Chapter 10
Phytomass, Litter and Net Primary Production of Herbaceous Layer

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10.1 Introduction

Understorey vegetation may form an important component of mineral cycling pathways in forest ecosystems. The important cycling processes are: nutrient uptake, storage, translocation and return by vegetation, litterfall and nutrient release from residues by mineralisation of litter and soil organic matter for further plant uptake (Duvigneaud and Denaeyer-DeSmet 1973; Charley and Richards 1983; Ellenberg et al. 1986; Eichhorn 1995). Although the biomass of herbaceous plants is low compared to that of the tree layer (Yarie 1980; Muller and Bormann 1976; Ellenberg et al. 1986; Giese et al. 2003; Peichl and Arain 2006), high element concentrations of herbaceous plants usually increase their importance in element cycling (Scott 1955; Turner et al. 1978; Blank et al. 1980; Rodenkirchen 1995; Bolte et al. 2004). Through short-term changes in species composition, element concentration and storage (Höhne 1963; Likens and Bormann 1970; Linke and Roloff 1995), the herbaceous vegetation forms a variable element pool that may reduce nutrient losses to external sinks of forest ecosystems (Eichhorn 1995; Mellert et al. 1998; Bartsch 2000; Schmidt 2002; Olsson and Falkengren-Grerup 2003; Bolte 2006).

Litter production of herbaceous layer may sometimes equal that of the tree layer (Höhne 1962). The amount and higher quality (particularly C/N ratio; Wittich 1944, 1961; Wolters 1999) of readily decomposable substrates produced by the herbaceous layer may alter the community of decomposers in a soil (Jandl et al. 1997) changing the element turnover rates (Wise and Schaefer 1994) that may affect C and N retention by forest soil (Bauhus et al. 2004).

The objective of this chapter is to describe the role of herbaceous vegetation in the nutrient cycling processes at the three beech forest sites of Göttinger Wald, Zierenberg and Solling through differences in the mass and quality of annually produced litter. The internal and external nitrogen balances in relation to the ground vegetation will be included in the discussion. For a valid assessment of any

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subsequent comparisons among sites involving quantitative parameters of the biomass and nitrogen, temporal and spatial dynamics in herbaceous biomass and N-cycling will be included, as well as the different methods used to assess changes in biomass and N-cycling.

10.2 Definitions and Methods

The *biomass* is defined as all the above- and belowground parts of live plant material. The *necromass* at the time of the inventory is the dead plant material, which includes the standing dead plant parts. The *phytomass* describes the combined amounts of biomass and necromass. Plant material shed to the surface organic layer is termed as *litter fall* and is not part of the phytomass. All parameters are expressed as dry matter (kg ha^{-1}, g m^{-2}). These definitions follow the terminology of the International Biological Program (I.B.P; Newbould 1967; Milner and Hughes 1968).

Two methods were used to assess various components of the herbaceous vegetation: (1) biomass harvesting to estimate net primary production (NPP) (Sect. 10.2.1), and (2) models using the mean shoot length and coverage of species or morphological groups for estimates of aboveground phytomass (Sect. 10.2.2).

10.2.1 Biomass and NPP Estimates using Harvesting Methods

Estimation of biomass by the harvest method is the basic procedure of assessing production components (Newbould 1967; Lieth and Whittaker 1975). *Net primary productivity* (NPP) (Whittaker 1975; Schütt et al. 1992) can be described by the following equation (Milner and Hughes 1968; Larcher 1994) (all values in weight per unit area and time):

$$\text{NPP} = \Delta B + \text{Ld} + \text{Lc},$$

where
$\triangle B$: biomass increase
Ld: biomass losses by death (necromass) and shedding (litter fall)
Lc: biomass losses through consumption (e.g. by herbivorous animals or insects)

Increase in biomass ($\triangle B$) of trees remains positive for a long period and leads to high storage values whereas for herbaceous plant communities it is usually assumed that $\triangle B$ value for a given stand when considered at the same time every year becomes close to 0 in the long-term (Larcher 1994). Biomass accumulation and decomposition then approach a 'quasi-equilibrium' state. Consequently, the annual NPP of the herbaceous communities is primarily given by the *necromass* plus *litterfall* values (Ld). However, Ld can only partially be determined by repeated inventories due to variations in the phenology of plant functional groups and the

highly dynamic biomass turnover of herbaceous plants, in particular of their root systems (Eggert 1985).

The proportion of NPP utilised by consumers (Lc) in the investigated stands is very low (less than 1% of NPP according to estimates by Schaefer 1989, 1996) and is thus not further considered here. For *Allium ursinum* in Göttinger Wald, Eggert (1985) and Hövemeyer (1995) determined an annual loss of 1–3% dry leaf matter consumed by hoverfly larvae (*Cheilosia fasciata*). These results were obtained from set of 120 uniform harvest plots with 1 m^2 surface. For *Mercurialis perennis*, Kothe (1983) reported a loss of 5% of the leaf area due to insect damage which was measured in 40 uniform harvest plots of 1 m^2 surface in a *Mercurialis* facies.

For the assessment of the annual NPP, the "maximum–minimum method" (Newbould 1967) is commonly used where the difference between the maximum and the minimum amount of phytomass is calculated. Usually, this annual NPP value equals the annual amount of litterfall plus necromass whereas Lc is neglected and $\triangle B$ equals zero. The assumption of $\triangle B = 0$ is not valid in all cases; therefore, modified calculation methods which include long-term changes in $\triangle B$ are used (Mrotzek 1998; Brünn 1999). The annual amount of nitrogen uptake by herbaceous vegetation was deduced by using a similar model as for the assessment of the biomass and litter production where the amounts of nitrogen in the litter fall, necromass and the storage ($\triangle B$) were used.

Harvest methods provide good estimates of the standing biomass for a given plot. However, these assessments are destructive and cannot be repeated at the same location. Thus, the accuracy of estimates of biomass increase ($\triangle B$), and consequently net primary production (NPP), depends on the structural homogeneity of the plots which are selected for the repeated harvesting. For vegetation monitoring purposes, e.g. within the EU Level II program (De Vries et al. 2002; Bolte et al. 2004), destructive harvest methods are often not applicable (Bolte et al. 2002).

10.2.2 Aboveground Phytomass Estimates by Dimension Analysis

Maximum aboveground storage of the herbaceous phytomass can be estimated by models which are based on biomass assessment of 31 widespread species and 13 morphological groups of the ground vegetation in forest stands of North Germany (Bolte 1999; Bolte et al. 2002; Tables 10.1, 10.2). These models were developed from ground vegetation structure and biomass data which originated from studies of 1,602 plots in 61 stands on various sites throughout northeast Germany and were sampled during 1993–1996. The selected plots covered the abundance range (coverage: 1–100%) for all selected species in forests predominantly dominated by European beech, oak and Scots pine. Based on plant species, shoot length and plant density, plot area selected for sampling varied from 0.05 m^2 (mosses) to 1.28 m^2 (tall ferns) which allowed the survey of sufficient number of shoots per plot (Donita 1972). In each plot, percentage coverage and the maximum length of 15 randomly

Table 10.1 Assessment functions for aboveground phytomass of different plant species according to Bolte (1999, modified)

No	MG	Species[b]	Empirical parameters[a] (eq. 10.1)			Cd$_{nlin}$
			A	B	C	
1	sh	*Adoxa moschatellina*	0.2919	1.0535	–	0.94
2		*Oxalis acetosella*	0.1520	1.1090	–	0.92
3	mh	*Anemone nemorosa, A. ranunculoides*	0.1853	1.2731	–	0.92
4		*Corydalis cava*	0.2027	1.2000	–	0.81
5		*Galium odoratum*	0.0038	1.0308	1.6429	0.86
6		*Lamium galeobdolon*	0.1618	1.2832	–	0.87
7		*Maianthemum bifolium*	0.0800	1.4286	–	0.87
8		*Mercurialis perennis*	0.0258	1.3338	0.6425	0.92
9		*Ranunculus ficaria*	0.3930	1.0699	–	0.90
10		*Stellaria holostea*	0.9375	0.9602	–	0.92
11	th	*Aegopodium podagraria*	0.0050	0.9901	1.4418	0.95
12		*Impatiens parviflora*	0.0013	1.5500	0.9015	0.88
13		*Urtica dioica*	0.0130	1.1055	0.9013	0.91
14	sg	*Deschampsia flexuosa*	0.1095	0.8900	0.7698	0.89
15		*Melica uniflora*	0.0289	0.9317	1.0126	0.89
16	mg	*Agrostis capillaris, Poa nemoralis*	0.0104	1.0786	1.2639	0.91
17		*Brachypodium pinnatum, B. sylvaticum*	0.0076	1.2545	1.0600	0.88
18		*Dactylis polygama*	0.0001	0.9228	2.5215	0.96
19	tg	*Calamagrostis epigejos*	0.0001	0.9927	2.2550	0.87
20		*Milium effusum*	0.1096	1.0918	0.4147	0.91
21		*Molinia caerulea*	0.0045	1.3120	1.1230	0.92
22	f	*Dryopteris carthusiana*	0.0039	1.2887	1.1811	0.85
23		*Dryopteris filix-mas*	0.0017	1.3997	1.0831	0.93
24	tf	*Pteridium aquilinum*	0.0003	1.2634	1.5391	0.96
25	dsh	*Calluna vulgaris*	0.1620	0.9808	1.0187	0.95
26		*Vaccinium myrtillus*	0.0373	0.9656	1.4117	0.93
27		*Vaccinium vitis-idaea*	0.1363	1.1427	0.8627	0.98
28	sh	*Rubus idaeus*	0.0003	0.9658	2.2250	0.92
29	pm	*Dicranella heteromalla, Dicranum polysetum Dicranum scoparium, Hypnum cupressiforme, Pohlia nutans*	0.8161	1.1543	0.4306	0.90
30	mm	*Brachythecium spec., Pleurozium schreberi, Scleropodium purum*	0.6937	0.8291	0.6726	0.87
31	dm	*Leucobryum glaucum*	1.8028	1.2476	0.4231	0.83

MG refers to morphological groups of species (for further description, refer to Table 10.2), Cd$_{nlin}$: non-linear coefficient of determination according to Sachs (1976) and (eq. 10.1)

[a]Values are rounded from 12 to 4 decimal points

[b]Nomenclature: vascular plants: Wisskirchen and Haeupler (1998), mosses: Koperski et al. (2000)

Table 10.2 Assessment functions for above ground phytomass of morphological groups of the forest understorey vegetation according to Bolte (1999, modified)

No	Morphological groups	Mean shoot length (cm)	Empirical parameters[a]			Cd_{nlin}
			A	B	C	
1	Small herb (sh)	5–**10**–15	0.1187	0.9663	0.4311	0.86
2	Middle herb (mh)	10–**15**–40	0.0687	1.2594	0.3624	0.81
3	Tall herb (th)	20–**55**–160	0.0037	1.5158	0.8057	0.80
4	Small grass (sg)	20–**35**–60	0.0426	0.9779	0.9083	0.88
5	Middle grass (mg)	30–**50**–80	0.0047	1.0748	1.4185	0.83
6	Tall grass (tg)	30–**70**–120	0.0001	1.2050	2.0590	0.88
7	Fern (f)	30–**55**–90	0.0445	1.4812	0.2582	0.81
8	Tall fern (tf)	50–**100**–215	0.0003	1.2634	1.5391	0.96
9	Dwarf shrub (dsh)	10–**20**–40	0.1641	1.0080	0.9028	0.86
10	Shrub (sh)	25–**55**–120	0.0003	0.9658	2.2250	0.92
11	Pad moss[b] (pm)	1–**3**–10	0.8161	1.1543	0.4306	0.90
12	Mat moss[c] (mm)	5–**7**–10	0.6937	0.8291	0.6726	0.87
13	Dense moss[d] (dm)	4–**5**–8	1.8028	1.2476	0.4231	0.83

Mean shoot length refers to the range (min, max) for the 129 plots, the bold value represents the mean for all plots; Cd_{nlin}: refers to non-linear coefficient of determination according to Sachs (1976) and (eq. 10.1)

[a]Values are rounded from 12 to 4 decimals

[b]Mostly acrocarpous moss species, growing in singular pads

[c]Pleurocarpous moss species, growing in more or less extended mats (carpets)

[d]Very dense pads of *Leucobryum glaucum*

selected shoots were recorded separately for all species analysed. Dry weight of species phytomass was measured after harvesting and drying aboveground shoots for 48 h at 105°C in the laboratory. Sampling was timed between blooming and fruiting of each species and ranged from April to September. During this period, aboveground plant growth of most herbaceous plant species occurred (Höhne and Fiedler 1963; Persson 1975; Rodenkirchen 1982).

A non-linear regression analysis was performed (Proc Nlin, iteration: Gauss-Newton, SAS 6.12; SAS Inst. 1989). Allometric functions of the following formula (10.1) were used to predict aboveground biomass of ground vegetation species or plant morphological groups relative to percentage cover (PC) and mean shoot length (MS):

$$P = a \, PC^b \, MS^c, \tag{10.1}$$

P: Aboveground phytomass (dry matter, 105°C, g m^{-2})

PC: Percentage cover (species, morphological groups)

MS: Mean shoot length (above ground, cm)

$a \ldots c$: Empirical parameters obtained by fitting the measured data

Fitting criteria for the optimal regression models were maximum values of the non-linear coefficient of determination (Cd_{nlin}, Sachs 1976) and the independence of the residuals from the dependent variable (Hartung 1989). Model derivation for both species (SP) and morphological groups (MG) allowed the estimation of those species that were not sampled by attributing them to morphological groups with

regard to morphology (fern, herb, grass, moss, shrub) and shoot length (Table 10.2). Standard deviation of estimations (standard deviation of the residuals) ranged between 18.8 and 20.7% of the predicted values for species models (SP) and for morphological group models (MG). Both model types were successfully validated comparing phytomass values of predicted (x) and measured (y) values of 50 independent samples ($y = x$, SP: $R^2 = 0.85$, MG: $R^2 = 0.85$; Bolte 1999).

Based on the allometric models in Tables 10.1 and 10.2, aboveground phytomass of the ground vegetation was calculated with MS Access 2002 using the macro package PhytoCalc 1.31 (Bolte and Parth 2004).

For the beech stands at Göttinger Wald and Solling, percent coverage and mean shoot length for each species with coverage of more than 1% were recorded in 2002 during the Level II survey for which four and six square subplots (each of 100 m²) were measured. At Göttinger Wald, these subplots were not systematically distributed in the stand, but covered characteristic facies of ground vegetation (see Chap. 5, Table 5.9). At Zierenberg, percent coverage of all and upper shoot length (UL: mean length of the dominant shoots, 90th percentile) of the most abundant species, stinging nettle (*Urtica dioica*) and dog's mercury (*M. perennis*) were assessed in 2002 in 80 small square subplots (4 m²) that were systematically distributed using a grid approach within ca. 4-ha area. For the calculation of mean shoot length ML from upper shoot length values UL (see (10.2)), conversion factors were deduced for each morphological group by linear regression analyses using the model samples ($n = 1,602$; Table 10.3). For less abundant species for which shoot lengths were not recorded, mean values (displayed bold values in Table 10.2) of the corresponding morphological species group were used.

$$\mathrm{ML} = a + b\,\mathrm{UL},\qquad\qquad(10.2)$$

where
ML: Mean shoot length (cm)
UL: Upper shoot length, 90th percentile (cm)
$a\ldots c$: Empirical parameters

Estimation of the above ground herbaceous phytomass was obtained for the beech stands by calculating: (1) the arithmetic mean of all six subplot values at Solling with a homogenous herbaceous structure, (2) the frequency weighted mean phytomass of all 80 subplots stratified according to bedrock type and relative irradiance intensity at Zierenberg, and (3) the area weighted phytomass mean of the four subplots attributed to different vegetation facies at Göttinger Wald (Dierschke 2006).

In contrast to the harvest methods, this non-destructive dimension analysis enables repeated estimations of plant phytomass for the same plot. Thus, it can be used for vegetation monitoring without any restriction. However, to date, the assessment models apply only to the aboveground parts of the understorey vegetation. The accuracy of the model predictions depends on data quality of the input parameters and the model errors described (18.8% for species models and 20.7% for morphological group models).

Table 10.3 Conversion functions for upper shoot length (90-%) to mean shoot length of morphological groups of the forest understorey vegetation (Bolte and Parth 2004)

No	Morphological groups of species	Sample number (n)	Empirical parameters (10.2)		R^2
			A	B	
1	Small herb (sh)	90	1.0471	0.6767	0.85
2	Middle herb (mh)	455	0.9175	0.6930	0.90
3	Tall herb (th)	149	−0.6697	0.7647	0.95
4	Small grass (sg)	158	7.9168	0.4758	0.83
5	Middle grass (mg)	158	5.3827	0.6557	0.84
6	Tall grass (tg)	173	−3.3267	0.7747	0.89
7	Fern (f)	52	−5.0700	0.8481	0.90
8	Tall fern (tf)	48	0.7862	0.8659	0.96
9	Dwarf shrub (dsh)	138	2.1576	0.6595	0.88
10	Shrub (sh)	50	4.9191	0.5994	0.96
11	Pad moss[a] (pm)	74	−0.0658	0.8326	0.97
12	Mat moss[b] (mm)	35	0.4573	0.6966	0.88
13	Dense moss[c] (dm)	22	−0.1319	0.8625	0.96

[a]Mostly acrocarpous moss species, growing in singular pads
[b]Pleurocarpous moss species, growing in more or less extended mats (carpets)
[c]Very dense pads of *Leucobryum glaucum*

10.3 Phytomass Estimates

The maximum phytomass determines the pool for matter and nutrient storage and turnover of the herbaceous vegetation. Thus, it is an important parameter for production studies. Biomass and necromass, both phytomass components, provide the basis for net primary production estimates.

10.3.1 Total Biomass Estimated from Harvest Studies

The maximum biomass values for below- and aboveground components, which were derived from harvest studies, indicated that markedly high amount of biomass in the herbaceous layer occurred at the nutrient-rich sites of Göttinger Wald and Zierenberg (Table 10.4). At each of these sites, high values (peak biomass aboveground plus belowground; see Table 10.4) between 1,865 kg in Zierenberg and 2,100 kg in Göttinger Wald dry matter per hectare were observed during two separate studies undertaken in 1981/1982 and 1995.

At the Solling site, the total phytomass of the herbaceous and moss layer ranged from 27 to 56 kg ha^{-1} which was only 1–3% of the maximum values obtained at the Göttinger Wald and Zierenberg sites. The calculated maximum aboveground biomass values were comparable to the modelled phytomass values shown in Table 10.5. It is, however, worth noting that necromass of herbaceous plants had already occurred

Table 10.4 Maximum biomass of the herbaceous layer (kg ha^{-1}, ± SD; *estimated from SD of *A. ursinum* populations, only) for different years derived from harvest studies

	Göttinger Wald[a]				Zierenberg[b]			Solling[c]
	1982	1981	1981	1981	1995	1995	1995	1968–1972
	Allium- facies	*Mercurialis-*facies	*Anemone-*facies	**Mean**	*Urtica-*facies	*Mercurialis-*facies	**Mean**	**B 1, mean**
aboveground	1,253 ± n.a.	976 ± 426	281 ± 103	**795 ± n.a.**	1,145 ± n.a.	469 ± n.a.	**560 ± n.a.**	**13–22 ± n.a.**
Belowground	1,932 ± n.a.	2,301 ± 563	623 ± 198	**1,548 ± n.a.**	1,765 ± n.a.	1562 ± n.a.	**1,589 ± n.a.**	**18–34 ± n.a.**
Peak biomass (aboveground plus belowground)[d]	2,801 ± 608*	2,952 ± 611	837 ± 224	**2,098 ± 500**	2,541 ± n.a.	1760 ± n.a.	**1,865 ± n.a.**	**27–56 ± n.a.**

n.a. Not available

[a]Hartmann (1982), Schultz (1982), Eggert (1985), Kothe (1988), Schmidt et al. (1989). Mean biomass values are area-weighted means of biomass values using proportion of the area under following facies according to Schmidt, Chap. 5, Table 5.5: *Anemone* facies: 6.3%, *Anemone-Mercurialis* facies (mean): 33.4%, *Mercurialis* facies: 6.3%, *Allium-Mercurialis* facies (mean): 9.1%, *Anemone-Allium-Mercurialis* facies (mean): 21.3%, *Allium* facies: 5.1%, *Anemone-Allium* facies (mean): 8.7%, other facies (mixture of previous facies according to their area proportion): 9.8%

[b]Mrotzek (1998). Mean biomass are the area-weighted means of biomass values considering the plot proportion of more than 7% relative irradiance intensity (*Urtica* facies, proportion of area: 13.5%) and less than 7% relative irradiance intensity (*Mercurialis* facies, proportion of area: 86.5%). The proportions were calculated from data that displays the classification of 192 plots into irradiance intensity classes according to Perona (1995) and Mrotzek (1998) (cf. Schmidt, this volume, Chap. 5)

[c]Eber (1972, 1982), Bennert (1973, 1980), Ellenberg et al. (1986). Vegetation type *Luzulo-Fagetum typicum*, *Oxalis acetosella*-facies

[d]Maximum total biomass is less than the sum of maximum above and belowground biomass because of different sampling dates

Table 10.5 Estimates of the aboveground phytomass of the herbaceous layer (dominant species and total sum) for spring (April–May) and summer 2002 (June–July) calculated with PhytoCalc 1.31 (Bolte and Parth 2004) (kg ha^{-1}, ± SD) at the Göttinger Wald, Zierenberg, and Solling sites (tree regeneration is not included)

| | Göttinger Wald | | | | | Zierenberg | | | | Solling |
	Allium ursinum	Anemone nemorosa	Asarum europaeum	Other species	Total[a]	Urtica dioica	Mercurialis perennis	Other species	Total[b]	B 1, total[c]
Spring 2002	508 ± 280	111 ± 140	6 ± 9	28 ± 26	**653 ± 123**	118 ± 201	235 ± 221	26 ± 27	**379 ± 306**	–
Summer 2002	3 ± 2	<1 ± <1	20 ± 20	14 ± 12	**37 ± 25**	238 ± 398	238 ± 229	39 ± 104	**515 ± 474**	**52 ± 47**

[a]Göttinger Wald: Phytomass values are area-weighted means considering the proportion of area of the central floristic variant in the east–west transect (2.81 ha) in 2001 with 22.1% (*Anemone* facies: 19.6%, *Mercurialis* facies: 2.5%) and the *Allium* variant with 77.9% (*Allium* facies: 61.5%, *Anemone-Alium* facies: 15.0%, *Aconitum* facies: 1.4%) according to Schmidt (this volume, Chap. 5, Table 5.5)

[b]Zierenberg: Frequency weighted-means of 80 regularly distributed plots (4 m² area, basalt $n = 35$, Limestone $n = 18$, Mixed basalt-limestone $n = 27$) according to Schmidt (this volume, Chap. 5, Table 5.2)

[c]Solling: Arithmetic means of six plots (100 m² area)
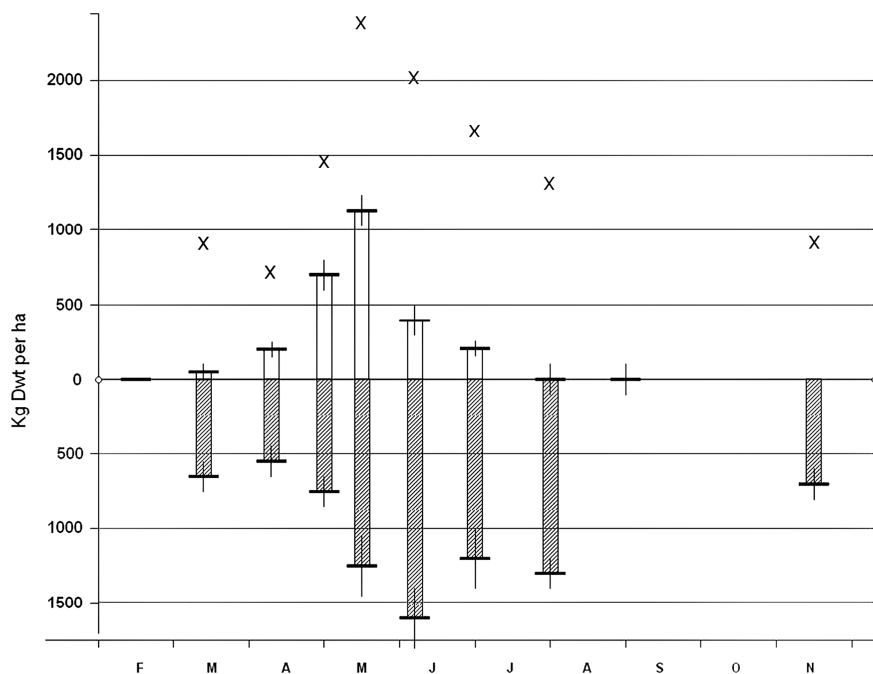
Fig. 10.1 Biomass and necromass of the herbaceous layer of *Allium* facies at Göttinger Wald in 1982 (according to Eggert 1985). *x* sum of aboveground and belowground biomass, *hatched boxes* belowground, *blank boxes* aboveground biomass

before maximum production of phytomass as shown for *A. ursinum* (Fig. 10.1, Eggert 1985).

At the Göttinger Wald site, the beech forest on limestone is characterised by a wide range of total biomass production according to the different species composition and small-scale heterogeneity of vegetation density ("patchiness", Rodenkirchen 1995). In the *Anemone nemorosa* facies with 837 kg ha^{-1}, considerably less biomass occurred compared to the *Allium* and *Mercurialis* facies. These differences reflected the morphological and growing properties of the dominant species and the low surface cover (about 50%) of the herb layer at this site.

At the Zierenberg site, *U. dioica* and *M. perennis* occurred in combinations where *Urtica* facies were characterised by a high coverage and a high biomass (2,541 kg dry weight per ha; peak biomass aboveground plus belowground). The differences in the aboveground biomass between the *U. dioica* facies and the *M. perennis* facies may be explained by the different morphology of the dominating species. *M. perennis* reaches a maximum height of 40 cm, whereas *U. dioica* can reach a height of up to 240 cm at the Zierenberg site.

In beech forests which are poor in understorey species, as at Solling, the biomass of the moss layer may be larger than that of the herbaceous layer. This was obvious in a single inventory of the quantitatively relevant moss *Polytrichum formosum* at Solling in 1970 that attained an aboveground biomass dry weigth of 18.5 kg ha^{-1}

and a similar value for the belowground biomass (Ellenberg et al. 1986). Total biomass of the herbaceous and the moss layer was about 62 kg ha^{-1}. Among the values reported in literature for beech forests throughout central Europe, the herb layer biomass in the nutrient poor beech forest at Solling (27–56 kg ha^{-1}) represented the lower end of the range. The mean values for aboveground biomass ranged from 10 to 460 kg ha^{-1}, and a maximum value of 1,700 kg ha^{-1} was reported (Hughes 1975; Leibundgut 1977; Kubiček 1980; Moldenhauer 1998; Anders et al. 2002; Weckesser 2003).

The nutrient-rich sites of Göttinger Wald and Zierenberg are close to the maximum value recorded in closed forests (Hughes 1975; Leibundgut 1977; Kubiček 1980; Moldenhauer 1998; Anders et al. 2002; Weckesser 2003). High amounts of herbaceous biomass of more than 4,000 kg ha^{-1} have been reported only for oak-dominated hardwood forests with geophytes (e.g. *A. ursinum, A. nemorosa*) in Southern Sweden (Olsson and Falkengren-Grerup 2003).

10.3.2 Aboveground Phytomass Estimated by Plant Dimension Analysis

Aboveground phytomass of the herbaceous layer on the three beech sites was calculated from percentage coverage and average shoot length using the model PhytoCalc 1.31 (Bolte and Parth 2004). Phytomass values given in Table 10.5 do not include the contribution of the tree regeneration.

Maximum total aboveground phytomass of the herbaceous layer were highest on the nutrient-rich soils at Göttinger Wald with 653 kg ha^{-1} and at Zierenberg with 515 kg ha^{-1} (Table 10.5). Low values occur at the nutrient-poor Solling beech site.

At Zierenberg, the dominant hemicryptophyte *U. dioica* accumulates the highest phytomass in summer. Its growth is stimulated by high irradiance intensity during the whole growing season. High light conditions were observed at the Zierenberg site mostly in the area of upper slope of basalt bedrock (Mrotzek 1998, Table 10.6). In contrast to *U. dioica*, phytomass of *M. perennis* is more evenly distributed within the different hillside situations and bedrock units on the site. An early increase of above ground phytomass was observed in spring (see Sect. 10.4) which was maintained until summer.

10.3.3 Comparison of Methods of Biomass Assessment

The comparison of harvest and plant dimension analysis (modelling) methods (Tables 10.4, 10.5) showed some differences. Modelled values were lower, 82% at the Göttinger Wald site and 68–92% at Zierenberg site, but of comparable size. However, at the Solling site, the modelled value of biomass was more than double

Table 10.6 Aboveground phytomass of the herbaceous layer for the dominant species and total values at Zierenberg for different hillside areas and bedrock units (means in kg ha^{-1}, ± SD) in 2002 estimates using PhytoCalc 1.31, Bolte and Parth (2004)

Zierenberg[1]	Upper side (n = 35 plots) Basalt			Middle side (n = 18 plots) Basalt/limestone			Lower side (n = 27 plots) Limestone		
	Urtica dioica	*Mercurialis Perennis*	Weighted mean for the site	*Urtica dioica*	*Mercurialis Perennis*	Weighted mean for the site	*Urtica dioica*	*Mercurialis Perennis*	Weighted mean for the site
Spring 2002	234^a ± 252	250^a ± 180	**518^a ± 288**	38^b ± 76	190^a ± 236	**257^b ± 296**	20^b ± 61	245^a ± 259	**275^b ± 266**
Summer 2002	466^a ± 459	251^a ± 182	**786^a ± 513**	86^b ± 160	204^a ± 231	**303^b ± 334**	45^b ± 129	244^a ± 283	**303^b ± 299**

n is the number of plots; species' and weighted means of the same season followed by different letters are significantly different at $P < 0.05$ (Kruskal–Wallace H test). Upper hillside site represents the main experimental area

[1]Zierenberg: Stratification of 80 plots of different hillside and bedrock sections according to Schulze and Eichhorn (2000), plot size 4 m^2

the value measured by the harvest method. Besides the methodological differences of assessing the biomass, the different values may have resulted from the temporal change of the vegetation structure and the different locations of the plots measured within the stands. At Zierenberg, the abundance of highly productive *U. dioica* (Mrotzek 1998) has decreased between 1993 (harvest studies) and 2002 (PhytoCalc study; Table 5.2). At Solling, a windthrow of one beech tree adjacent to the monitoring plots in 1990 increased the ground vegetation cover values. The high small-scale heterogeneity of ground vegetation structure may have caused major differences at the Göttinger Wald site reflected in the plots used for harvest and those used for monitoring for modelling purposes. Moreover, the more detailed description of the vegetation facies in 1981 (Dierschke and Song 1982) was used for mean biomass calculation from the harvest study made during the same year. For the following considerations, only values based on the harvest method are used.

10.4 Phenological Patterns of Annual Development of Herbaceous Biomass

The herbaceous vegetation showed a strong seasonal dynamic of increasing and decreasing phytomass that allowed the separation of time intervals between biomass and litter production of the aboveground components (Fig. 10.1; Jandl et al. 1997). Through regular measurement of above- and belowground biomass production, it was possible to recognise internal translocation processes related to species-specific patterns and strategies.

The herbaceous layer at Göttinger Wald is dominated by spring geophytes like *A. usinum* (Schmidt et al. 1989; Ellenberg 1996; Schmidt, Chap. 5, this volume) that are most competitive in the shade of forests with closed canopies (Ernst 1979, 1983; Eggert 1985; Hellmold and Schmidt 1989; Kriebitzsch 1989; Böhling 2003; Schmidt, Chap. 5, this volume). Aboveground growth of *A. ursinum* at Göttinger Wald (Fig. 10.1), started early in the year in March before leaf flushing of the beech trees and reached its maximum in mid-May (1,253 kg ha^{-1}). Under leafed canopy from mid-May, the relative irradiance intensity declined to 2–5% compared to open field conditions (Dierschke and Brünn 1993; Lambertz and Schmidt 1999). During this time, *Allium*'s biomass decreased and at the beginning of June aboveground biomass was only 1/3 (418 kg ha^{-1}) of the amount measured in May. Root growth started later than growth of the aboveground parts in mid-April, but lasted for about 14 days longer, leading to an increase in the biomass proportion belowground during the second half of the year. This specific temporal course of aboveground biomass also reflected the phenological adaptation of other geophytes like *A. nemorosa* to changes in light and soil temperature conditions under beech stands (Hellmold and Schmidt 1989; Heine-Koch 1993; Dierschke 2000). An extended period of belowground development, when compared to the shoot growth, pointed to processes of element mobilisation in the geophytes, which survive through belowground storage components (Eggert 1985; Demars and Boerner 1997).
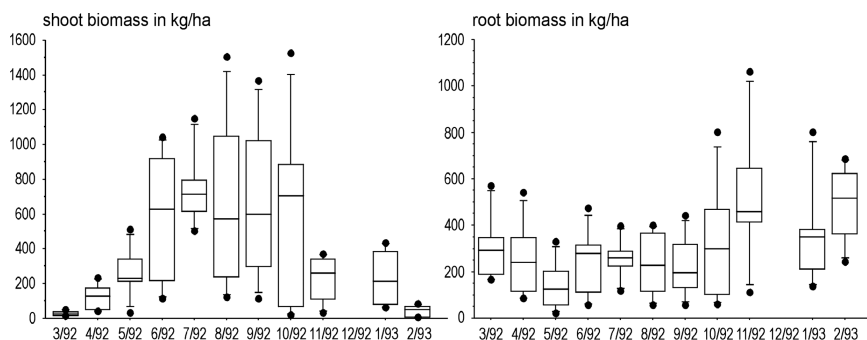
Fig. 10.2 Aboveground and belowground biomass of *U. dioica* at Zierenberg 1992/1993 (Eichhorn 1995). Box-whisker-plots with range (*points*), 10/90th percentiles (whisker plot), 25/75th percentiles (*box plot*), median (*middle line*)

At the Zierenberg site, with higher below-canopy irradiance intensity compared to Göttinger Wald site (Perona 1995; Mrotzek 1998), the dominant species were *U. dioica* and *M. perennis* of which first *M. perennis* and then *U. dioica* became the dominating fraction of the understorey. The shoot biomass of the nettle *U. dioica*, e.g., reached high values during June to October with a median value of about 650 kg ha^{-1} (Fig. 10.2). During these months, the aboveground biomass showed a large spatial variability and, for some areas with high and densely growing nettle, shoot biomass of up to 1,520 kg ha^{-1} was calculated for October (Eichhorn 1995). *U. dioica* may prolong its photosynthetic activity during summer when aboveground parts of the geophytes dominating at the Göttinger Wald site have already died (Teckelmann 1987). There is an annual course of the aboveground and belowground biomass with low amounts of shoot biomass and high values of the root biomass occurring after the growing period. In February, the highest value of 510 kg ha^{-1} (median value) of root biomass was determined at Zierenberg.

The shoot/root ratios are indications of the ecological adaptation of the species to different resources including water, light and nutrients. In the *Allium* facies of Göttinger Wald, the dominating spring and summer geophytes *A. ursinum*, *M. perennis* and *A. nemorosa* showed a shoot/root ratio < 1 over the entire year (Table 10.7). Their belowground components acted as storage for survival and therefore dominated over the aboveground plant parts most of the year with peak in May. However, the shoot/root ratios of *U. dioica* at Zierenberg ranged from 2.37 to 3.07 during periods when aboveground values peaked (Table 10.7) pointing to a strategy of aboveground competitive advantage (Mrotzek 1998).

At the Solling site, *Luzula luzuloides* and *Avenella flexuosa* were the dominant species, besides tree seedlings of *Fagus sylvatica*, and showed a distinct seasonal development with increasing biomass until summer and decreasing towards autumn (Ellenberg et al. 1986). At the Solling site, the total biomass ranged from 11 to 27 kg (1969) and 14 to 25 kg (1970) per hectare (mosses excluded). The biomass in 1969 did not peak until early July and in 1970 until the beginning of August. The

Table 10.7 Annual course of shoot/root ratio of the *Allium* facies at Göttinger Wald[a] and of *Urtica dioica* at Zierenberg[b]

Harvest month	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Allium-facies[a]	0.06	0.13	0.40	0.82	0.18	–	0.04	–	–	0.04
Urtica dioica[b]	0.10	0.09	0.54	1.84	2.48	2.74	2.52	3.07	2.37	0.57

[a]Eggert (1985)
[b]Eichhorn (1995)

reason for these annual fluctuations may be related to climatic conditions, masting and competitive effects of tree seedlings, herbivory and the influence of fungal infections on the herbaceous vegetation (Ellenberg et al. 1986; Schmidt 1988).

10.5 Annual Production of Biomass and Litterfall of the Herbaceous Layer

Mean annual biomass production (NPP) was high at Göttinger Wald with a mean value of 1,035 and at Zierenberg with 1,069 kg ha^{-1} (Table 10.8). However, the herbaceous layer at the Solling site produced per year only 1–3% of the biomass produced annually at both other beech forests. Depending on the model used (Eggert 1985; Mrotzek 1998), the annual maximum litter production at Göttinger Wald was only half of the amount at Zierenberg.

At the Göttinger Wald site, the amount of biomass produced annually by different facies showed that *Allium* facies was the most productive (1,907 kg ha^{-1}) followed by the *Mercurialis* facies (1,139 kg ha^{-1}) and the *A. nemorosa* facies (256 kg ha^{-1}). At Zierenberg, high annual NPP values of 2,117 kg dry matter per ha were determined for *U. dioica* in the *Urtica* facies. These exceeded the values for the *Allium* facies at Göttinger Wald.

The *Mercurialis* facies at Zierenberg and at Göttinger Wald showed comparable biomass production values. The *Anemone* facies, however, produced at Göttinger Wald very low biomass during the same phenological period (Hellmold and Schmidt 1989). A lower base saturation (Schmidt et al. 1989) and reduced light conditions (Dierschke and Brünn 1993) in the *Anemone* facies may result in differences in NPP values.

Net primary production was markedly lower than the maximum biomass accumulated (compare Table 10.6), especially in the belowground components (Mrotzek 1998). Belowground values underestimate the actual production, because it was not possible to accurately determine the fine root turnover (Eggert 1985; Mrotzek 1998).

The highest annual litter production was observed under *U. dioica* in the *Urtica* facies at Zierenberg with a mean value of 1,950 kg ha^{-1}, and under *M. perennis* in the *Mercurialis* facies, 853 kg ha^{-1} was observed (Table 10.8). In *Urtica* facies, the mean litter production of the dominating *U. dioica* slightly exceeded the biomass

Table 10.8 Maximum biomass (NPP) and litter production of the herbaceous layer at the Göttinger Wald, Zierenberg and Solling sites expressed as kg ha^{-1} a^{-1}. Value ranges (in parentheses)

	Göttinger Wald[a]				Zierenberg[b]			Solling[c]
	1982	1981	1981	1981	1995	1995	1995	1968–1972
	Allium- facies	Mercurialis- facies	Anemone- facies	**Weighted mean**	Urtica-facies[e]	Mercurialis- facies[f]	**Weighted mean**	**B 1, mean**
Max. biomass production (NPP)	1,907	1,139	256	**1,035**	1,915 (1,713–2,117)	938 (703–1,172)	**1,069**	**14–30**
Max. litter production (=Ld)	970 (370–1,570)	479[d]	94	**481**	1,950 (1,748–2,152)	853 (618–1,087)	**1,001**	**16**

[a]Hartmann 1982; Schultz 1982; Eggert 1985; Kothe 1988; Schmidt et al. 1989. Mean biomass values are the area-weighted means of biomass values referred to the area proportion of following facies according to Schmidt, Chap. 5, Table 5.9: *Anemone*-facies: 6.3%, *Anemone-Mercurialis* facies (mean): 33.4%, *Mercurialis* facies: 6.3%, *Allium-Mercurialis* facies (mean): 9.1%, *Anemone-Allium-Mercurialis* facies (mean): 21.3%, *Allium* facies: 5.1%, *Anemone-Allium* facies (mean): 8.7%, other facies (mixture of previous facies according to their area proportion): 9.8%

[b]Mrotzek (1998). Mean biomasses are the area-weighted means of biomass values considering the plot proportion with more than 7% open field irradiance (*Urtica* facies, area proportion: 13.5%) and less than 7% open field irradiance (*Mercurialis* facies, area proportion: 86.5%). The proportion was calculated from data in Table 5.4 (Schmidt, this volume, Chap. 5) that includes the classification of 192 plots based on irradiance intensity classes according to Perona (1995) and Mrotzek (1998)

[c]Eber (1972, 1982), Bennert (1973, 1980), Ellenberg et al. (1986). Vegetation type *Luzulo-Fagetum typicum*, *Oxalis acetosella* facies (relevé no. 2/1991)

[d]Minimum value according to Hartmann (1982)

[e]Value only for *U. dioica*

[f]Value only for *M. perennis*

production (Table 10.8). These results supported the observations carried out on permanent plots at Zierenberg over several years. The cover and growth of *U. dioica* has reduced in some parts of the site during the last few years. This was mainly caused by reduced light conditions after closing of the beech forest canopy. This process became more obvious in those parts of the research areas where nettle growth was poor and was less evident where it was vigorous. In the formation dominated by the shade tolerant plant *M. perennis*, a continuous increase was observed (Mrotzek 1998; Schulze et al. 2000).

10.6 N-storage, Dynamic and Internal N-Cycling

Herbaceous vegetation in forests may constitute a sink for nitrogen when annual net balance is considered. However, ground vegetation may also be a source for nitrogen when herbaceous phytomass decreases due to a shortage of growth resources as may occur in summer droughts (Bolte et al. 2004). Once a stable amount of understorey has been established which is in balance with the conditions of the stand, no further annual biomass increment is expected. However, the seasonal changes in herbaceous growth may influence the internal element budget. Olssen and Falkengren-Grerup (2003) found that, in spring, excessive nitrate (more than 90%) was assimilated by the understorey which was dominated by geophytes in an oak forest, when tree canopy showed little activity and nitrogen availability was high. During the growing period, the uptake of nitrate and ammonium by the ground vegetation may contribute to a decrease in the N-concentration in the soil solution (Eichhorn 1995).

The amount of N retained by the herbaceous vegetation (Table 10.9) was determined by the biomass and the high N concentrations of the dominant species *A. nemorosa*, *M. perennis*, *A. ursinum* and *U. dioica*. A comparison of the three stands showed that the highest mean N storages occurred at Zierenberg with 52 kg N ha^{-1}. Similar values of 48 kg N ha^{-1} were determined for the *Allium* facies in Göttinger Wald and 51 kg N ha^{-1} for the *Mercurialis* facies at Zierenberg. These amounts are high compared to the value of 11 kg N ha^{-1} that was recorded by Moldenhauer (1998) at a 131-year-old beech stand on a comparable nutrient-rich site at Knüll (Hessia). The nitrogen retained by the herbaceous vegetation at Solling was comparatively low with 1.2 kg N ha^{-1}. For a mature beech stand on Pleistocene sandy sediments of lower nutrition, Anders et al. (2002) reported 4.6 kg N ha^{-1} in aerial parts of the ground vegetation. In different deciduous forests, maximum values of nitrogen in the herbaceous layer ranged from 1 to 55 kg ha^{-1} (Höhne 1962; Eggert 1985; Ellenberg et al. 1986; Anders et al. 2002). Thus, the Zierenberg site and the Solling site represented the upper and the lower ends of the range.

In the *Allium* facies of Göttinger Wald (Table 10.9), the annual nitrogen returned via the litter fall and decomposition ranged between 21 and 31 kg ha^{-1}. In comparison, the nitrogen in all facies of the Zierenberg site is higher. The highest amounts of N-uptake by *U. dioica* at Zierenberg was a maximum of 77 kg ha^{-1} per year. The stinging nettle contributed 65 kg ha^{-1} per year and *M. perennis* 12 kg ha^{-1}

Table 10.9 Maximum N-storage (kg ha^{-1}), amount of N-uptake (kg ha^{-1} a^{-1}), and amount of N-flux with the litterfall (kg ha^{-1} a^{-1}) of the herbaceous vegetation at the Göttinger Wald, Zierenberg, and Solling sites

	Göttinger Wald[a]		Zierenberg[b]			Solling[c]
	1982	1982	1995	1995	1995	1968–1972
	Allium-facies	Weighted mean	*Urtica*-facies	*Mercurialis*-facies	Weighted mean	B 1, mean
N-storage	48	**42**	68	51	**52**	**1.2**
N-uptake	–	**21**	77	30	**36**	**0.4**
N-litterfall	–	**21–31**	78	30	**36**	–

[a]Hartmann (1982), Schultz (1982), Eggert (1985; 1989), Kothe (1988), Schmidt et al. (1989, unpublished data) and Sah (1990). Mean values are calculated from biomass shown in Table 10.4 or production values of Table 10.8 and nitrogen concentrations of the dominating species *A. nemorosa, M. perennis* and *A. ursinum* (living plant material and shed dead material, compare also Sah 1990)

[b]Mrotzek (1998). Mean values are the area-weighted means considering the plot proportion with more than 7% relative light intensity (*Urtica* facies, proportion of area: 13.5%) and less than 7% relative light intensity (*Mercurialis* facies, proportion of area: 86.5%) according to Perona (1995) and Mrotzek (1998)

[c]Eber (1972, 1982), Bennert (1973, 1980), Ellenberg et al. (1986). Vegetation type *Luzulo-Fagetum typicum, Oxalis acetosella* facies (Table 5.1)

per year to the total amount. The annual amount of N-uptake of 30 kg ha^{-1} was determined for the facies dominated by *M. perennis*. On average, similar amounts of 36 kg ha^{-1} per year are taken up as released with the litterfall in the annual course. This is lower than those values between 48 and 55 kg ha^{-1} per year reported by Höhne (1962) for comparable stands. With an annual N-uptake of only 0.4 kg ha^{-1} by the herbaceous vegetation, the Solling site represents a base-poor site with low turnover rates for N.

The low values of nitrogen storage and uptake at the Solling site are supported by Anders et al. (2002) who estimated 3.3 kg ha^{-1} annual nitrogen uptake by the herbaceous plants aboveground of a closed beech forest on a base-poor sandy site in northeastern Germany. This is contrasted by Höhne (1962) who reported 19 kg ha^{-1} nitrogen uptake for the ground vegetation under the canopy of a mixed beech-pine stand on a site with comparably poorer nutrition.

10.7 Annual Changes in N-Contents

The N-contents in the shoots and leaves of stinging nettles at the Zierenberg site were about 70 g kg^{-1} at the time of bud break in March (Fig. 10.3, Eichhorn 1995; Mrotzek 1998). During the growing period from April to September, the N-content decreased to 60 g kg^{-1} and showed markedly lower N-content in the shoots than in the leaves. This phenological variance of element concentration in herbaceous
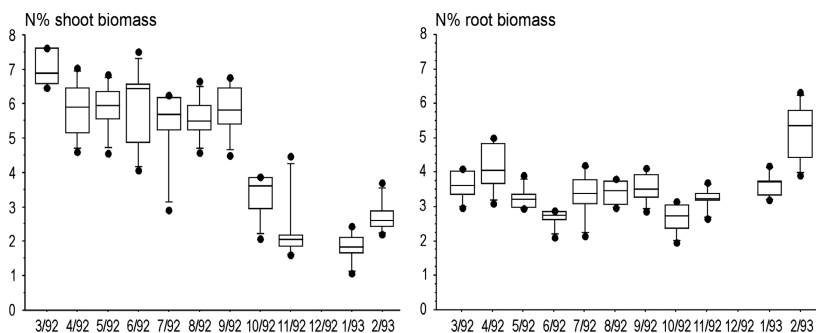
Fig. 10.3 N-contents in the above and belowground biomass of *U. diocia* expressed as % dry matter (Eichhorn 1995)
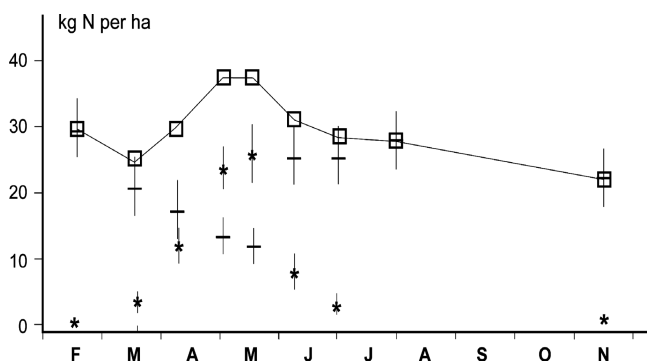
Fig. 10.4 Nitrogen storages (kg ha^{-1}) of the herbaceous layer at Göttinger Wald, *Allium* facies 1982 (Eggert 1985). *Star* N in aboveground biomass, *line* N in belowground biomass, *box* total N in biomass

plants is also described by Höhne and Fiedler (1963), Bennert (1973) and Chapin (1980). Plant tissue is diluted for N due to fast spreading of leaves at the beginning of the growing period (Eggert 1985). From October onwards, the N-content decreased below 40 g kg^{-1}. Due to a parallel accumulation of N in the throughfall below the densely growing nettles and very little increase in the N-concentration in the roots, it was assumed that the shoots of the nettles release nitrogen (Eichhorn 1995). N-content of roots varied very little from March to November (median values around 30–40 g N kg^{-1}). The highest N-content of roots occurred in February and reached 60 g N kg^{-1}. Fine roots were always richer in nitrogen than the coarse roots and rhizomes. This result leads to concepts of whole plant perspectives as proposed by Givnish (1988).

In the *Allium* facies at Göttinger Wald (Fig. 10.4; Eggert 1985), total N-content of 48 kg ha^{-1} was determined during May and June. In November, there was still found 27 kg N ha^{-1}. Re-translocation and mobilisation of nitrogen become obvious as development of the above- and belowground components takes place. From

February to May, nitrogen was transported from the belowground organs into the aboveground ones. In mid-May, after a sudden reduction of the aboveground biomass, N increased in roots and continued until August when it began to decrease again.

The extent of N translocation usually depends on the plant species and may be considered an adaptation to the nitrogen supply, especially when nitrogen is limiting growth. Species growing at nutrient poor sites often show a higher internal N re-translocation than plants at nutrient-rich sites. The amount of internal N-mobilisation depends on plant parts (Werner 1983) and can constitute up to two-thirds of the total N required by the plant (Eggert 1985). For *A. ursinum*, translocation of 25 kg N ha^{-1} was observed (Fig. 10.4) indicating high translocation ability. Eichhorn (1995) calculated for *U. dioica* an annual re-translocation of nitrogen at the end of the growing period from the aboveground to the belowground organs of 10–45 kg N ha^{-1}, and Mrotzek (1998) reported for *M. perennis* 2–5 kg N ha^{-1}. Compilation of data on element re-translocation by Aerts (1996) indicates values between 25 and 80% (mean: 41%) for most herbaceous species. A comparably low re-translocation of nitrogen is typical for species on nutrient-rich sites (Chapin 1980; Chapin et al. 1990).

10.8 C/N Ratios

The C/N ratio is used as a measure of litter quality determining decomposition (Wittich 1961); and herbaceous plants usually have low C/N ratios. They ranged between 8.1 (*M. perennis*) and 18.8 (*A. ursinum*) in the leaf components of understorey plants on these three sites (Table 10.10). Aboveground litter of almost all species had higher C/N ratios. A comparison of these values suggests that Re-translocation of nitrogen occur at the time of leaf senescence to varying extents in plants.

The C/N ratio in the leaf litter of beech is about 40 (Rademacher et al., Chap. 8, this volume). The C/N ratios of the herbaceous vegetation may be related to the humus form. Bolte (1999) showed that with an improvement of the humus form the

Table 10.10 C/N-ratios of the leaf biomass at the time of maximum aboveground biomass and the aboveground leaf litter of herbaceous species

	C/N leaf biomass	C/N leaf litterfall
Allium ursinum[a]	18.8	19
Anemone nemorosa[a]	10.1–12.8	24.3
Arum maculatum[a]	13.2	27
Mercurialis perennis[a]	8.1	6.9
Asarum europaeum[a]	10.7	15.5
Lamiastrum galeobdolon[a]	8.7	27.3
Urtica dioica[b]	11.2–14.6	–

[a]Eggert (1985): Göttinger Wald
[b]Teckelmann (1987)

C/N ratios of the Oh/Ah-horizon decreased whereas the N-contents of herbaceous plants growing on these sites increased and the C/N ratio in the aboveground plant material was reduced from 31 (raw humus) to 12 (mull). Plant litter on nutrient-rich sites provides readily decomposable substrates and thus more favourable conditions for the activity of decomposers.

10.9 Ground Vegetation as a Part of Internal N-Cycling in Beech Stands

Contribution of the herbaceous vegetation to the annual nitrogen turnover may be significant in some cases (Alriksson and Eriksson 1996; Buchmann et al. 1996). For example, herbaceous vegetation at Göttinger Wald contribute with 25% and at Solling with less than 1% to the total annual N-uptake by vegetation (Table 10.11). The herbaceous layer in forest ecosystems thus forms an intermediate nutrient store for cycling (Muller and Bormann 1976; Eichhorn 1995; Bolte 1996; Olsson 2002). This was of particular significance at the beginning of the growing period or after tree removals when the element uptake of the actively growing herbaceous vegetation may reduce nutrient losses and nitrate leaching from forests (Mellert et al. 1998; Olsson and Falkengren-Grerup 2003). However, due to the seasonal nature of the understorey growth, the release of N during mineralisation in autumn or early spring may not always synchronise with the demand for element uptake by trees (Jandl et al. 1997) and may cause significant N losses in drainage water during

Table 10.11 Component of vegetation in the nitrogen balance of beech stands at Göttinger Wald and Solling (storage and uptake by trees adopted from Chap. 8, belowground N-litter from Chap. 9 and aboveground litter from Chap. 11)

	Göttinger Wald	Solling
N-storage [kg ha^{-1}]		
Tree layer		
Aboveground[a]	941	894
Belowground	397	173
Total tree layer	1,338	1,067
Herb layer	42	1.2
N-uptake [kg ha^{-1} a^{-1}]		
Tree layer		
Aboveground[b]	81	74
Herb layer	21	0.4
N-litter [kg ha^{-1} a^{-1}]		
Tree layer		
Aboveground	63	68
Belowground	18–26	36–39
Herb layer	21–31	–

[a]Leaf biomass not considered
[b]Litter fall plus increment

winter and early spring (Eichhorn 1995). High nitrate uptake by vegetation dominated by geophytes during summer may reduce nitrate losses from the ecosystem even when their biomass is low due to a high nitrate reductase activity (NRA) per unit biomass (Olsson and Falkengren-Grerup 2003).

Differences in the quality of litter between herbaceous and woody vegetation are important for the supply of readily decomposable substrates for mineralisation (Wittich 1944; Scott 1955; Wise and Schaefer 1994). For example, at the Zierenberg site, the N-content in the herbaceous litter for decomposition was as high as N-content in the beech leaf litter. Moreover, the litter of the herbaceous vegetation has lower C/N ratios than that of beech trees indicating better litter quality (Jandl et al. 1997). Positive effects of *A. ursinum* ground cover on the soil fauna, particularly collembolans and earthworms, have been reported for a beech forest which may enhance decomposition processes (Kopeszki and Jandl 1994; Wolters 1999). Herbaceous species like *Melica uniflora* and *Epilobium angustifolium* may facilitate decomposition (Ponge and Delhaye 1995; Bauhus et al. 2004). Wise and Schaefer (1994) hypothesised that for an accelerated decomposition of beech litter the contribution of high quality herbaceous litter is required. For the biotic incorporation by earthworms, high quality herbaceous litter plays an important role by triggering decomposition processes after liming (Bauhus et al. 2004). Thus, the retention of C and N by mineral soil may be positively affected by species-rich and highly productive herbaceous vegetation.

10.10 Conclusion

Important issues and implications of the study are:

- The three beech stands have a similar age, but differ in site conditions, forest history and management. Herb layer vegetation is mainly affected by the chemical soil site conditions and irradiance intensity which may vary in time and space.
- The Solling site has a poorly developed herbaceous layer, while the Göttinger Wald site is rich in number of species with high variability at a small spatial scale. The dominant species at the Zierenberg site include *U. dioica* and *M. perennis*.
- Two methods were used to assess the maximum aboveground biomass of the herbaceous layer at the three sites. The first method involved biomass harvests conducted in different years from 1968 to 1995. With this method, the total above- and belowground biomass was 56 kg ha^{-1} at Solling, 2,100 kg ha^{-1} at Göttinger Wald and 1,865 kg ha^{-1} at Zierenberg. The amount of mean biomass production (NPP: "maximum–minimum") was 1,035 kg ha^{-1} per year at Göttinger Wald, 1,069 kg ha^{-1} per year at Zierenberg and 30 kg ha^{-1} per year at Solling. The second method made use of the PhytoCalc 1.31 model which involved percent coverage and average shoot length. The calculated maximum

aboveground phytomass of the herbaceous layer from relevés in 2002 were 653 kg ha^{-1} at Göttinger Wald and 515 kg ha^{-1} at Zierenberg, and 52 kg ha^{-1} at the nutrient-poor Solling site.

- Amount of N retained by the understorey vegetation depends on the biomass and N concentrations in the plant parts. The herbaceous vegetation at Zierenberg (*U. dioica* and *M. perennis*) stored a significant amount (mean: 52 kg ha^{-1}, *Urtica*-facies: 68 kg ha^{-1}) when compared to Göttinger Wald (mean: 42 kg ha^{-1}, *Allium* facies: 48 kg ha^{-1}) and particularly the Solling site (1.2 kg ha^{-1}). Different values were recorded also for mean annual N-uptake (Göttingen Wald: 21 kg ha^{-1} per year, Zierenberg: 36 kg ha^{-1} per year, Solling: 0.4 kg ha^{-1} per year) and mean annual N-losses with the litterfall (Göttingen Wald 21–31 kg ha^{-1} per year, Zierenberg: 36 kg ha^{-1} per year) of the understorey vegetation indicating high proportion of total turnover of N at the Zierenberg and Göttingen Wald sites.
- Intermediate store of nutrients is probably the most important function of the herbaceous layer in forest ecosystems. At times of low tree uptake at the beginning of the growing period or after tree removals, the element uptake by the ground vegetation may reduce leaching losses. However, due to the seasonality in the growth of understorey plants, the release of N during mineralisation of herbaceous litter may not always synchronise with the demand for plant uptake and may cause significant N losses in drainage water.
- High quality litter of the understorey vegetation plays an important role in the decomposition processes of overstorey components by enhancing the activity of the soil fauna (collembolans, earthworms) and triggering litter decomposition.

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