: 7°C
Length growing season: 230 days
Altitude: 120 m
Latitude: 55° 59′ N
Institution: Univ. Lund,
Sweden

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	5000	121	26.7	24.5	7.0	7.5
Overstory branches	99000	660	228	381	55.2	40.9
Overstory boles		290	201	201	22.4	57
Overstory roots	51000	150	79	42	15.6	13.5
Understory vegetation	200	10	8	0.9	0.7	0.1
Forest litter layer	5200	86	104	34.2	5.8	4.8
Soil-rooting zone	207000	7800	56	175	38	84
Increments (kg/ha/yr)						
Overstory foliage	5000	121	26.7	24.5	7.0	7.5
Overstory branches						
Overstory boles	10100	8.3	16.6	24.8	3.5	3.4
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		8.2	1.9	3.5	0.1	0.9
Atmosphere particulates						
Overstory litterfall	5690	69	14.4	31.7	5	4.3
Leaf wash	Data included in stem flow					
Stem flow		1.0	11.2	6.6	0.1	2.5
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

Stand No. 35
Site: Thompson Research Center, Washington, USA
Investigator(s): Turner
Forest type: Red alder (*Alnus rubra*)
Geology: Glacial till
Soil type: Typic haplorthod, alderwood gravelly sandy loam
Stand age: 30 yr
Annual precipitation: 1360 mm
Mean annual temperature: 9.8°C
Length growing season: 214 days
Altitude: 210 m
Latitude: 47° 23′ N
Institution: Univ. Washington,
USA

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	4060	100	43	42	5	8.4
Overstory branches	19380	20	4	77	2	6.8
Overstory boles	127580	120	27	51	16	45.1
Overstory roots	35230	176	7	123	4	12.4
Understory vegetation	9530	103	132	95	7	16
Forest litter layer	66350	877	91	391	45	57.
Soil-rooting zone	158520	5450				
Increments (kg/ha/yr)						
Overstory foliage	4060	100	43	42	5.0	8.4
Overstory branches	1150	3	4.5	2	0.4	0.6
Overstory boles	7570	16	30.0	12	2.7	3.8
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		1.7	2.2	2.2	0.3	0.5
Atmosphere particulates						
Overstory litterfall	15972	87	39	67	6.2	10
Leaf wash		8.8	12.2	10	1	5
Stem flow		0.1	0.4	0.2		0.08
Leaching–forest floor		15	42.5	77	10.1	14.7
Leaching–rooting depth						
Leaching–watershed						

Stand No. 36
Site: Rouquet, France
Investigator(s): Lossaint, Rapp
Forest type: Mediterranean evergreen oak forest (*Quercus ilex*)
Geology: Portlandien–Kimmeridgien limestone
Soil type: Brunified Mediterranean red soil
Stand age: 150 yr
Annual precipitation: 987 mm
Mean annual temperature: 12.4°C
Length growing season: 365 days
Altitude: 180 m
Latitude: 43° 42′ N
Institution: CNRS, Montpellier, France

		Elements				
	Org. Mat.	N	K	Ca	P	Mg
Amounts (kg/ha)						
Overstory foliage total	7000	93	43	70	10	9
Overstory branches	27000	135	90	493	40	25
Overstory boles	235000	517	493	3290	174	117
Overstory roots	45000	153	85	1147	81	7.2
Understory vegetation	340	2.3	17	4.1	0.1	1.1
Forest litter layer	11400	124.7	10.2	361.2	4	19.7
Soil-rooting zone						
Increments (kg/ha/yr)						
Overstory foliage	4500	64	28	38	6	6
Overstory branches	1100	9.9	5.8	21.7	1.6	1.5
Overstory boles	1500	3.3	3.1	4.0	1.0	0.7
Overstory roots						
Understory vegetation						
Fluxes (kg/ha/yr)						
Atmosphere precipitation		15.6	2.4	11.7	1.0	2.1
Atmosphere particulates						
Overstory litterfall	3842	32.8	16.2	63.9	2.8	4.6
Leaf wash		0.5	21.3	23.3	1.6	3.6
Stem flow		1.2	6.5	7.8	0.3	0.8
Leaching–forest floor						
Leaching–rooting depth						
Leaching–watershed						

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