Chapter 11
Biomass and Element Content of Foliage and Aboveground Litterfall on the Three Long-Term Experimental Beech Sites: Dynamics and Significance

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11.1 Introduction

The amount and dynamics of litterfall in a forest stand is recognised as an integrated response, reflecting biologically (hereditary defined) controlled processes of shedding of leaves, roots, bark, fruits and other plant components and the physiologically controlled factors of environmental nature (climate, water availability, nutritional supply and toxicity parameters). Changes in the dynamics of litterfall components (leaves, fruits, florescence, seeds, twigs, etc.), in the short-term, is primarily a reflection of climatic perturbations affecting water and nutrient supply. For example, drought conditions in the early summer preceding mast year (mast year−1) were found to be a very strong predictor of mast production in beech stands of Europe and eastern North America (Piovesan and Adams 2001). An unusually moist, cool summer the year before the drought (mast year−2) increased the predictability of mast production which was associated with carbohydrate build up within the trees which might prime them for floral induction the following year (mast year−1). There is, however, very little known of the accumulation and redistribution of nutrients in association with masting in beech.

Litterfall constitutes the transfer of energy between different trophic levels, where energy-rich plant materials are transferred for use by microbial and faunal populations in and on the soil. Despite the significance of litterfall in many ecosystem processes, the main emphasis on litterfall studies during the earlier periods had been to describe the fluctuations, distribution and composition of litterfall (Viro 1955; Kittredge 1948). Emphasis has now shifted to study the role of litterfall in ecosystem functioning especially its role in nutrient cycling processes in forest ecosystems (Khanna and Ulrich 1991). The aim of many studies in forest ecosystems is to develop management options where sustainability of ecosystem productivity and ecological functioning have been appropriately achieved, and for that purpose litterfall can act as a useful indicator. One such parameter is leaf biomass that is related to the health of forest ecosystems, which can be directly deduced from leaf litter, especially in deciduous stands. Another one is

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the decomposition rate of litterfall components which depends on the quality of litter fall and is thus closely related to the functionality and activity of microbial and faunal populations in soils (Chaps. 12, 20, this volume). Thus, litter fall quality of overstorey and understorey vegetation is closely related to the biodiversity on a forest site. Some essential components of the multi-functions of a forest ecosystem that are closely related to the amount and quality of litterfall are: C source for microbial activity, food for animals (biodiversity) and the use of nutrients for the growth and activity of flora and fauna.

Due to continually changing input conditions and climatic factors, site factors and stand parameters strongly and differently affect forest productivity and nutrient cycling processes. Leuschner et al. (2006) evaluated 50 beech stands in Central Europe to assess the important soil factors which describe the niche breadth of their growth. The stands could be delineated into three main groups depending upon the exchangeable base cations, C/N ratio in the mineral soil and C/P of the surface organic layer. In order to manage such ecosystems in a landscape context, it is essential to develop suitable knowledge based on such interactions, e.g. on the role of litter fall parameters which may enable one to extend site-specific information to landscape level.

In this chapter, the relative amounts of leaf and fruiting bodies will be considered in relation to climatic and other variables which may affect their production. The question will be addressed as to how does the annual leaf litter relate to the productivity on these sites?

Mast production in beech is a significant event involving the transfer of huge amounts of C and nutrients. Both high plant productivity and high amount of atmospheric nutrient inputs may cause the high frequency and amount of mast produced (Gruber 2006). This has further consequences for the amount of nutrients retained by the trees for mast production, leading to low values of Mg, K, and P as cycling fractions in these stands. Mast production may also affect the production of foliage and/or wood. Thus, the consequences of changes in mast production (increase in the frequency of mast years has been observed during recent decades; Paar et al. 2000) for the growth and functioning of beech stands will be specifically discussed in this chapter.

All the three stands studied have been receiving high amounts of atmospheric inputs of elements and acidity (Chap. 15), which may have a long-term effect on their foliage chemistry either through direct effects on the amount of leaf nutrients leached from the leaves or indirectly through nutrient uptake. Foliage chemistry and leaf litter chemistry are intimately related, thus affecting the nutrient turnover processes in the soil and litter layer. There are many other factors which affect the concentration of nutrients in the total litterfall. For example, season of litterfall, moisture and other stress factors, relationships with other elements and nutrient withdrawal patterns during leaf senescence will determine the concentration and amount of nutrients transferred through litterfall. Some of these factors will be described in this chapter.

The patterns of element withdrawal at the time of leaf senescence form an important process which affects the nutrient status of the stand and may depend upon the absolute and annual variation in the element concentrations in the foliage. The following questions will be addressed. What types of annual patterns of element withdrawal are observed on different sites? How do they relate to the supply of nutrients by soils and to the stand productivity?

The amount of leaf litter and foliar mass are related; however, this relationship depends upon a number of factors (Stachurski and Zimka 1975). Usually, the amount of leaf litter collected at the surface organic layer does not equal the amount of leaf produced because of the unaccountable losses of leaf material. There are direct losses of leaf material where it is consumed by insects and undergoes microbial decomposition and indirect losses where leaf material is transferred to other plant components prior to or at the time of senescence. Is it possible to make an assessment of these losses, for example by using marker element such as Ca and then assess the foliar mass from the amount of leaf litter? As it is hard to directly measure changes in the amount of foliar mass, the possibility of assessing the amount through leaf litter will be tested in this chapter.

11.2 Site Description and Collection and Measurements of Aboveground Litterfall Components and Green Foliage

The three experimental sites at Solling, Göttinger Wald and Zierenberg differ in their stand, climatic and soil characteristics, which are expected to affect the amount and chemistry of litterfall. Some of the relevant stand and site parameters are given in Table 11.1. The stands contained mostly beech with very small fractions of other trees in the overstorey, but differed in their understorey which was a reflection of stand and soil parameters (Chaps. 5, 10). The stands were aged

Table 11.1 Some relevant parameters for site description of the three beech stands in relation to the amount and chemistry of litter fall. Range of soil properties are given for 0–50 cm soil depth

Site	Solling	Göttinger Wald	Zierenberg
Age (years) (2003)	165	120–130	160
Density (trees ha^{-1})	199	245	132
Mean tree height (m)	29.6	33.7	36.7
Mean tree diameter (cm)	46.8	45.7	59.9
Basal area (m^2)	34.2	39.5	32.0
Mean annual temp. °C (rainfall mm)	6.9 (1,193)	7.4 (709)	6.9 (754)
Understorey components	Luzulu-Fagetum	Hordelymo-Fagetum	Hordelymo-Fagetum
Soil pH (H_2O)	3.5–4.5	5.5–7.9	5.3–5.8
N (g kg^{-1})	0.8–3.2	1.4–6.1	1.4–4.1
P (g kg^{-1})	0.30–0.51	0.35–0.70	1.1–1.2

more than 130 years but differed in their stand density and basal area due to different management history. Amounts of annual rainfall and minimum and maximum temperatures varied among the sites with highest rainfall and lowest temperature values on the Solling site. Forest sites vary in their soil properties due to differences in parent materials (Solling – loess overlying Triassic red sandstone, Göttinger Wald – Triassic limestone, Zierenberg – basalt). They show differences in chemical characteristics and proton buffering, and in biological processes and climatic conditions (altitude, annual precipitation) (see Chaps. 1–7, this volume, for more information on the three beech sites).

Litterfall was collected periodically by using litter traps, the number of which varied on different sites, but they were commonly 12–16 on each site, which were usually combined into four replicates for chemical analysis. The period of collection was mostly after long intervals of one or more months during winter and the initial periods of foliage production. During the active leaf litter period, it was collected at fortnightly or shorter periods. Litter was dried, sorted into various components, weighed, ground and analysed for different elements. Leaves and other components were always analysed. The other components included floral or leaf buds, twigs, flower buds, seeds, seed capsules and small bark. The seeds were analysed separately, while all other components were merged together and analysed as residue. Any non-plant component was discarded.

The period of measurements of litterfall on the various sites were periodically prior to 1991 starting in the 1960s on the Solling site, in the 1980s on the Göttinger Wald site and in 1990 on the Zierenberg site. However, since 1991, measurements were made regularly on all three sites, so that this period provided the possibility of making a comparison among the three sites. Most years, the amount of leaf litter on all the three sites showed a narrow range with values lying between 2.5 and 3.5 Mg ha^{-1}.

Fully expanded leaves were collected periodically once a year from the upper third of the tree canopy of the beech stands. They were dried, ground and analysed for element contents. Since 1995, concentrations of elements have been followed on all three sites allowing a comparison among the sites. As the weight of leaves was not known, it was not possible to calculate the amount of nutrients in the green foliage. However, an attempt was made by using Ca as an indicator of constancy in the values to calculate the weights of leaves prior to their shedding.

For assessing the total litterfall on the forest site together with the above ground litter components, the belowground component of fine root litter should be considered. Estimated values of fine root litter production is provided by Murach et al. (Chap. 9, this volume) for the Göttinger Wald and Solling sites. A value of 2,600 kg ha^{-1} per year for the Solling site was assessed where data for 50 cm soil depth were available, and 1,200 kg ha^{-1} per year for the Göttinger Wald site for 20 cm soil depth. In terms of nutrients, fine root litter contained (kg ha^{-1} per year) for the two sites Göttinger Wald and Solling, respectively: N (26 and 39), P (0.9, 1.9), K (2.4, 9.0), Ca (3.2, 2.1) and Mg (0.7, 1.4). These are significant and comparable values with those of aboveground litterfall which should be considered appropriately when nutrient budgets are developed. The rest of the chapter will only consider the aboveground components of the litterfall.

11.3 Components and Annual Patterns of Aboveground Litterfall

Total aboveground litterfall under beech stands has a number of components which include leaf, as the main component, and other components of twigs, discarded buds, small pieces of woody components and pieces of bark. Periodically, a significant proportion of litterfall may contain inflorescence and fruit components during mast years.

The three sites varied in the annual total aboveground litterfall. The highest values were observed on the Zierenberg site (Table 11.2). As a mean for the measurement period, the amount of litter fall followed the decreasing order of sites – Zierenberg site (5,763 kg ha^{-1} per year) < Göttinger Wald (5,032 kg ha^{-1} per year) < Solling (4,894 kg ha^{-1} per year). These mean values of total litterfall

Table 11.2 Annual weights and N contents of total litterfall and leaf litter at the three experimental sites Solling (*SO*), Göttinger Wald (*GW*) and Zierenberg (*ZB*). Mean, minimum and maximum values (kg ha^{-1}) are given for different periods and single years respectively

Site	Mean	Period	SD	Min	Year	Max	Year[a]
		Aboveground litterfall – weights					
SO	4,894	1991–2003	1,287	3,569	1993	7,657	2000
GW	5,032	1990–2003	1,572	3,519	1993	8,517	2000
ZB	5,763	1990–2002	2,065	3,817	1991	9,363	2000
		Leaf litter – weights					
SO	2,772	1991–2003	253	2,423	1992	3,160	2001
GW	2,902	1990–2003	279	2,506	1992	3,450	2000
ZB	3,080	1990–2002	436	2,254	1990	3,882	1994
		N in aboveground litterfall					
SO	67.5	1991–2003	32.5	39.0	1993	128	2000
GW	63.3	1990–2003	31.5	29.5	1993	139	1995
ZB	74.9	1990–2002	33.9	43.6	1993	131	2000
		N in leaf litter					
SO	34.1	1991–2003	4.0	27.8	2001	40.2	1991
GW	32.7	1990–2003	4.6	23.5	1993	40.4	2000
ZB	39.6	1990–2002	5.4	31.1	1990	48.2	1991
		C in the aboveground total litter					
SO	2,581	1991–2003	705	1,871	1993	4,132	2000
GW	2,586	1990–2003	835	1,775	1993	4,450	2000
ZB[b]	2,651	1990–2002	950	1,775	1997	4,207	2003
		C in the leaf litter					
SO	1,456	1991–2003	132	1,262	1992	1,662	2001
GW	1,482	1990–2003	154	1,243	1992	1,783	2000
ZB	1,431	1990–2002	191	1,048	1990	1,773	1994

[a] Years of heavy mast were: 1992, 1995, 1998(?), 2000, 2002

[b] Values for ZB site were calculated by using average values of 46% C content. These values may be underestimated

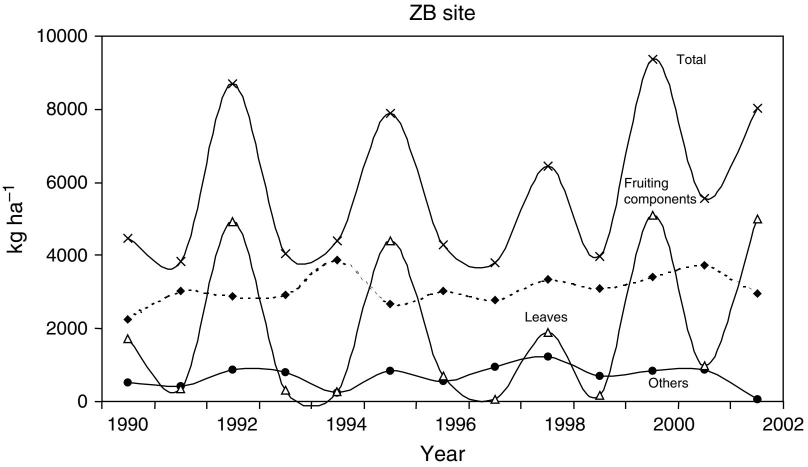

Fig. 11.1 Different components of litterfall measured at Zierenberg site from 1990 to 2002

depended on the frequency and the amount of mast produced on each site. For example, in the heavy mast year of 2000, the total amount of litterfall was 1,700 kg ha^{-1} more on the Zierenberg site than on the Solling site (9,363 kg ha^{-1} on the Zierenberg site and 7,657 kg ha^{-1} on the Solling site). Temporal patterns of various components of total litterfall are shown in Fig. 11.1 as an example for the Zierenberg site. In the common years, the leaf litter component of the litterfall is the major fraction (more than 70%) of aboveground litterfall. Leaf litter values of 60–70% of the total litter have been commonly reported in the literature, which amount to 1.8–4.7 Mg ha^{-1} (Santa-Regina and Tarazona 1999; Pedersen and Bille-Hansen 1999). Meentemeyer et al. (1982) calculated that leaf litter contributed 70% of the total litterfall in forests around the world. Lebret et al. (2001) reported that leaves represented 90% of the total litterfall in the young stand and 70% in the oldest stand, thus age and basal area provided a good prediction of leaf litter in the beech stands. But, as shown in Fig. 11.1, during mast years the fruiting components of litterfall were high, ranging for a year from 1.7 to 5.1 Mg ha^{-1}; the high value was even more than the total leaf litter in some cases. In the mast years, amount of leaf litter constituted less than 40% of the total litterfall. On average over the measuring period of 12 years, leaf litter formed about 53–57% of the total aboveground litterfall.

The mean annual weights of leaf litter measured for more than 10 years ranged from 2,254 to 3,882 kg ha^{-1} with similar overall means for different sites where a difference of about 150–300 kg ha^{-1} among the various sites (Table 11.2) was observed. This small difference in the leaf litter on different sites during the measurement period of 1990–2002 indicates that these stands had a stabilised canopy with very small variation in the amount of foliage. As the mass of leaves would depend on the number and size of leaves, and the size of leaves would be determined by the current year weather conditions at the time of leaf expansion (intensity and pattern of rainfall, sun light conditions and period of sunshine), the similarity in the leaf fall on the three sites indicates that these and other factors determining foliage mass were similar on the three sites. In a recent study of 36 old growth stands of *Fagus sylvatica* across a broad gradient of soil fertility covering nine mesozoic and kaenozoic parent material types (three limestones, two sandstones, two clay stones, one sand and one loess substrate), Meier et al. (2005) reported similar annual leaf litter masses irrespective of soil fertility or acidity of the sites.

When the minimum and maximum values of annual leaf litter are considered, the inter-annual variation, given as the difference in percentage of the mean, on each of the three sites is quite high, 26% on Solling, 33% on Göttinger Wald and 53% on Zierenberg. This is, however, not strictly related to the mast years (Table 11.2). As is evident from Fig. 11.1, the amount of mast did not affect the leaf litter in any significant way though a small trend was observed in the year following the mast years when low amounts of leaf litter were recorded. However, in some of the mast years or the year following the mast year, the highest value of annual leaf litter was recorded. It is expected that any diversion of resources for the production of mast will have only a limited effect on the weight of leaf litter. There are other retranslocation processes which may affect the weight occurring at or prior to the shedding of leaf, suggesting that the mast production and the leaf weights are not related. Due to lack of additional data it was not possible to further explain and evaluate the small differences in the leaf litter at the three beech stands (Fig. 11.2). Despite the small differences among the three sites in the annual amount of leaf litter, the three sites differed in their tree density and BA values (Table 11.1), and these were also reflected in their annual productivity values. Average annual volume increments (m^3 ha^{-1} per year) on the three sites were reported in Chap. 8 (this volume) as 7.7 (Solling), 14.3 (Göttinger Wald) and 9.3 (Zierenberg). These differences in productivity were not reflected by the leaf litter values indicating that there are other factors which determine the productivities.

No long-term trend was observed in the amount of leaf litter during the period of measurement in this study (Fig. 11.2). However, at Göttinger Wald where longer term measurements extending over the last 20 years were taken, a slight increase in leaf litter over time was recorded, though it was only a weak trend (Schmidt 2006). It is possible that high amount of atmospheric N inputs has prolonged the growing period, causing higher plant productivity including an overall increase in the frequency of mast production.

11.4 Amount of Nutrients in Litterfall

The amount of N transfer through litterfall varied among the three sites but more significantly from year to year, which was related to the periodical occurrence of mast years (Table 11.2). In the mast year of 2000, 128, 139 and 131 kg N ha^{-1} were transferred through litterfall at the Solling, Göttinger Wald and Zierenberg sites,

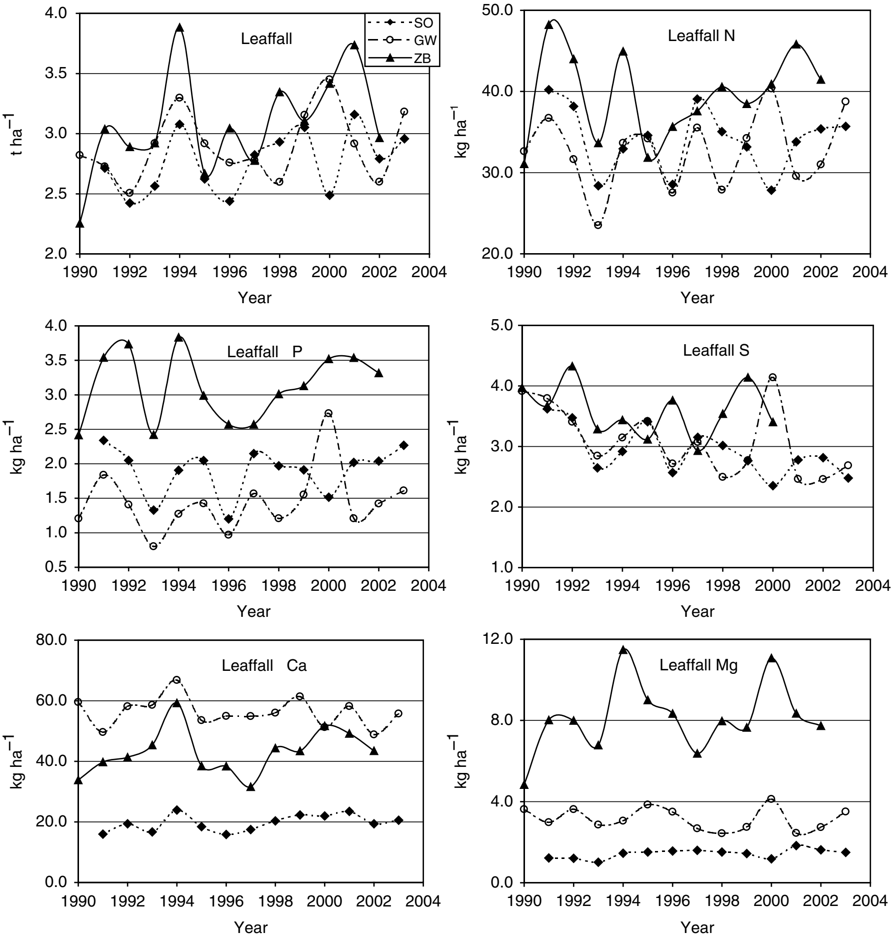

Fig. 11.2 Annual amount of leaf fall and a number of nutrients on the Zierenberg (*ZB*), Göttinger Wald (*GW*) and Solling (*SO*) sites from 1990 to 2003

respectively. As a 10-year average, the amount of N in the litterfall ranged between 63 and 75 kg N ha^{-1}. For the nitrogen budgets, it is customary to take the leaf litter data, usually measured on a short-term basis. Nitrogen content in leaf litter ranged from 24 to 48 kg ha^{-1}annually depending mostly on the site and N content of the leaves shed, but as long-term means for the three sites, the values of leaf litter were 34, 33 and 40 kg ha^{-1}for Solling, Göttinger Wald and Zierenberg sites, respectively (Table 11.2). For the 36 old growth beech forests Meier et al. (2005) reported an annual N transfer through leaf litter of 25–38 kg ha^{-1}, which were not related to any of the soil parameters measured (soil N pool, available P, exchangeable Ca, K and Mg, soil acidity or exchangeable Al). A similar mean value of 45 kg N ha^{-1} (range 31–69 kg ha^{-1}) was reported for 13 IBP sites by Cole and Rapp (1981). When annual leaf litter data are used to define N status, disregarding the other litter

Table 11.3 Mean and SD values of nutrients in the litterfall for the mast years (mast years were based on the information in literature and the relative amount of fruiting components to leaves) 1992, 1995, 2000, 2002 for all sites, plus, for the Zierenberg site, 1998, and for the Göttinger Wald site, 1990, and normal years on the three beech sites. All values are given in kg ha^{-1}

	N	P	S	Ca	K	Mg
Solling						
Mast years ($n = 4$)	111.1	8.1	8.0	33.5	25.9	4.9
SD	21.8	2.1	1.8	4.8	7.4	1.0
Normal years ($n = 9$)	48.1	2.7	4.0	24.6	10.8	2.0
SD	5.7	0.6	0.5	3.6	2.6	0.4
Overall mean	67.5	4.3	5.2	27.4	15.5	2.9
SD	37.0	3.2	2.5	5.7	9.0	1.6
Göttinger Wald						
Mast years ($n = 5$)	97.9	6.0	7.9	98.9	26.6	7.1
SD	28.6	1.9	2.1	17.7	5.1	2.0
Normal years ($n = 9$)	44.0	1.9	3.8	70.3	13.6	3.9
SD	6.4	0.4	0.5	9.7	3.1	0.7
Overall mean	63.3	3.4	5.3	82.5	18.9	4.9
SD	31.5	2.3	2.3	17.8	7.0	2.1
Zierenberg						
Mast years ($n = 5$)	112.7	11.2	8.5	67.3	nd	16.2
SD	21.6	2.7	1.5	6.8	nd	3.4
Normal years ($n = 8$)	51.3	4.1	4.4	50.0	nd	9.0
SD	7.2	0.8	0.6	8.1	nd	1.6
Overall mean	74.9	6.9	5.9	56.6	nd	11.8
SD	33.9	3.9	2.4	11.4	nd	4.3

components, they underestimate the amount of N taken up, transferred through litterfall and added to soils. However, to assess the real amount of N transfer on a site, long-term measurements of litterfall are needed. In order to understand the functioning of ecosystems, it is important that events such as production of mast should be appropriately included in the measurement period. For example, the amount of N taken up for mast production would increase many fold over that of a normal year. This poses the question of physiological changes required in the tree to cope with a very high (Table 11.3) requirement of N and other elements for the production of mast.

Amounts of P and other elements in the litterfall are given for the three sites in Table 11.3 where the years with clear mast production are separated from those of normal years. The long-term mean values of P in the litterfall were 4.3, 3.4 and 6.9 kg ha^{-1} on the Solling, GW and Zierenberg sites, respectively, indicating clearly the high P levels on the site with basaltic soil parent material, and the low values on soil developed from calcareous material. P inputs are similar to N (in pattern as well as in relative amounts in leaf litter and in fruiting components). Leaves contribute 3.1 kg of P (range 2.4–3.7 kg) annually to the litter on all three sites.

The fruiting components have higher P contents than the leaf litter (2.7–3.2 times). P contribution of the twigs and buds, etc. to the total litter is small, less than

1 kg ha^{-1} (mean 0.6 kg ha^{-1}), whereas total P input can vary between 3.3 and 12.9 kg depending upon the amount of mast produced. It is very hard to assign an annual P transfer value from litter to the soil because the final fate and the decomposition constants for fruiting bodies are not precisely known. Fruit shell will decompose much more slowly than the fruits with high nutrient levels.

Differences among the three sites were small for the overall mean amount of S in the litterfall, (5.2–5.9 kg ha^{-1}) and the mean difference between mast years and non-mast years was similar (about 4 kg S) on all sites. Litterfall at Göttinger Wald site is richer in Ca whereas that at Zierenberg showed much higher values of Mg in the total litterfall. However, the amount of Ca in the fruiting components was relatively low, contrasting with that of P, and therefore fruiting components of litter had a relatively small effect on the long-term total transfer of Ca through litterfall. Ca levels in the leaves are much higher than in the fruit components. The leaves therefore determine the Ca inputs to the soil through litterfall. This is probably an indication of the lower mobility of Ca from the cell walls. Zierenberg site has a higher amount of Mg than the Solling and Göttinger Wald sites, Solling being the lowest of the three. Differences in Mg amounts on the three sites are also reflected in the mast components. Data on K was only available for the Solling and Göttinger Wald sites with Göttinger Wald showing slightly higher values than Solling.

The data on the amount of nutrient show the importance of long-term measurements of litterfall to include the mast years in assessing the overall mean of nutrients involved in the nutrient cycling processes.

11.5 Nutrient Concentrations in the Total Litterfall and Leaf Litter Components of the Different Sites

Annual weighted mean values of concentration of nutrients in the litterfall and leaf litter are given in Table 11.4 and the changes in time are shown in Fig. 11.3. Differences between the nutrient concentrations of litterfall and leaf litter point mostly to the composition of fruiting components. The mean values of nitrogen, sulphur, potassium and magnesium did not differ much in the total litterfall and the leaf components at the individual sites, whereas Ca was low but P was high in the fruiting components. Therefore, N/P ratios were relatively lower in the total litter fall than in the leaf litter (Table 11.4).

Of the three sites, leaf litter at the Göttinger Wald site showed continuously low values of N and P but higher values of Ca (Ca-rich soil at Göttinger Wald site) (Fig. 11.3), though there was no evident continuous trend in the concentration of these elements in the leaf litter during the course of these measurements. However, concentrations of S decreased in all cases with time which was the reflection of a decrease in atmospheric S inputs in these systems (Chap. 15, this volume). This decrease in S concentrations increased the N/S ratios on all sites, especially on the Göttinger Wald sites where N/S ratio of 8.3 in 1990 increased to 12.0 in 2001. Usually, a constant N to S ratio of 16 is expected in the plant tissue and values

Table 11.4 Weighted mean and standard deviation (SD) values of concentration (g kg^{-1}) and ratios of different elements in the leaf litter and total litterfall on the three beech sites

	Solling		Göttinger Wald		Zierenberg	
	Mean	SD	Mean	SD	mean	SD
			Leaf litter			
C	525.2	4.07	510.3	6.18	465.0	9.59
N	12.4	1.63	11.3	1.40	12.9	1.44
P	0.79	0.12	0.50	0.13	1.02	0.13
S	1.06	0.19	1.07	0.20	1.14	0.11
Ca	7.10	0.79	19.5	1.98	14.0	1.22
K	3.13	0.68	4.03	0.63	nd	nd
Mg	0.52	0.07	1.09	0.19	2.63	0.38
C/N	43.2	5.38	46.0	6.36	36.4	3.65
N/P	18.2	2.14	23.6	3.67	12.8	1.13
N/S	11.7	1.06	10.7	1.74	11.0	1.15
			Total litterfall			
C	526.5	6.09	512.6	5.59	nd	nd
N	13.2	2.85	12.1	2.31	12.7	1.74
P	0.82	0.31	0.62	0.23	1.12	0.27
S	1.04	0.18	1.03	0.17	1.02	0.09
Ca	5.69	0.80	16.9	2.37	10.4	2.03
K	3.01	0.89	3.71	0.59	nd	0.00
Mg	0.57	0.13	0.95	0.15	2.06	0.29
C/N	41.3	7.82	43.8	7.59	nd	nd
N/P	17.1	3.74	20.7	4.01	11.7	1.51
N/S	12.7	1.32	11.8	1.61	12.1	1.52

lower than that indicate excessive amounts of sulphate present in the senescent leaf. An increase in that ratio indicates that the amount of free sulphate is decreasing slowly over the period as the atmospheric depositions of S are decreasing.

These differences in the element composition of the leaf litter reflected in general the differences in composition of the three soils suggesting the composition of the cell wall components (Ca and P) and the nutrient withdrawal patterns in association with plant sinks are the major factors affecting the element composition on the three beech sites. Khanna and Ulrich (1991) and Meier et al. (2005) have provided evidence of the role of soil composition on the levels of Ca and other elements in the leaf litter.

11.6 Foliar Chemistry

Mean values of N concentration were quite high on all sites (22.3–24.6 mg g^{-1}) with very little differences among them. This is related to high atmospheric N inputs. Most of the N concentrations lie between high and very high diagnostic

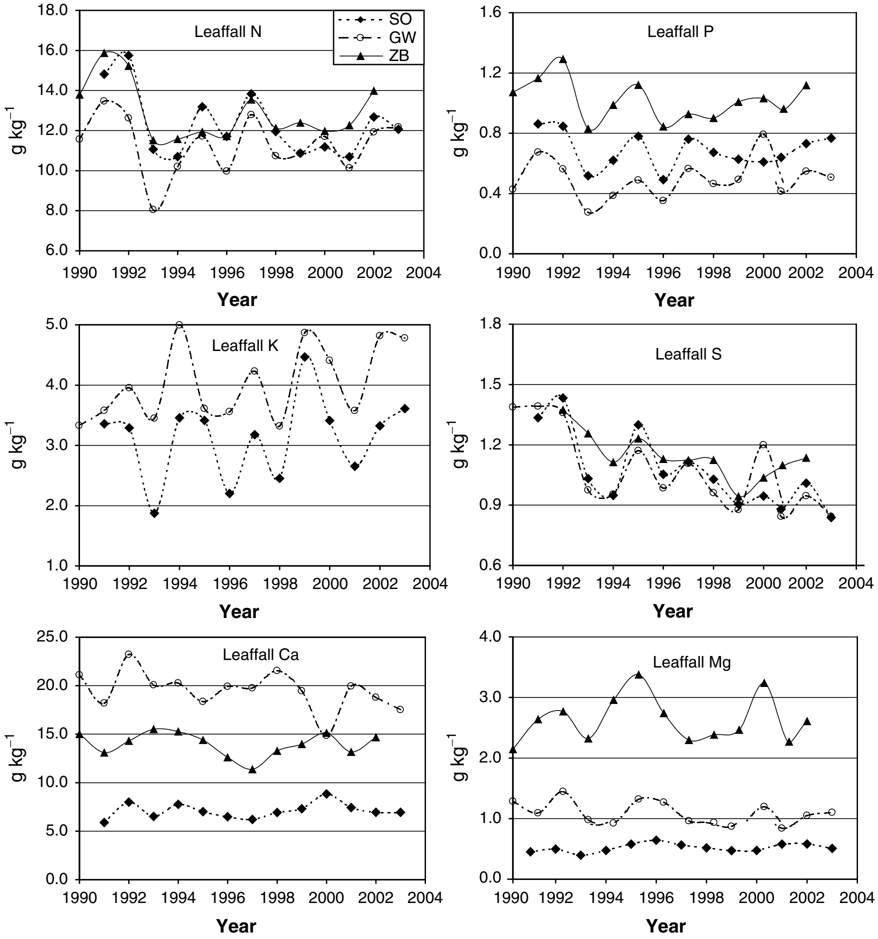

Fig. 11.3 Mean annual concentrations of nutrients in the leaf litter on the Zierenberg (*ZB*), Göttinger Wald (*GW*) and Solling (*SO*) sites during the measurement period

values (Hüttl 1992). However, the concentrations of Ca, Mg, P and Mn in the foliage varied on different sites depending upon the chemical soil characteristics (Table 11.5).

Concentrations of P in the green foliage of the Göttinger Wald and Solling sites were <1.3 mg g^{-1}, ranging from 0.98 to 1.18 mg P g^{-1} in Göttinger Wald and from 1.14 to 1.37 mg P g^{-1} for Solling. Foliar concentrations of P at the Zierenberg site were high, ranging from 1.14 to 1.69 mg g^{-1}. Different values are given in literature to define the critical values of P in beech stands. For example Krauß and Heinsdorf (2005) suggested that the values of 1.14–1.52 mg P g^{-1} are in the optimum range and values less than 1.14 should be considered low. Hüttl (1992) gives much lower values as critical values (<1.3 mg g^{-1} will be considered low). Considering these

Table 11.5 Annual mean and SD values of concentrations of a number of elements in the live foliage of beech from three sites (data for the period 1995–2002)

	Solling		Göttinger Wald		Zierenberg	
	Mean	SD	Mean	SD	Mean	SD
Nutrient and other elements (mg g^{-1})						
C	526	6.20	514	8.04	469	16.0
N	24.6	1.14	24.14	1.76	22.30	1.22
P	1.26	0.07	1.06	0.08	1.33	0.18
S	1.52	0.14	1.58	0.11	1.44	0.13
K	5.01	0.58	7.42	1.06	6.05	0.62
Ca	3.65	0.44	10.80	0.79	8.75	0.71
Mg	0.71	0.10	0.98	0.22	2.84	0.39
Mn	1.88	0.24	0.55	0.10	nd	nd
Fe	0.09	0.04	0.09	0.03	nd	nd
Al	0.06	0.04	0.04	0.04	nd	nd
Heavy metals (mg kg^{-1})						
Zn	27.02	4.23	26.19	4.87	nd	nd
Cu	7.18	0.57	6.84	0.74	nd	nd
Cr	0.31	0.10	0.31	0.07	nd	nd
Co	0.03	0.04	0.04	0.04	nd	nd
Ni	0.60	0.16	0.73	0.24	nd	nd
Cd	0.04	0.03	0.05	0.04	nd	nd
Pb	0.52	0.27	0.76	0.35	nd	nd
Element ratios						
C/N	21.42	0.97	21.40	1.59	21.08	1.32
N/P	19.50	0.86	22.92	1.51	16.97	1.92
N/Ca	6.82	0.83	2.24	0.22	2.56	0.23
P/Ca	0.35	0.03	0.10	0.01	0.15	0.02
Mg/Ca	5.24	0.79	11.52	2.61	3.11	0.27
N/S	16.29	1.29	15.31	0.67	15.53	0.93

criteria, one can safely say that the foliar P indicates adequate to high levels at the Zierenberg site and probably at the borderline to deficient range for the Göttinger Wald site. For the Solling site, the foliar levels cannot be assigned to a definite group of low or adequate levels. As the foliage data represented a short period of measurements (1995–2002), it is very hard to assess any long-term trends in these values. However, it seems certain that at present the productivity values are not related to foliar P values. Beech is considered to have a high level of physiological plasticity, and whether it can also adjust to low content of P is a possibility which has not received sufficient attention (Meier et al. 2005). Due to the short period of measurements it is hard to study the retranslocation patterns of P on each site and if the patterns have undergone any changes.

If the critical values (Hüttl 1992) for K, Ca and Mg in the beech leaves are compared with the measured concentrations (Table 11.5), all the three elements are in the very low range on the Solling site whereas their values for the other two sites lie in the adequate to high levels. Again, the low values of these elements on the Solling site are associated with the highly acid soil.

No change in the concentration of most of the elements was measured in the foliage samples during 1995–2002 on all sites except that the concentration of S on the Zierenberg site, and that of K on the Solling and Zierenberg sites, has decreased continuously during the last 10 years (Fig. 11.4). However, when long-term measurements were considered on the Solling site, decreasing trends in P and K concentrations with time were observed (Fig. 11.5). Prior to 1975, the values of K concentrations in the foliage ranged from 8 to 12 mg g^{-1} which had dropped to

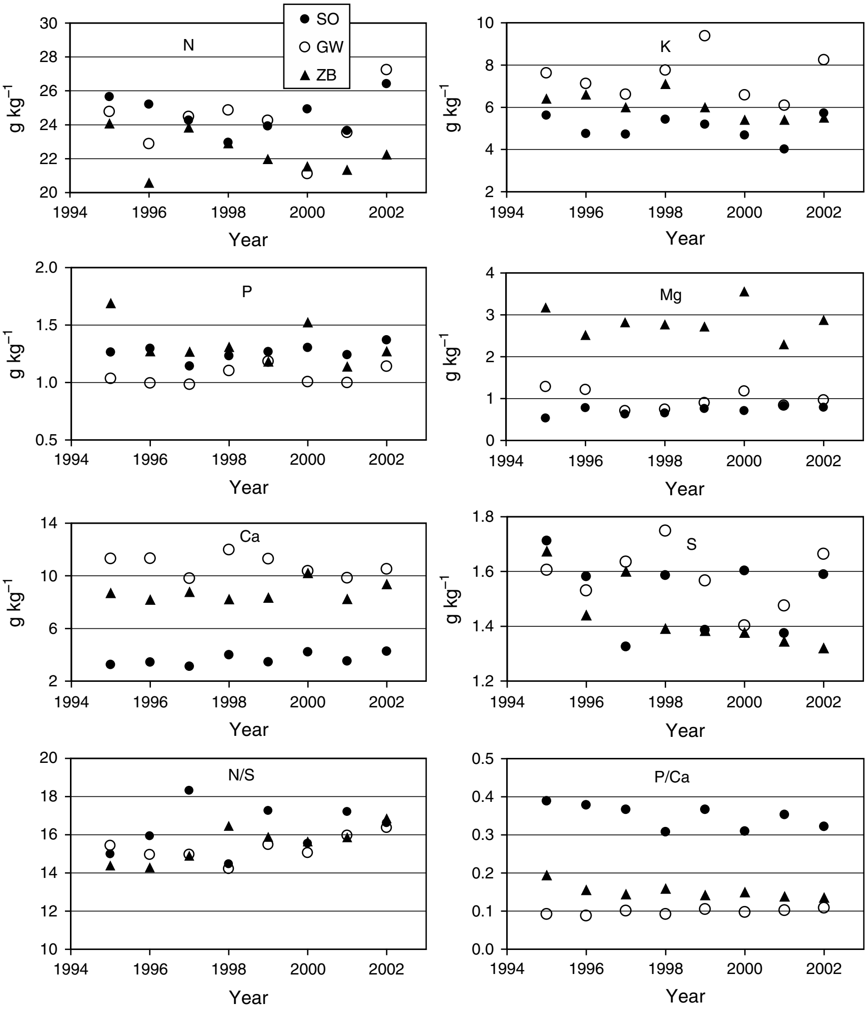

Fig. 11.4 Annual mean values of nutrient concentrations and nutrient ratios in the foliage of the Zierenberg (*ZB*), Göttinger Wald (*GW*) and Solling (*SO*) sites for 1995–2002

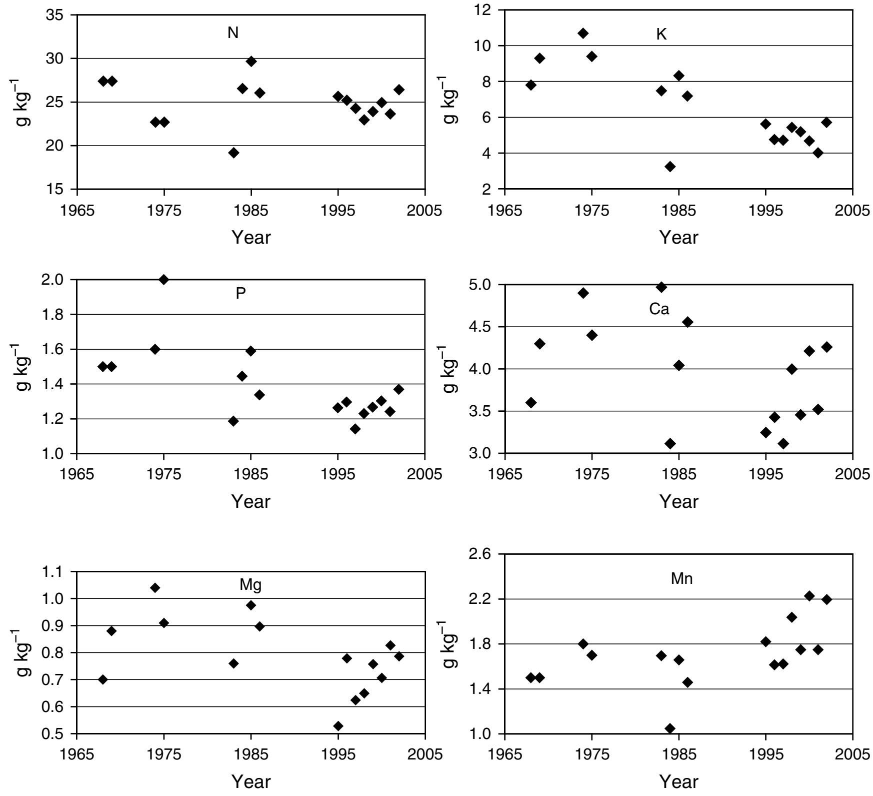

Fig. 11.5 Long-term trends in the foliar concentration of some nutrients at the Solling site

4–6 mg g^{-1} after 1995. For the same periods, the values of P concentrations ranged from 1.5–2 mg g^{-1} (prior to 1995) to 1.0–1.5 mg g^{-1} (after 1995).

In a study on changes in foliar nutrient levels in northeastern France, Duquesnay et al. (2000) sampled 118 beech stands in 1996–1997 and compared the analysed values with those obtained in 1969–1971. Between the two sampling periods, the concentration of foliar N increased (+12%), whereas that of others decreased by 23% (P), 38% (Mg) and 16% (K). Ratios of N/P and N/Mg increased by 42 and 77%. This decrease in concentrations of P and cations was particularly marked for trees growing on acidic soils. They assigned this decrease in P concentration in the foliage of beech trees to increasing atmospheric CO_2 concentrations and acidification of forest soils. In a parallel study where the foliage concentrations of beech stands were monitored continuously for 5 years, a decrease in P levels was observed, which resulted in an increase in N/P ratios. Similarly, Flückiger and Braun (1998, 1999) reported an increase in nitrogen concentration and a continuous decrease in phosphorus concentration measured every 3–4 years in the beech foliage. The values of P decreased from 1.25 mg P g^{-1} in 1984 to 1.08 mg P g^{-1} in 1995 in 51 beech stands in northwestern Switzerland, with an accompanying increase in the N to P ratios from 18.6 to 25.0.

In a study of 49 stands European beech (60-or more years-old) in the Werdenfelser Land region, Ewald (2000) analysed foliage and soil samples from eight sites for nutrient composition. High crown transparency and slow tree growth were related to low availability of P, Mn and N in soils. Sites could be divided into two groups. Moderate P levels were found in trees from well-developed mineral soils, and extremely low P levels (0.6–1.0 mg g^{-1}) in immature carbonate soils where total P levels in soils were low and Ca saturation very high. Very high N/P ratios of 30 or more were associated with low P level. P was a critical element in the nutrition of beech in the calcareous Alps, which may be partly responsible for the poor vitality of this species in mixed mountain forests. In their study of 50 European beech stands, Leuschner et al. (2006) observed that N/P values of the surface organic layers were higher on acid soils under beech stands than on the calcareous soils, indicating the possibility of P limitation on acid soils, probably in association with high atmospheric N inputs. Composition of surface organic layer for N and P is expected to relate strongly with their litterfall values.

Of 17 beech forests, which are part of the German contribution to the Forest Focus initiative of the EU (Level II sites), those with inadequate levels of nutrients were seven sites for Ca, four for Mg, three for P and two for K. None of the sites showed deficiency of N in the foliage (Chap. 23, Table 23.3). On a wide ranging dataset from beech stands ($n = 75$) in Lower Saxony, Brandenburg and Bavaria, Wolff and Riek (1997) reported that about 54% of the sites would show P deficiency using the commonly used critical values for beech foliage.

On the three sites under investigation N/P ratios of the live foliage was always >20 on the Göttinger Wald site and <18 on the Zierenberg site though the ratios did not change in time during 1991–2002 reflecting the P status of the sites. However, a decrease in P/Ca ratios were observed during this period on the Solling and Zierenberg sites (Fig. 11.4). As the value of Ca concentration was not expected to vary much on each site, a decrease in P/Ca ratio indicated a decrease in P concentration on the Solling and Zierenberg sites. Similarly, K/Ca ratio in the foliage decreased indicating a decrease in K concentrations on the Solling site (data not shown). However, as discussed above, only longer term measurements indicate a decrease in P and K foliar levels on the Solling site. Usually, a constant N/S ratio of 16 is expected in the plant tissue when no protein-free S and N are stored. Foliage samples prior to 1998 showed values of <16 on all the three sites, but after 1998 the ratio has slowly increased towards 16 (Fig. 11.4). A value of <16 would indicate a high amount of free sulphate in the tissue (excessive amount of sulphate) which would have occurred due to high amounts of atmospheric inputs of S.

11.7 Nutrients and Heavy Metals in Green Foliage and Litterfall in Relation to Atmospheric Inputs

The atmospheric inputs of nutrients and heavy metals have changed during the last 30 years (low acidity, low S, low Ca and other cations, low content of heavy metals) (Chap. 15). For example, at the Solling site, atmospheric inputs of S were around

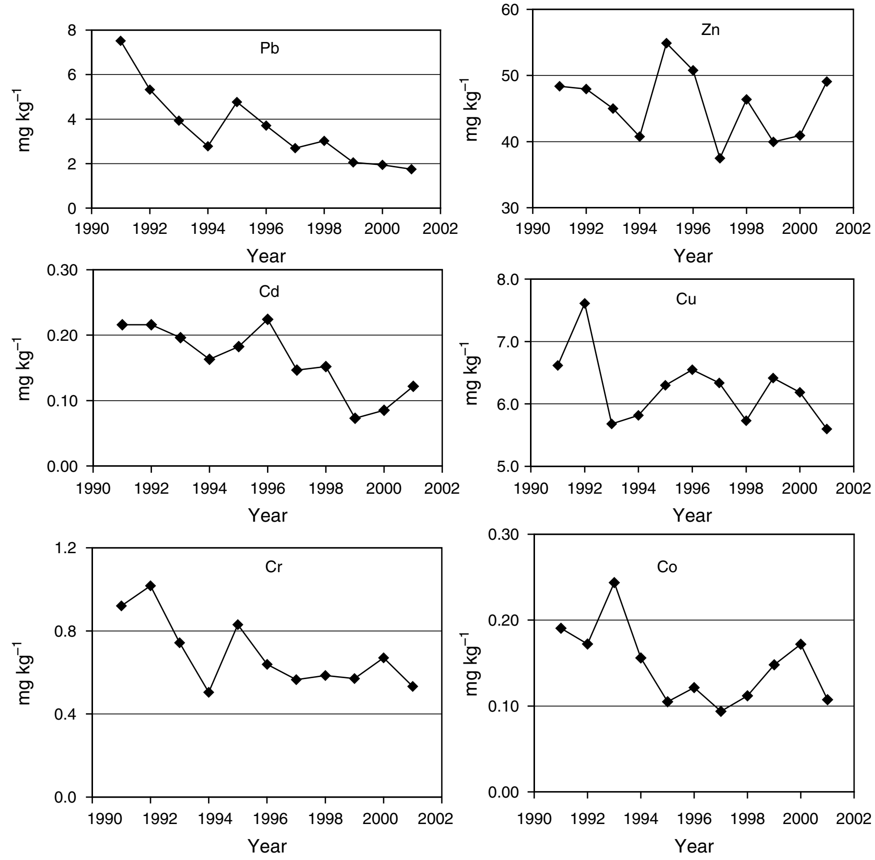

Fig. 11.6 Mean values of some heavy metals in the leaf litter at the Solling site from 1990 to 2001

60 kg ha^{-1} in 1968 which have decreased to 10 kg ha^{-1} in 2002. However, atmospheric inputs of N, which were about 20 kg ha^{-1} in the early 1970s had increased to 28 kg ha^{-1} in the 1980s, but have since decreased to 20 kg ha^{-1} and have remained constant for the last 13 years (Chap. 15). During the last 20 years, atmospheric inputs of heavy metals have also decreased (low Pb, Cd and other heavy metals). This decrease in atmospheric depositions is reflected in the concentration of S (Fig. 11.4), and a number of heavy metals in the leaf litter (Fig. 11.6). For example, the concentration of Pb in the leaf litter decreased from 7.5 mg kg^{-1} in 1991 to 1.7 mg kg^{-1} in 2001.

There is very little known of the consequences of changes in heavy metal concentrations of the litter on the decomposition and mineralisation processes. Some of the factors related to litter decomposition processes would be the content and solubilities of heavy metals, the interactions of heavy metals with other elements, the formation of stable complexes with organic matter, and the toxicity effects on soil fauna and microbial populations.

Dynamics of heavy metals in decomposing litter are particularly poorly known, with only a few studies on decomposition processes involving heavy metals as pollutants (Coughtrey et al. 1979; Killham and Wainwright 1981; Bengtsson et al. 1988; Grodzinski et al. 1990; Laskowski et al. 1994). During litter decomposition, the concentrations of heavy metals increase (Ruhling and Tyler 1973; Berg et al. 1991). Staaf (1980) and McBrayer and Cromack (1980) found significant accumulations of Fe, Zn, Pb, Cu and Cd in the litter of beech, oak, Scots pine and oak–hornbeam forests.

11.8 Autumn Withdrawal of Nutrients at the Time of Leaf Senescence

The amount of nutrients measured in the leaf litter is the net amount present after their withdrawal into the old tissue and any subsequent losses that may have occurred due to leaching during the period when the leaf is shed and when it is collected and measured. The leaching component could be quite significant for a number of elements such as K, Mg, P and N. Chapin and Moilanen (1991) reported that leaching by autumn rains accounted for 25% of the N disappearance and 55% of the P disappearance from senescing leaves of birch in a high-fertility field. From our presently available data, it is not possible to assess the amount or the fraction of nutrients which will be leached. This creates some uncertainty in the interpretation of the results by describing the whole amount as the withdrawal fraction, especially for K which is most mobile element and is easily lost.

Retranslocation of nutrients from senescing tissues, often referred to as ‘resorption’ (Killingbeck 1986), is an important plant strategy to economically use the accumulated nutrients. For example, Aerts (1996) suggested that 40–65% of nitrogen and phosphorus from leaves may be resorbed by plants before leaf abscission. Resorption of nutrients thus acts as an important feed-back mechanism in the nutrient cycling and litter decomposition processes in forests (Staaf 1982; Killingbeck 1996; Cherbuy et al. 2001; Cote et al. 2002). A higher rate of nutrient resorption would cause a low amount of nutrient uptake for the next growing season, but at the same time would produce litter of low quality affecting its decomposition.

Another unknown factor in the calculation of the nutrient withdrawal amount is the concentration of nutrients at the time of leaf senescence. Usually, the leaf samples are collected from a specific part of the canopy to assess the nutritional levels through critical amounts or balance of elements in the fully grown leaves. Some nutrients are constantly transferred in and out of leaves, probably affecting the value for the nutrients used as the amount in the live foliage at the time of leaf senescence (Nambiar and Fife 1991).

Another error involved is the assessment of foliage biomass from the litter biomass measured on the surface organic layer, even of deciduous foliage. It is well known that some components of the leaf are retranslocated to the living tissue for future use. This involves nutrients and also organic components. There are additional losses of organic components through decomposition and respiration of C during leaf shedding and prior to leaf shedding through consumption by insects. This has been estimated to be about 15% as a mean value for beech forests, though this value can be quite high in some cases.

By assuming no losses of organic components from the leaf litter following leaf senescence, i.e. foliage mass equals the measured leaf litter weights, one can calculate the minimum amount of nutrients which may have been withdrawn at leaf senescence. The values of nutrient withdrawal will thus be approximate as it is hard to define the amount present in the foliage sample prior to its becoming leaf litter. The time of sampling is crucial in such studies which have not been actually taken into consideration in most studies.

The results obtained from this study are presented in Table 11.6 where mean values of nutrient withdrawal for the three sites during the period of study are given. It also gives the fraction of nutrients removed or lost from the initial amount in the foliage. The results are approximate values due to deficiency of related data on different processes during leaf senescence as described above:

(a) All nutrients, except Ca and in some individual years Mg, were withdrawn in significant amounts.
(b) The amount of N withdrawn was high (31–37 kg ha^{-1}) despite high atmospheric N inputs in these systems. As a mean, the fraction of N withdrawn was 51% on the Solling, 53% on the Göttinger Wald and 44% on the Zierenberg sites.
(c) The amount of P withdrawn was similar on the Solling and Göttinger Wald sites (1.5 kg ha^{-1}) but was low (1.1 kg ha^{-1}) on the Zierenberg site. As the P

Table 11.6 Mean and SD values of amount of nutrients withdrawn at leaf senescence (kg ha^{-1}) and the amount withdrawn as a percentage of the amount in the live foliage. Live foliage mass was assumed to be equal to the measured leaf litter

Site		N	P	S	Ca	K	Mg
		kg ha^{-1}					
Solling	Mean	34.6	1.6	1.3	−10.0	4.9	0.4
	SD	4.19	0.35	0.38	1.87	2.16	0.35
Göttinger Wald	Mean	36.6	1.5	1.6	−23.8	9.7	−0.2
	SD	3.47	0.46	0.50	4.53	2.92	0.29
Zierenberg	Mean	30.6	1.1	1.0	−15.1	nd	0.5
	SD	3.86	0.47	0.28	3.56	nd	0.81
		Percentage of amount in live foliage					
Solling	Mean	51.1	47.4	31.5	−102	36.4	19.7
	SD	4.72	9.52	8.57	15.51	14.48	16.06
Göttinger Wald	Mean	53.2	51.3	34.7	−77.3	45.3	−9.8
	SD	5.26	15.06	11.28	21.66	9.06	15.09
Zierenberg	Mean	43.9	25.1	23.0	−55.3	nd	5.9
	SD	3.82	9.17	6.38	12.14	nd	9.54

concentration in the foliage of the three sites differed significantly, the proportion of P withdrawn was low on the Zierenberg site (25%) but high (47–51%) on the other two sites. The high values lay in the same magnitude as the amount present in the leaf litter, indicating that the tree has the capacity to develop half of its foliage with similar element concentrations without depending upon any uptake during the next growing season.

(d) Values for Ca withdrawal were negative, pointing to the error involved in assessing the mass of the foliage or the concentration of Ca in the leaves prior to senescence.

(e) The Göttinger Wald and Zierenberg sites have Mg-rich soils showing very little withdrawal of Mg or the withdrawal is of the same proportions as the organic substances removed or lost during the leaf litter. The fraction of Mg withdrawn at the Solling site was high (20%).

(f) Nutrient withdrawal in autumn during leaf senescence was related to the nutrient status of the three sites either in relation to nutrient inputs (N and S) or chemical soil properties influencing the concentration of nutrients in the live foliage.

An attempt was made to determine the weight of the live foliage by assuming the conservation of Ca in the leaf litter. This method was tested by using the total amount of Ca in the leaf litter collected a number of times during autumn. For leaf analysis, only one sample was taken. This produced two to three times higher values of foliage mass than measured at litterfall suggesting that these values were far too high to be plausible. It seems that Ca content in the leaves goes on increasing until they are shed, and conservation of Ca can only be valid and useful if the live leaves prior to leaf senescent are taken. In the present scheme of sampling, live leaves were collected a few months in advance of when the leaves were shed.

There are two common hypotheses pertaining to the fraction and amount of nutrients re-absorbed from leaves.

(a) The first one considers that the amount of nutrient resorption increases as an inverse function of soil nutrient availability (Grime 1979; Chapin 1980; Berendse and Aerts 1987). Nutrient resorption from senescing leaves is therefore expected to be more highly developed on sites of low fertility. For example, Cote et al. (2002) reported 56–71% N re-absorption efficiency for eight hardwood species on two sites of contrasting fertility. However, Staaf (1982) did not find any relationship between translocation efficiency of N and P and soil factors for beech trees on 24 sites. The retranslocation for N and P was always more than 55% of the amount present in the leaf prior to its senescence. For elements N, P, K, and S, the amount withdrawn at leaf senescence was related to the concentration of respective element in the leaf prior to its senescence. This was not the case with Ca and Mg where site factors such as soil pH and site index were also important. From a literature review, Aerts (1996) concluded that trees and shrubs showed poor intra-specific responses to soil nutrient availability with 63% of experiments reporting no response by 60 plant species.

(b) The second hypothesis considers that resorption is influenced by sink strength within the plant (Nambiar and Fife 1991) so that resorption efficiency is positively correlated with plant growth rates, because the production of new tissues constitutes a strong nutrient sink. Thus, one can consider the significance of nutrient withdrawal in terms of growth phases as suggested by Oron and Schulze (1989) which act as strong sinks for an element and can thus lead to nutritional disharmony when the demand of an element for the new growth is higher than its supply either through resorption or through uptake. However, Chapin and Moilanen (1991) noted that sink strength was unlikely to explain the strong resorption shown by many deciduous trees in autumn and concluded that nutrient resorption efficiency was influenced more strongly by carbohydrate flux from leaves (i.e. source-sink interactions) than by factors governing hydrolysis of nutrient-containing fractions in leaves. In our study, relationships between nutrient concentrations and nutrient withdrawal for some elements depended on nutrient status of the sites.

11.9 Conclusions

1. Leaf litter constituted about 70% of the total litterfall in normal years and about 40% in mast years with absolute values showing only small differences among the three sites and during 12 years of measurements. This was despite the major differences observed in the productivity on the three beech sites.
2. There was no clear evidence of any change in the amount of nutrients in litterfall in time over the measuring period. However, the amount of nutrients differed among the sites depending upon the soil bedrock material. Litterfall was high in P and Mg at the basaltic sites and in Ca in the calcareous Göttinger Wald soil.
3. Frequency and the amount of fructification were the most important factors affecting the amount of nutrients transferred in litterfall to the surface organic layer, due to very high amount of nutrient (especially P) contained in the fruit components (except Ca) and doubling of the frequency of masting. However, due to the periodicity and irregular nature of mast production, long-term measurements of litterfall are required to make an useful assessment of nutrient transfer that would include mast production.
4. Foliar concentration indicated that, different from the Zierenberg site, the Solling and Göttinger Wald sites were low to very low in P, and Solling also in K, Ca, Mg.
5. Following the Clean Air policies, atmospheric inputs of S and heavy metals have decreased during the course of the measurements, which reduced the amount of these elements in the litterfall, especially those of some heavy metals. For example, concentration of Pb in the leaf litter decreased from 7.5 mg kg^{-1} in 1991 to 1.7 mg kg^{-1} in 2001.

6. Nutrient withdrawal during leaf senescence in autumn was related to the nutrient status of the three sites either in relation to nutrient inputs (N and S) or chemical soil properties influencing the concentration of nutrients in the live foliage. A significant amount of N (44–53%) was withdrawn on the three sites whereas that of P varied according to the P status of the sites, low withdrawal on the Zierenberg site (25%), but high (47–51%) on the Solling and Göttinger Wald sites. Similarly, Mg was withdrawn mostly on the Solling site. The amount of nutrient withdrawn will provide the nutrients for the growth of at least half the amount of canopy without any further uptake.

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