Chapter 5
Vegetation

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5.1 Introduction

Beech forests, i.e. deciduous forests dominated by *Fagus sylvatica*, form the potential and in part the current dominant climax vegetation over large parts of Central Europe (Ellenberg 1996; Bohn et al. 2003; Dierschke and Bohn 2004). *F. sylvatica* has a competitive advantage over most other Central European tree species due to its high growth performance, robust natural regeneration, broad ecological amplitude and its high degree of shade tolerance and canopy closure (Leuschner 1998). This results in different sub-communities and micro-habitats dependent on the canopy layer, and the processes that take place within them (Schaefer 1989, 2003; Leuschner 1999; Dierschke 2003; Dierschke and Bohn 2004; Schaefer and Schauermann, Chap. 7, this volume).

One of these canopy-dependent components is the ground vegetation (herb layer, under-storey vegetation), which in the strictest sense includes dwarf shrubs, herbs, grasses and terricolous mosses and lichens at various successional stages, and in the broadest sense includes also the tree regeneration itself (Schmidt 1991, 1999). The composition of the ground vegetation reacts very sensitively to edaphic and micro-climatic site factors. In beech forests, these factors include a low light regime and strong differences in the nutrient (base cations) and moisture regimes (Ellenberg 1996; Leuschner 1999; Schmidt 1999). These factors are in turn connected to the ecological function of the ground vegetation for the entire ecosystem, e.g. in its contribution to biomass production or nutrient cycling in the beech forests (Bolte et al. 2004; Schulze et al., Chap. 10, this volume).

Ecologically, three main beech forest ecosystems can be distinguished in Central Europe (Ellenberg 1996; Dierschke and Bohn 2004):

- Acidic, oligotrophic, predominantly species-poor beech forests
- Meso- to eutraphic, species-rich beech forests of mesic sites
- Meso- to eutraphic, species-rich beech forests of warm–dry sites

R. Brumme and P.K. Khanna (eds.), *Functioning and Management of European Beech Ecosystems*, Ecological Studies 208,
DOI: 10.1007/b82392_6,

The Solling Project, beginning in 1966, (Ellenberg 1971; Ellenberg et al. 1986), marked for the first time in Central Europe the comprehensive investigation of the ecology of an acidic beech forest (*Luzulo-Fagetum*). Later on, in 1980, the acidic, species-poor beech forest in the Solling was compared to a species-rich beech forest on limestone (*Hordelymo-Fagetum*). The comparative study site was established near Göttingen (Schaefer 1989; Schmidt et al. 1989). Research on the causes of the new types of forest decline in the 1980s placed the stability of forests with respect to the increased input of nitrogen and acidity in the spotlight of forest ecosystem research. In the Zierenberg case study, a species-rich, mesic beech forest was likewise selected, which, unlike the Göttinger Wald site, had experienced the strong spread of nitrogen-indicators, especially stinging nettle (*Urtica dioica*), in recent decades (Eichhorn 1995; Mrotzek 1998).

The present contribution pursues three goals:

- To provide a floristic and ecological characterisation of the vegetation of the three beech forest ecosystems of the Solling, Zierenberg, and Göttinger Wald research sites.
- To describe patterns of vegetation dynamics during the last few decades.
- To include baseline data to describe the function of ground vegetation in the biomass production and nitrogen cycling of beech forest ecosystems (Schulze et al., Chap. 10, this volume).

For nomenclature of vascular plants Wisskirchen and Haeupler (1998) was followed, and for mosses, Koperski et al. (2000).

5.2 Vegetation Structure and Phyto-sociological Classification

5.2.1 Solling

This approximately 156-year-old beech stand (2003) was established through natural regeneration. Until its designation as an international biological programme (IBP) area in 1966, the stand received regular silvicultural treatments, with particularly intense logging during the Second World War (Ellenberg 1971; Ellenberg et al. 1986). Since 1966, no regular forest management practice has been employed. Windthrow patches, including those from the 100-year-storm of November 1972, have so far played a subordinate role in the dynamics of the stand. However, since the 1990s, white rot has infected some of the beech trees. Individual infected trees, mainly from the lower canopy, were removed between 1997 and 2000 wherever they possibly threatened existing research programmes. This has resulted in small gaps in the canopy of the beech forest. The main research plot (B1) has been continuously fenced to exclude hoofed game and has been neither limed nor fertilised, with the exception of a small subplot.

The beech forest site at Solling was assigned to the wood sorrel (*Oxalis*) variant of the typical woodrush-beech forest, *Luzulo-Fagetum typicum* (Gerlach 1970), the most commonly encountered close-to-nature forest community in the Solling area (Table 5.1). The tree layer is dominated exclusively by European beech (*F. sylvatica*), which in its optimal phase forms “cathedral forests” (Ellenberg 1996). A shrub layer is lacking, due either to deficiency of light (Eber 1972) or to the influence of the high game populations, which also prevented the establishment of natural beech regeneration outside the fenced areas in the 1960s (Gerlach 1970). Indicators of acidic soils are typical of the sparse, species-poor herb and moss layers, which according to Heinken (1995) and Ellenberg (1996) distinguish the acidic *Quercetalia* communities and the *Luzulo-Fagetum* from the nutrient-rich

Table 5.1 Vegetation of beech stands in the *Oxalis* variant of the *Luzulo-Fagetum typicum* in the Solling region 1966–1968 (Gerlach 1970) and 1999–2000 (Weckesser 2003)

	1966–1968 ($n = 15$) (Gerlach 1970)		1999–2000 ($n = 25$) (Weckesser 2003)	
Tree layer, cover (%)	89.0 ± 8.3		87.2 ± 6.8	
Shrub layer, cover (%)	0.0		**0.8 ± 2.9**	
Herb layer, cover (%)	**29.8 ± 26.9**		7.2 ± 8.5	
Moss layer, cover (%)	**4.5 ± 4.0**		0.7 ± 0.5	
Number of species	11.7 ± 3.1		14.6 ± 5.8	
	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)
Species that increased				
Rubus idaeus	33	1.1	**76**	**2.0**
Dryopteris dilatata	7	+	**40**	+
Urtica dioica	–	–	**36**	+
Brachythecium rutabulum M	–	–	**32**	+
Cardamine flexuosa	–	–	**28**	**0.1**
Species that decreased				
Oxalis acetosella	**100**	**8.8**	72	2.9
Luzula luzuloides L, S	**100**	**6.7**	100	1.4
Polytrichum formosum L, S, M	**100**	**4.6**	96	0.4
Deschampsia flexuosa L, S	**87**	**3.0**	60	0.1
Carex pilulifera L, S	**87**	**1.1**	72	0.1
Calamagrostis arundiancea L				
Indifferent species				
Fagus sylvatica	80	2.0	100	2.7
Dicranella heteromalla L, S, M	60	0.4	68	0.1
Sorbus aucuparia	47	0.2	60	+
Dryopteris carthusiana	47	0.4	48	+
Agrostis capillaris L	40	1.3	56	0.1
Hypnum cupressiforme L, M	40	0.3	48	+
Mnium hornum L, S, M	33	0.2	20	+
Picea abies	20	0.1	56	+

Frequency (% of the relevés in which the species were recorded) and mean cover (%, +: $\leq 0.1\%$) of the most important species in the herb and moss layer. Significantly higher values are bolded ($p \leq 0.05$, Mann-Whitney U test). *L* Character or differential species (separating species) of the *Luzulo-Fagetum* (Heinken 1995, Härdtle et al. 1997), *S* soil acidity indicator (reaction figure $R \leq 3$ according to Ellenberg et al. 2001), *M* moss species beech forest (*Fagetalia*) communities: *Luzula luzuloides, Deschampsia flexuosa, Carex pilulifera, Dicranella heteromalla, Mnium hornum*, and *Polytrichum formosum*. Two species that are absent in the lowlands, *L. luzuloides* and *Calamagrostis arundinacea*, characterise the sub-montane and montane altitude of the *Luzulo-Fagetum typicum*. *Oxalis acetosella* and *Dryopteris carthusiana* are typical for the more mesic and somewhat more nutrient-rich sites on deeper soils in the low mountains.

5.2.2 Zierenberg

The approximately 159-year-old Zierenberg beech stand (2003) is on the north-eastern slope of a basalt knoll on the mountain Kleinen Gudenberg and has a strong gradient and pronounced heterogeneity in the soil parent material caused by the different thickness of the basalt cover over the adjacent layer of limestone. After about 1840, the former coppice with standards system was converted to a high forest system. In 1970, the stand was thinned to provide the appropriate conditions for natural regeneration (Eichhorn 1995; Mrotzek 1998; Schulze and Eichhorn 2000). Since 1972, the expansion of stinging nettle (*U. dioica*) was documented and was treated chemically in the thinned areas to further tree regeneration. In 1980, the soil was scarified, and in 1980 and 1983, the stand was further thinned, though still without the establishment of any successful natural beech regeneration. Low intensity shelterwood treatment was applied in 1996/97 and again in 1999 (Mrotzek 1998; Schulze and Eichhorn 2000). The thinned areas covered to a large extent the basalt-influenced upper slope. Although the plot has been fenced since 1989, roe deer have been sighted repeatedly within the experimental plot.

The ground vegetation of Zierenberg area has been determined on the one hand by the geological gradient from limestone- to basalt-influenced sites, and on the other by the different thinning operations done to the forest. The tree layer exhibits the highest degree of cover on the limestone-influenced lower slope, while the herb layer reaches its highest cover on the basalt-influenced upper slope (Table 5.2). The low tree cover on the upper slope resulted in greater light intensity for the herb layer (5.4% of relative light intensity) when compared to the lower slope (3.4%). Moreover, the basalt-influenced upper slope is characterised by lower pH values than the limestone-influenced lower slope (5.2 vs 5.7; see Meesenburg et al., Chap. 3 of this volume). The herb layer is dominated by either *Mercurialis perennis* or *U. dioica*. *M. perennis* cover increases from basalt (average 30% cover) to limestone (average 42% cover), whereas *U. dioica* occupies on average only a quarter of the area on limestone that it occupies on the basalt areas. This classification as well as the floristic composition as a whole (Table 5.2) reflects the ample nitrogen and moisture supply of the basalt-influenced sites on the upper slopes (Reif et al. 1985; Eichhorn 1995; Mrotzek 1998; Ellenberg et al. 2001). For *U. dioica*, however, basalt influence does not determine its herb layer cover as much as the relative light intensity on the surface organic layer as stratified sampling on the research plot

Table 5.2 Vegetation of 80 permanent plots (4 m^2 each) at the Zierenberg research site between 1993 and 2002. The stratification was based on the geological substrate (Schulze and Eichhorn 2000; *mixed* transitional zone between basalt and basalt-influenced limestone area)

	Total (*n* = 80)				Basalt (*n* = 35)				Mixed (*n* = 18)				Limestone (*n* = 27)			
Year	1993		2002		1993		2002		1993		2002		1993		2002	
Number of species 4 m^{-2}	7.2 ± 3.1		**7.9 ± 2.2**		7.9 ± 3.1		8.5 ± 2.3		6.7 ± 2.5		7.9 ± 2.3		6.6 ± 3.2		7.1 ± 1.9	
	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C
Tree layer																
Fagus sylvatica	nd	nd	98	64.1	nd	nd	100	59.1	nd	nd	94	68.1	nd	nd	96	67.8
Shrub layer																
Fraxinus excelsior N	30	2.2	**61**	**20.3**	17	1.0	**43**	**12.1**	39	3.2	**67**	**27.6**	41	3.0	**81**	**25.9**
Acer pseudoplatanus N	3	+	**31**	**1.1**	–	–	**26**	**1.2**	–	–	**39**	**1.2**	7	+	**33**	**1.0**
Herb layer																
Urtica dioica F, N	**75**	**29.6**	53	21.6	97	46.8	80	39.9	67	23.7	44	11.3	**52**	**11.4**	22	4.9
Oxalis acetosella	**43**	**0.8**	23	0.2	40	0.8	29	0.2	39	0.8	17	+	**48**	**1.0**	19	0.2
Viola reichenbachiana	**25**	**0.5**	11	+	11	0.2	9	+	22	0.4	–	–	**44**	**0.9**	22	0.1
Vicia sepium	**20**	**0.5**	5	+	17	0.6	9	+	6	0.1	–	–	**33**	**0.7**	4	+
Galium odoratum	90	2.7	95	4.2	89	2.6	94	6.8	94	2.8	100	2.5	**89**	**2.6**	93	1.9
Fagus sylvatica	45	0.2	**61**	**1.4**	40	0.2	43	0.6	50	0.3	**78**	**2.1**	48	0.2	**74**	**2.0**
Circaea lutetiana F, N	14	0.3	**43**	**1.0**	17	0.4	**46**	**1.1**	17	0.3	56	1.0	7	0.2	**30**	**0.9**
Galium aparine N	15	0.3	**33**	**0.6**	20	0.5	34	0.7	11	0.4	39	0.3	11	0.1	26	0.8
Mercurialis perennis HF	99	34.3	98	42.9	100	29.5	**97**	**47.0**	94	31.3	94	36.4	100	42.4	100	41.9
Acer pseudoplatanus N	43	0.5	48	1.1	29	0.2	29	0.6	50	0.5	56	1.0	56	0.8	**67**	**1.8**
Lamiastrum galeobdolon	35	2.8	49	1.4	54	3.2	69	2.1	44	6.5	61	1.7	–	–	**15**	**0.2**
Fraxinus excelsior N	66	4.6	68	2.2	54	2.3	46	1.6	56	5.7	83	2.4	89	6.9	85	2.7
Milium effusum	25	0.7	20	0.2	40	1.1	29	0.4	28	0.8	22	0.1	4	+	7	+
Arum maculatum HF, N	21	0.6	26	0.2	29	1.0	20	0.2	11	0.2	28	0.2	19	0.4	33	0.2
Hordelymus europaeus HF	18	0.4	14	0.2	20	0.4	17	0.3	28	0.6	17	0.1	7	0.2	7	0.1
Anemone nemorosa	11	0.3	11	+	20	0.5	14	0.1	6	0.1	17	0.2	4	+	4	+
Athyrium filix-femina F	10	0.2	4	0.1	17	0.4	9	0.3	11	0.2	–	–	–	–	–	–
Alliaria petiolata N	9	0.2	14	0.2	17	0.4	17	0.3	–	–	6	+	4	+	15	0.1
Stachys sylvatica F, N	6	0.3	11	0.2	11	0.4	17	0.4	6	0.6	11	0.2	–	–	4	+

Frequency (*F* % of the plots in which the species were recorded) and mean cover (*C* %, +: $\leq$ 0.1%) of the most important species. *HF* Character or differential species (separating species) of the *Hordelymo-Fagetum*, *F* moisture indicator of the *Circaea*-Gruppe (Dierschke 1989a), *N* indicator of places rich in available nitrogen (nitrogen figure N $\geq$ 7 according to Ellenberg et al. 2001). Significantly higher values are in bold type ($p \leq 0.05$, Mann-Whitney U test), *nd* no data showed. In a typical beech forest light regime of less than 3.5% of the ambient light intensity (Eber 1972; Ellenberg 1996), *U. dioica* achieves less than 5% cover on average. However, if the relative light intensity is more than 7% of the ambient, *U. dioica* increases its cover to more than 50%. No other under-storey species reacts with similar vigour to the increased light supply. *M. perennis* is evenly represented along the light gradient with about 40% cover. Because the light values were measured above the herb layer, the true light availability for the lower-growing *M. perennis* under the taller-growing *U. dioica* is not reflected here. Mrotzek et al. (1996) were able to show that *M. perennis* reached its maximum cover where *U. dioica* occurred with less than 20% cover without, however, becoming completely excluded under almost closed patches of *U. dioica*.

This difference in behaviour of the two dominant species, *U. dioica* and *M. perennis*, with respect to the light regime and chemical soil factors, was demonstrated by a linear regression analysis using data from all 192 subplots (Mrotzek et al. 1996, Table 5.3). The respective correlation coefficient (r^2) values for the dependency of cover and height of *U. dioica* are consistently smaller for the soil factors pH, cation exchange capacity, and calcium content (each in the upper 0–15 cm of mineral soil) than for light intensity. For *M. perennis*, no linear correlation could be found between percent cover and the relative light intensity above the herb layer. However, for height, a weak correlation was found. Similarly low r^2 values were calculated with soil factors for combined growth of both *M. perennis* and *U. dioica*. According to the studies of Mrotzek (1998), there were no differences in the nitrogen supply between areas dominated by *U. dioica* or *M. perennis*. All studied plots showed high net nitrogen mineralisation rate of ca. 140 kg N ha^{-1} per year (Table 5.5), of which over 95% of the mineralised nitrogen was available in the form of nitrate. However, a clear difference in the soil nitrate content was observed during summer and autumn for the areas dominated by *U. dioica* and *M. perennis*. In the late summer and autumn, nitrate concentrations in the mineral soil were many times higher in areas where *M. perennis* had already died back and *U. dioica* was only weakly represented than in areas where *U. dioica* had dense cover.

Table 5.3 Correlation coefficients (r^2) of a linear regression between cover and growth height of *Urtica dioica* and *Mercurialis perennis* and various site factors at the Zierenberg research site (Mrotzek et al. 1996)

Independent factor	Dependent factor	*Urtica dioica*	*Mercurialis perennis*
Relative light intensity (% of full sun light intensity)	Cover	0.54*	0.00 n.s.
	Height	0.52*	0.18*
pH value (KCl) (0–15 cm)	Cover	0.11*	0.13*
	Height	0.15*	0.05*
Cation exchange capacity (mmol ieq l^{-1}) (0–15 cm)	Cover	0.08*	0.15*
	Height	0.14*	0.06*
Ca content (mval kg^{-1}) (0–15 cm)	Cover	0.20*	0.07*
	Height	0.28*	0.13*

n.s. Not significant, *$p \leq 0.001$; $n = 196$

The dominance of *U. dioica* and *M. perennis* overshadows the base floristic composition of the beech forest at Zierenberg and renders more difficult the already complex classification of species-rich beech forests on mesic sites in Central Europe (Dierschke 1989a, 2000a). Because of the presence of *M. perennis, Hordelymus europaeus, Arum maculatum*, and *Anemone ranunculoides* together with indicator species of moist soils with persistent, constant water supply species like *Carex remota, Circaea lutetiana, Ranunculus ficaria, Stachys sylvatica* and *U. dioica*, the *Hordelymo-Fagetum circaeetosum* (Dierschke 1989a) plant community type was assigned. Similarly, to the beech forests described by Seibert (1954) and Hakes (1991) from Hessian basalt sites, the *Hordelymo-Fagetum circaeetosum* with its dominance of *U. dioica* and/or *M. perennis* is species-poorer than the familiar *Hordelymo-Fagetum* on limestone sites (Dierschke 1989a; Hermy et al. 1993).

5.2.3 Göttinger Wald

The research site in the Göttingen Forest was established on a ca. 12-ha area in 1980. Following the management conversion from coppice with standards 100 years ago, the then-customary management method of thinning from below was implemented on the 120–130-year-old (2003) mixed deciduous beech forest stand until 1960. After the increased occurrence of beech slime flux (beech bark disease) at the beginning of the 1960s, silvicultural management was halted, and the stand remained unmanaged until today. However, the forest structure did not remain unchanged. Individual trees, especially those of *F. sylvatica* and *Acer platanoides*, were occasionally blown down or fell after being weakened by white rot. The resulting gaps have rapidly closed, however (Lambertz and Schmidt 1999).

F. sylvatica dominates the closed tall forest stand. The most common associated species is *Fraxinus excelsior*; in addition, *Acer pseudoplatanus, A. platanoides, Ulmus glabra, Quercus robur*, and *Q. petraea* can be found in the tree layer (Dierschke and Song 1982; Dierschke and Brünn 1993). Yield surveys carried out in 1983 at the beginning of studies indicated a younger stand age and smaller basal area in the NW than in the SE of the research plot (Pellinen 1986; Brünn 1992; Dierschke and Brünn 1993). In 1983, relatively high numbers of stems and higher standing volumes than expected in a managed beech forest were noted, which can be attributed to the lack of silvicultural treatment. A shrub layer was scarcely present at the beginning of the studies in 1980 (cover 5.2%; Table 5.4). Of the natural regeneration of *F. excelsior, A. pseudoplatanus, A. platanoides* and *F. sylvatica* which were richly represented in the herb layer, only the *F. excelsior* achieved the height of the shrub layer in scattered areas with better light conditions. The natural regeneration strongly suffered from roe deer browsing until the fencing of the experimental plot in the winter of 1980/81 (Dierschke and Song 1982; Eggert 1985).

Detailed analysis of the area showed a strongly horizontal structure of ground vegetation. The forest can be considered a sub-oceanic, sub-montane, mesic

Table 5.4 Vegetation of 281 permanent plots (100 m^2 each, east–west transect) at the Göttinger Wald research site from 1981 (vegetation relevés: Dierschke and Song 1982; Dierschke 1989b), 1991 (vegetation releves: Brünn 1992; Dierschke and Brünn 1993) and 2001 (vegetation releves: Rudolph 2002; Dierschke 2003, 2004, 2006)

	1981		1991		2001	
Tree layer, cover (%)	78.7		81.5		**89.0**	
Shrub layer, cover (%)	5.2		12.4		**17.1**	
Herb layer, spring, cover (%)	86.3		82.6		**97.0**	
Herb layer, summer, cover (%)	47.9		45.2		**53.8**	
Total number of species	76		72		56	
Number of herb layer species 100 m^{-2}	**24.0**		**22.4**		18.5	
	F	C	F	C	F	C
Woody species (shrub and herb layer, increase)						
Fraxinus excelsior	99	3.8	97	4.2	**100**	**12.1**
Fagus sylvatica	93	1.3	89	1.2	**99**	**12.4**
Acer platanoides	96	1.0	98	1.3	**98**	**3.9**
Acer pseudoplatanus	70	0.5	71	0.5	**90**	**2.3**
Ulmus glabra	48	0.3	48	0.3	**42**	**0.7**
Crataegus laevigata L	38	0.2	37	0.2	**43**	**0.4**
Species of the herb layer						
Species that increased						
Allium ursinum	91	37.6	91	54.2	**95**	**66.0**
Hedera helix	19	0.1	25	0.6	**25**	**2.0**
Species that decreased						
Mercurialis perennis DG	**90**	**28.7**	88	17.2	49	2.2
Lamiastrum galeobdololon DC	**92**	**9.0**	96	6.7	94	3.2
Oxalis acetosella DC	**84**	**7.0**	88	3.0	69	3.8
Galium odoratum	**96**	**6.7**	92	4.2	57	0.6
Hordelymus europaeus C	**100**	**3.0**	100	3.3	94	1.4
Melica uniflora	**64**	**2.1**	71	3.5	64	0.6
Primula elatior	**78**	**1.1**	54	0.5	39	0.2
Polygonatum verticillatum	**68**	**0.7**	37	0.7	53	0.4
Vicia sepium	**46**	**0.5**	33	0.4	12	+
Carex sylvatica DC	**60**	**0.4**	38	0.2	17	0.1
Euphorbia amygdaloides	**40**	**0.4**	11	+	8	+
Viola reichenbachiana	**62**	**0.3**	59	0.3	5	+
Ranunculus auricomus L	**50**	**0.3**	32	0.4	11	0.1
Lathyrus vernus L	**40**	**0.3**	40	0.3	34	0.2
Phyteuma spicatum	**50**	**0.2**	15	0.1	1	+
Indifferent species						
Anemone nemorosa	100	11.4	100	13.0	100	11.3
Asarum europaeum L	97	6.6	98	6.6	100	9.8
Anemone ranunculoides C	100	1.2	100	4.3	100	4.6
Arum maculatum C	94	2.7	93	1.7	100	1.8
Dryopteris filix-mas	74	1.6	72	1.8	82	1.0
Dentaria bulbifera	72	1.1	79	1.8	74	0.8

Frequency (*F* % of the plots in which the species were recorded) and mean cover (*C* %, +: $\leq$ 0.1%) of the most important species. *C* Character species of the *Hordelymo-Fagetum*, *DC* differential species separating from the *Carici-Fagetum*, *DG* differential species separating from the *Galio-Fagetum*, L differential species of the *Hordelymo-Fagetum lathyretosum* (Dierschke 1989a). Higher values are in bold type (only mean values published, therefore no statistics) limestone beech forest (*Hordelymo-Fagetum lathyretosum*, Dierschke 1989a), in which species such as *Anemone ranunculoides, Arum maculatum, Asarum europaeum, Hordelymus europaeus*, and *Lamiastrum galeobdolon* are equally represented. This basic floristic structure is overlain by small-scale spatial change of dominant species, conspicuous among which are *Allium ursinum, Mercurialis perennis*, and *Aconitum vulparia* with cover values of up to 100% in spring and early summer. In addition to dominance types (facies) there are also mixed types within the research plot, with different proportions of dominant species, resulting in greatly varied horizontal structure of the ground vegetation (Dierschke and Song 1982; Dierschke 1989a, 2003; Dierschke and Brünn 1993). In 1991, five of the most important communities within the association *Hordelymo-Fagetum lathyretosum* at the Göttinger Wald site were classified by Brünn (1992) to two variants: first, a central (typical) variant (percent cover of *Allium* less than 40%, often less than 5% or absent) and second, an *Allium ursinum* variant (percent cover of *Allium* more than 50% and often 70–100%; Dierschke 1989a) (Table 5.5). In the central variant, the *Anemone nemorosa* facies has relatively low cover in the herb layer. Only *A. nemorosa* and *Galium odoratum* achieved higher cover values. In 1991, the

Table 5.5 Distribution of small-scale vegetation types (facies of dominant herb layer species) within the total area (12 ha, 1,200 plots, 100 m^2 each) and along an East–west transect in 1981, 1991, and 2001 (2.81 ha, 281 plots, 100 m^2 each) of the *Hordelymo-Fagetum lathyretosum* on the Göttinger Wald research site (vegetation relevées: Dierschke and Song 1982, Brünn 1992, Dierschke and Brünn 1993, Rudolph 2002, Dierschke 2003, 2004, 2006)

Vegetation unit	Total area (12 ha)	East–west transect (2.81 ha)		
	1981	1981	1991	2001
Central (typical) variant				
***Anemone* facies**	**6.3%**	**4.4%**	**16.0%**	**19.6%**
Melica facies	0.8%	[a]	[a]	[a]
Anemone–Mercurialis facies	33.4%	[a]	[a]	[a]
Anemone–Aconitum facies	0.3%	[a]	[a]	[a]
***Mercurialis* facies**	**6.3%**	**24.5%**	**10.6%**	**2.5%**
Mercurialis–Melica facies	1.9%	[a]	[a]	[a]
Mercurialis–Aconitum facies	0.6%	[a]	[a]	[a]
Allium variant				
***Allium–Mercurialis* facies**	**9.1%**	**44.1%**	**26.5%**	**0.0%**
Anemone–Allium–Mercurialis facies	21.3%	[a]	[a]	[a]
Allium–Mercurialis–Melica facies	3.6%	[a]	[a]	[a]
***Allium* facies**	**5.1%**	**26.3%**	**45.8%**	**61.5%**
***Anemone–Allium* facies**	**8.7%**	**0.0%**	**0.0%**	**15.0%**
Allium–Melica facies	1.2%	[a]	[a]	[a]
***Aconitum* facies**	**1.2%**	**0.7%**	**1.1%**	**1.4%**
Stachys variant				
Ranunculus ficaria facies	0.2%	[a]	[a]	[a]
Sum total	100%	100%	100%	100%

[a] Denotes absence from the transect and/or not distinguished from the neighbouring (in bold type) units. Forms previously assigned to the *Galium* facies have been assigned to the *Anemone* units in their entirety

A. nemorosa facies was concentrated in the shadiest parts, in which the relative light intensity reached an average of only 3.4% (Brünn 1992; Dierschke and Brünn 1993). The *M. perennis* facies of the central variant had denser cover in spring and summer than the *Anemone* facies. Edaphically, the *Mercurialis* facies reached its optimum on rather shallow soils (mull rendzinas), which suffered slightly from moisture deficit in dry summers. *M. perennis* showed reduced vitality where soil pH dropped below 5.2, as was often the case in the *A. nemorosa* facies colonising relatively deep terra fusca, brown loam rendzina or para brown earth, where the upper horizons were more strongly acidified (Dierschke and Song 1982; Dierschke 1989b; Schmidt et al. 1989; Brünn 1992; Dierschke and Brünn 1993).

Within the *A. ursinum* variant, the *Allium* and *Allium-Mercurialis* facies harboured the highest cover values of *A. ursinum*, a spring geophyte which prefers to colonise nutrient-rich mull soils. The *A. ursinum* facies was optimally developed in areas of moderate light conditions (4.0% relative irradiance intensity) on deep, loamy and humus-rich terra fusca-rendzinas, which are often even moister in spring than the rather shallow mull-rendzina of the *Allium-Mercurialis* facies.

Based on the prevalence of *Allium ursinum, Corydalis cava*, and of other species of the same nutrient requirements, the *Aconitum vulparia* facies was assigned to the *Allium ursinum* variant of the *Hordelymo-Fagetum lathyretosum* (Dierschke and Song 1982; Brünn 1992; Dierschke and Brünn 1993). *Aconitum vulparia* occurred with high cover on a few small spots over the entire research plot; this may be an example of random colonisation of a highly competitive but dispersal-limited species.

5.3 Vegetation Ecology of the Beech Forest Ecosystems: Impact of Site Conditions

Floristic and structural differences of Central European forest communities can be attributed to a great extent to differences in soil chemistry (Tüxen 1954; Ellenberg 1996; Leuschner 1999). Following the mean indicator values of Ellenberg et al. (2001), the main site differences between the beech forest ecosystems of the Solling, Zierenberg, and Göttinger Wald research plots may be related to their differing degrees of acidity and their nutrient status, whereas differences in water supply and light intensity are comparably low (Table 5.6).

The acidic *Luzulo-Fagetum* of the Solling site clearly distinguishes itself from the more base-rich *Hordelymo-Fagetum* of the Zierenberg and Göttinger Wald sites in both cation exchange capacity and base saturation (Meesenburg et al., Chap. 3 of this volume). Species number and cover of the herb (and shrub) layer increases with increasing pH values, while the cover of the mosses decreases. The preponderance of acid-tolerant, or calcifuge, plants on the Solling site and the predominance of calcicolous plants (Runge and Rode 1991) on the Zierenberg and Göttinger Wald sites also reflect the differences in the acidity of the soils.

Table 5.6 Vegetation structure, diversity, and ecological indicator values of Ellenberg et al. (2001) for the three beech forest ecosystems of the Solling (based on 15 relevés from Gerlach 1970), Zierenberg (based on 192 relevés from Perona 1995) and the Göttinger Wald (based on 209 relevés from Brünn 1992) research sites

	Solling *Luzulo-Fagetum typicum*	Zierenberg *Hordelymo-Fagetum circaeetosum*	Göttinger Wald *Hordelymo-Fagetum lathyretosum*
Tree layer, cover (%)	**89.0 ± 8.3**	64.4 ± 22.5	**82.8 ± 14.5**
Shrub layer, cover (%)		**2.9 ± 3.7**	**12.4 ± 21.6**
Herb layer, cover (%)	29.8 ± 26.9	69.1 ± 23.4	**85.6 ± 18.6**
Moss layer, cover (%)	**4.5 ± 4.0**	0.1 ± 0.8	
Number of species (Herb layer)	7.9 ± 2.4	15.7 ± 4.9	**21.5 ± 4.2**
Mean indicator values of Ellenberg et al. (2001)			
Temperature	3.67 ± 0.37	5.29 ± 0.12	**5.33 ± 0.09**
Continentality	**3.44 ± 0.33**	3.09 ± 0.15	**3.28 ± 0.11**
Light	**4.51 ± 0.38**	3.44 ± 0.30	3.33 ± 0.21
Moisture	5.33 ± 0.27	**5.62 ± 0.19**	5.38 ± 0.09
pH reaction	3.05 ± 0.23	6.53 ± 0.19	**6.59 ± 0.15**
Nitrogen	4.14 ± 0.35	**6.56 ± 0.28**	6.26 ± 0.19
Site factors			
Relative light intensity (%)	4.4 ± 0.7	4.5 ± 2.2	4.2 ± 1.0
Organic layer (humus type)	Hemimor/humimor	Moder/vermimull	Vermimull
Thickness of organic layer (mm)	110	30–50	5
pH (0–5 cm, KCl, CaCl$_2$)	2.9–3.4	5.4 ± 0.5	**6.2 ± 0.7**
C/N (0–5 cm)	**18.8 ± 2.1**	11.8 ± 0.9	12.6 ± 0.4
N mineralisation (kg N ha^{-1} per year)	100 ± 11	**141 ± 23**	**137 ± 40**

The site data for the Solling (*SO*), Zierenberg (*ZI*) and the Göttinger Wald (*GW*) research sites were compiled based on studies by Eber (1972, SO), Ellenberg et al. (1986, SO), Brünn (1992, *GW*), Dierschke and Brünn (1993, *GW*), Perona (1995, *ZI*), Mrotzek et al. (1996, *ZI*), Mrotzek (1998, *ZI*), Leuschner (1999, *SO*, *ZI*, *GW*), Schmidt (2002b, *SO*, *GW*), Leuschner et al. (2004, *SO*, *GW*), and Meiwes et al. (Chapter 1.4, this volume, *SO*, *ZI*, *GW*). Significantly higher means (± standard deviation) are in bold type ($p \leq 0.05$, Mann-Whitney U test, not for thickness of organic layer and pH at *SO*)

Differences in the average nitrogen indicator value of Ellenberg et al. (2001) are not striking but still quite clear with values of 4.1 (Solling), 6.6 (Zierenberg) and 6.3 (Göttinger Wald). If one compares this with the annual nitrogen mineralisation, the Solling site with its average of 100 kg N ha^{-1} per year is about 40 kg N ha^{-1} per year lower than that of Zierenberg or Göttinger Wald (Mrotzek 1998; Schmidt 2002b). The differences in nitrogen availability are comparably low, such that this alone cannot explain the differences in the floristic composition and especially not the differences in diversity and cover values in the herb layers of the three beech ecosystems. The nitrogen mineralisation rate in the montane-influenced Solling is somewhat lower due to low average temperatures (Rehder 1970; Ellenberg 1977, 1996), but it is unlikely to be significantly limited by dryness at any of the three sites. The form of nitrogen may be equally as important for the species composition and productivity of the herb layer as the amount that is received. Since the studies of Bogner (1968), it has been known that a number of plants are physiologically not competitive in the presence of pure ammonium or nitrates, and thus are absent from certain forest communities. In the Solling site, nitrogen supply occurs both as ammonium and nitrates (Runge 1974; Ibrom and Runge 1989), while at the Zierenberg and the Göttinger Wald sites, it is primarily in the form of nitrate (Mrotzek 1998; Schmidt 2002b). Liming consistently enhances nitrification and is most likely the main reason why the ground vegetation of limed areas supports not only more indicators of base-rich sites but also of indicators of nitrogen-rich soils (Schmidt 2002a).

The high cover values of the herb layer with the dominance of *U. dioica* at Zierenberg is in part an expression of the high phosphorus availability of this basalt-influenced site (Mrotzek 1998, Meesenburg et al., Chap. 3 of this volume). According to Pigott and Taylor (1964), *U. dioica* is an indicator of soils with good phosphorus supply, and the species reacted in culture experiments more strongly to P-fertilisation than it did to N-fertilisation. Mrotzek (1998) found an unusually high P-uptake at Zierenberg with up to 10 kg P ha^{-1} per year through the *U. dioica*-dominated herb layer. The herb layer may have assimilated more phosphorus than the tree layer in the aboveground biomass (5.1 kg P ha^{-1} per year, Rademacher et al., Chap. 8, this volume). In the Solling and Göttinger Wald sites, the phosphorus supply is sufficient and not limiting for the development of beech forest communities according to the previous studies by Schmidt (1970). However, it would be necessary to investigate whether atmospheric inputs (Meesenberg et al., Chap. 15, this volume) have not strongly altered soil acidity and nitrogen supply such that phosphorus supply on these sites would require re-evaluation.

Differences in the nutrient supply are also reflected in differences of the humus form and the thickness of the organic litter layer. The thickness of the humus layer is 20 times greater in the *Luzulo-Fagetum typicum* in the Solling site than in the *Hordelymo-Fagetum lathyretosum* of the Göttinger Wald site. This is concomitant with a significant decrease in species number and cover of the herb layer (Table 5.6). Various litter accumulation experiments in forests have observed the negative relation between the amount of litter and species richness and biomass production of the herb layer (Grime 1979; Facelli and Pickett 1991; Xiong and Nilsson 1997; Xiong et al. 2001).

In addition to the nutrient supply and soil chemical conditions, fine root development is decisive for species richness and cover values of the herb layer in closed beech forests. In the *Luzulo-Fagetum* of the Solling site, 165 mg fine root mass per 100 ml soil volume was found in the upper soil horizons (O_f/O_h or A_h), while in the *Hordelymo-Fagetum* of the Zierenberg and the Göttinger Wald sites, only 110–140 mg 100 ml^{-1} was found. Together with three other beech sites, Leuschner

(1999) established a correlation between species number of the herb layer and a combination of the factors including soil pH value and density of fine roots (and thickness of topsoil). Herb layer cover showed a stronger relationship with exchangeable magnesium or base saturation, and with root density. However, no relationship with pH value was found. A high density of fine roots in the topsoil and upper mineral soil of poor, acidic beech forest sites can effectively exclude many species of the herb layer, because intense competition for nutrients and water hinders the establishment and growth of plants. However, when mean value of fine roots is expressed on an area basis there is hardly any difference between the Göttinger Wald and the Solling (320–350 g m^{-2} fine root biomass) sites, even if one includes the biologically very active deeper mineral soil horizons of the Göttinger Wald site (Leuschner et al. 2004). Area-based differences with higher values in the *Luzulo-Fagetum* were found only in the density of fine root tips and fine root necromass. Leuschner et al. (2004) therefore hypothesise that high root tip densities in acidic infertile soils compensate for low nutrient supply rates, and large necromasses are a consequence of adverse soil chemical conditions.

5.4 Vegetation Dynamics

5.4.1 Solling

In a comparison of 15 vegetation relevés (sample stands) of the *Oxalis* variant of the *Luzulo-Fagetum typicum* from Solling from 1966–1968 (Gerlach 1970) with 25 relevés from 1999–2000 (Weckesser 2003), the average cover values of the tree and shrub layers have scarcely changed (Table 5.1, Weckesser and Schmidt 2004) during that period. The cover values of the herb and moss layers, by contrast, have decreased significantly. However, the total number of herb and moss species per relevé has increased, mainly species such as *Rubus idaeus, Dryopteris dilatata, U. dioica*, and *Cardamine flexuosa* in the herb layer and *Brachythecium rutabulum* in the moss layer. These are not typical forest species of base- and nutrient-poor sites (Ellenberg et al. 2001; Schmidt et al. 2003) but rather species that react equally positively to increased nitrogen input, liming, and soil disturbance (Bobbink et al. 1998; Fischer 1999; Schmidt 1999, 2002a; Diekmann and Falkengren-Grerup 2002; Weckesser and Schmidt 2004). This contrasts with the decrease of the indicators of acidic and nutrient-poor sites (Ellenberg et al. 2001) such as *Luzula luzuloides, Deschampsia flexuosa, Carex pilulifera, Polytrichum formosum*, and *Oxalis acetosella*. Therefore, the disappearance of the typical species combination of the *Luzulo-Fagetum typicum* could be expected in future at the Solling site (Weckesser and Schmidt 2004), in agreement with the results of Wilmanns and Bogenrieder (1986) from the Kaiserstuhl region and of Röder et al. (1996) from the Spessart. This species-poor subunit of the *Luzulo-Fagetum*, which once covered large areas of the forest landscape of Central Europe (Ellenberg et al. 1986, Ellenberg 1996, Bohn et al. 2003), is increasing being displaced by more nutrient-demanding vegetation types, in which indicators of nitrogen, liming, and disturbance predominate (Fischer 1999, Schmidt 1999, 2002a, Weckesser and Schmidt 2004).

5.4.2 Zierenberg

Vegetation was monitored in the years of 1989 (Hubeny 1991) and 1995 (Perona 1995) on 40 subplots (2 × 2.5 m) along a transect from the basalt-influenced upper slope to the limestone-influenced lower slope. During this period, the percent cover of *U. dioica* has generally decreased, while that of *M. perennis* slightly increased. For both species, a close relationship to the relative light intensity on the sites was detected, which had markedly decreased by more than 2.5% during this period on over 40% of the subplots. This may be attributed to the increased canopy closure following the thinnings done in 1983 and 1985. The percent cover of *U. dioica* decreased especially in areas of low relative light intensity.

The change towards low light conditions continued in the following years, as shown by a comparison of 80 permanent plots that have been re-sampled since 1993 at intervals of 1–2 years (Table 5.2) in the context of the Europe-wide Level II biomonitoring programme (Schulze and Eichhorn 2000). From 1993 until 2002, the percent cover of *U. dioica* has significantly declined and at the same time the cover of *M. perennis* has increased (albeit not significantly). The decrease in frequency of occurrence of under-storey as documented by Schulze and Eichhorn (2000) until 1999 has thus continued. Whereas *U. dioica* was found on three-quarters of all permanent plots in 1993, it was observed on only around one-half of all plots in 2002. The low intensity shelterwood treatments that took place especially in edge areas in 1996/97 and 1999 (Mrotzek 1998; Schulze and Eichhorn 2000) did not improve the light situation for *U. dioica* in the central part of the research plot. Besides the increase in *M. perennis*, the increase of *Fraxinus excelsior* and *A. pseudoplatanus* in the shrub layer, and *F. sylvatica, Circaea lutetiana*, and *Galium aparine* in the herb layer was striking. Tree regeneration (*F. excelsior, A. pseudoplatanus, F. sylvatica*) has certainly benefitted directly from reduced game browsing and indirectly from the reduced competitiveness of *U. dioica*. The increase in the above-mentioned herbs, and the decrease of *Oxalis acetosella, Viola reichenbachiana* and *Vicia sepium*, are difficult to correlate with any changed habitat factor or competitive relationships.

5.4.3 Göttinger Wald

From 1981 to 2001, permanent plot studies along the east–west transect showed extraordinarily strong temporal dynamics of the limestone beech forest (Dierschke and Song 1982; Dierschke 1989b, 2003, 2006; Brünn 1992; Dierschke and Brünn 1993; Rudolph 2002, Table 5.4). The lack of silvicultural treatment was responsible for the increase in cover of the tree layer, and sufficient protection from game browsing was responsible for the strong development of the shrub layer. The shade-tolerant *F. sylvatica*, which at the beginning of the studies was less represented in the regeneration than *Fraxinus excelsior*, has now the highest cover in the understorey. Valuable broadleaved tree species such as *F. excelsior, A. pseudoplatanus*, and *A. platanoides* are only competitive against the beech on base-rich sites when they are thinned using group selection (Schmidt 1997, 2002b; Lambertz and Schmidt 1999; Wagner 1999) or when the stands are affected by large-scale wind-throw events (Schmidt 2002c, 2005; Kompa and Schmidt 2006).

Strong changes were observed in the herb layer (Table 5.4). The most prevalent trend was the loss in the number of species: since 1981, the total number of species decreased from 76 vascular plant species to 56 and the average number of species per relevé (100 m^2) decreased from 24.0 to 18.5. This result agrees with the observations of floristic and phyto-sociological studies in forest nature reserves of Lower Saxony and Hessia, in which the diversity of vascular plants was lower than in comparable, semi-natural managed forests. Greater amounts of light and soil disturbance are primarily responsible for this, allowing species that grow mainly in open areas to occur in woodlands (Schmidt 1999, 2003, 2005; Schmidt and Schmidt 2007).

Among the facies-forming species that decreased strongly were *M. perennis* and *Galium odoratum*. *Allium ursinum*, whereas *Anemone nemorosa* and *Aconitum vulparia* were among the dominant species whose frequency and cover had remained constant over the last 20 years. Changes in the facies-forming species resulted in a corresponding shift in the dominant vegetation of the research units (Table 5.5). For instance, while the *Mercurialis* facies of the central variant occupied almost a quarter of the east–west transect in 1981, it had nearly completely disappeared by 2001. In a reverse trend, the area occupied by the *Allium* facies in 1981 more than doubled to the current 60%. A more detailed analysis of the individual subplots, however, showed that *A. ursinum* in fact scarcely expanded its range, i.e. it colonised only few new plots. More commonly, the many small gaps present between existing patches of *A. ursinum* became covered with facies-forming species during the past two decades. This happened especially in the plots formerly mapped as the *Allium-Mercurialis* facies, but also in some areas earlier mapped as *Mercurialis* facies that contained small individual patches of *A. ursinum* in 1981. The majority of the *Mercurialis* facies has now been replaced by the *Anemone* facies, which increased its area from around 5% to almost 20%. A new map unit, the *Allium-Anemone* facies, was distinguished in 2001, which along with the *Allium* facies observed in this research study includes large parts of the former *Allium-Mercurialis* facies. The *Aconitum* facies remained largely constant over the study period.

There are various explanations for the observed changes. A tendency towards both a general spread and increased density of *A. ursinum* has been reported for more than a decade, for instance in southern German forests (Buck-Feucht 1989; Bücking 1989; Böhling 2003) and in Hainich National Park (Ahrns and Hofmann 1998). Strong decline of *A. ursinum* in the light gradient of group-selected shelterwoods (Schmidt 1997) and following the resumption of a coppice with standards system (Stegmann and Schmidt 2005), Winterhoff (1977) suggested that open, drier conditions were unfavourable for the hygromorphically constructed *A. ursinum* than closed, more densely shaded mature beech forest. The increase of layers of woody plants with a densely closed canopy and the absence of silvicultural intervention have benefitted *A. ursinum*, which with its large leaves can take advantage of the irradiation with high productivity photosynthesis before the leafing of the over-storey. This is less the case for species with leaves that remain green through the deep shade of the summer and persist on the surface organic layer, such as *M. perennis, Galium odoratum, Lamiastrum galeobdolon, Hordelymus europaeus* and *Melica uniflora* (Hellmold and Schmidt 1989; Kriebitzsch 1989). A growing season that starts early and lasts longer, which has been observed in the Göttinger Wald site (Dierschke 2000b) and in Central Europe for two decades (Chmielewski and Rötzer 2001), has had positive effects on *A. ursinum*; but it has not been experimentally proven nor the spread of *A. ursinum* through increased nitrogen inputs (Ahrns and Hofmann 1998). Ongoing fertilisation experiments at Göttinger Wald site since 1996 have so far not revealed any nitrogen effects, which may be due to the site being relatively rich in nitrogen (Schmidt 1999, 2002b, Table 5.6).

The decline of *M. perennis* can be in part attributed to reduced light conditions on the surface organic layer. The more densely closed tree layer and the rise in natural regeneration results in decreased available irradiation, especially in the M*ercurialis* facies, which was still widespread in 1981. Available light under a closed canopy and under the natural regeneration has decreased to less than 2% of full sun light intensity (Lambertz and Schmidt 1999). Under canopy gaps where the relative irradiance intensity was above 5%, however, dense patches of *M. perennis* were found (Dierschke and Brünn 1993). In addition to its decline due to light reduction, *M. perennis* reacted sensitively with strong losses of vitality in subsequent years to extreme summer dryness and fungal infection with *Synchytrichum mercurialis* and *Melampsora rostrupii* (Schmidt 1988, 1997; Dierschke and Brünn 1993; Dierschke 2003, 2006).

Browsing is another factor in the dynamics of under-storey species. According to Klötzli (1965) and Schmidt (1978), *A. ursinum* and *M. perennis* are not the preferred food species of the roe deer. *Anemone nemorosa* and *Hedera helix*, by contrast, are preferred food species and thus benefit immediately from the fencing of forested areas (Schmidt 1978; Morgenroth 1992; Gerber and Schmidt 1996; Gill 2006). *Hedera helix* in particular is favoured as a browse species especially during winters with high snowfall, as the evergreen liana can be reached at any time by the deer on the tree trunks. Corresponding effects were observed in late winter 2003 at the Göttinger Wald site, when two roe deer were accidentally trapped inside the enclosure for several weeks and within a short period of time browsed back all ivy within reach on the trunks of the beeches. Whereas severe winters limit the spread into the herb layer and ascent into the canopy of *Hedera helix*, a sub-Atlantic–sub-Mediterranean species, mild winters probably facilitate its spread (Oberdorfer 2001, Dierschke 2005a, b). Similar observations of the invasion of deciduous forests by evergreen plants (laurophyllisation) have been made in southern Switzerland

(Klötzli et al. 1996; Walther 1997, 1999; Walther and Grundmann 2001, Grund et al. 2005).

5.5 Conclusion

Tree and herb layer vegetation of the beech forest research sites, Solling, Zierenberg, and Göttinger Wald, resulted primarily from differences in soil fertility. The water supply and the light regime on the surface organic layer was found to be of minor importance. The nutrient-poor acid soil at the Solling site had species-poor, sparse ground vegetation (*Luzulo-Fagetum*) while the base-rich soils at the Zierenberg and Göttinger Wald sites supported species-rich, dense herb layers (*Hordelymo-Fagetum*). Although soil characteristics support similar herb layers on the Göttinger Wald and Zierenberg beech forests, the vegetation of the Zierenberg site is strongly influenced by anthropogenic disturbances (opening of the canopy, scarification of the soil, higher atmospheric nitrogen deposition).

Under-storey vegetation of all the three beech forests changed significantly during the past decades:

- Species richness and the proportion of non-forest plant species (indicators of disturbances, e.g. *U. dioica, Cardamine flexuosa*) depended on the intensity of forest management and declined significantly after forest harvesting had stopped.
- Atmospheric N deposition supported the increase of some herb layer species (e.g. *A. ursinum, U. dioica*); whereas acid-tolerant species of the nutrient-poor beech forests (e.g. *Oxalis acetosella, Luzula luzuloides*) have declined significantly.
- The protection or reduction from hoofed-game browsing was responsible for an overall increase of woody regeneration and of some few herb layer species (e.g. *Hedera helix*) which were particularly preferred food species of deer.
- The increase of evergreen broad-leaved (laurophyllous) species such as *Hedera helix* and spring geophytes such as *A. ursium* has profited from the trend of mild winters and the earlier start of the vegetation period, which can be attributed to global warming (global climate change).

These vegetational changes have been documented due to long-term permanent plot studies on the three beech forest research sites. For causal explanations of vegetation pattern and process, experiments with under-storey vegetation or important herb layer species in the field or under controlled condition in greenhouse or climatic chambers are urgently needed.

Acknowledgments In addition to the cited data sources, unpublished field data of Bernadett Lambertz, Ina–Maria Schulze, and Marcus Schmidt were evaluated for this publication. Andreas Parth supported data analysis and preparation of the figures. The manuscript benefited from comments by Andreas Bolte, Hartmut Dierschke, Partap K. Khanna, and Marcus Schmidt. Gina Gemma Lopez and Toby Spribille improved the English version. All this assistance is gratefully acknowledged.

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