Herr, segne die Gewerken / und gib Gedeihen hier, /
laß deine Kraft mich stärken / zur Arbeit für und für.

Harzer Gesangbuch, Clausthal, 1698

Influence of forest age dynamics on ground vegetation and epiphytic diversity in montane spruce forests

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General introduction

1.1 Plant diversity in temperate forests

In the naturally forest-dominated biome of Central Europe (BOHN et al. 2003), forest areas have been influenced by human activities since the Neolithic (PICHLER et al. 2011). This led to large-scale deforestation and replacement of forests by grassland, fields and settlements (BOGUCKI 1988). While forests have covered the greatest part of the land area in primeval times (ELLENBERG & LEUSCHNER 2010), the present forest cover in Central Europe barely reaches 50 % of the total land area (EUROSTAT 2010). Simultaneously to the deforestation, the remaining forest stands faced considerable structural and ecological changes due to extensive management including logging (coppicing, pollarding) as well as pasture, litter removal, drainage, and propagation of economically significant tree species (POTT & HÜPPE 1991, GRAAE & HESKJÆR 1997, ELLENBERG & LEUSCHNER 2010). Thus, human actions have become the major determinant of plant diversity in European forests (ELLENBERG & LEUSCHNER 2010, SCHMIEDINGER et al. 2012). Some species bound to habitats provided by traditional management have become more abundant than in primeval forest ecosystems (POTT & HÜPPE 1991, KRATOCHWIL & ASSMANN 1996, HANSSON 2000). While traditional forest management partly increased the structural and species diversity of forests, intensified modern forestry since the late 18th century led to a decline in forest species diversity. In particular, the introduction of large-area clearcuts and establishment of planted monocultures led to changes in tree species, understorey and epiphytic vegetation as well as animal und funghi communities (GUSTAFSSON & HALLINGBÄCK 1988, ABS et al. 1999, JUNNINEN & KOMONEN 2011, ZMIHORSKI 2011). Altogether, traditional and recent management led to considerable turnover in forest organisms and forest structure, resulting in strong differences to natural, particularly primeval forest ecosystems (GRAAE & HESKJÆR 1997, STÖCKER 1997, ABS et al. 1999).

Numerous studies have described the importance of old trees and deadwood for species diversity in forests (JONSSON et al. 2005). Old trees and large, lying trunks offer a wide range of different microhabitats for epiphytes (ÓDOR & VAN HEES 2004, HAUCK 2011, LARRIEU & CABANETTES 2012). Consequently, epiphytic lichens and bryophytes strongly rely on high amounts of large-sized lying and standing deadwood as well as old, high-diameter trees (MONING et al. 2009, ÓDOR & STANDOVÁR 2001, HAUCK 2011). Even the establishment of bryophytes on the forest ground is supported by lying deadwood (FENTON et al. 2007). Overmature trees and deadwood are widely lacking in managed forests. Hence, numerous old trees and high volumes of lying or standing deadwood characterize

late successional stages of natural forests (KORPEL' 1995, STÖCKER 1997, STURTEVANT et al. 1997). The higher species richness of unmanaged, near-natural forests is particularly pronounced in cryptogams (AUDE & POULSEN 2000, PAILETT et al. 2009). Additionally, the diversity of lichens and bryophytes strongly relies on a forest continuity of several centuries (ROSE 1976, EDWARDS 1986). This is mainly due to the dispersal limitations of many cryptogam species, hindering the colonization of newly-established forests (HILMO & SÅSTAD 2001). However, most ancient forests have been strongly influenced by management, thus lacking old trees beyond rotation age and deadwood (RACKHAM 2003, LÕHMUS & LÕHMUS 2008). Effects of the presence of deadwood and overmature trees versus forest continuity on cryptogamic diversity have rarely been separated (NORDÉN & APPELQUVIST 2001, MARMOR et al. 2011). The importance of stand continuity has also been substantiated for vascular plants (PETERKEN & GAME 1984, VERHEYEN et al. 2003). Unlike cryptogams, richness of vascular plant species is slightly higher in managed forests (PAILLET et al. 2009). Though, in unmanaged forests, some herbs preferably colonize sites with deadwood accumulation (FALINSKI 1978). Lying deadwood also provides safe sites for tree seedlings with low competition and is, therefore, essential for the natural tree and forest regeneration (BAČE et al. 2012).

1.2 Natural forest dynamics and late successional stages

Most temperate natural forests underlie cyclic age dynamics with subsequent development stages (KORPEL' 1995, STÖCKER 1997). Different from boreal forests, large-scale, stand-replacing disturbances are comparably rare in Central Europe (FISCHER et al. 2012). Consequently, the different forest development stages occur in small-scale mosaics comprised of unevenly-aged patches differing in the tree vitality. The ageing and dieback of small tree groups or single trees leads to the formation of canopy gaps in advanced development stages (HOLEKSA & CYBULSKI 2001). Light availability, microclimate and soil conditions below canopy gaps can strongly deviate from neighbouring closed-canopy forest (HOLEKSA 2003, NADKARNI & SUMERA 2004). Therefore, the variations in size and age of gaps in natural forests can influence the diversity and abundance of forest ground species (KIRCHNER et al. 2011) as well as epiphytes on trees (COOTE et al. 2007). In contrast to comparisons between managed and unmanaged forests, the importance of overmature and decaying tree stands for plant diversity within natural forest dynamics has rarely been addressed yet (VON OHEIMB et al. 2004, STÖCKER 1997, UOTILA & KOUKI

2005). The significance of advanced and late successional stages in forests has been shown for epiphytes (KUUSINEN & SIITONEN 1998, HAUCK 2011). Few studies suggest a comparably low significance of overmature and decaying forest patches for ground vegetation diversity (ZUKRIGL 1982, VON OHEIMB et al. 2004, JONÁŠOVÁ & PRACH 2008).

In many forest ecosystems, the response of epiphytes as well as ground vegetation to senescent and decaying tree stands is difficult to estimate, as the forest areas have not been solely affected by forest management. Other site factors include the input of different elements by agriculture and industry, e.g. pollution by atmospheric nitrogen or sulphurous deposition (ELLENBERG & LEUSCHNER 2010, HAUCK et al. 2012, HRUŠKA et al. 2012). As both direct and indirect human influences, such as forestry and air pollution, affect forest vegetation (HEDL 2004), the investigation of unmanaged forests, particularly overmature and naturally declining stands, is necessary for the separation of these effects (HAUCK 2000). The impacts of pollution-induced substrate acidification, heavy-metal influx and related forest dieback on both ground vegetation and epiphytes have been intensively studied (BUSSOTTI & FERETTI 1998, HAUCK 2000). Possible reverse effects under low $S0_2$ or nitrogen deposition have rarely been explored yet (STRENGBOHM et al. 2001, SUJETOVIENE & STAKENAS 2007). This especially applies to cryptogamic epiphytes, which are strongly affected by atmospheric pollutants, leading to markedly different diversity and distribution patterns across different levels of pollution (HAUCK 2005). Studies under high levels of air pollution have revealed the higher diversity of lichens and bryophytes on damaged and dead trees compared to live trees (HAUCK et al. 2002). This has been relativized by studies under lower pollution levels (HAUCK 2005). Further studies have to clarify the actual importance of late successional stages, and the differences in the epiphyte diversity of live, overmature and decaying trees in natural, lowly-polluted forests.

Recent research activities in natural, old-growth forests do not only include the diversity patterns of forest organisms, but also other ecosystem services (HÜTTL et al. 2000, WIRTH 2009). With regard to global change, the role of natural forests as carbon sinks is widely discussed (VINSON et al. 1996). Though the productivity, and with it, the carbon uptake declines in late forest development stages old tree stands can still be important carbon sinks (ZHOU et al. 2006, DOLMAN et al. 2010). Carbon is not only accumulated in the biomass, but also in the soil (ZHOU et al. 2006, GLEIXNER et al. 2009) Therefore, much more than managed forests, old-growth forests could serve as a carbon sink (KNOHL et al. 2009). Consequently, a better knowledge on carbon stocks in over-mature and decaying

forest development stages, together with biodiversity assessments would certainly underline their exceptional importance.

In Central Europe, studies on natural forest vegetation and natural forest ecosystem services are strongly hampered. Protected forests, which have been excluded from management, make up less than 0.4 % of the total forest area (PARVIAINEN 2005). Old-growth forests are rare and long-term management continuously affects the structure, site factors and plant diversity even in forests, where the management has ceased (GRAAE & HESKJÆR 1997, LAMEDICA et al. 2010). Many relevant studies have been performed in managed or otherwise anthropogenically disturbed forests. Most studies in natural forests have focussed on single plant groups and their responses to forest structure-related habitat traits (THOMSEN et al. 2005, MONING et al. 2009, KIRCHNER et al. 2011) rather than differences in the plant diversity of different forest development stages. Gaps in the knowledge of diversity patterns and other functions of senescent and decaying forest stands are particularly critical for the numerous conflicts between nature conservation and forest economics (EID et al. 2002, YOUNG et al. 2005, BOUGET et al. 2012). Both the exclusion of single large trees from management as well as the retention of larger old-growth patches from logging implies economic burdens for forest stakeholders (BERGSENG et al. 2012). To support the protection of forest species diversity and ecosystem services against the demands of commercial forestry, it is necessary to elucidate the ecological importance of the late forest development stages.

While earlier successional stages of natural forests are roughly included in the age classes of managed forests, common rotations do not admit over-mature and decay stages (STÖCKER 1997, KUULUVAINEN 2009). Therefore, the present study focussed on the dynamics of an unmanaged, old-growth forest ecosystem with special emphasis on the late successional stages. The investigations included both ground and epiphyte vegetation. Additionally, the forest structure in the different development stages was analysed, including aspects of forest history and biogeochemical features of natural stand structures providing epiphyte habitats. The main objectives of this thesis were to

(1) Outline the importance of late successional stages for the diversity and species richness of the forest vegetation,
(2) assess the diversity patterns of deadwood-inhabiting vegetation and the significance of deadwood to the plant diversity in natural forests,

(3) examine the effect of stand history and tree age on the plant diversity.

Additional studies were to address

(4) the ecological response of epiphytic lichens to site conditions in natural forests and
(5) the possible function of senescent and decaying tree stands as carbon sinks.

1.3 Study design and chapter outline

To investigate the plant diversity patterns and plant ecology in natural forests, the present study was conducted in the years 2009-2012 in one of the few old-growth forest stands in Northern Germany with at least 400 years of forest continuity unaffected by management. The study area is located on Mt. Brocken between 950 and 990 m a.s.l. (GK: 51°47' N, 10°38' E), influenced by a regional climate with an annual precipitation of 1600 mm and mean annual temperature of 2.9 °C (GLÄSSER 1994). The studied forest is situated in a strict reservation ("Brockenurwald", 300 ha) within Harz National Park, and was protected as a hunting ground since the early middle ages (SCHADE 1926). The area is widely dominated by spruce forests (*Picea abies* [L.] Karst.) growing on acidic, fresh and waterlogged soils, interspersed with open swamps (DAMM 1994, KARSTE et al. 2006). As the site was banned for logging, the natural forest age dynamics remained widely untouched for centuries. This offered the rare opportunity for comprehensive studies on the plant diversity across the development stages of a forest type common in Central European mountainous regions (ELLENBERG & LEUSCHNER 2010). The forest development stages defined by the intensive studies of STÖCKER (1997) in the same area formed the basis for the present study.

For all studies, data were obtained by plot-based sampling, particularly by vegetation relevés in even-shaped, 100 m² plots, including ground vegetation and epiphytes on the lower tree trunks (between 0-2.0 m height) and lying deadwood (objects >2.0 cm diameter). Chapters 2, 3 and 4 present the approaches and results of the main projects, which focussed on the diversity and composition of the natural forest vegetation. Results of additional studies on biogeochemical issues, published in co-authored papers published in co-authored papers with contributions of the author, are outlined in the chapters 5, 6 & 7, while Chapter 8 gives a synopsis and general discussion of the main results.

In Chapter 2, the response of the forest vegetation to structural changes within the forest ageing cycle was analysed. By plot-based vegetation records in five structurally defined forest development stages, the diversity and community composition of ground and epiphyte vegetation was investigated. In relevés of the ground vegetation (shrublayer, herblayer, cryptogam layer) and of epiphytic communities on single lying trunks and lower tree trunks, the cover of lichens, bryophytes and vascular plants was estimated. Additionally, structural features and soil properties of the forest development stages were assessed in the plots. From upper soil, the C/N ratio and pH values were obtained. Of the structural characteristics for the different stages, stem density, deadwood amount and canopy cover were measured. Diversity indices as well as frequency and abundance of lichen, bryophyte and vascular plant species were calculated as average of the mean values obtained from ground vegetation and epiphyte relevés. Vegetation data were subjected to multivariate analyses and tested for significance. By comparing the plant diversity, community composition and the frequency and abundance of plant species, differences between the forest development stages were examined. Thereby, the hypotheses were to be tested that (i) the composition and diversity of the ground vegetation and epiphytes is affected by stand age-related shifts in forest structure and soil conditions, (ii) that cryptogamic epiphytes respond more sensitively to changes associated with the forest development stages than the ground vegetation, and (iii) that later (advanced) forest development stages support a larger number of characteristic vascular plants, bryophytes and lichens than earlier stages, underlining their exceptional importance.

In Chapter 3, special emphasis was laid on deadwood-inhabiting epiphytes, particularly on lying trunks. The vegetation data obtained in the plots in the old-growth forest (Chapter 2) were used. Additionally, the approach included substrate traits of the lying trunks (trunk diameter and decay class). Besides, the community composition of the epiphytes was tested for significant differences between differently sized and differently decayed deadwood objects. Furthermore, the abundance of single epiphyte species on live and dead trees, differently-decayed trees and ground vegetation was compared to identify deadwood-specialized species of lichens, bryophytes and vascular plants and the response of single species to wood decay. To assess the significance of deadwood-inhabiting vegetation to the total plant diversity of the forest, the β-diversity of epiphytes on trees, lying trunks and the ground vegetation were compared. In addition, the cryptogamic and vascular plant diversity on deadwood was compared with the plant diversity on the trunks

of live trees and the forest floor. The different analyses were to prove the hypotheses that deadwood is a key factor to the total plant diversity of natural forest ecoystems and that the diversity of deadwood-inhabiting lichens, bryophytes and vascular plants increases with increasing diameter and proceeding decay of the deadwood pieces.

For the studies in Chapter 4, the study site originally confined to the old-growth forest was expanded on an adjacent secondary forest (> 215 yrs) on a drained bog site. In both forests, plots were established in live (overmature) and standing dead tree groups. Within the plots, relevés of the ground vegetation and epiphytes on trees were made. Additionally, structural characteristics and soil variables were assessed. In soil properties, the C/N ratio, pH value, and content of several elements in the upper soil were included. Vegetation data were analyzed by multivariate statistics, and the distribution of epiphyte and ground species in the old-growth and secondary forest was tested for significance. The comparison of live and dead tree groups in the old-growth and the secondary forests aimed on testing the hypothesis that both ground vegetation and epiphyte vegetation are more diverse in the old-growth (primary) forest than in the secondary forest despite similar tree age, thus evidence on age-dependent effects of habitat continuity on plant diversity.

The chapters 5 & 6 include studies on the ecology of selected epiphyte lichen species. While both the abundance as well the biochemistry of lichens have been strongly affected by air pollution since the early industrialisation, present analyses performed under low-level pollution, were compared with previous studies at higher levels of pollution. Studies on the formerly frequent, pollution-tolerant lichen *Lecanora conizaeoides* Nyl. ex Crombie included analyses of the bark chemistry of the sampling trees in the plots, while studies on the lichen *Hypogymnia physodes* (L.) Nyl. focussed on the uptake of heavy metals and the biochemistry of related lichen substances under the currently low pollution of the study site. On *L. conizaeoides*, studies focussed on proving the hypothesis that (i) only a slight decrease in substrate acidity may cause the decline of this lichen species. Within the analysis of *H. physodes* samples, it was hypothesized that (ii) the concentration of lichen substances varies with the metal concentrations of the substratum and (iii) lichen substance concentrations vary less between lichen thalli from the same tree than from different trees (with different metal concentrations in the bark). More specifically, it was also tested that (iiii) the concentration of physodalic acid in *H. physodes* thalli increases with the concentration of Cu^{2+} and Mn^{2+} in the substratum.

After studies on plant diversity patterns and plant ecology, chapter 7 deals with studies on the possible function of old-growth forests as carbon sinks. By assessing the wood-bound carbon in the different forest development stages, as well as the carbon stock in the soil, the potential of the differently-aged forest stands to bind carbon was evaluated. Thereby, the hypotheses were to be proven that (i) stages dominated by overmature and decaying trees are characterized by a higher above-ground biomass and (ii) higher soil carbon stocks.

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Chapter

2

Response of ground vegetation and epiphyte diversity to natural age dynamics in a Central European mountain spruce forest

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Abstract

Question: Natural forest age dynamics is often more or less cyclic with profound temporal changes in stem density and tree size, tree age structure, deadwood frequency and the abundance of canopy gaps. We investigated the response of ground and epiphyte vegetation to the natural forest age dynamics of an old-growth spruce forest focussing on (1) the influence of stand age related shifts in forest structure and related changes in soil conditions on the diversity and composition of plant communities, (2) differences in the species turnover of cryptogamic epiphytes and ground vegetation in relation to forest age development, (3) the importance of later (advanced) forest development stages for characteristic epiphyte communities.

Location: High-montane old-growth spruce forest (*Picea abies* (L.) Karst.) on Mt. Brocken, Harz Mountains, Germany.

Methods: Five defined forest development stages (regeneration to decay) were investigated with five 100 m² plots for each stage, in which we studied forest structure, ground vegetation, and the epiphytes of living trees and dead trunks.

Results: The ground vegetation did not significantly change across the forest development stages. Epiphyte diversity on dead standing trees markedly increased towards later stages, exhibiting the highest diversity in the overmature and decay stages. Diversity of epiphytes on lying trunks was highest in early development stages. Trees in decay as well as regeneration stage included a set of characteristic epiphytes, being rare or absent in the other stages.

Conclusions: Deadwood, i.e. trees and lying trunks and its epiphytes outlast the oldest individuals of the tree layer and are still present in the early stages of the following forest generation. Epiphyte diversity on lying deadwood was higher in young than late forest development stages. Habitat continuity presents a fundamental difference to managed forests; it promotes species with dispersal limitations, which are common among cryptogamic epiphytes.

Keywords: forest age dynamics, lichens, bryophytes, deadwood, ground vegetation, nature conservation.

2.1 Introduction

Unmanaged forest communities have a cyclic, long-term dynamic which is triggered by tree ageing and disturbance. This results in small-scale mosaics of unevenly aged patches (KORPEL' 1995; STÖCKER 1997; OHEIMB et al. 2004). The duration of individual development stages varies between forest ecosystems according to the life-span of the dominant tree species and the disturbance regime. Development stages are characterized by differences in tree age, tree vitality, and associated differences in forest structure (STÖCKER 2001, 2002). Typical features changing within the course of natural forest succession are tree size, stem density, tree regeneration, deadwood abundance and quality, as well as gap size and abundance (SIPPOLA et al. 1998; HOLEKSA & CYBULSKI 2001; MCCARTHY & WEETMAN 2006).

Tree size, which is often not closely related to tree age, strongly influences epiphyte diversity, as big trees offer more diverse microsites differing in the exposure to precipitation and insolation as well as the local availability of nutrients (KUUSINEN & SIITONEN 1998; HAUCK 2011). Stem density affects light, temperature and moisture conditions for both epiphytes and ground vegetation (FENTON & FREGO 2004; MA et al. 2010). Forest stands with canopy gaps differ in microclimate, atmospheric nutrient deposition and rates of litter decomposition from closed-canopy forests (HOLEKSA 2003; NADKARNI & SUMERA 2004). Canopy gaps also play an important role for tree regeneration (BAIER et al. 2007). The availability of deadwood is a key factor for the diversity of lichens, bryophytes, fungi and invertebrates in forest ecosystems (JONSSON et al. 2005). Coarse standing and lying deadwood offers a much wider range of microhabitats than fine wood debris (ÓDOR & VAN HEES 2004; BUNNELL & HOUDE 2010). With progressive decay, deadwood becomes inhabitable for an increasing number of organisms. Finally, strongly decomposed deadwood can even be colonized by vascular plants, and promotes tree regeneration by supplying safe sites for tree seedlings because competition intensity with other vascular plants is typically low (SÖDERSTRÖM 1988; ZIELONKA & PIĄTEK 2004).

In Central Europe, effects of natural forest dynamics on biodiversity can rarely be studied, as most forests are managed and lack old trees beyond rotation age. The prevailing cutting regimes generate age-class forests with a comparatively homogenous structure. Deadwood is generally scarce in managed forests (KRUYS et al. 1999; ÓDOR & STANDOVÁR 2001). In

the present study, we made use of one of the rare opportunities in Central Europe, where the natural forest dynamics was not disturbed for several centuries and a small-scale pattern of different development stages coexists and is mixed with occasional canopy gaps. The forest examined in this study is a natural high-altitude forest of Norway spruce (*Picea abies* (L.) H. Karst.) on Mt. Brocken, Harz Mountains, Germany, which has not been influenced by forest management since the introduction of modern forestry practice 300 years ago and has been protected as a hunting sanctuary for many centuries prior to that. The main objective of this study was to study the influence of natural age-related dynamics of spruce on the composition of the ground vegetation and the tree- and deadwood-inhabiting epiphytes. The study focussed on vascular plants, bryophytes and lichens. As supplementary information for our diversity analysis, we also studied forest structure and the abundance of deadwood in the different development stages. Based on the findings on ground vegetation and epiphytes in other forests ecosystems studied (OHEIMB et al. 2004, UOTILA & KOUKI 2005, MONING et al. 2009), we expected a response of both epiphyte and ground vegetation to forest age dynamics. Ground vegetation may respond to changes in soil variables and light availability, whereas epiphytes additionally benefit from deadwood and old trees in later forest development stages. Therefore, the specific aims of the study were to test the hypotheses that (1) the composition and diversity of the ground vegetation and epiphytes is affected by stand age-related shifts in forest structure and soil conditions, (2) cryptogamic epiphytes respond more sensitively to changes associated with the forest development stages than the ground vegetation, and (3) later (advanced) forest development stages support a larger number of characteristic vascular plants, bryophytes and lichens than earlier stages, underlining their exceptional importance.

2.2 Material and Methods

Study area

The study site (Fig. 2.1) is located in a strictly protected area ("Brockenurwald", 300 ha) within the Harz National Park on Mt. Brocken, Saxony-Anhalt, Germany. Our investigations were carried out between 950 and 990 m a.s.l. The regional climate is characterised by a high annual precipitation of 1600 mm (including 1.9 m of snow) and mean annual temperature of + 2.9 °C (GLÄSSER 1994). The bed rock of the study area is iron-rich granite. Dominant soil types include cambisols and stagnogleys, depending on the

groundwater level. The predominant humus form on the strongly acidic soil is mould. As the area was reserved as a hunting ground for the nobility and clergy since the early middle ages (ca. 800 AD, JACOBS 1870; SCHADE 1926), the forest was banned for logging and forest pasture, and was never exploited for local charcoal production (KORTZFLEISCH 2008). The low human influence is also reflected in the stem diameter distribution of the sampled trees (Fig. 2), which is similar to that reported for other old-growth forests (WESTPHAL et al. 2006). The natural disturbance regime includes the creation of canopy gaps by tree ageing and decay, largely enhanced by bark-beetle damage (GMELIN 1787; WEGENER et al. 2003) and windbreak. Since the studied spruce stand has not been harvested for timber for at least three to four centuries, the stand follows natural age dynamics; these processes have been studied extensively by STÖCKER (1997, 2001, 2002). STÖCKER (1997) assigned the development stages to five classes that cover the complete succession cycle of the forest community. STÖCKER's definitions of the five development stages are compiled in Table 2.1. These stages occur in a small-scale mosaic of patches of several hundred m² size in the studied forest. A similar distribution pattern exists for gaps, which are formed at the end of the forest dynamics cycle and persist to the early stages of a new cycle (KATHKE & BRUELHEIDE 2010 a, b).

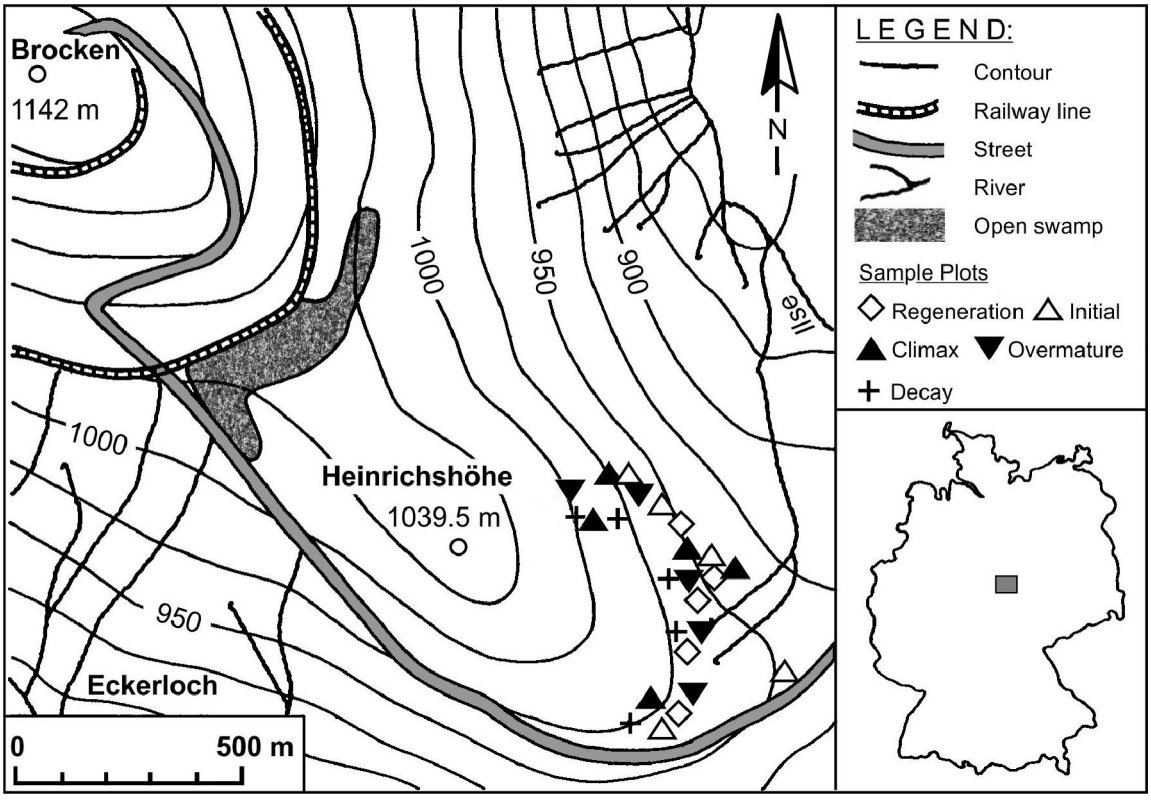

Fig. 2.1 Location of the study site and the sample plots.

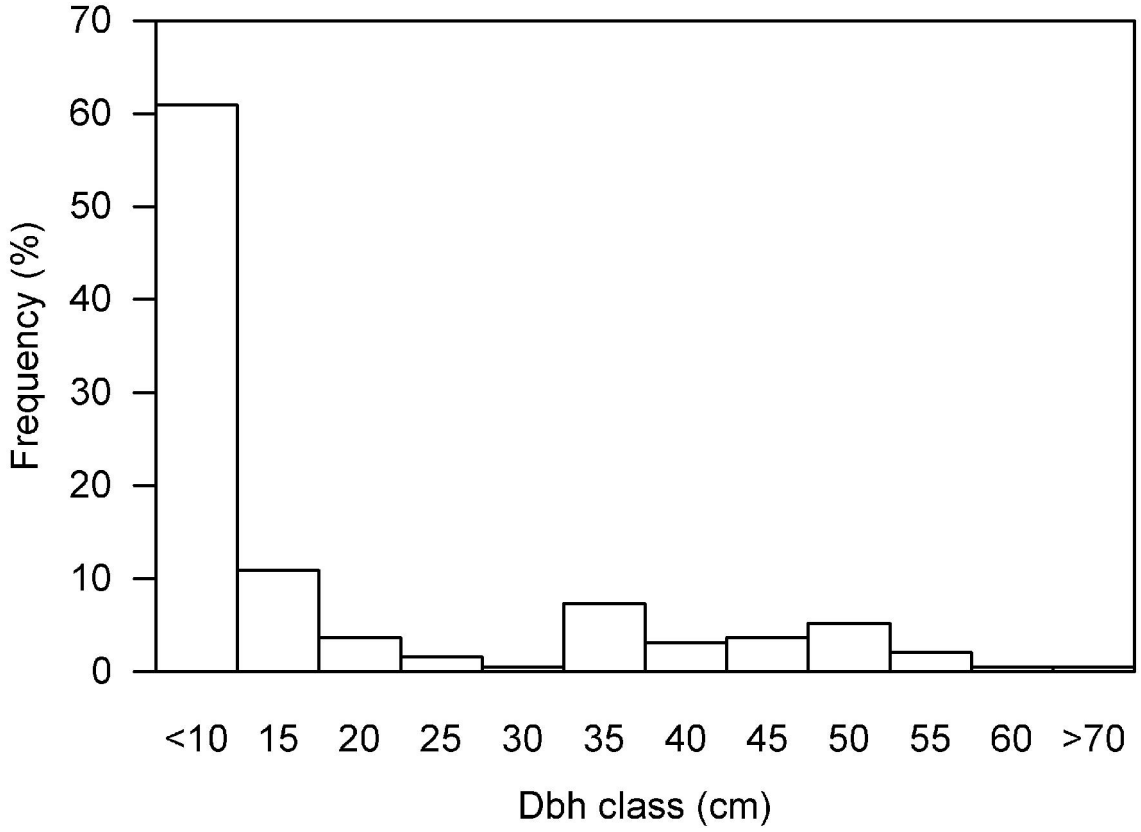

Fig. 2.2 Frequency distribution of living trees in the sample plots (*N*=192) in different diameter classes (diameter at breast height or basal diameter of saplings). Values on the x-axis specify the lower limit of a diameter class.

Forest age dynamics and sample plot selection

The dominant forest association in the study area is the reedgrass-spruce forest (*Calamagrostio villosae-Piceetum*) which is characteristic of acidic mineral soils. This forest is replaced by spruce mires (*Bazzanio-Piceetum*) on water-logged soils and birch-spruce forest (*Betulo carpaticae-Piceetum*) at places with many granite boulders. The forest development stages defined by STÖCKER (1997, Table 2.1) formed the basis for plot selection. Five sample plots of 10 m x 10 m were selected per forest development stage. Because the study design required a minimum of five replicate plots for each of the five forest development stages, i.e. 25 plots in total, in a limited area (300 ha) of unmanaged forest, a random selection procedure was not possible. For reasons of comparability, all plots were selected only in the *Calamagrostio villosae-Piceetum*. The main plot selection criteria were a stand structure that met the criteria of one of the five stand development classes and a more or less even spatial distribution of the plot classes across the area of the

studied natural forest to avoid local clumping of the replicate plots which could introduce 'hidden treatments'.

Table 2.1: Structural attributes characteristic for five forest development stages in the old-growth forest on Mt. Brocken (based on Stöcker 1997, modified)

	A	B	C	D	E
Stages	Regeneration	Initial	Climax	Overmature	Decay
Number of tree individuals	low-high, increasing	very high, decreasing	high, stagnating	high, decreasing	medium-low, decreasing
Canopy cover	low, steadily increasing	medium-high, closure of gaps	high, closure of gaps	decreasing, gaps remain	medium-low, decreasing
Tree mortality	low	medium	low	medium-high	high
Deadwood	remainder from decay phase	small-sized wood debris	increasing	increasing in canopy layer	dead trees dominate
Height structure	very few mature trees	heterogeneous structure	low variance in tree height	low variance in tree height	Disintegration of canopy layer
Tree size, age structure	saplings dominate	medium-sized trees, low variance	large-medium-sized trees, low variance	large trees, low variance	large (dead) trees, saplings
Tree vitality	very high	high	stagnating-decreasing	low	low, dieback
Tree regeneration	abundant	medium-low, partly suppressed	very low, suppressed	low, partly suppressed	starting in groups

Vegetation analysis

The ground vegetation was analyzed by estimating the cover of all species of vascular plants, bryophytes and lichens in the 100 m² plots. For woody plants, data were recorded separately for the tree (> 2.0 m height), shrub (<2.0 m) and herb layers (< 0.5 m). Ground-inhabiting bryophytes and lichens were noted as a separate cryptogam layer. The relevé size of 100 m² coincides with the recommended plot size for vegetation analyses in temperate and boreal forest (DIERSCHKE 1994). The cover of the taxa was estimated in percent of total plot area using 5 %-classes for species covering ≥ 10 % of the plot and 1%-classes for the remaining species. Species with a cover < 1 %, were put to 0.5 % (if more than one individual was present) or 0.1 % cover (one individual). Epiphytic bryophytes and lichens as well as vascular plants growing on deadwood were assessed for their relative cover on all living and standing dead stems with a minimum height of 2.0 m as well as on lying trunks. On the studied trees, the cover of all taxa present was recorded from the entire

stem or trunk surface area below 2.0 m height above soil surface covering all aspects (HAUCK et al. 2002). Data from lying trunks refer to the entire upper surface area and the flanks. Cover was estimated in the same manner as with ground vegetation. Strongly decayed lying trunks were included in the survey. All relevés were recorded between June and August 2009. The nomenclature of plant species follows WISSKIRCHEN & HAEUPLER (1998, vascular plants), KOPERSKI et al. (2000, bryophytes) and WIRTH et al. (2011, lichens). Nomenclature of forest associations is based on SCHUBERT et al. (2001).

Analysis of stand properties

Selected structural characteristics of the sample plots are compiled in Table 2.2. In the sample plots, the diameter at breast height (dbh) was measured for all trees with a diameter tape at 1.3 m. Height of all trees with a dbh > 7 cm was recorded with a Vertex IV sonic clinometer and a T3 transponder (Haglöf, Långsele, Sweden). Length and diameter of lying trunks were also measured with a measuring tape. In the centre of every plot, a hemisperical photograph of the canopy was taken with a fisheye lens (Coolpix 8400, Fisheye converter UR-E16; Nikon, Tokio, Japan). To avoid interference with the ground vegetation, the camera was positioned at 1.0 m above the ground. The hemispherical photos were taken on overcast days with evenly clouded sky. By greyscale-reduction photo pixels were assigned to gaps or areas covered by the canopy. Canopy closure (i.e. photographed area covered by canopy) is given in percent of the total area.

Data analysis

Statistical analyses were calculated with R 2.14.0 software (R Development Core Team, Vienna, Austria). All data were tested for normal distribution with the Shapiro-Wilk test. The cover percentages of the individual plant species were not transformed before data analysis. . The significance of differences between the five development stages was tested with the Kruskal-Wallis test, as the data were not normally distributed. Furthermore, Dunn's test was used for subsequent pairwise comparisons in the cases were the result of the Kruskal-Wallis test indicated a significant difference, though the discriminatory power of this test is limited. The dominance structure of the communities was analyzed by calculating N_1-diversity which is defined as a modified Shannon function $N_1 = e^{H'}$ (KREBS

1999). In this equation, H' is the Shannon function ($H' = -\sum p_i \cdot \ln p_i$; p_i = cover of species i divided by the total cover of all species per sample). N_1 specifies the number of equally abundant species producing the same diversity value as the calculated Shannon-Wiener function H'. Large differences between N_1 and the total number of species (α-diversity) in a relevé indicate the dominance of few species (i.e. reduction of plant diversity according to Shannon). Detrended Correspondence Analysis (DCA, HILL & GAUCH 1980) was applied to examine differences between the five forest development stages in terms of ground vegetation and epiphyte cover and composition using the program PC-Ord 5.14 (MjM Software, Glenneden Beach, Oregon, U.S.A.). The length of the gradients along the ordination axes are given in standard deviations and represent the average standard deviation of species turnover. The significance of differences in the community composition was tested with an analysis of similarities (ANOSIM; CLARKE et al. 1993) using the software package PAST 2.15 (Ø. Hammer, Natural History Museum, University of Oslo, Norway).

2.3 Results

Ground vegetation

The herb layer in all five development stages was dominated by *Deschampsia flexuosa*, *Calamagrostis villosa*, *Galium saxatile* and *Vaccinium myrtillus* (Table 2.3). Mean cover values did not differ significantly between the stages for most species of the ground vegetation. A significant response was only found for *Picea abies* saplings in the shrub layer in the Kruskal-Wallis test, though no significant difference between the individual stages was found in Dunn's posthoc test. The cover of *Picea* saplings was highest in the regeneration stage (A), strongly decreased toward the initial stage (B) and was lowest in the decay stage (E). *Galium saxatile* and *Dryopteris dilatata* showed highest mean cover regeneration stage (A). The cryptogam layer was well developed, covering more than 40 % of the ground in most plots. The total number of bryophyte species in the ground vegetation was higher than that of vascular plant species (Table 2.3). The cryptogam layer was dominated by *Plagiothecium undulatum*, which was accompanied by *Sphagnum girgensohnii*, *Dicranum scoparium, Polytrichum formosum* and *Rhytidiadelphus loreus* as other frequent species. Significant differences between single stages were found for the bryophytes *Sphagnum girgensohnii* (maximum mean cover in the initial stage) and

Polytrichum formosum (maximum mean cover in the decay stage). Most other species in the herb- and moss-layer occurred with mean cover values <1%.

Table 2.2: Soil and stand characteristics of the sample plots in the five forest development stages (A, regeneration; B, initial; C, climax; D, overmature; E, decay stage, mean±standard error of five replicates, min-max ranges in brackets).

	A	B	C	D	E	P[5]
C/N ratio[1]	23.2±0.6	23.1±1.0	27.6±4.0	24.5±1.6	23.3±0.9	
pH (KCl)[1]	3.2±0.1	3.2±0.2	3.1±0.1	2.9±0.1	3.2±0.1	
Canopy closure (%)	82±3a	91±2a	90±1a	85±1a	74±2a	**
Living trees[2] (ha^{-1})	640±260a	1500±427a	480±44a	420±34a	0±0a	**
Dbh of living trees (cm)	3.8±0.4a (2-8)	9.7±0.5a (2-49)	43.2±3.0a (22-68)	46.8±2.0a (20-64)	0±0a (0)	***
Height of living trees (m)	2.6±0.2a (2-4)	5.4±0.2a (2-17)	22.5±1.2a (17-27)	21.4±1.2a (9-28)	0±0a (0)	*
Saplings[3] (ha^{-1})	8360±1208a	1580±168ab	840±327b	2560±1024ab	1660±598ab	*
Dead trees[2] (ha^{-1})	260±151	220±153	180±100	140±46	360±36	
Dbh of dead trees (cm)	32.8±7.4a (4-57)	21.2±11.7ab (2-50)	12.6±3.2b (5-20)	21.6±5.9ab (9-56)	50.0±4.8ab (6-71)	*
Height of dead trees (m)	6.8±2.1a (2-22)	2.5±0.2ab (2-6)	3.6±1.2b (2-15)	6.5±1.2ab (3-18)	13.5±2.8ab (2-26)	*
Lying trunks (ha^{-1})	720±52	720±223	960±154	760±187	920±131	
Diameter of lying trunks (cm)	23.9±2.7a (13-30)	23.4±2.0ab (15-28)	12.1±1.4b (8-16)	16.3±3.1ab (7-27)	16.0±3.7ab (2-24)	*
Total deadwood ($m^3\ ha^{-1}$)	351±101a	156±39a	50±8a	242±89a	1280±319a	**
Lying trunks ($m^3\ ha^{-1}$)	146±31	101±30	37±5	72±13	136±57	
Dead trees[2] ($m^3\ ha^{-1}$)	183±105ab	48±24ab	11±8a	169±78ab	1134±305b	*
Stumps[4] ($m^3\ ha^{-1}$)	22±9	7.4±4.9	2±2	2.3±1.1	9.4±4.5	

[1] Soil depth 0-10 cm
[2] Spruce trees > 2.0 m
[3] Spruce trees < 2.0 m
[4] < 2.0 m
[5] Statistics: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$ (Kruskal-Wallis test). Additional testing with Dunn's posthoc test for multiple comparisons; within a row, equal letters behind mean values indicate that means do not differ significantly between the single stages.

Both the herb and the cryptogam layers were strongly dominated by a few species which is reflected by a large deviation of total species numbers (α-diversity) and N_1-diversity (Fig. 3). N_1-diversity did not differ significantly between the five different forest development stages for either the herb or the cryptogam layer in the Kruskal-Wallis test (Fig. 3). Community composition of the ground vegetation did not differ between the development stages either, as was shown by the results of the ANOSIM (P>0.05) and the DCA plot of the ground vegetation relevés, which yielded one cluster without any subdivisions that were caused by the forest development stages (Appendix S1).

Table 2.3: Cover (in %) of species (mean±standard error) occurring in the ground vegetation in the five forest development stages (A, regeneration; B, initial; C, climax; D, overmature; E, decay stage).

	A	B	C	D	E	P^2
Total cover	77±4	72±6	72±5	63±14	81±2	
Shrub layer:						
Picea abies	20±5a	4.1±2.5a	0.5±0.2a	0.4±0.2a	0.3±0.2a	*
Herb layer[1]:						
Deschampsia flexuosa	36±6	23±5	39±6	46±11	28±11	
Calamagrostis villosa	23±9	21±6	25±6	20±6	41±8	
Galium saxatile	21±12	7.5±3.7	2.2±1.8	5.4±2.7	12±3	
Vaccinium myrtillus	12±8	21±10	9.3±4.9	17±5	9.0±5.8	
Luzula sylvatica	1.0±0.9	0.5±0.4	3.0±2.7	3.1±2.7	0.1±0.1	
Picea abies	1.0±0.4	1.3±0.8	1.2±0.9	0.7±0.2	0.5±0.1	
Dryopteris dilatata	1.0±0.2	3.6±1.6	0.6±0.3	0.4±0.2	0.6±0.2	
Oxalis acetosella	0.9±0.3	1.3±0.8	2.6±1.7	1.1±0.4	1.0±0.2	
Trientalis europaea	0.5±0.2	0.7±0.3	0.6±0.1	0.4±0.2	0.5±0.1	
Sorbus aucuparia	0.2±0.1	0.3±0.2	0.3±0.2	0.1±0.1	<0.1	
Dryopteris expansa	<0.1	0.1±0.1	-	-	-	
Cryptogam layer[1]:						
Plagiothecium undulatum	28±5	27±2	20±2	27±5	18±2	
Sphagnum girgensohnii	6.8±2.3	0.5±0.4	0.7±0.3	5.1±3.4	0.8±0.5	
Dicranum scoparium	5.1±2.8	3.5±2.6	9.6±5.9	5.9±3.2	0.7±0.3	
Polytrichum formosum	2.5±1.1	7.0±5.2	5.6±3.3	2.8±0.8	13±2	
Rhytidiadelphus loreus	1.6±0.8	2.1±1.8	6.0±3.6	0.9±0.3	1.3±0.8	
Pleurozium schreberi	1.2±0.9	0.3±0.2	0.2±0.2	0.2±0.2	0.2±0.1	
Plagiothecium denticulatum	0.2±0.2	0.3±0.1	0.4±0.4	0.5±0.2	0.1±0.1	
Cladonia polydactyla	<0.1	<0.1	0.1±0.1	<0.1	0.1±0.1	
Dicranum fuscescens	3.0±1.8	3.4±2.6	0.2±0.2	-	2.4±1.7	
Sphagnum russowii	0.2±0.2	0.6±0.6	-	0.1±0.1	0.1±0.1	
Barbilophozia lycopodioides	0.1±0.1	-	0.1±0.1	0.1±0.1	0.2±0.2	
Lophocolea bidentata	<0.1	0.4±0.2	-	<0.1	0.2±0.1	
Plagiothecium curvifolium	0.1±0.1	-	0.1±0.1	-	0.1±0.1	
Calliergon stramineum	<0.1	-	<0.1	-	-	
Amblystegium serpens	-	0.1±0.1	-	0.1±0.1	-	
Lophocolea heterophylla	-	0.1±0.1	-	-	<0.1	
Lophozia ventricosa	-	0.1±0.1	-	<0.1	-	
Diplophyllum albicans	-	<0.1	-	-	0.2±0.2	
Pohlia nutans	-	<0.1	-	<0.1	-	
Plagiothecium laetum	-	-	-	2.0±1.8	0.1±0.1	

[1] Rare species (occurrence in only one stage with ≤ 0.2% mean cover): *Carex canescens, Digitalis purpurea, Maianthemum bifolium, Molinia caerulea, Phegopteris connectilis, Senecio sylvaticus*; *Barbilophozia floerkei, Calypogeia azurea, Lepidozia reptans, Lophozia incisa, Mnium hornum, Mylia taylorii, Plagiomnium affine, Polytrichum commune*.

[2] Statistics: * $P \leq 0.05$ (Kruskal-Wallis test). Additional testing with Dunn's posthoc test for multiple comparisons; within a row, equal letters behind mean values indicate that means do not differ significantly between the single stages.

Epiphytes on trees

The epiphyte vegetation on living and standing dead trees was dominated by lichens, with *Cladonia polydactyla*, *C. digitata*, *Lepraria jackii* and *Hypocenomyce scalaris* being the most dominant species (Table 2.4). Frequent bryophyte species included *Tetraphis pellucida*, *Polytrichum formosum*, *Plagiothecium denticulatum* and *Dicranum fuscescens*. Bryophytes as well as occasionally occurring epiphytic vascular plants were primarily restricted to the trunk bases. Most lichen species occurred with their highest frequency and cover values in the later stages of the forest dynamics cycle (C-E), but were still frequent in the regeneration stage (A), which follows the decay stage (E). The initial stage (B) was characterized by lowest mean frequency and cover values or even absence, of most epiphyte species. This was also evident from the lowest values of total cover of species and total species numbers in this stage (Table 2.5). *Lecanora conizaeoides*, which was highly frequent (though with always low cover values) in the climax (C) and ageing (D) stages, but was rare in the regeneration (A) and decay (E) stages (Table 2.4). There was also a trend for higher cover of *L. conizaeoides* in the climax (C) and ageing (D) stages, but this trend was only supported by the Kruskal-Wallis test, but not Dunn's test for multiple posthoc comparisons (Table 2.4). Some lichen species, which were mainly found on dead trees showed highest cover values in the regeneration (A) and decay (E) stages (e.g. *Cladonia pyxidata* s.l., *C. ramulosa*, *Parmeliopsis ambigua*). Distribution patterns in the most frequent bryophyte species resembled those of many lichens. Some liverwort species (e.g. *Lophozia ventricosa*, *Cephalozia lunulifolia*) were exclusively or mostly found in the decay stage (E). N_1-diversity was mostly only slightly lower than α-diversity (Fig. 4a). N_1-diversity was highest in the later stages (C-E), moderately decreased in the regeneration stage and was lowest in the initial stage (B); however, this difference was only significant in the Kruskal-Wallis test (P 0.05), but not in Dunn's test. The DCA (Appendix S2) suggested a clear difference in the epiphyte vegetation between the early (A, B) and the more advanced stages of development (C, D, E). The results of the ANOSIM revealed significant differences in the epiphyte vegetation between all development stages, except between the climax (C) and overmature stages (D) (Appendix S3).

Table 2.4: Mean frequency (Fr., in %) and cover (in %, ±standard error) of epiphytes on live or dead standing trees ≥ 2.0 m in the five forest development stages (A, regeneration; B, initial; C, climax; D, overmature; E, decay stage).

	A		B		C		D		E	E	P[3]
	Fr.[2]	Cover	Fr.	Cover	Fr.	Cover	Fr.	Cover	Fr.	Cover	
Lichens[1]:											
Cladonia polydactyla	35	5.5±2.6a	+	<0.1a	94	6.4±0.7a	91	7.0±1.1a	95	0.6±2.7a	**
Cladonia digitata	35	4.6±3.4ab	+	<0.1a	80	2.6±0.5ab	93	5.9±1.1ab	95	7.8±0.8b	**
Lepraria jackii	50	2.9±1.9	61	6.2±4.0	90	5.6±1.3	75	5.8±1.8	87	9.2±2.8	
Hypocenomyce scalaris	21	1.6±1.4ab	+	<0.1a	43	1.3±0.3ab	51	3.5±1.3ab	63	3.6±1.8b	*
Platismatia glauca	21	1.5±1.3	2	-	28	0.2±0.1	28	0.3±0.1	50	0.6±0.2	
Hypogymnia physodes	20	0.9±0.8	5	<0.1	44	0.3±0.1	60	0.5±0.2	57	1.2±0.4	
Lecanora conizaeoides	6	<0.1a	25	<0.1a	87	1.4±0.5a	84	0.7±0.2a	36	0.1±0.0a	***
Mycoblastus fucatus	3	<0.1	0	-	7	0.1±0.0	6	<0.1	22	0.1±0.0	
Cladonia pyxidata s.l.	20	0.4±0.3a	0	-	5	0.1±0.1a	0	-	29	0.3±0.2a	*
Parmeliopsis ambigua	12	0.1±0.0a	0	-	4	-	0	-	53	0.3±0.1a	*
Pseudevernia furfuracea	0	-	0	-	8	<0.1	7	<0.1	23	0.2±0.1	
Cladonia ramulosa	10	<0.1a	0	-	0	-	0	-	22	0.1±0.0a	*
Parmeliopsis hyperopta	0	-	2	<0.1	3	0.1±0.1	0	-	0	-	
Trapeliopsis flexuosa	0	-	0	-	2	<0.1	0	-	5	0.5±0.5	
Bryophytes[1]:											
Tetraphis pellucida	41	1.6±0.9a	7	<0.1a	73	0.5±0.1a	45	0.7±0.2a	61	0.8±0.3a	*
Polytrichum formosum	32	1.1±0.9	2	<0.1	23	0.3±0.1	35	0.6±0.4	44	0.3±0.1	
Plagiothecium denticulatum	26	0.6±0.5	20	0.3±0.2	67	1.1±0.6	66	0.6±0.2	76	0.8±0.3	
Dicranum fuscescens	23	0.4±0.4a	10	0.2±0.1a	59	0.7±0.3a	59	1.5±0.8a	78	2.4±0.7a	*
Plagiothecium undulatum	23	0.1±0.0	+	<0.1	8	0.2±0.1	3	<0.1	4	<0.1	
Lepidozia reptans	+	<0.1	0	-	7	<0.1	19	0.1±<0.1	5	<0.1	
Lophocolea heterophylla	0	-	5	<0.1	4	<0.1	9	<0.1	10	0.1±0.0	
Lophozia ventricosa	+	<0.1a	0	-	0	-	0	-	22	0.1±0.1a	*
Lophocolea bidentata	0	-	+	<0.1	0	-	0	-	9	<0.1	
Mylia taylorii	0	-	0	-	6	<0.1	0	-	0	-	
Ptilidium ciliare	0	-	0	-	5	0.1±0.1	3	<0.1	0	-	
Pohlia nutans	0	-	0	-	19	0.1±0.1	6	0.1±0.0	17	<0.1	
Amblystegium serpens	0	-	0	-	0	-	5	<0.1	5	<0.1	
Cephalozia lunulifolia	0	-	0	-	0	-	2	<0.1	10	<0.1	
Vascular plants[1]:											
Oxalis acetosella	20	0.3±0.2	0	-	6	<0.1	12	<0.1	22	0.2±0.1	
Vaccinium myrtillus	11	<0.1	0	-	20	0.1±0.1	12	0.2±0.1	30	0.3±0.1	
Picea abies	10	0.1±0.0	0	-	0	-	6	<0.1	7	0.1±0.1	
Deschampsia flexuosa	0	-	0	-	11	0.1±0.0	13	0.1±0.1	17	0.1±0.1	
Calamagrostis villosa	0	-	0	-	4	<0.1	0	-	5	0.1±0.0	

[1] Rare species (occurence in only one stage with <10 % mean frequency): *Bryoria fuscescens*; *Calypogeia azurea*, *Brachythecium salebrosum, Plagiothecium laetum*, *Ptilidium pulcherrimum*; *Dryopteris dilatata*, *Galium saxatile*.

[2] +: mean frequency <1 %.

[3] Statistics: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$ (Kruskal-Wallis test). Additional testing with Dunn's posthoc test for multiple comparisons; within a row, equal letters behind mean values indicate that means do not differ significantly between the single stages.

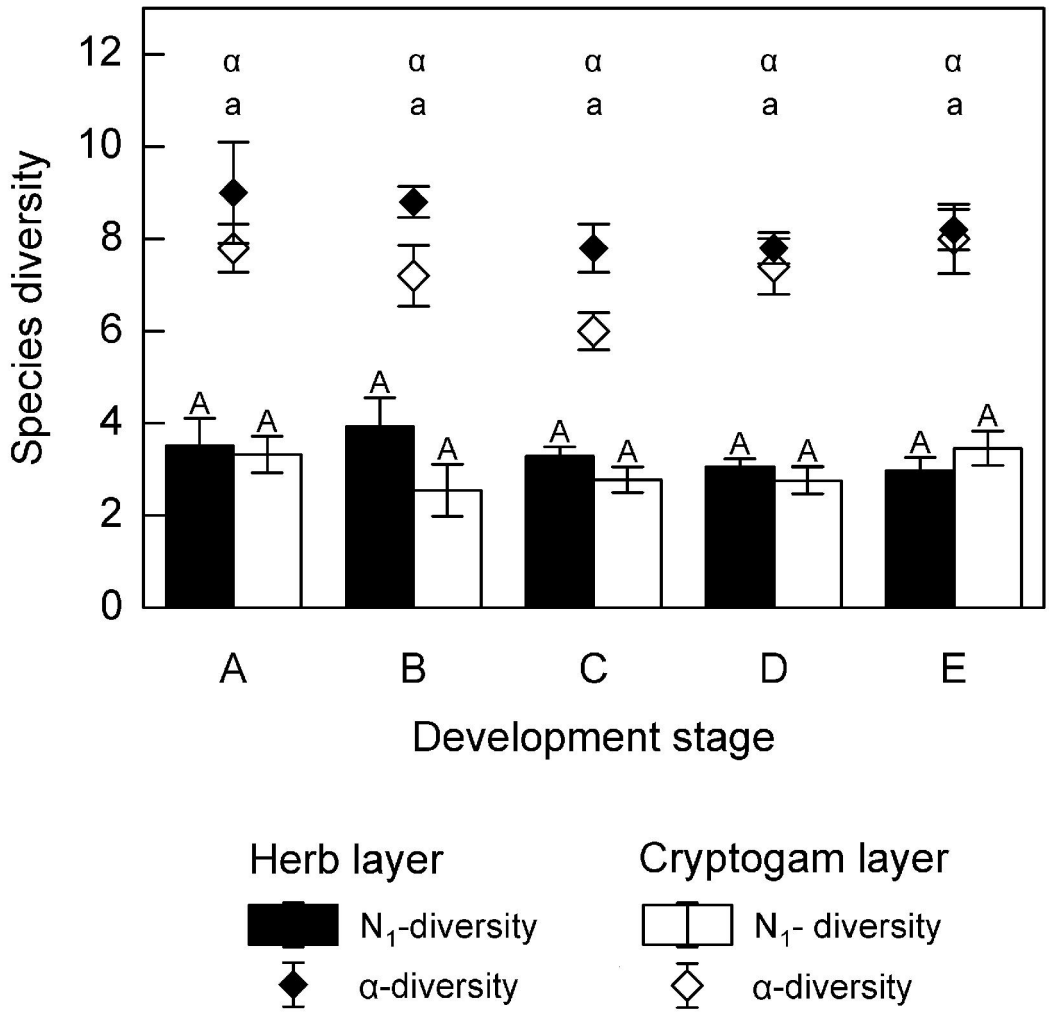

Fig. 2.3 Mean±standard error of N_1-diversity and α-diversity of ground vegetation in the five development stages (A, regeneration; B, initial; C, climax; D, overmature; E, decay stage). Equal letters in the panels indicate that means do not differ significantly (Kruskal-Wallis test, P□0.05): capital letters, N_1-diversity; greek letters, α-diversity of the herb layer; lower-case letters, α-diversity of the cryptogam layer.

Table 2.5: Total cover and total number of species on standing live or dead trees and lying deadwood trunks in the five forest development stages (A, regeneration; B, initial; C, climax; D, overmature; E, decay stage).

	A	B	C	D	E	P[1]
Standing trees:						
Total cover (%)	19±11ab	6.9±4.1a	19±2ab	26±5ab	37±6b	*
Total of species:						
Lichens	2.4±1.3ab	0.9±0.1a	5.0±0.5ab	5.1±0.4ab	6.5±0.8b	*
Bryophytes	1.5±0.6ab	0.4±0.1a	2.8±0.5ab	2.6±0.4ab	3.7±0.4b	**
Vascular plants	0.4±0.3	0.0±0.0	0.4±0.2	0.5±0.3	0.9±0.2	
Lying trunks:						
Total cover (%)	39±9ab	40±6a	14±4ab	16±6ab	15±4b	*
Total of species:						
Lichens	1.9±0.2	2.3±0.4	0.9±0.3	1.2±0.4	2.5±0.8	
Bryophytes	4.4±0.5a	4.0±0.5a	1.2±0.4a	2.1±0.6a	2.0±0.4a	*
Vascular plants	2.2±0.4a	2.0±0.4a	0.3±0.0a	0.9±0.3a	0.9±0.3a	*

[1] Statistics: * $P \leq 0.05$, ** $P \leq 0.01$ (Kruskal-Wallis test). Additional testing with Dunn's posthoc test for multiple comparisons; within a row, equal letters behind mean values indicate that means do not differ significantly between the single stages.

Epiphytes on lying trunks

Species diversity on lying trunks (Table 2.6) was higher than on standing deadwood or living trees. Most of the species were bryophytes, and many species were found on few logs and with small cover values only. The most abundant and dominant species include the bryophytes *Dicranum fuscescens*, *Polytrichum formosum*, *Tetraphis pellucida* and the lichens *Cladonia digitata*, *C. polydactyla*, and *C. pyxidata* s.l. On strongly decayed logs, seedlings and saplings of *Picea abies* and shrubs of *Vaccinium myrtillus* were regularly found. The majority of species were most frequent and reached the highest cover values in the regeneration (A) and the initial (B) stages; this was also reflected by the high total cover of all epiphytes in these stages (Table 2.5). Cover and frequency of most species were much lower in the climax stage (C), but increased in the ageing (D) and decay (E) stages. This pattern was particularly pronounced in *Polytrichum formosum*, *Plagiothecium denticulatum, Vaccinium myrtillus* and *Cladonia digitata*, though the trends for differences in the cover were not confirmed by Dunn's test (Table 2.6).

Table 2.6: Mean frequency (Fr.) and cover (±standard error) of epiphytes on lying tree trunks in the five forest development stages (A, regeneration; B, initial; C, climax; D, overmature; E, decay stage).

	A		B		C		D		E		P^2
	Fr.	Cover	Fr.	Cover	Fr.	Cover	Fr.	Cover	Fr.	Cover	
Lichens[1]:											
Cladonia digitata	58	5.7±2.6a	52	3.5±0.7a	16	1.0±0.5a	19	0.9±0.2a	34	2.0±1.0a	*
Cladonia polydactyla	51	3.2±0.9	53	2.0±0.6	21	1.0±0.6	31	2.2±1.4	30	3.8±2.3	
Cladonia pyxidata s.l.	32	0.4±0.1	29	1.5±0.8	11	1.3±0.9	4	0.2±0.2	22	0.4±0.2	
Lepraria jackii	16	0.3±0.1	19	0.4±0.2	8	0.2±0.1	14	0.1±0.1	43	1.8±0.6	
Cladonia coniocraea	11	0.3±0.1	3	0.2±0.1	7	0.1±0.1	6	<0.1	13	0.4±0.3	
Parmeliopsis ambigua	9	0.1±0.1	5	0.2±0.1	1	<0.1	2	-	30	0.2±0.1	
Hypocenomyce scalaris	6	0.3±0.2	10	0.7±0.6	0	-	4	<0.1	8	0.1±0.0	
Mycoblastus fucatus	3	<0.1	17	0.2±0.1	3	<0.1	0	-	4	<0.1	
Hypogymnia physodes	3	0.2±0.2	0	-	2	<0.1	7	0.2±0.2	16	0.5±0.4	
Platismatia glauca	3	<0.1	0	-	2	<0.1	7	0.1±0.1	10	0.1±0.1	
Cladonia squamosa	6	0.6±0.3	0	-	3	<0.1	2	<0.1	0	-	
Cladonia fimbriata	0	-	0	-	6	0.1±0.1	8	<0.1	5	<0.1	
Lepraria elobata	0	-	0	-	5	<0.1	8	<0.1	5	<0.1	
Pseudevernia furfuracea	3	<0.1	0	-	0	-	0	-	13	0.1±0.1	
Bryophytes[1]:											
Dicranum fuscescens	68	6.7±1.5	71	8.4±3.8	29	3.5±1.1	36	5.7±3.2	42	3.0±1.3	
Polytrichum formosum	59	8.8±4.3a	47	4.6±1.9a	8	0.4±0.4a	20	0.8±0.5a	14	0.5±0.2a	**
Tetraphis pellucida	56	3.9±2.3	54	4.7±2.6	16	2.5±1.4	29	1.3±0.7	28	0.3±0.1	
Plagiothecium undulatum	37	0.8±1.0	24	2.0±1.5	23	1.3±0.5	22	0.4±0.2	8	0.3±0.3	
Pohlia nutans	28	0.4±0.2a	52	0.7±0.2a	1	<0.1a	5	<0.1a	18	0.1±0.0a	**
Lepidozia reptans	24	0.5±0.2	23	0.1±0.1	2	0.0±0.0	2	<0.1	5	<0.1	
Plagiothecium denticulatum	22	0.3±0.1	24	0.8±0.5	17	0.2±0.1	23	0.3±0.2	22	0.4±0.2	
Lophozia ventricosa	16	0.6±0.5	3	0.1±0.0	4	0.1±0.1	7	<0.1	4	0.1±0.0	
Lophocolea heterophylla	15	0.1±0.0	15	0.5±0.4	11	0.4±0.3	15	0.1±<0.1	12	0.2±0.1	
Amblystegium serpens	13	0.6±0.5	8	0.3±0.2	3	0.4±0.4	8	<0.1	3	0.1±0.1	
Mylia taylorii	7	<0.1	10	0.1±0.1	2	<0.1	2	<0.1	1	0.3±0.2	
Sphagnum girgensohnii	3	0.4±0.3	1	<0.1	4	0.2±0.2	4	0.1±0.1	0	-	
Lophocolea bidentata	13	0.1±0.1	5	0.1±0.1	0	-	3	<0.1	3	<0.1	
Brachythecium salebrosum	9	0.4±0.3	1	<0.1	0	-	1	<0.1	10	0.1±0.1	
Calypogeia azurea	22	0.2±0.1	4	<0.1	0	-	7	0.2±0.1	0	-	
Calypogeia muelleriana	12	0.1±0.1	3	<0.1	0	-	4	<0.1	0	-	
Pleurozium schreberi	12	0.6±0.4a	2	0.2±0.2a	0	-	0	-	3	0.1±0.0a	*
Hypnum cupressiforme	0	-	0	-	0	-	2	<0.1-a	6	<0.1a	*
Vascular plants[1]:											
Picea abies	47	6.2±1.4	55	5.5±2.4	4	<0.1	33	2.2±1.8	25	0.2±0.1	
Vaccinium myrtillus	47	2.9±1.5a	65	5.4±2.4a	13	0.7±0.5a	16	0.7±0.4a	9	0.1±0.0a	**
Oxalis acetosella	37	0.4±0.1	10	0.1±<0.1	4	<0.1	16	0.1±0.1	5	<0.1	
Dryopteris dilatata	23	0.1±0.0	13	<0.1	2	<0.1	2	<0.1	8	<0.1	
Deschampsia flexuosa	17	19±0.9	19	0.4±0.2	6	<0.1	15	0.3±0.2	13	0.2±0.1	
Galium saxatile	18	0.1±0.0	8	0.2±0.2	5	<0.1	0	0.0±0.0	8	0.2±0.2	
Calamagrostis villosa	17	0.3±0.1	15	2.0±1.8	0	-	4	0.1±0.1	13	0.2±0.1	
Trientalis europaea	15	0.1±0.0	5	<0.1	2	<0.1	0	-	10	0.1±0.0	

[1] Rare species (two or less development stages, ≤10 % mean frequency in single stages): *Cladonia macilenta*, *Cladonia sulphurina*, *Hypocenomyce caradocensis*, *Lecanora conizaeoides*, *Mycoblastus sanguinarius*, *Parmelia saxatilis*, *Parmeliopsis hyperopta*, *Placynthiella icmalea*, *Pycnora leucococca, Trapeliopsis flexuosa*; *Barbilophozia attenuata*, *Barbilophozia lycopodioides*, *Cephalozia bicuspidata*, *Cephalozia leucantha*, *Cephalozia lunulifolia*, *Cephaloziella hampeana*, *Dicranoweisia cirrata*, *Dicranum scoparium*, *Lophozia incisa*, *Plagiothecium laetum*,

Footnotes Table 2.6 (continued)
[1] Rare species: *Ptilidium ciliare*, *Ptilidium pulcherrimum*, *Rhytidiadelphus loreus*, *Sphagnum russowii*, *Tritomaria exsectiformis; Gymnocarpium dryopteris*, *Lycopodium annotinum*, *Sorbus aucuparia*.
[2] Statistics: * $P \leq 0.05$, ** $P \leq 0.01$ (Kruskal-Wallis test). Additional testing with Dunn's posthoc test for multiple comparisons; within a row, equal letters behind mean values indicate that means do not differ significantly between the single stages.

In the climax (C), overmature (D) and decay (E) stages, values of N_1-diversity differed only moderately from those of α-diversity (Fig. 4b). In the regeneration (A) and initial (B) stages, however, where *Dicranum fuscescens*, *Polytrichum formosum*, *Tetraphis pellucida*, *Cladonia digitata* and *C. polydactyla* were most dominant (Table 2.6), α-diversity was about twice as high as N_1-diversity (Fig. 4b); while Kruskal-Wallis test revealed the existence of significant difference ($P \leq 0.05$), there was no significant difference detected in Dunn's posthoc test. Like α-diversity, N_1-diversity was lowest in the climax stage (C) and highest in the regeneration (A) and initial (B) stages. Despite the differences in the frequency and cover data between the forest development stages (Table 2.6), the composition of epiphyte communities on lying trunks was not markedly different between the five development stages. In the DCA plot, a grouping of the epiphyte communities on lying trunks according to the forest forest development stages was not evident (Appendix S2). However, the ANOSIM suggested the existence of differences between the stages, except between the regeneration (A) and initial (B) as well as between the climax and overmature (D) and between the climax (C) and the overmature stages (D) (Appendix S3).

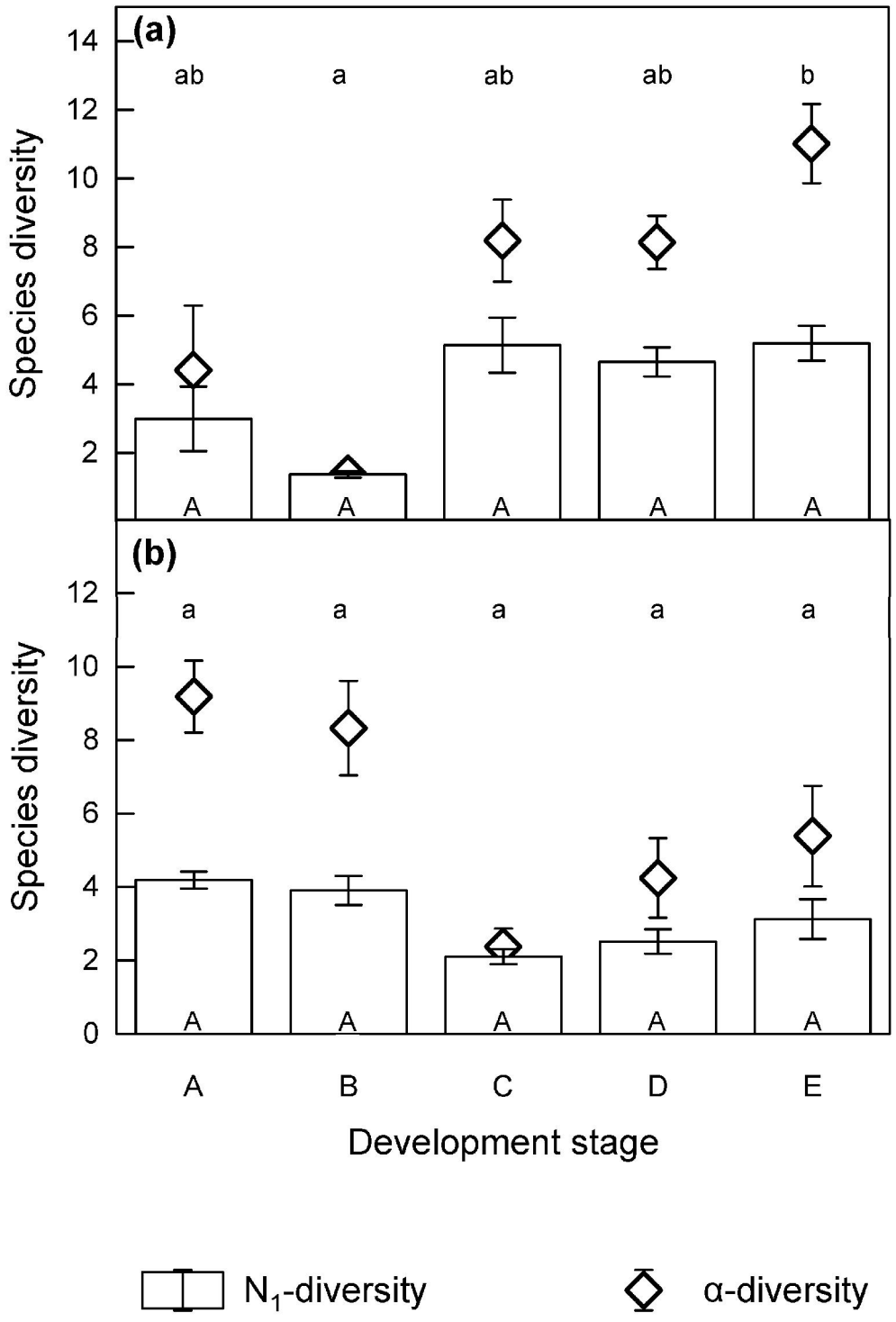

Fig. 2.4 Mean±standard error of N_1- and α-diversity of epiphytes on **(a)** trees > 2.0 m, **(b)** lying trunks in the five development stages (A, regeneration; B, initial; C, climax; D, overmature; E, decay stage; 5 replicates per stage). Equal letters in the panels indicate that means do not differ significantly (Dunn's posthoc test for multiple comparisons after positive test result with the Kruskal-Wallis test, $P \leq 0.05$): capital letters, N_1-diversity; lower-case letters, α-diversity.

2.4 Discussion

Our results showed that epiphytes on trees and lying dead trunks responded strongly to structural changes related to natural forest age dynamics, whereas the ground vegetation was little influenced. The community composition of epiphytes clearly differs between the stages, particularly between the early and more advanced stages. On living trees and standing deadwood, epiphyte diversity (α and N_1-diversity) and cover are highest on trees of the ageing (D) and decaying (E) forest stages. Preference of many epiphytic lichens and bryophytes for old and decaying trees is well documented and is attributable to the higher diversity of microhabitats with different structural, microclimatic and chemical features (ÓDOR & VAN HEES 2004; MONING et al. 2009; HAUCK et al. 2012b).

Remarkably, epiphyte diversity and cover on living and standing dead trees are not lowest in the earliest forest development stage, the regeneration stage (A), but in the second stage, i.e. the initial stage (B). The relatively high epiphyte diversity in the regeneration stage (A) is due to the still abundant occurrence of standing dead trees that persist from the decay (E) to the regeneration (A) stage, whereas the epiphyte cover on spruce seedlings and saplings is very low. In the initial stage (B), most standing dead trees from the previous forest generation have collapsed and thus are no longer present in the tree layer. For the same reason, epiphyte diversity on the lying trunks of the regeneration (A) and initial (B) stages is even higher than in the other stages. Epiphyte vegetation on lying trunks is least diverse in the climax stage (C), because most trunks from the previous forest generation are already decomposed and little deadwood is produced by the current forest generation. In contrast to the abundance of standing deadwood, there is only a slight increase of epiphyte diversity from the climax (C) to the decay (E) stage, as the number of lying trunks remains low, while the community composition changes.

Age dynamics and their effects on vegetation strongly differ between near-natural old-growth as in our case and managed age-class forests, especially if they are plantations which are harvested by clear-cutting. Managed spruce forests in Central Europe differ to old-growth forests by the near absence of trees in the ageing (D) and decay (E) stages and thus the stages with highest epiphyte diversity, because trees are harvested in the climax stage (C) before tree productivity declines. Rotation age in Central European spruce plantations mostly varies between 80 and 120 years (MOOG & BORCHERT 2001; HILMO et al. 2009), while trees in the unmanaged study site are up to 280 years old (HAUCK et al.

2012a). Managed spruce forests also show increasing epiphyte diversity with increasing age, despite the reduced life span (FRISVOLL & PRESTØ 1997; HILMO et al. 2009), but their epiphyte diversity never reaches that of old forest stages beyond the climax stage (C). In addition, managed spruce stands usually differ from near-natural forests by the absence of dead tree trunks and their characteristic epiphytes from the previous forest generation in the early development stages of the current regeneration.

The deadwood volumes measured in the present study correspond to those assessed in other old-growth spruce forests (SVOBODA et al. 2010). The coarse deadwood legacy and its epiphyte vegetation, which form a continuum between consecutive tree generations in near-natural forests, is a very important difference to managed stands. The presence of deadwood is essential for species diversity in early successional forest stages (LINDENMAYER et al. 2006; SWANSON et al. 2011). This applies for epiphytes and other groups of organisms, including invertebrates and birds (EHNSTRÖM 2001; SWANSON et al. 2011). Similar to the forest structure, which is often predetermined by the previous forest generation (KORPEL' 1995), epiphyte diversity is also strongly influenced by the diversity patterns in the previous forest generation in near-natural forests. This contrasts with forest plantations created following clear-cutting, where epiphytes must invade the stand from the surrounding woodlands. Therefore, the epiphyte diversity in managed spruce forests gradually increases with stand age, but starts from the lowest level and is cut off with tree harvesting (HILMO et al. 2009). The need for re-colonization from other stands excludes many species with limited dispersal potential from managed forests, leading to lower epiphyte diversity even on suitable substrates (HILMO & SÅSTAD 2001). Alternating clear-cutting of neighboring stands gradually leads to the extinction of epiphytes from larger areas (WIRTH 1978). The higher frequency and cover of bryophytes, including liverworts, on lying than on standing dead spruce trunks is attributable to the better water supply on lying, strongly decayed trunks than on standing deadwood (SÖDERSTRÖM 1988; LAAKA-LINDBERG et al. 2005). Characteristic for unmanaged forest stands is the growth of spruce seedlings on strongly decayed, lying trunks where the competition by other vascular plants is low (ZIELONKA & PIATEK 2004; KATHKE & BRUELHEIDE 2011b).

Even though light limitation is the strongest growth-controlling factor of the ground vegetation of temperate forests (ELLENBERG & LEUSCHNER 2010; VAN COUWENBERGE et al. 2011), forest age-related structural changes did not have an influence on the ground vegetation of this upper-montane spruce forest. The apparent insensitivity to changes in

light availability and a remarkable resilience of forest ground vegetation after disturbances found in the present work agrees with the results of other studies from European spruce forests where effects of wind throw, insect infestations or forest dieback were examined (KUKLA et al. 2003; JONÁŠOVÁ & PRACH 2008; EWALD et al. 2011). Even gaps do not lead to strong changes in the vegetation composition or diversity in near-natural spruce forests (KIRCHNER et al. 2009, 2011). Nevertheless, the cover of some frequent herb layer species, including *Calamagrostis villosa*, *Vaccinium myrtillus* and *Trientalis europaea* was found to decrease with gap age (KIRCHNER et al. 2011). This is also reflected in the (non-significant) variation of species cover and community composition in the different forest development stages in the present study. In contrast to near-natural stands, the succession stages in managed forest ecosystems are characterized by a considerable species turnover in the understory vegetation (UOTILA & KOUKI 2005; AAVIK et al. 2009). In managed boreal forests, the ground vegetation diversity was found to be considerably higher in young or pre-mature stands than in mature stands (WIDDENFALK & WESLIEN 2009) in accordance with the intermediate disturbance hypothesis (CONNELL 1978). In spruce plantations, thinning of mature stands leads to the increase in non-forest plant species (ZERBE 1993). Grasses and herbs are more abundant in young, managed coniferous forest stands and strongly decline in mature stands (UOTILA et al. 2005). In contrast, cover values of dwarf shrubs and mosses are lowest in the early stages, strongly increasing in advanced stages while liverworts are rare across all stages (UOTILA et al. 2005; UOTILA & KOUKI 2005). In contrast to old-growth spruce forests, natural age dynamics in old-growth lowland beech forests (*Fagus sylvatica* L.) resulted in marked cyclic changes in ground vegetation composition and diversity in a study of OHEIMB et al. (2004), possibly due to the lower light transmissivity of beech as compared to spruce in the initial and climax stages of the forest development cycle.

2.5 Conclusions

Our results confirmed the significance of natural forest dynamics for plant diversity, particulary epiphytes. Forest age dynamics yield structural changes within the forest ageing cycle, particularly in the increasing tree size and deadwood creation and tradition. Although forest age dynamics had little effect on the diversity of the ground vegetation, the diversity of epiphytic lichens and bryophytes on living trees as well as on standing and lying dead tree trunks clearly benefited from the presence of ageing and decaying forest

stages. Standing and lying deadwood not only increases the epiphyte diversity in old forest stages, but even more in regenerating and young stands, as the deadwood from the previous forest generation is still present at the beginning of the next. This continuum of substrata for epiphytes represents a strong contrast to managed forests, especially to plantations created after clear-cutting. The continuous persistence of the deadwood across consecutive tree generations is of major importance, since many epiphytes are threatened by their limited capability for dispersal in managed forests. Therefore, a certain percentage of senescent and dead trees beyond the rotation age should be kept in all forests (and not only in small conservation areas) for conserving species (1) which depend on old trees, (2) which are specialized on deadwood, and (3) with dispersal limitations. The economic burden is relatively small, but the benefit for protecting characteristic forest biota is large. The protection of unmanaged forest patches within managed forests would certainly not only be beneficial to epiphytic lichens and bryophytes, but also to other groups of organisms, such as various invertebrate groups and fungi.

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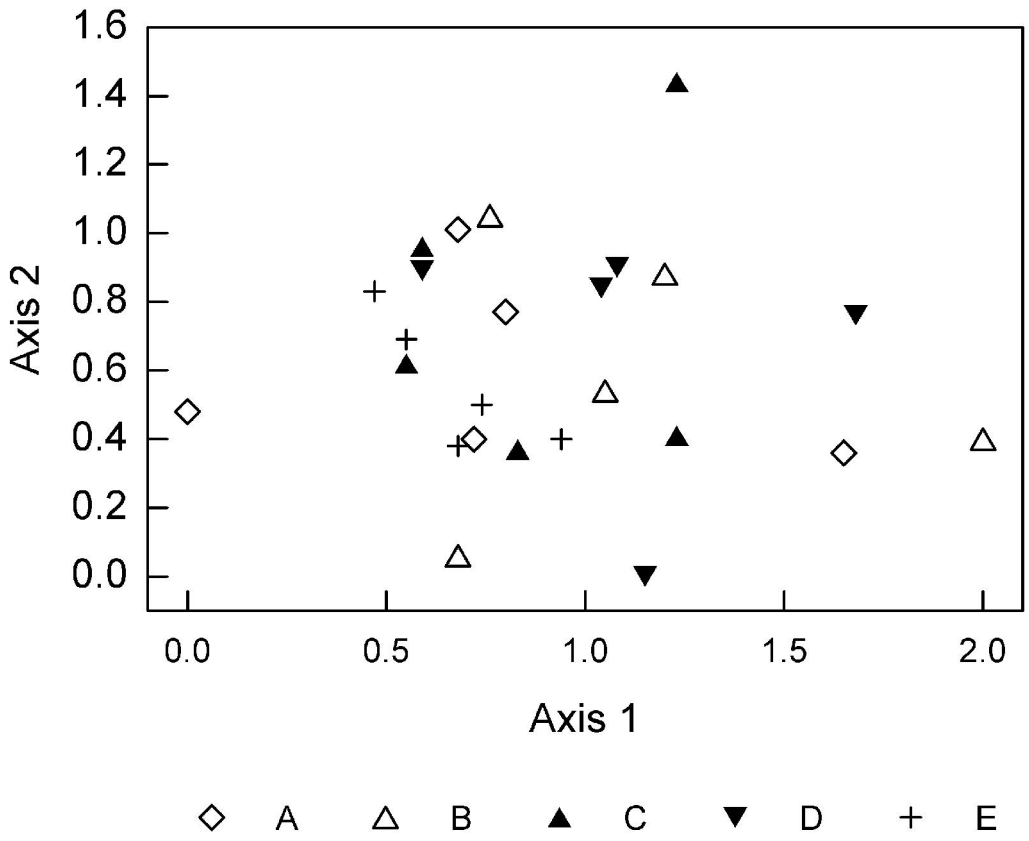
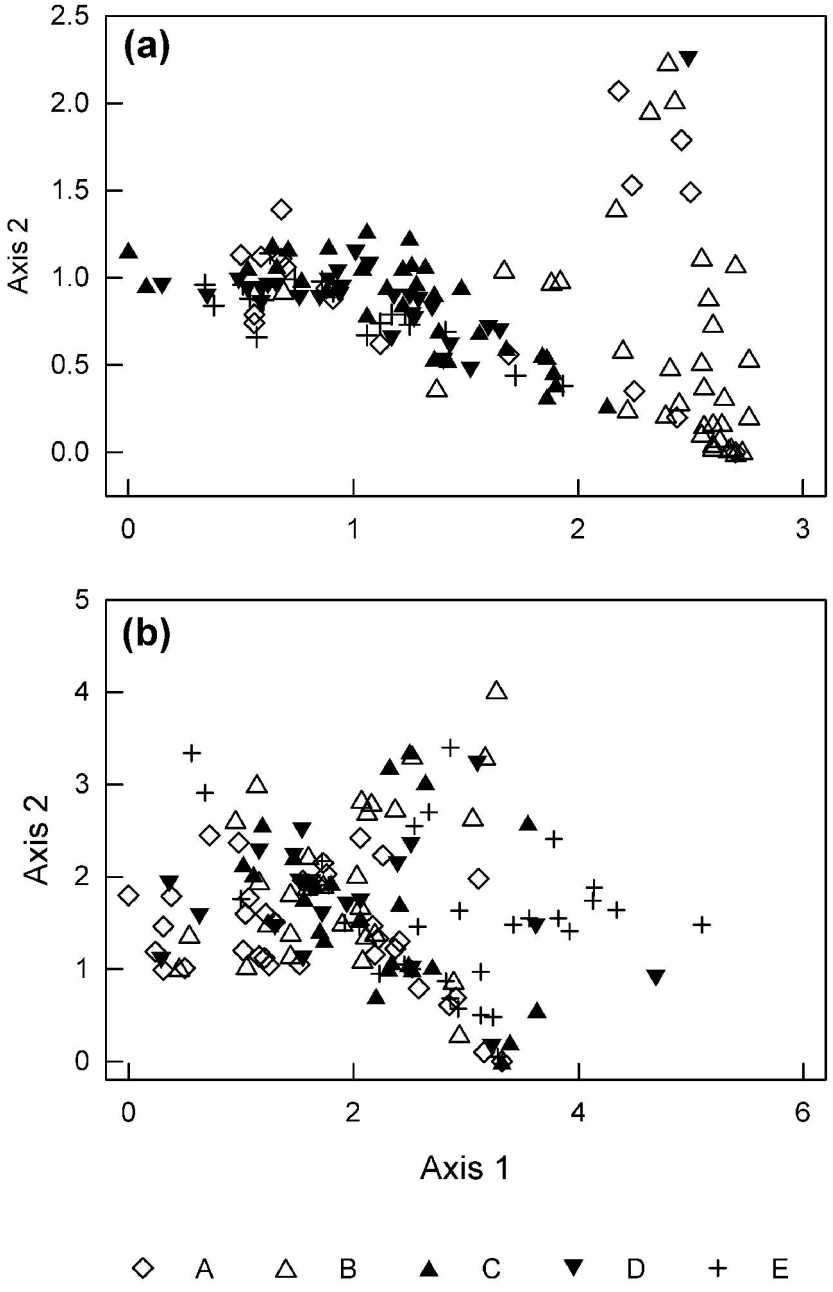
Appendix



Appendix S1 DCA of ground vegetation plots in the five development stages (A, regeneration; B, initial; C, climax; D, overmature; E, decay stage; 5 replicates per stage). Total variance in species data: 0.965. Eigenvalues: 0.21 (axis 1), 0.12 (axis 2). Gradient length 2.00 (axis 1), 1.45 (axis 2),



Appendix S2 DCA of epiphyte communities in the five development stages (A, regeneration; B, initial; C, climax; D, overmature; E, decay stage). **(a)** Trees > 2.0 m (N = 148). Total variance in species data: 3.14. Eigenvalues: 0.43 (axis 1), 0.26 (axis 2). Gradient length: 7.40 (axis 1), 3.68 (axis 2). **(b)** Lying trunks (N = 140). Total variance in species data: 6.93. Eigenvalues: 0.59 (axis 1), 0.50 (axis 2). Gradient length: 5.10 (axis 1), 4.08 (axis 2).

Appendix S3 Results of the ANOSIM analyzing the significance of differences in the epiphyte vegetation on live and dead standing trees or lying trunks between the five forest development stages (A, regeneration; B, initial; C, climax; D, overmature; E, decay stage).

	A	B	C	D
Trees:				
B	<0.001			
C	<0.001	<0.001		
D	<0.001	<0.001	0.10	
E	<0.001	<0.001	<0.001	0.03
Lying trunks:				
B	0.10			
C	0.01	0.04		
D	0.007	0.04	0.60	
E	<0.001	<0.001	0.007	0.002

Chapter

3

The significance of deadwood for total bryophyte, lichen and vascular plant diversity in an old-growth spruce forest

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Submitted.

Abstract

Deadwood plays a key role in forest conservation, since silviculture reduces the amounts especially of large-diameter deadwood. We analyzed the significance of deadwood for the total species diversity in three plant groups (bryophytes, lichens, vascular plants) in one of Central Europe's few remnants of unmanaged old-growth forest. The site was a montane forest of *Picea abies* on Mt. Brocken, Harz Mountains, Germany, which has not been managed for at least several centuries, underlies natural forest dynamics, and thus harbors large amounts of standing and downed deadwood. Epiphyte vegetation of live trees and the ground vegetation were studied for comparison. We did not find any species which was obligately bound to deadwood. Nevertheless, 84 % (70 species) of the total species were found on standing or downed deadwood. One third of these species or 28 % of the total species in the forest were restricted to deadwood, whereas the remaining species were also found on live trees and/or the ground. Bryophytes were the largest group of species on deadwood (47 % of the deadwood-inhabiting species), followed by lichens (37 %) and vascular plants (16 %). Large-diameter and strongly decayed deadwood harbored more species than small-sized, hardly decayed wood. Species richness of lichens tended to decrease on soft deadwood, where the decay was most progressed and the richness of bryophytes and vascular plants increased. Despite the lack of obligate deadwood colonizers, deadwood apparently plays a key role for forest plant diversity mainly by facilitating the establishment of species due to reduced competition.

3.1 Introduction

Large amounts of deadwood are the most apparent feature of old-growth forests compared to managed forests (SIPPOLA et al. 1998; WINTER et al. 2005; GIBB et al. 2006). Especially deadwood of large diameter is rare in managed forests (ANDERSSON & HYTTEBORN 1991; BADER et al. 1995). Dying and collapsed trees as well as downed branches provide a continuous supply of deadwood to the forest floor (JONSSON 2000; AAKALA 2011). Deadwood is an important habitat for many specialized organisms including invertebrates, fungi, bryophytes and lichens (LESICA et al. 1991; EHNSTRÖM 2001; JONSSON et al. 2005). The deadwood legacy, which is created in forest stages with over-mature trees, increases species diversity in early successional stages of the next forest generation (SWANSON et al. 2011; DITTRICH et al. 2013a). Deadwood is the habitat of specialized species, which decompose the wood and, therefore, need enzymes for lignin degradation (BLANCHETTE 1991; HAMMEL et al. 2002). However, deadwood is also inhabited by species, which do not contribute to deadwood decay with regard to lignin decomposition, but benefit from the low competition on the wood surface. Such species include cryptogamic epiphytes, some of which are highly specialized on decorticated wood, whereas others grow on both live and dead trees (HUMPHREY et al. 2002; HAUCK 2011). Late decay stages of deadwood can become the habitat of terricolous species of bryophytes, lichens and even vascular plants, which take advantage of lower competition than on the ground (FALINSKI 1978; FENTON et al. 2007). In natural forests, downed deadwood is important for forest regeneration, since tree seedlings emerge more easily on the surface of strongly decayed wood than in dense vegetation (KATHKE & BRUELHEIDE 2010; BAČE et al. 2012).

Deadwood is a major issue in the territory between the opposing poles of the conservation and economic exploitation of forests, since every bole which is kept for conservation lowers the potential profit from wood sales (HALE et al. 1999; FRIDMAN & WALHEIM 2000; Grove 2001). Since deadwood-inhabiting species are only partly mandatory colonizers of this substratum, we became interested in the question which share deadwood has in the total plant diversity of an old-growth forest. Therefore, we analyzed the species diversity of bryophytes, lichens, and vascular plants in one of the rare examples of unmanaged Central European old-growth forests in a montane spruce forest of Germany. We compared plant diversity of deadwood with that of the ground vegetation and with the epiphyte diversity on live trees to test the hypotheses that (1) deadwood makes a major contribution to the total bryophyte, lichen and vascular plant diversity of this ecosystem and that (2) some species of these taxonomic groups are restricted to deadwood in the studied old-growth forest.

In addition to the total deadwood volume, the quality of deadwood in terms of the size and the decomposition stage of the individual deadwood pieces are significant for species diversity. The diversity of deadwood-inhabiting bryophytes and lichens increases with the trunk diameter (ÓDOR & VAN HEES 2004; HAUCK 2011). Large pieces of deadwood are much slower overgrown by ground vegetation and their decay takes longer than that of small and thin pieces of wood (SÖDERSTRÖM 1988; HOLEKSA et al. 2008). Large trunks also provide a broader variety of microhabitats and, thus, can support more species (ÓDOR et al. 2006; HAUCK et al. 2013a). Wood decay causes a marked species turnover with time (BARKMAN 1958; ÓDOR & VAN HEES 2004; POUSKA et al. 2011). Fresh, poorly decayed deadwood shares a considerable proportion of epiphyte species with live trees, whereas strongly decayed trunks are finally overgrown by the ground vegetation. Early stages of succession in temperate and boreal forests are often dominated by lichens, or liverworts in moist habitats, which are later replaced by moss-dominated communities (SÖDERSTRÖM 1988; DANIELS 1993; CARUSO & RUDOLPHI 2009). Strongly decomposed wood is overgrown by dwarf shrubs, grasses and herbs (ZIELONKA & PIĄTEK 2004). Since both deadwood size and deadwood decay are known to shape species diversity, we included this aspect into our study and analyzed our data for the effect of the two parameters on plant diversity. With this analysis, we tested the hypothesis that the diversity of deadwood-inhabiting lichens, bryophytes and vascular plants increases with increasing diameter and proceeding decay of the deadwood pieces. The combined study of bryophytes, lichens and vascular plants as well as the assessment of plant diversity on deadwood relative to the total plant diversity of the entire forest ecosystem separates our study from many other studies on the significance of deadwood for plant diversity in forest ecosystems.

3.2 Material and Methods

Study area

The study was carried out in a montane old-growth forest of *Picea abies* (L.) H. Karst. on Mt. Brocken (51°47' N, 10°38' E) in the Harz Mountains, Germany. The studied stand is a strictly protected area on the eastern and south-eastern slopes of Mt. Brocken between 950 and 990 m a.s.l. and has a size of 300 ha. The forest has never been logged since the introduction of modern forestry in the area in the 17th century (DITTRICH et al. 2013b); the oldest trees are at least 280 years old (HAUCK et al. 2012). GREGER (1992) supplied evidence that the forest was spared from logging also in the 16th century when logging activities took places at lower elevations of Mt. Brocken. The lack

of charcoal remnants in the vicinity of the studied stand is another indicator, which speaks against logging in the stand; charcoal remnants are otherwise frequent on Mt. Brocken and in other parts of the Harz Mountains, as large amounts of charcoal were produced for the booming local mining industry (KORTZFLEISCH 2008). Between the plague pandemics of 1347-51 and the early 16th century the human population of the Harz Mountais was low. Before that time, the upper elevations of Mt. Brocken were reserved as a hunting ground and were banned for logging and forest pasture since the early Middle Ages (c. 800 AD; GREGER 1992; HAUCK et al. 2013b). All this evidence suggests that our study site was unmanaged for at least three to four centuries and perhaps even represents a virgin forest. Due to the limited human influence, the stand follows natural age dynamics (STÖCKER 2001, 2002) and harbors substantial amounts of standing and downed deadwood (Table 3.1). The cold mountain climate also favors the accumulation of deadwood by decelerating deadwood decomposition. The regional climate is characterized by high annual precipitation of 1600 mm (including 1.9 m yr^{-1} of snow) and a mean annual temperature of 3-3.5 °C (GLÄSSER 1994).

Table 3.1 Stand structure including quantities of standing and downed deadwood in the 25 plots of 10 m × 10 m in the *Picea abies* old-growth forest

	Means±standard error
Canopy closure (%)	84±2
Live trees (>2 m height)	
Density (trees ha^{-1})	608±144
Diameter at breast height (cm)	21±4
Height (m)	10.3±2.0
Volume (m^3 ha^{-1})	66±17
Standing deadwood (>2 m height)	
Density (trees ha^{-1})	232±52
Diameter at breast height (cm)	21±4
Height (m)	5.3±1.2
Volume (m^3 ha^{-1})	69±26
Downed deadwood (>1 m length, >2 cm in diameter)	
Density (trees ha^{-1})	816±76
Diameter (cm)	18±2
Height (m)	2.4±0.2
Volume (m^3 ha^{-1})	52±39

Sample plot selection

The dominant forest community in the study area is the reedgrass-spruce forest (*Calamagrostio villosae-Piceetum*), which is characteristic of acidic mineral soils at montane elevations. This forest is replaced by spruce mires (*Bazzanio-Piceetum* s.l.) on water-logged soils and birch-spruce forest

(*Betulo carpaticae-Piceetum*) at places with many granite boulders. For reasons of comparability, our study was restricted to the *Calamagrostio villosae-Piceetum*. Twenty-five plots of 10 m x 10 m size were selected for vegetation analysis. These 25 plots were intended to cover the full forest ageing cycle, including regeneration, initial, climax, over-mature and decay stages (STÖCKER 2001, 2002). For this reason and because of the limited size of the studied old-growth forest, the selection of the sample plots was a non-random procedure. Rather, we selected the plots to represent all forest development stages equally and to be as evenly distributed over the studied forest as possible (DITTRICH et al. 2013a).

Analysis of deadwood and stand properties

All live spruce trees and the complete standing deadwood with a minimum height of 2 m were included in the analysis. The diameter at breast height (*dbh*) of these trees was measured with a measuring tape at 1.3 m above the ground. Tree height was recorded with a Vertex IV sonic clinometer and a T3 transponder (Haglöf, Långsele, Sweden). Downed deadwood was included in the analysis, if it was >1 m long and > 2 cm in diameter. On the 25 plots, altogether 39 live trees, 25 standing dead trees and 122 pieces of downed deadwood met the criteria for inclusion into the study. The dead wood volume (V, in m³) was calculated using the equation $V = \pi\,(dbh/2)^2\,l$, with l being the length of downed deadwood or the height of standing deadwood, respectively.
The standing and downed deadwood was assigned to diameter classes based on the stem diameter, viz. class 1, <10 cm; 2, 11-20 cm; 3, 21-30 cm; 4, 31-40 cm; 5, 41-50 cm; 6, 51-60 cm; 7, >60 cm.
The wood decay of the deadwood was assessed by classifying all standing and downed deadwood pieces in the field using an 8-graded scale (Table 2); this classification was based on scales proposed by STÖCKER (1998) and HOLEKSA (2001).

Table 3.2 Definition of classes to assess the decay of downed deadwood (after STÖCKER 1998, HOLEKSA 2001, modified)

Class	Substrate group[1]	Wood surface structure	Penetration by sharp objects	Bole profile	General appearance
1	DDa	Smooth	Not penetrable	Round	Thin twigs and remaining needles present
2	DDa	Smooth	Surface bends	Round	Twigs breaking off
3	DDb	Crevices of few mm depth	≤ 1 cm	Round	Parts of crown still present
4	DDb	Crevices of ≤ 0.5 cm depth	≤ 3 cm	Round	Loss of crown, few side branches remain
5	DDc	Crevices 1 cm deep, thick wood pieces tear off from surface	≤ 5 cm	Round	Only trunk left
6	DDc	Thick pieces tear off from sides	Solid parts in center	Round	Only trunk left
7	DDd	Entire trunk with crevices of several cm depth, high vegetation cover	Completely penetrable	Flattened	Only trunk left, deep crevices, cavernous or filled by litter
8	DDd	Almost completely covered with cryptogams and vascular plants	Completely penetrable	Irregular, elevated	Irregular, almost completely covered by vegetation

[1] Downed deadwood: DDa, early decay; DDb, early advanced decay; DDc, late advanced decay; DDd, strong decay.

Vegetation analysis

Our studies focused on the vegetation of downed stems and branches of >2 cm in diameter and >1 m length. For comparison, we also quantified the ground vegetation of the plots and epiphytes on live trees and standing deadwood. The vegetation was analyzed by estimating the cover of all species of bryophytes, lichens and vascular plants. The cover of the individual plant species was estimated in percent using 5 %-classes for species covering ≥10 % of the plot and 1%-classes for the remaining species. Species with a cover <1 % were put to 0.5 % (if more than one individual was present) or 0.1 % cover (one individual). The reference area for vegetation sampling was the entire upper surface and the flanks of the individual deadwood pieces, the lower 2 m of the trunks of standing deadwood and live trees, or the entire 10 m × 10 m plots in the case of the ground vegetation. The number of all species of a plant group (lichens, mosses, hepatics, vascular plants) present on the substrate surfaces (forest floor, downed deadwood, standing deadwood, live trees) within the 10 × 10 m plots was taken as α-diversity. Nomenclature of species is based on WISSKIRCHEN & HAEUPLER (1998, vascular plants), KOPERSKI et al. (2000, bryophytes) and WIRTH et al. (2013, lichens).

Data analysis

Arithmetic means ± standard errors are presented throughout the paper. Statistical analyses were made with R 2.14.0 software (R Development Core Team, Vienna, Austria), if not specified otherwise. All data were tested for normal distribution with the Shapiro-Wilk test. To obtain a higher *N* for the comparative analyses of single species responses to different substrate types (standing [SD] and downed deadwood [DD], live trees [LT] and forest ground [FG]), we merged the eight decay classes of downed deadwood to four groups (Table 2), viz. early decay (decay class 1-2), early advanced decay (3-4), late advanced (5-6) and strong decay (7-8). In standing trees, we only distinguished between live trees and standing dead trees. The Kruskal-Wallis test was applied to test significant differences of cover values of individual species and species richness between the substrate types. The β-diversity was calculated for each of the compared substrate types as $\beta = \gamma/\alpha$, with γ being the total richness of species found in the 25 plots and α being the species richness found in the relevant substrate type, respectively. Two subtypes of β-diversity are used in the paper: β_{stand} refers to the total α-diversity found in the relevant substrate group; β_{object} was calculated with the α-diversity of individual trees or deadwood pieces, respectively. To test for significant differences in the α- and β-diversities between the substrate types, we used Tukey's test. To avoid overly conservative conclusions (GARCIA 2004), we did not apply Bonferroni corrections in the statistical analyses. Intercorrelation between the α-diversities of the studied species groups (lichens, mosses, hepatics, vascular plants) was examined by calculating Pearson correlation coefficients. Differences in community composition between different diameter classes and decay classes were tested for significance with the non-parametric analysis of similarities (ANOSIM) using the software package PAST 2.15 (Ø. Hammer, Natural History Museum, University of Oslo, Norway). The *R* value resulting from the ANOSIM is defined as $R = (r_B - r_W)/(N[N-1]/4)$, with r_B and r_W being the mean between-group and within-group ranks and *N* being the number of samples; $R=\pm 1$ indicates perfect grouping, whereas $R=0$ indicates random grouping (Clarke 1993). The estimated percentage cover values of plants were not transformed before ANOSIM or the the statistical testing of the means of values from different substrates.

3.4 Results

Variation of deadwood across the forest dynamics cycle

A total of 70 plant species was found on standing and downed deadwood (Table 3). Remarkably, this equals 84 % of the total of 83 species recorded from the sample plots. The 70 wood-dwelling species included bryophytes (47 %, with 24 % of hepatics and 23 % of mosses), lichens (37 %) and vascular plants (16 %). One third (= 23 species) of the species occurring on deadwood or 28 % of the total species in the forest were restricted to this substratum; this included 50 % of the deadwood-inhabiting lichens, 35 % of the liverworts, and 13 % of the mosses found in the studied spruce forest. Even two species of vascular plants (*Gymnocarpium dryopteris*, *Lycopodium annotinum*) were only found on deadwood. Among the lichens, *Cladonia* species were particularly characteristic of deadwood with a total of six species, which were not found on other substrata. Most species (74 %, 17 species) that were restricted to deadwood in the sample plots were rare species in the studied forest. Thus, the restriction of these species to deadwood might be coincidental in many cases. However, even among the more frequent species, four lichens (*Cladonia coniocraea*, *C. fimbriata*, *C. ramulosa*, *Lepraria elobata*) and two liverworts (*Calopogeia muelleriana*, *Cephaloziella hampeana*) were only recorded from deadwood (Table 3.3). Twenty-three percent of the frequent species (frequency >10 %) and 50 % of the rare species (frequency <10 %) found in the sample plots were only recorded from deadwood. The majority of vascular plant species found on deadwood mostly grew on the forest floor and only occasionally colonized deadwood (e.g. *Vaccinium myrtillus*, *Oxalis acetosella*, *Deschampsia flexuosa*).

The α-diversity of all studied plant groups was significantly higher on standing than downed deadwood (Fig. 3.1). Lichens and bryophytes had also high α-diversities on live trees. The species richness of mosses and vascular plants was higher in the ground vegetation than on live trees and deadwood. Across all taxonomic groups, β_{stand}-diversity was highest on live trees and lowest in the ground vegetation. In contrast, there were marked differences between the taxonomic groups for β_{object}-diversity (Fig. 3.1). The species turnover for lichens was low on live trees and standing deadwood, high on downed deadwood and at an intermediate level in the ground vegetation. Mosses had a very low species turnover in the ground vegetation and an intermediate β_{object}-diversity on trees and deadwood. Liverworts did not show significant differences in the species turnover between the substrates due to high variation in the data, but there was an insignificant trend for higher β_{object}-diversity in the ground vegetation and on downed deadwood than on live trees and standing deadwood. Vascular plants had little species turnover in the ground vegetation,

intermediate values of β_{object}-diversity on standing and downed deadwood, and low β_{object}-diversity on live trees.

Impact of deadwood traits on deadwood-inhabiting species

The total α-diversity of the sum of all lichen, bryophyte and vascular plant species increased with increasing diameter of the deadwood (Fig. 3.2a). The α-diversity reached saturation at a stem diameter of c. 40 cm (diameter class 4). The total α-diversity also increased with the decay class (Fig. 3.2b). Saturation of α-diversity was almost reached in decay class 4, while there was only an insignificant additional increase from decay class 7 to 8. The saturation curves for total species richness were reflected by the results of ANOSIM (Table 3.4) showing significant differences in the community composition of the vegetation on downed deadwood only between the thinnest deadwood pieces (class 1) and most other diameter classes (classes 2-6). As for the decay classes, the community composition of classes 1-3 differed significantly from that of classes 4-8.

Species richness of bryophytes and vascular plants was correlated with each other (Table 3.5). Vascular plant α-diversity was more strongly correlated with species richness of mosses than of liverworts. In contrast, species richness of lichens varied independently of that of vascular plants and liverworts and was only weakly correlated with moss α-diversity. The α-diversities of bryophytes and vascular plants principally followed the responses to deadwood diameter and decay that were observed for total species richness of all investigated taxonomic groups (Fig. 3.2). In contrast to bryophytes and vascular plants, lichen species richness was highest in medium-progressed stages of wood decomposition (decay classes 4 and 5) and slightly decreased afterwards (Fig. 3.2b). However, this trend for lower lichen species richness in decay classes 6-8 than in classes 4-5 was statistically insignificant. Significant decreases of the cover of individual lichen species from decay class 4 to class 8 (Table 3.3) match with the concurrent trend for declining α-diversity of lichens. Such declines were, for example, observed in *Hypogymnia physodes* and *Parmeliopsis ambigua*. Several lichen species had decreasing frequencies towards decay class 8 (Table 3.3; e.g. *Hypogymnia physodes*, *Lepraria jackii*, *Parmeliopsis ambigua*, *Platismatia glauca*, *Pseudevernia furfuracea*).

Although bryophyte species richness remained more or less constant during wood decay from classes 4-8, there was significant variation on the species level (Table 3.3). Some species preferred intermediate decay stages (*Lophocolea heterophylla*, *Pohlia nutans*, *Brachythecium salebrosum*), whereas some others grew mostly on strongly decayed wood (*Dicranum fuscescens*, *Tetraphis*

pellucida, *Calypogeia azurea*, *Polytrichum formosum*, *Lophocolea bidentata*, *Pleurozium schreberi*). Preference for intermediate or late decay stages was independent of the affiliation to liverworts or acrocarpous or pleurocarpous mosses.

Table 3.3 Distribution of bryophyte (M, mosses; H, hepatics), lichen (L) and vascular plant (V) species[1] for live trees (LT), standing deadwood (SD), downed deadwood (DD)[2] and the forest ground (FG). For each substratum type, the first column of the main body of the table represents the frequency (in %) and the second column represents mean cover ± standard error (in %). Frames indicate species with similar behavior in terms of the response frequency and cover to the substratum type

		LT		SD		DDa		DDb		DDc		DDd		FG		P[3]
	Decay class	-		3.3±0.3		1.4±0.2		3.5±0.1		5.6±0.1		7.7±0.1		-		***
	Number of replicates	39		25		5		47		50		20		25		
	Total cover	20.6±1.9		40.8±3.6		14.0±10.4		20.8±3.0		36.8±4.3		54.7±7.3		76.2±2.1		***
	α-diversity lichens	5.3±0.2		6.2±0.5		0.6±0.5		2.8±0.3		2.4±0.3		1.8±0.3		0.3±0.1		***
	α-diversity bryophytes	3.1±0.2		3.8±0.3		1.0±0.6		2.9±0.3		4.1±0.4		4.2±0.6		6.8±0.4		***
	α-diversity vascular plants	0.4±0.1		1.0±0.2		-		1.0±0.2		1.8±0.2		3.3±0.5		8.4±0.3		***
	- Preference for live and standing dead trees and logs[2]:															
M	*Dicranum fuscescens*	74	1.3±0.3	80	2.2±0.5	0	-	55	4.7±1.2	74	11.9±2.6	75	6.7±2.1	28	1.8±0.8	***
M	*Tetraphis pellucida*	62	0.5±0.1	72	1.4±0.4	0	-	40	1.2±0.6	48	2.4±0.8	65	10.9±3.8	0	-	**
H	*Lophocolea heterophylla*	13	<0.1	12	0.1±<0.1	0	-	19	0.3±0.2	34	0.5±0.3	0	0	8	<0.1	**
H	*Lepidozia reptans*	13	0.1±<0.1	4	<0.1	20	<0.1	6	0.1±0.1	12	0.2±<0.1	20	0.1±0.1	4	<0.1	
L	*Cladonia pyxidata*	3	0.1±0.1	28	0.4±0.2	0	-	28	0.9±0.3	32	0.4±0.1	15	0.9±0.7	0	-	**
	- Preference for live and standing dead trees:															
L	*Cladonia polydactyla*	100	7.2±0.8	92	10.1±1.7	0	-	45	2.7±0.9	44	3.7±1.2	55	4.8±2.0	28	<0.1	***
L	*Lepraria jackii*	97	5.1±0.7	96	11.0±2.4	20	0.4±0.4	40	1.0±0.3	28	0.5±0.2	15	0.6±0.5	0	-	***
L	*Lecanora conizaeoides*	97	1.4±0.2	36	0.1±<0.1	0	-	2	<0.1	0	-	0	-	0	-	***
L	*Cladonia digitata*	90	3.5±0.5	92	8.7±1.2	0	-	51	3.2±1.0	56	5.1±1.5	45	2.8±1.5	0	-	***
L	*Hypogymnia physodes*	59	0.4±0.1	56	1.3±0.3	0	-	15	0.5±0.3	2	0.1±0.1	5	<0.1	0	-	***
L	*Hypocenomyce scalaris*	39	1.7±0.8	72	3.7±1.0	0	-	9	0.5±0.4	10	0.2±0.1	0	-	0	-	***
L	*Platismatia glauca*	31	0.2±0.1	48	1.1±0.4	0	-	9	0.1±0.1	4	<0.1	0	-	0	-	***
L	*Pseudevernia furfuracea*	10	<0.1	16	0.1±0.1	0	-	9	0.1±<0.1	4	<0.1	0	-	0	-	
L	*Violella fucata*	5	<0.1	16	0.1±0.1	0	-	6	<0.1	10	0.1±0.1	0	-	0	-	
L	*Parmeliopsis ambigua*	3	0.1±<0.1	44	0.3±0.1	0	-	28	0.2±<0.1	12	0.2±0.1	10	0.1±<0.1	0	-	**
L	*Trapeliopsis flexuosa*	3	<0.1	4	0.4±0.4	0	-	2	<0.1	0	0	5	<0.1	0	-	
H	*Cephalozia lunulifolia*	3	<0.1	8	<0.1	0	-	2	<0.1	2	<0.1	5	<0.1	0	-	
L	*Cladonia ramulosa*[4]	0	-	20	0.1±<0.1	0	-	0	-	0	-	0	-	0	-	**
	- Preference for logs:															
M	*Amblystegium serpens*	0	-	4	<0.1	20	3.0±2.7	13	0.9±0.5	8	0.1±0.1	10	0.05	8	<0.1	
L	*Cladonia coniocraea*[4]	0	-	0	-	0	-	13	0.2±0.2	12	0.4±0.2	10	0.2±0.2	0	-	
H	*Calypogeia azurea*	0	-	0	-	0	-	2	<0.1	12	0.2±0.1	20	0.3±0.1	4	<0.1	**
L	*Lepraria elobata*[4]	0	-	0	-	20	0.2±0.2	9	<0.1	0	0	5	<0.1	0	-	**
L	*Cladonia fimbriata*[4]	0	-	0	-	0	-	4	<0.1±0.1	8	<0.1	10	0.1±0.1	0	-	
H	*Calypogeia muelleriana*[4]	0	-	0	-	0	-	2	<0.1	4	<0.1	10	<0.1	0	-	
H	*Cephaloziella hampeana*[4]	0	-	0	-	0	-	2	<0.1	2	<0.1	5	<0.1	0	-	

Table 3.3 (continued)

		LT		SD		DDa		DDb		DDc		DDd		FG		P[2]
	- More frequent on the ground than on trees or deadwood:															
M	*Polytrichum formosum*	38	0.5±0.2	48	0.7±0.4	0	-	32	2.1±0.8	44	4.0±1.6	60	6.7±2.3	96	6.2±1.5	***
V	*Vaccinium myrtillus*	15	0.1±<0.1	28	0.2±0.1	0	-	26	0.5±0.3	48	1.5±0.6	60	7.4±2.5	88	13.8±3.2	***
V	*Oxalis acetosella*	10	<0.1	28	0.3±0.1	0	-	9	<0.1	26	0.2±0.1	40	0.4±0.1	76	1.4±0.4	***
V	*Deschampsia flexuosa*	10	0.1±<0.1	16	0.1±0.1	0	-	15	0.1±<0.1	26	0.4±0.1	40	2.9±1.5	88	34.4±4.0	***
M	*Plagiothecium undulatum*	10	0.1±0.1	12	0.1±<0.1	20	8.0±7.2	26	1.3±0.5	34	0.7±0.2	30	1.7±1.0	100	24.0±2.0	***
V	*Picea abies*	3	<0.1	12	0.1±0.1	0	-	26	0.3±0.1	44	3.8±1.4	60	7.5±3.4	96	5.9±1.9	***
H	*Lophocolea bidentata*	0	-	8	<0.1	20	1.0±0.9	2	<0.1	12	0.1±<0.1	10	<0.1	28	0.1±0.1	**
V	*Calamagrostis villosa*	3	<0.1	4	<0.1	0	-	6	<0.1	6	0.2±0.1	40	1.4±1.0	100	26.2±3.6	***
V	*Dryopteris dilatata*	0	-	4	<0.1	0	-	6	<0.1	12	0.1±<0.1	25	0.2±0.1	96	1.3±0.4	***
V	*Galium saxatile*	0	-	4	<0.1	0	-	6	<0.1	12	0.1±0.1	25	0.5±0.3	80	9.7±3.0	***
M	*Plagiothecium laetum*	0	-	4	<0.1	0	-	0	-	0	-	0	-	12	0.4±0.4	**
	- Forest ground species, occasionally on logs:															
V	*Trientalis europaea*	0	-	0	-	0	-	2	<0.1	6	<0.1	30	0.3±0.1	84	0.6±0.1	***
M	*Pleurozium schreberi*	0	-	0	-	0	-	2	<0.1	6	0.3±0.2	15	0.9±0.7	36	0.4±0.2	**
M	*Rhytidiadelphus loreus*	0	-	0	-	0	-	0	-	0	-	10	1.4±1.2	60	2.4±0.9	***
M	*Sphagnum girgensohnii*	0	-	0	-	0	-	2	<0.1	0	-	5	0.2±0.1	60	2.8±1.0	***
M	*Dicranum scoparium*	0	-	0	-	0	-	0	-	2	0.1±0.1	5	0.8±0.7	72	5.0±1.7	***
H	*Barbilophozia lycopodioides*	0	-	0	-	0	-	0	-	2	<0.1	5	0.1±0.1	20	0.1±0.1	***
V	*Sorbus aucuparia*	0	-	0	-	0	-	2	<0.1	0	-	0	-	52	0.2±0.1	***
M	*Sphagnum russowii*	0	-	0	-	0	-	0	-	2	<0.1	0	-	20	0.2±0.1	**
V	*Luzula sylvatica*	0	-	0	-	0	-	0	-	0	-	0	-	32	1.6±0.8	***
M	*Calliergon stramineum*	0	-	0	-	0	-	0	-	0	-	0	-	12	<0.1	***
	Indifferent species:															
M	*Plagiothecium denticulatum*	72	1.0±0.2	80	0.9±0.1	20	0.6±0.5	21	0.1±<0.1	46	1.0±0.4	30	0.8±0.5	68	0.4±0.1	**
M	*Pohlia nutans*	15	0.1±<0.1	12	<0.1	0	-	26	0.2±0.1	36	0.4±0.1	20	0.1±0.1	12	<0.1	*
H	*Mylia taylorii*	5	<0.1	0	-	0	-	6	<0.1	4	<0.1	5	0.1±<0.1	8	<0.1	
M	*Brachythecium salebrosum*	0	-	16	0.4±0.2	0	-	13	0.3±0.2	6	0.1±<0.1	0	-	4	<0.1	
H	*Lophozia ventricosa*	0	-	16	0.1±<0.1	0	-	2	<0.1	14	0.1±<0.1	10	<0.1	8	<0.1	
H	*Lophozia incisa*	0	-	0	-	0	-	2	<0.1	0	-	5	<0.1	4	<0.1	

[1] Rare species (occurence in two or less substrate types, <10% frequency in each substrate type): *Ptilidium ciliare*, *Parmeliopsis hyperopta* (LT, DDb); *Ptilidium pulcherrimum* (SD, DDb); *Cladonia squamosa*[4], *Gymnocarpium dryopteris*[4], *Hypnum cupressiforme*[4], *Parmelia saxatilis*[4] (DDb, DDd); *Placynthiella icmalea*[4] (DDc, DDd); *Bryoria fuscescens*[4] (SD); *Dicranoweisia cirrata*[4], *Tritomaria exsectiformis*[4] (DDb); *Barbilophozia attenuata*[4], *Cephalozia bicuspidata*[4], *C. leucantha*[4], *Cladonia macilenta*[4], *C. sulphurina*[4], *Hypocenomyce caradocensis*[4], *Mycoblastus sanguinarius*[4], *Pycnora leucococca*[4] (DDc); *Lycopodium annotinum*[4] (DDd); *Barbilophozia floerkei*, *Carex canescens*, *Digitalis purpurea*, *Diplophyllum albicans*, *Dryopteris expansa*, *Maianthemum bifolium*, *Mnium hornum*, *Molinia caerulea*, *Phegopteris connectilis*, *Plagiomnium affine*, *Polytrichum commune* (FG).

[2] DDa, early decay; DDb, early advanced decay; DDc, late advanced decay; DDd, strong decay.

[3] Significance of differences between cover values: * P<0.05, ** P<0.01, *** P<0.001 (Kruskal-Wallis test).

[4] Species was only found on standing or downed deadwood in the scope of this study.

Table 3.4 Results of ANOSIM (*R* values) analyzing the differences in community composition on downed deadwood for diameter and decay classes. Levels of significance: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

	1	2	3	4	5	6	7
Diameter class:							
2	0.32***						
3	0.40***	0.02					
4	0.31***	–0.11	–0.02				
5	0.36***	–0.24	–0.21	–0.23			
6	0.36**	–0.22	–0.25	–0.19	0.00		
7	0.35	–0.30	–0.35	–0.18	–0.25	0.00	
Decay class:							
2	0.00						
3	0.00	–0.11					
4	0.50***	0.56***	0.23***				
5	0.93***	0.71***	0.29***	–0.01			
6	0.55***	0.26***	0.18***	–0.01	–0.05		
7	0.90**	0.73***	0.16*	0.03	–0.10	–0.10	
8	0.63***	0.63***	0.29***	0.19	0.22	0.01	–0.01

Table 3.5 Pearson correlations between species richness of the individual taxonomic groups on standing and downed deadwood (*N*=147 relevés; * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$)

	Mosses	Hepatics	Lichens
Vascular plants	0.54***	0.42***	0.06
Mosses		0.48***	0.20**
Hepatics			-0.04

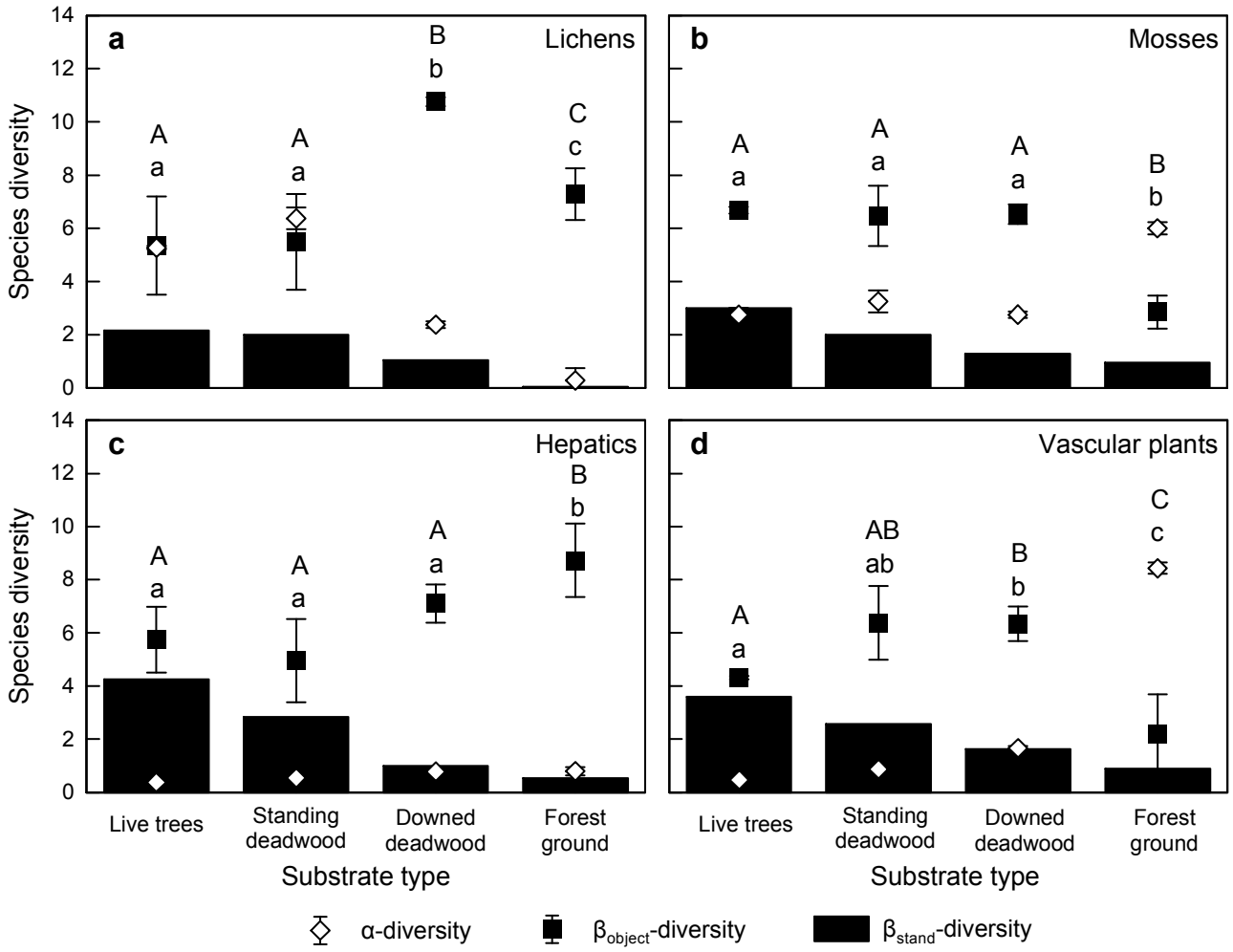

Fig. 3.1 Response of α- and β-diversities of (a) lichens, (b) mosses, (c) hepatics and (d) vascular plants on the substrate types (LT, live trees; SD, standing deadwood; DD, downed deadwood, FG, forest ground). Different letters above the markers indicate significant differences (Tukey's test); capital letters refer to α-diversity, lower-case letters to β-diversity (β_{object})

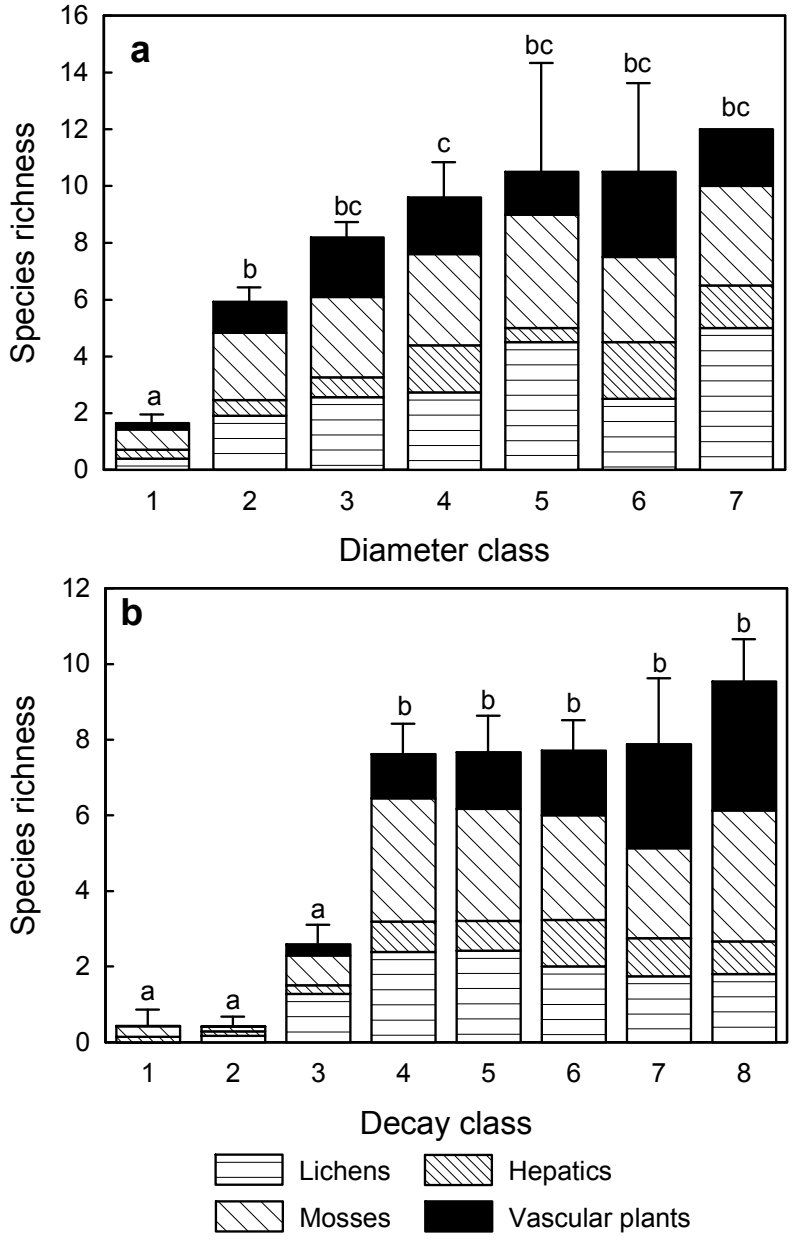

Fig. 3.2 Species richness (α-diversity) of all deadwood-inhabiting plant groups in the different (a) diameter and (b) decay classes of downed deadwood in the 100 m² plots (bars represent standard error for the total of species). The total species richness of columns with the same letter does not differ significantly ($P \leq 0.05$; Tukey's test)

3.5 Discussion

In accordance with the first hypothesis, deadwood was an important substrate for lower and higher plants in the investigated unmanaged spruce old-growth forest. More than 80 % of the species colonized deadwood, at least, as one suitable substratum. Our results also support the second hypothesis that a notable proportion of the total species of the old-growth forest is

restricted to deadwood. However, checking with the literature (e.g. DIERßEN 2001; JÄGER 2011; WIRTH et al. 2013) and based on our regional field experience, none of the 28 % of the total species which were exclusively found on deadwood in our study was an obligate inhabitant of deadwood.

In lichens, obligate dependence on deadwood exists, but is not common. Such species are usually specialized on decorticated wood (lignicolous species) and might also colonize longly decorticated parts of live trees. SPRIBILLE et al. (2008) classified 8 % of the deadwood-inhabiting lichen species in the Pacific Northwest of North America and 11 % of the deadwood-inhabiting lichen species in Fennoscandia as obligately lignicolous species. In bryophytes, lignicolous species usually also inhabit other substrata. This is also true for most species which were termed as 'epixylic specialists' and contrasted with more 'generalistic' species in other studies (e.g. ANDERSSON & HYTTEBORN 1991; ARSENEAULT et al. 2012). Especially most liverworts (e.g. *Calopogeia azurea*, *C. muelleriana*, *Cephalozia lunulifolia*, *Cephaloziella hampeana*, *Lepidozia reptans*, *Lophocolea heterophylla*, *Lophozia incisa*) and a few mosses (*Amblystegium serpens*, *Tetraphis pellucida*) found in our study are known for their preference for deadwood (DIERßEN 2001; KOPERSKI 2011), but most of these species also occurred on live trees and/or soil in the studied forest. The vascular plants flora of Central Europe lacks any 'true' epiphytes or lignicolous species. All species found on deadwood or live trees our study are essentially ground-dwelling species.

Notwithstanding the lack of any obligate colonizer of deadwood in the studied old-growth forest, the high number of species which occurred among others on deadwood or were even restricted to this type of substratum, evidences that deadwood plays a pivotal role for the diversity of lower and even higher plant species in unmanaged old-growth forests. The promotional effect of deadwood on many plant species is due to the facilitation of establishment at reduced competition compared to the ground (KIRBY et al. 1998; HUMPHREY et al. 2002). Facilitation by reduced competition has been discussed repeatedly in the context of forest regeneration (ZIELONKA & NIKLASSON 2001; BAČE et al. 2012). This type of facilitation is a weak relationship, but nevertheless significant to maintain forest biodiversity. The lack or rarity of obligate deadwood inhabitants is, thus, not a criterion that would inevitably lower the value that must be attributed to deadwood for conserving plant diversity. Meta-analyses that would address the significance of deadwood for the establishment of

ground-dwelling forest species on a biome level or the global scale are, to our knowledge, unfortunately lacking so far.

The increase in the total species richness of the sum of all studied plant groups with increasing diameter and decay of the deadwood generally supports our third hypothesis and is in line with studies from other forest ecosystems (KRUYS et al. 1999; ÓDOR et al. 2006; BUNNELL et al. 2008). However, with respect to both diameter and decay stage, species richness reaches a saturation point relatively early. In the case of the decay stage, saturation is reached, since epiphytes which colonize the early stages of decay are increasingly displaced by species which can colonize both soft wood and the ground (HUMPHREY et al. 2002; ÓDOR & VAN HEES 2004). The former group is primarily represented by lichens, which receive less intense competition by the more productive vascular plants and bryophytes in early decay stages than on soft wood (CRITES & DALE 1998; ZIELONKA & PIĄTEK 2004). The latter group includes even dominant vascular plant species of the ground vegetation, like *Calamagrostis villosa*, *Deschampsia flexuosa*, *Vaccinium myrtillus*, and *Galium saxatile*. The colonization of downed deadwood by both epiphytes of live trees and standing deadwood and, in later stages, of species from the ground vegetation explains the low species turnover on downed deadwood on the stand level (β_{stand}). Between the individual deadwood pieces, species turnover (β_{object}) was much higher (and especially high for lichens) reflecting the effect of decay and diameter on the species composition. In a study of *Picea abies* stumps in Belgium, Cornelissen & KARSSEMEIJER (1987) concluded that wood in early decay stages would be preferred by pleurocarpous mosses and adpressed liverworts, whereas late decay stages would be dominated by ascending liverworts and acrocarpous mosses. Any such pattern was not found in our data, even though the study of CORNELISSEN & KARSSEMEIJER (1987) was conducted in plantations of the same tree species under a similar oceanic climate.

3.6 Conclusions

Our study demonstrated the significance of deadwood for total forest plant diversity for lichens, bryophytes and vascular plants despite the lack of any obligate deadwood colonizers in the studied forest. The high proportions of species which occur on deadwood in addition to the forest floor and/or the bark of live trees (84 % of the total species) as well as of species which were only found on deadwood despite their ability to grow on the ground and/or live

trees (28 %) show that deadwood has an outstanding function for forest biodiversity, even if few or (as in the present example) no species which are obligately bound to deadwood are present. As found repeatedly in other studies, large-diameter deadwood is richer in species than small-sized deadwood pieces. Though strongly decayed deadwood is richer in species than wood that is hardly decomposed, species richness remains constant from intermediate to final decay stages, whereas a high species turnover indicates the succession from species of early (mostly lichens) to late (mostly bryophytes and vascular plants) stages of deadwood-inhabiting vegetation.

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Chapter 4

Separating forest continuity from tree age effects on plant diversity in the ground and epiphyte vegetation of a Central European mountain spruce forest

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***Flora* 208: 238-246.**

Abstract

Forest continuity has been identified as an important factor influencing the structure and diversity of forest vegetation. Primary forests with centuries of continuity are usually more diverse than young, secondary forests as forest are colonized only slowly and because they are richer in old tree individuals. In the present study, performed in unmanaged high-elevation spruce forests of the Harz Mountains, Germany, we had the unique opportunity to separate the effects of forest continuity and tree age on plant diversity. We compared an old-growth spruce forest with century-long habitat continuity with an adjacent secondary spruce forest which had naturally established on a former bog after 1796 when peat exploitation halted. Comparative analysis of the ground and epiphyte vegetation showed that the plant diversity of the old-growth forest was not higher than that of the secondary forest with a similar tree age of > 200 years. Our results suggest that a period of > 200 years was sufficient for the secondary forest to be colonized by the whole regional species pool of herbaceous and cryptogam forest plants and epiphytes. Therefore, it is likely that habitat structure, including the presence of old and decaying trees, was more important for determining plant diversity than the independent effect of forest continuity. Our results are probably not transferrable to spruce forests younger than 200 years and highly fragmented woodlands with long distances between new stands and old-growth forests that serve as diaspore sources. In addition, our results might be not transferable to remote areas without notable air pollution, as the epiphyte vegetation of the study area was influenced by SO_2 pollution in the second half of the 20th century.

Keywords old-growth forest; secondary forest; plant diversity; bryophytes; lichens

4.1 Introduction

The distribution and abundance of forest plants is strongly influenced by forest age and stand history (PETERKEN & GAME 1984). Many forest species of vascular plants, lichens and bryophytes are assumed to be restricted to forests with a habitat continuity of at least several centuries (ROSE 1976, PETERKEN & GAME 1981, EDWARDS 1986, Brunet 1993). The same is true for invertebrates, fungi and other organism groups (NILSSON et al. 1995, BREDESEN et al. 1997, ALEXANDER 1998). The main cause of these restrictions is the limited dispersal ability of many forest species (SILLETT ET AL. 2000, HILMO & SÅSTAD 2001, VERHEYEN et al. 2003). Therefore, such species are bound to (primary) old-growth forests or at least ancient secondary forests with long habitat continuity. Managed forests with repeatedly interrupted habitat continuity lack many species of old-growth forests (GUSTAFSSON & HALLINGBÄCK 1988, KUUSINEN & SIITONEN 1998). Young, small forest patches in fragmented landscapes can even be largely devoid of typical forest species (DZWONKO & LOSTER 1988).

In Central Europe, where humans began to interrupt the continuity of forest cover with the import of agriculture from the Middle East already in the Neolithic (HAAK et al. 2010, PICHLER et al. 2011), completely undisturbed forests are lacking. However, a few primeval forest patches do still exist where stand history can be tracked back for many centuries and at the same time, stand structure suggests that these stands have likely never experienced stand-level disturbance by humans (ELLENBERG & LEUSCHNER 2010). In such forests, it is often difficult to separate the effect of forest continuity on species diversity from the effect of tree age. This is because such primeval forests are today often located in conservation areas, whereas most woodland with interrupted habitat continuity are managed forests, which lack overmature and decaying trees.

Though many species have been classified as to be characteristic of ancient forests in the sense of long habitat continuity in expert assessments (e.g. ROSE 1976, WULF 1997), those do not distinguish between species whose reproduction biology restricts them to forests with uninterrupted or, at least, long-term continuity (GRASHOF-BOKDAM & GEERTSEMA 1998, HILMO et al. 2011) and species with a preference for site conditions which are mainly found in forests with old tree individuals (MCGEE & KIMMERER 2002, MONING et al. 2009, HAUCK 2011). The higher importance of substrate specificity and habitat persistence over forest continuity and dispersal limitations has been discussed for species in boreal forests (NORDÉN

& APPELQVIST 2001, GIBB et al. 2006, LÕHMUS & LÕHMUS 2011). In Central Europe, options for the comparative study of forests with old trees with or without interrupted continuity are naturally limited because of the scarcity of relevant forest stands. Comparative approaches partly include forests with contrasting site conditions and different tree species composition, limiting conclusions (KÜHN 2000).

In the present study, we had the unique opportunity to directly compare two montane stands of Norway spruce (*Picea abies* (L.) Karst.) with contrasting history. Both stands were comprised of more than 200-year old trees, but strongly differed in the duration of forest cover. One stand is an old-growth forest, which had been banned for logging since the early Middle Ages. The other stand developed through natural succession on an exploited and drained bog at the end of the 18th century and was, like the old-growth forest, never logged afterwards and, thus, has a cohort structure. Since both the old-growth forest and the secondary forest share old trees with an age far beyond the rotation age in managed forests, but strongly differ in the continuity of their existence, we used this setting for an attempt to separate the effect of forest age (or continuity) on plant diversity from that of tree age. Our study covered the ground vegetation as well as epiphytic lichens and bryophytes on live and dead trees. The aim of the study was to test the hypothesis that both ground vegetation and epiphyte vegetation are more diverse in the old-growth (primary) forest than in the secondary forest despite similar tree age, thus evidence on age-dependent effects of habitat continuity on plant diversity.

4.2 Material and Methods

Study sites

The study was conducted in a forest of Norway spruce (*Picea abies* (L.) Karst.) in Harz National Park on Mt. Brocken in Germany (51°47’ N, 10°38’ E, Fig. 4.1). Our investigations were carried out on the eastern and south-eastern slopes of Mt. Brocken between 950 and 1025 m a.s.l. The regional climate is characterized by high annual precipitation of 1600 mm (including annual snowfall of 1.9 m) and a mean annual temperature of 2.9 °C (GLÄSSER 1994). The local bed rock is iron-rich granite, creating strongly acidic soils. Dominant soil

types (FAO 2006) include cambisol and stagnogley, depending on the groundwater level. The predominant humus form is mor-like mold.

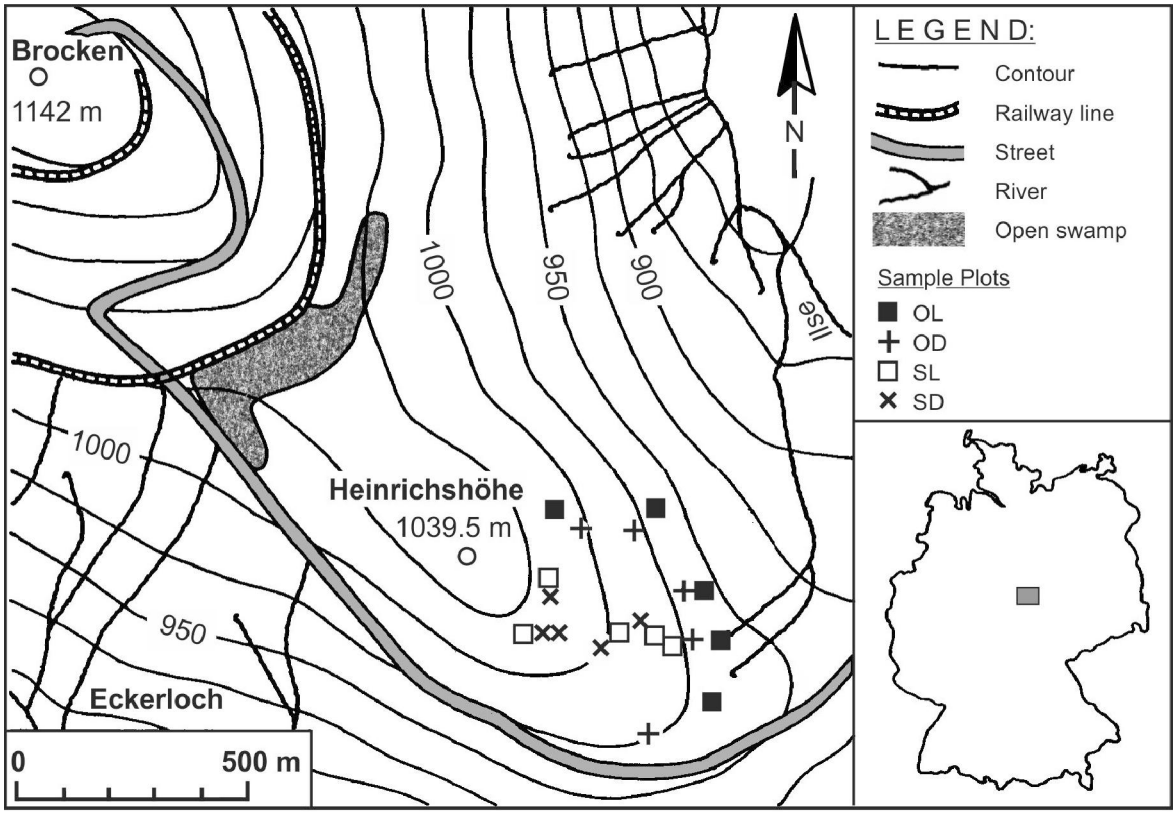

Fig. 4.1 Location of the study area within Germany and location of the sample plots (old growth forest, live [OL] and dead trees [OD]; secondary forest, live [SL] and dead trees [SD]) on Mt. Brocken

The old-growth (putatively primary) spruce forest ("Brockenurwald", 300 ha) had been banned for logging and forest pasture, as it was part of a hunting ground for nobility and clergy since the time of Charles the Great (ca. 800 AD, JACOBS 1870, SCHADE 1926) and was afterwards never subjected to timber harvest since the introduction of systematic forest management in the region in the late 17th century (BEI DER WIEDEN & BÖCKMANN 2010). This stand is, therefore, considered as a forest with uninterrupted habitat continuity and therefore probably a primary forest. Characteristic of this old-growth forest is the co-occurrence of different forest age stages in a small-scale pattern of irregularly distributed patches (STÖCKER 2001, 2002; KATHKE & BRUELHEIDE 2010). The oldest trees in this stand are more than 280 years old (HAUCK et al. 2012a).

The nearby secondary forest has evolved on a former bog site which has been exploited for peat since ca. 1740 (KORTZFLEISCH 2008). The extraction of peat, which was partly dug down

to the bedrock (BEUG et al. 1999), was finally abandoned in 1796 (KORTZFLEISCH 2008). Afterwards, the drained and exploited sites were colonized by Norway spruce, creating uniform stands (WEGENER & KISON 2002), which are now more than 200 years old. Throughout the paper, we use the terms "old-growth" and "secondary" forest to differentiate the probably never-logged stand from the stand which has been established on the former bog in the course of secondary succession.

Sample plot selection

In both forest sites, groups of old, living and dead trees were selected, structurally corresponding to the overmature and decay stages of natural spruce forest dynamics (STÖCKER 1997). Most of the dead trees had been damaged by bark beetle (*Ips typographus* L.), which is in the recent time a common cause of spruce dieback in the upper Harz Mountains (WEGENER et al. 2003); Most of the dead trees had been damaged by bark beetle (*Ips typographus* L.), which is a common cause of spruce dieback in the upper Harz Mountains (WEGENER et al. 2003); others are probably the remnants of the dieback from SO2 pollution during the second half of the 20th century (HAUCK et al. 2012a). Each plot type was represented by five replicate sample plots of 10 m x 10 m. Random plot selection was not possible due to the limited size of the study area. Plots are abbreviated as OL (old-growth forest, dominated by live trees), OD (old-growth forest with many dead trees), SL (secondary forest, live trees) and SD (secondary forest, dead trees) throughout.

Vegetation surveys

Ground vegetation was recorded by estimating the cover of all species of vascular plants, bryophytes and lichens. For woody plants, data were recorded separately for the tree (> 2 m height), shrub (< 2 m) and herb layers. Ground-inhabiting bryophytes and lichens were noted as a separate cryptogam layer. Each relevé was recorded from the entire plot size of 100 m², which follows the range of plot sizes recommended for vegetation analyses in temperate and boreal forests (DIERSCHKE 1994). The cover of the individual species was estimated in percent using 5 %-intervals for species covering ≥ 10 % of the plot area and 1%-intervals for the other species. Species covering less than 1 % were put to 0.5 % (if more than one individual was present) or 0.1 % (one individual). Epiphytic bryophytes and lichens as well as vascular plants occasionally growing on wood were recorded from the trunks of all live and standing dead

trees with a minimum height of 2 m. On the studied trees, cover of all species was recorded from trunk segments including the lower 2 m above the ground and all aspects (HAUCK et al. 2002). Cover was estimated in the same manner as with ground vegetation. Nomenclature of species is based on WISSKIRCHEN & HAEUPLER (1998, vascular plants), KOPERSKI et al. (2000, bryophytes) and WIRTH et al. (2011, lichens).

Structural characteristics and soil properties

Some structural characteristics of the sample plots are compiled in Table 4.1. Within the plots, diameter at breast height (dbh) of all sample trees was measured with a diameter tape. Height of all trees with a dbh > 7 cm was measured with a Vertex IV sonic clinometer and a T3 transponder (Haglöf, Långsele, Sweden). Length and diameter of lying trunks were also measured with a measuring tape. A photograph of the canopy was taken in every plot using a hemispherical lens (Coolpix 8400, Fisheye converter UR-E16; Nikon, Tokio, Japan). To avoid interference with the ground vegetation, the camera was positioned at 1.0 m above the ground. The hemispherical photos were taken on days with evenly overcast sky. By greyscale-reduction photo pixels were assigned to gaps or areas covered by the canopy. Canopy closure (i.e. photographed area covered by canopy) is given in percent of the total area.

Soil samples were taken from a soil profile in the centre of each plot. The pH was measured in aqueous suspension. To analyze concentrations of Ca, K, and Mg, fresh soil samples were extracted in 0.2 M $BaCl_2$ solution and measured with ICP-OES (Optima 5300 DV, Perkin Elmer, Waltham, Massachusetts, USA). Concentrations of C and N, as well as the C/N ratio were obtained from dry soil samples measured with a CN analyzer (Vario EL III, Elementar Analysensysteme, Hanau, Germany). Results of the soil analyses revealed marked differences in the soil-properties between old-growth and secondary forests, particularly in the nutrient concentrations (Table 4.1).

Table 4.1 Structural characteristics and soil properties of the studied old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees). Arithmetic means ± standard error (*N*=5), minimum and maximum values in brackets

	OL	OD	SL	SD	P^f
Soil profile depth (cm)	50.6±3.9	50.6±1.9	65.3±5.6	64.6±2.6	*
Soil water content[ab]	95.7±10.6	128.7±19.1	108.2±11.6	120.2±15.2	
C/N ratio[c]	19.4±1.0	19.0±0.9	19.3±0.5	20.6±0.4	
C_{total}[bc]	28.4±2.8	23.7±3.4	20.9±0.63	20.2±2.0	
Ca[c] (mol/g)	0.17±0.07	0.15±0.04	0.03±<0.01	0.02±<0.01	**
K[c] (mol/g)	0.08±0.01	0.06±0.01	0.03±<0.01	0.03±<0.01	**
Mg[c] (mol/g)	0.05±0.01	0.05±0.01	0.01±<0.01	0.01±<0.01	**
N[c] (mol/g)	0.8±0.11	1.03±0.13	0.68±0.06	0.66±0.05	
pH_{H2O}[c]	3.6±1.0	3.7±0.7	3.7±0.7	3.8±1.0	
Canopy cover (%)	85.4±1.3	74.3±2.1	91.6±0.5	89.6±0.9	**
Living trees[d] ha^{-1}	420±36	0±0	400±40	60±36	**
Dbh of living trees (cm)	47±2 (20-64)	0±0 (0)	34±1 (6-60)	45±2 (28-38)	**
Height of living trees (m)	21±1 (9-28)	0±0 (0)	18±<1 (2-26)	18±1 (15-20)	**
Saplings[e] ha^{-1}	2560±1024	1660±598	1560±395	700±265	*
Dead trees[d] ha^{-1}	140±46	360.0±36	160±46	1120±131	**
Dbh of dead trees (cm)	22±6 (9-56)	50±5 (6-71)	21±1 (10-31)	22±2 (3-47)	*
Height of dead trees (m)	7±1 (3-18)	14±3 (2-26)	7±<1 (2-7)	5±<1 (2-22)	

[a] Soil depth 0-60 cm
[b] % of dry weight
[c] Soil depth 0-20 cm
[d] Spruce trees ≥ 2.0 m
[e] Spruce trees < 2.0 m
[f] Level of significance * $P<0.05$, ** $P<0.01$, *** $P<0.001$ (Kruskal-Wallis test)

Data analysis

Arithmetic means ± standard errors are presented throughout the paper. Statistical analyses were calculated with R 2.14.0 software (R Development Core Team, Vienna, Austria). All data were tested for normal distribution with the Shapiro-Wilk test. The significance of differences between different plot types was tested with the Kruskal-Wallis test, as the data were not normally distributed. The dominance structure of the vegetation was quantified by calculating N_1-diversity which is defined as a modified Shannon function $N_1 = e^{H'}$ (KREBS 1999). In this equation, H' is the Shannon function ($H' = -\sum p_i \cdot \ln p_i$; p_i = cover of species i divided by the total coverage of all species per sample). N_1 specifies the number of equally abundant species producing the same diversity value as the calculated Shannon-Wiener

function H'. Strong differences between N_1 and the total number of species (α-diversity) in a relevé illustrate the dominance of single species (i.e. reduction of plant diversity according to Shannon). Non-Metric Scaling ordination (NMDS) was applied to study differences between different forest development stages in variation of ground plant and epiphyte cover. In the ground vegetation, response of single plant species to selected soil variables (Ca, K, Mg, pH, water content and C/N ratio) and canopy cover was tested with Canonical Correspondence Analysis (CCA). Both ordinations were performed using the program PCord 5.14 (MjM Software, Glenneden Beach, Oregon, U.S.A.). To test for significant differences in the community composition between the forest structure types, epiphyte and ground vegetation relevés were subjected to the multivariate, non-parametric analysis of similarities (ANOSIM, CLARKE et al. 1993) using the PAST 2.15 software (Ø. Hammer, Natural History Museum, University of Oslo, Norway).

4.3 Results

Ground vegetation

The ground vegetation in the old-growth forest and the secondary forest was dominated by the vascular plant species *Deschampsia flexuosa*, *Calamagrostis villosa*, *Vaccinium myrtillus* and *Galium saxatile* (Table 4.2). *Trientalis europaea* (and with an insignificant trend also *Oxalis acetosella*) were more abundant in the secondary forest. *Luzula sylvatica* was mainly found in the old-growth forest. The cryptogam layer in all forest types was dominated by *Plagiothecium undulatum*, *Dicranum scoparium* and *Polytrichum formosum*. The latter was most abundant in old-growth plots dominated by dead trees. The abundance of *Dicranum scoparium* was significantly higher below living than dead trees in either forest type. The mean cover of *Plagiothecium denticulatum*, *Lophocolea heterophylla*, *Amblystegium serpens* and *Tetraphis pellucida* was significantly higher in the secondary than in the old-growth forest. The secondary forest was richer in liverwort species than the old-growth forest, though all liverwort species only reached low cover values.

Table 4.2 Cover (in %; arithmetic means ± standard error, *N*=5) of vascular plant, bryophyte and lichen species occurring in the ground vegetation of the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees)

	OL	OD	SL	SD	*P*[b]
Cover herb layer	71.0±1.7	74.0±2.6	70.0±2.8	78.0±3.0	
Cover cryptogam layer	46.0±7.7	38.0±7.3	55.0±4.7	45.0±5.8	
Herb layer[a]					
Deschampsia flexuosa	46.0±10.7	28.0±10.8	42.0±6.6	31.6±6.2	
Calamagrostis villosa	20.4±6.1	41.0±8.4	19.2±6.1	53.0±10.0	
Vaccinium myrtillus	17.2±4.7	9.0±5.8	11.6±4.2	4.6±1.2	
Galium saxatile	5.4±2.7	12.3±3.4	3.8±1.0	7.4±3.0	
Luzula sylvatica	3.1±2.7	0.1±0.1	0.0±0.0	0.1±0.1	
Oxalis acetosella	1.1±0.4	1.0±0.2	10.8±4.5	3.4±1.7	
Picea abies	0.7±0.2	0.5±0.1	0.7±0.1	0.5±0.1	
Dryopteris dilatata	0.4±0.2	0.6±0.2	1.0±0.2	0.9±0.1	
Trientalis europaea	0.4±0.2	0.5±0.1	2.3±0.7	3.6±0.7	**
Sorbus aucuparia	0.1±0.1	<0.1	0.4±0.1	0.2±0.1	
Cryptogam layer[a]					
- Mosses					
Plagiothecium undulatum	27.0±5.4	18.0±2.3	34.0±3.3	27.0±4.6	
Dicranum scoparium	5.9±3.2	0.7±0.3	4.2±0.7	1.2±0.9	*
Polytrichum formosum	2.8±0.8	13.0±2.3	9.2±1.5	9.8±4.7	*
Plagiothecium laetum	2.0±1.8	0.1±0.1	0.6±0.4	1.9±1.4	
Rhytidiadelphus loreus	0.9±0.3	1.3±0.8	1.4±0.1	0.8±0.3	
Plagiothecium denticulatum	0.5±0.2	0.2±0.1	2.4±0.7	2.1±0.8	*
Sphagnum girgensohnii	5.1±3.4	0.8±0.5	0.6±0.2	0.0±0.0	
Pleurozium schreberi	0.2±0.2	0.2±0.1	0.0±0.0	0.3±0.1	
Dicranum fuscescens	0.0±0.0	2.4±1.7	1.8±0.3	2.1±0.6	
Amblystegium serpens	0.1±0.1	0.0±0.0	0.0±0.0	0.4±0.2	**
Pohlia nutans	<0.1	0.0±0.0	0.0±0.0	0.3±0.2	
Tetraphis pellucida	0.0±0.0	0.0±0.0	0.1±0.1	0.1±0.1	*
- Liverworts					
Barbilophozia lycopodioides	0.1±0.1	0.2±0.2	0.1±0.1	0.3±0.2	
Lophocolea bidentata	<0.1	0.2±0.1	0.1±<0.1	0.2±0.2	
Lophocolea heterophylla	0.0±0.0	<0.1	0.2±0.1	0.2±0.1	*
Lepidozia reptans	0.0±0.0	<0.1	<0.1	0.1±0.1	
Lophozia ventricosa	<0.1	0.0±0.0	<0.1	0.0±0.0	
Lophozia incisa	0.0±0.0	0.1±0.1	<0.1	0.0±0.0	

[a] Rare species (one or two structure types, ≤0.2 % mean cover) – old-growth forest: *Senecio sylvaticus*; *Brachythecium salebrosum*, *Cladonia polydactyla*, *Plagiomnium affine*, *Polytrichum commune*, *Sphagnum russowii*; *Diplophyllum albicans*. Secondary forest: *Carex canescens*, *Urtica dioica*; *Herzogiella seligeri*, *Rhytidiadelphus squarrosus*; *Barbilophozia floerkei*, *Calypogeia azurea*, *Calypogeia muelleriana*, *Cephaloziella hampeana*, *Cephalozia leucantha*, *Cephalozia lunulifolia, Chiloscyphos polyanthus*.

[b] Level of significance * $P<0.05$, ** $P<0.01$, *** $P<0.001$ (Kruskal-Wallis test)

The N_1-diversity and α-diversity of the herb layer were each similar across the different forest structure types, with a high deviation of N_1- from α-diversity in all plot types (Fig. 4.2). N_1-diversity of cryptogams did not differ between the plot types either, whereas the α-diversity of the cryptogam layer was higher in the secondary forest than in the old-growth forest; in the latter, α-diversity deviated more from N_1-diversity the in the former. Moss and especially liverwort α-diversity was higher in the ground vegetation of the secondary than of the old-growth forest ($p < 0.05$), whereas there was no such difference for the vascular plants (Fig. 4.3a). The different forest types did not form clearly differentiated clusters in the NMDS; nevertheless live trees of either site had a trend for low axis 1 scores, whereas dead trees clustered preferentially at high scores along axis 1 (Fig. 4.4a). In the CCA, Monte Carlo-Test results on the response of forest ground species to canopy cover and soil variables proved no significance of the measured site factors to species distribution. In the ANOSIM, no significant differences were found between the forest types, except between old-growth stands with dead trees and live secondary stands (Table 4.4).

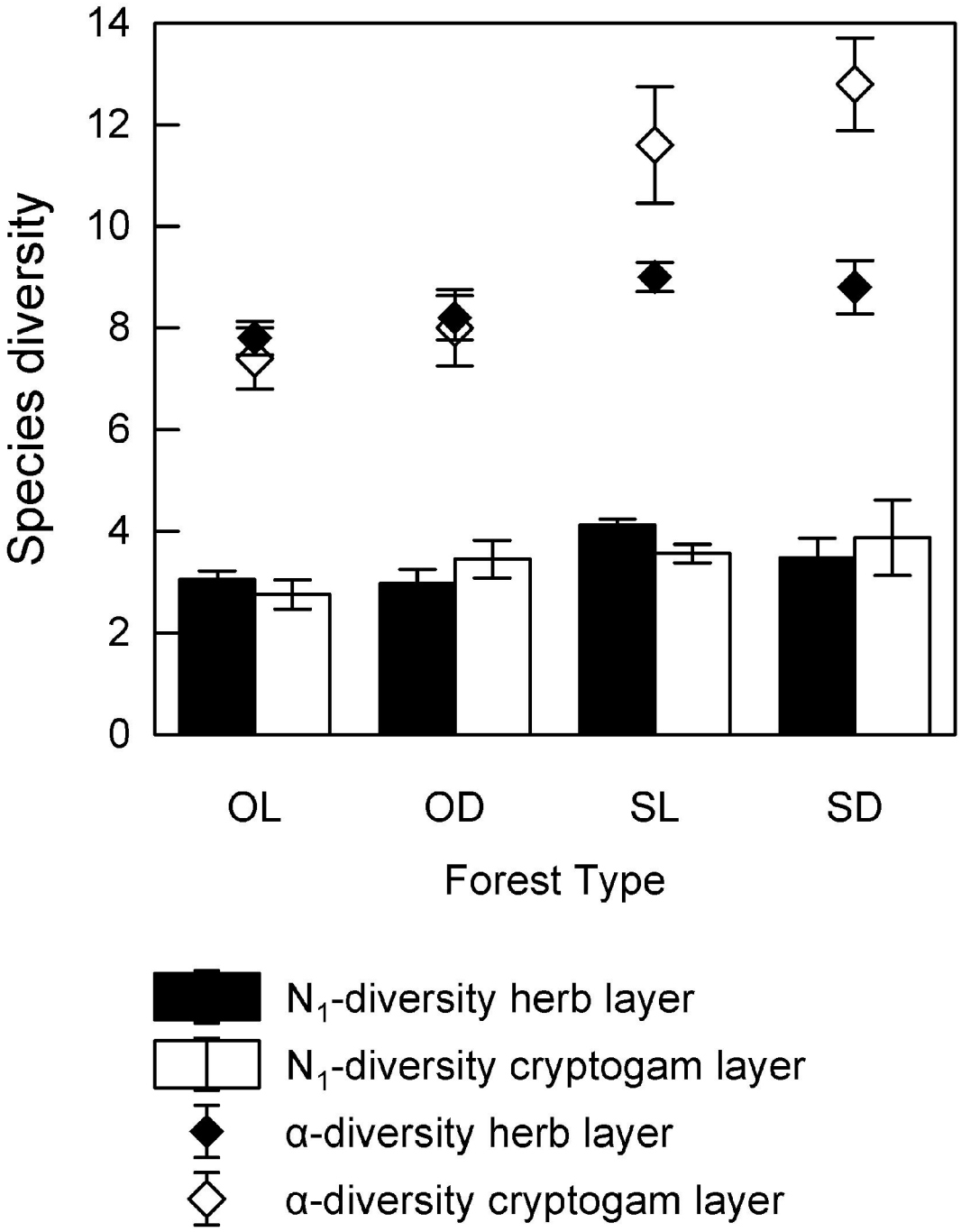

Fig. 4.2 N_1- and α-diversity of ground vegetation plots in the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees).

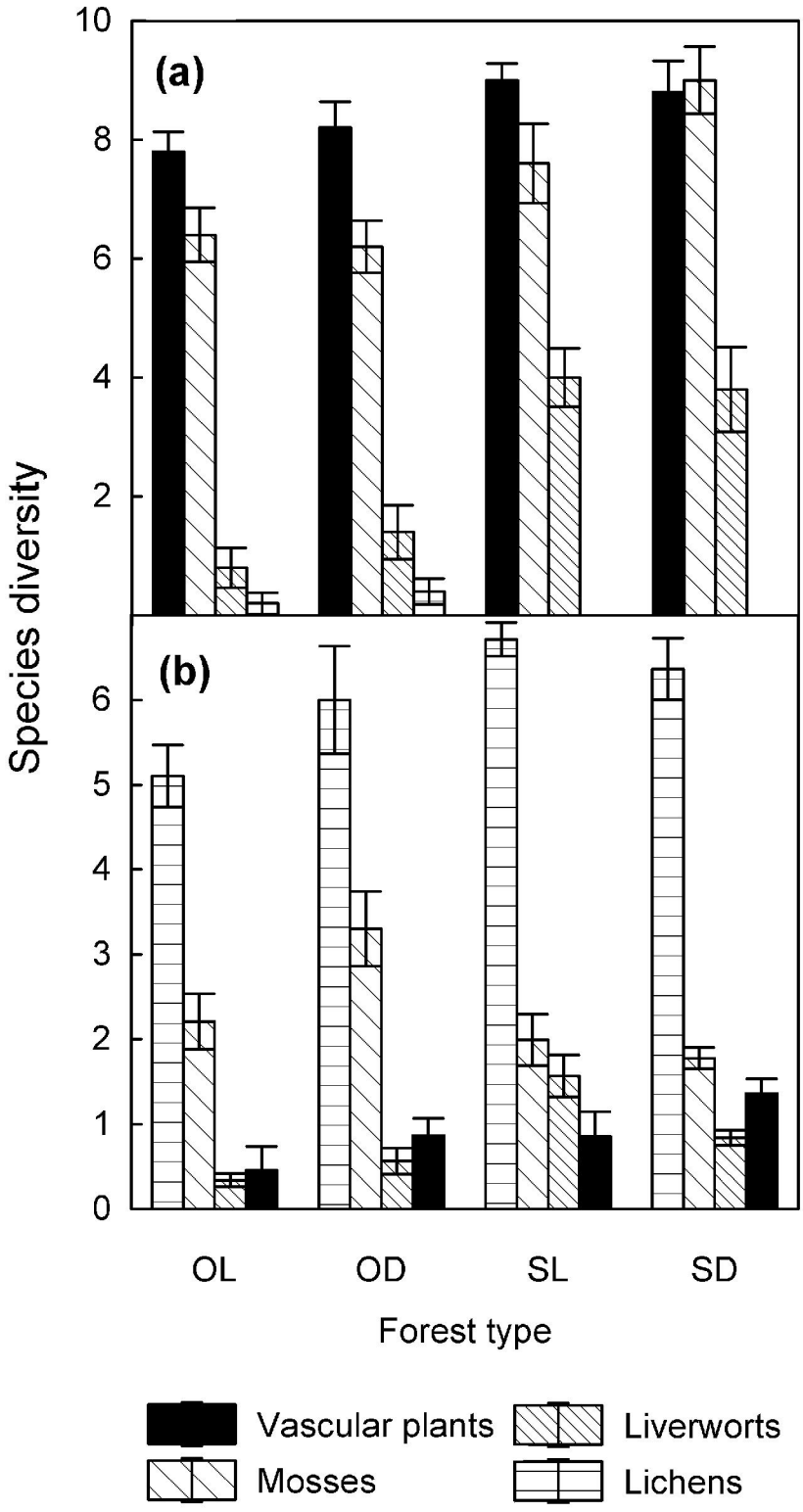

Fig. 4.3 α-diversity of different species groups in (a) the ground vegetation, (b) the epiphyte assemblages in the in the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees)

Table 4.4 ANOSIM-analysis of significant differences ($P < 0.05$) in the ground vegetation and epiphyte assemblages among the he studied old-growth forest (OL, live trees; OD, dead trees) and the secondary forest plots (SL, live trees; SD, dead trees).

	OL	OD	SL
Ground vegetation			
OD	0.17		
SL	0.12	<0.001	
SD	0.06	0.6	0.07
Epiphytes on trees			
OD	0.02		
SL	<0.001	<0.001	
SD	0.73	0.76	0.58

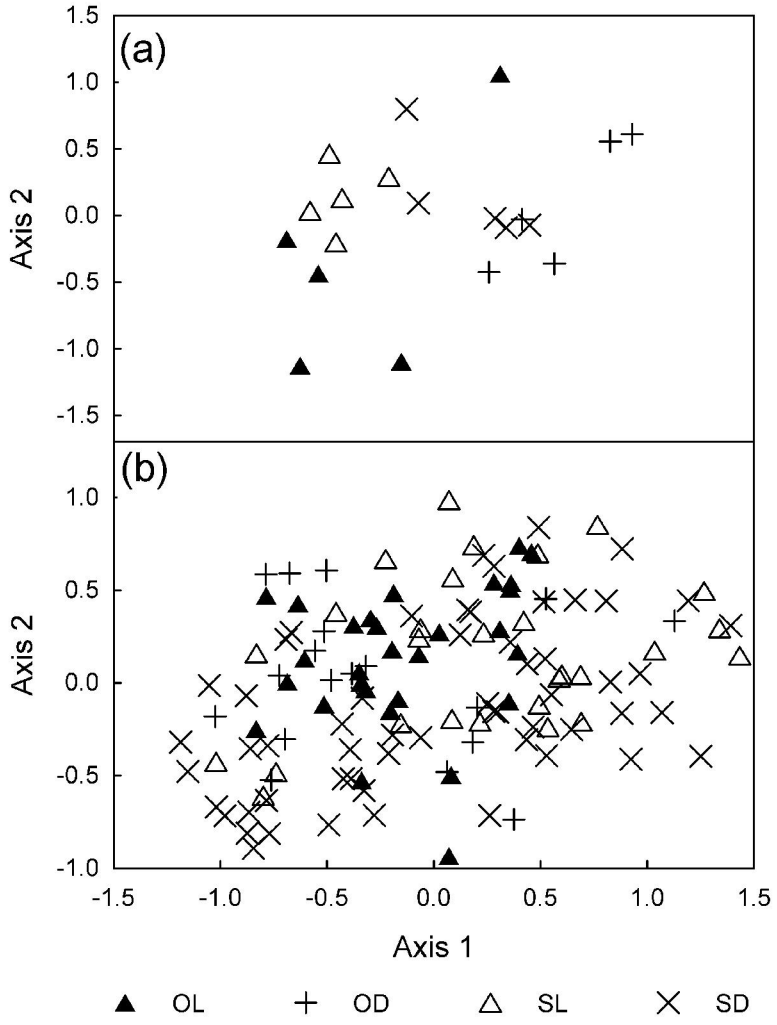

Fig. 4.4 NMDS ordination of vegetation relevés in the in the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees). (a) Ground vegetation (N=20 plots). Mean stress in real data: Axis 1, 45.453; Axis 2, 17.244. (b) Epiphytes on trees ≥ 2.0 m (N=133 trees). Mean stress in real data: Axis 1, 42.761; Axis 2, 21.433.

Epiphytes

The most abundant epiphytes across all plot types included the lichens *Cladonia digitata*, *C. polydactyla*, *Lepraria jackii* as well as the bryophytes *Plagiothecium denticulatum* and *Dicranum fuscescens* (Table 4.3). The lichen *Pseudevernia furfuracea* and the bryophytes *Polytrichum formosum* and *Pohlia nutans* were more frequent in the old-growth forest than in the secondary forest. *Cladonia ramulosa* was restricted to dead trees in the old-growth forest. Differences in the frequency and abundance of *Cladonia pyxidata* s.l., *Mycoblastus fucatus*, *Bryoria fuscescens*, *Lepidozia reptans* and *Lophozia ventricosa* between plots dominated by living and dead trees were more pronounced in the old-growth than the secondary forest. Like the ground vegetation, epiphyte vegetation in the secondary forest included more liverwort species than in the old-growth forest. Among the epiphytic occurrences of vascular plants, *Vaccinium myrtillus* was most frequent across the forest types. *Trientalis europaea* and *Calamagrostis villosa* were significantly more frequent in the secondary than in the old-growth forest.

The N_1-diversity of epiphytes did not differ strongly between the forest types, whereas the α-diversity of epiphytes was lower on live trees of the old-growth stand than in the other plot types (Fig. 4.5). The α-diversity of liverworts and vascular plants was higher in the secondary than in the old-growth forest, whereas it was the other way round for mosses (Fig. 4.3). The species number of lichens did not strongly differ between the different forest types (Fig. 4.3). In the NMDS, no separate clusters were found for different forest types (Fig. 4.4b). The ANOSIM was more sensitive and revealed differences between the live trees of the secondary forest and the trees in the old-growth forest as well as between live and dead trees of the old-growth plots (Table 4.4).

Table 4.3 Frequency (in % of trees, arithmetic mean of plot-wise mean values) and cover (in %; arithmetic means ± standard error) of trunk-inhabiting epiphytes growing at 0-2 m height above the soil level on trees of a minimum height of 2 m in the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees) (*N*=5)

	OL	OD	SL	SD	*P*[b]
Total Cover	25.8±4.6	36.5±5.5	20.0±2.6	26.2±6.2	
Lichens[a]					
Cladonia digitata	93 5.8±1.1	95 7.8±0.8	73 2.2±0.6	75 5.5±1.3	**
Lepraria jackii	92 5.8±1.8	87 9.1±2.7	95 7.7±2.7	88 11.1±4.8	
Cladonia polydactyla	91 7.0±1.1	95 10.6±2.7	80 4.3±1.1	76 2.7±0.9	
Lecanora conizaeoides	79 0.7±0.2	26 <0.1	64 0.5±<0.1	48 0.3±0.1	
Hypogymnia physodes	60 0.5±0.2	57 1.2±0.4	72 0.4±0.1	60 1.1±0.2	
Hypocenomyce scalaris	51 3.5±1.3	63 3.6±1.8	77 0.8±0.2	70 2.0±1.2	
Parmeliopsis ambigua	28 0.3±0.1	58 0.3±0.1	71 0.2±<0.1	59 0.2±0.1	
Pseudevernia furfuracea	7 <0.1	18 0.2±0.1	<0.1	7 <0.1	
Mycoblastus fucatus	6 <0.1	22 <0.1	27 0.1±<0.1	55 0.3±0.1	*
Platismatia glauca	0 0.0±0.0	50 0.6±0.2	14 <0.1	17 0.1±0.1	
Cladonia ramulosa	0 0.0±0.0	29 0.1±<0.1	0 0.0±0.0	0 0.0±0.0	*
Cladonia pyxidata s.l.	0 0.0±0.0	24 0.3±0.2	37 0.5±0.1	30 0.4±0.2	*
Bryoria fuscescens	0 0.0±0.0	7 <0.1	5 <0.1	3 <0.1	
Mosses[a]					
Plagiothecium denticulatum	66 0.6±0.2	76 0.8±0.3	39 0.2±<0.1	18 0.3±0.1	**
Dicranum fuscescens	56 1.5±0.8	78 2.4±0.7	71 1.2±0.9	49 0.4±0.1	
Tetraphis pellucida	41 0.7±0.2	61 0.8±0.3	59 0.2±0.1	33 0.2±0.1	
Polytrichum formosum	35 0.6±0.4	44 0.3±0.1	17 0.1±0.1	13 0.1±<0.1	*
Pohlia nutans	6 0.1±<0.1	12 <0.1	0 0.0±0.0	0 0.0±0.0	*
Amblystegium serpens	5 <0.1	5 <0.1	0 0.0±0.0	2 <0.1	
Plagiothecium undulatum	3 <0.1	4 <0.1	13 <0.1	5 <0.1	
Brachythecium salebrosum	0 0.0±0.0	17 0.4±0.2	0 0.0±0.0	0 <0.1	
Liverworts[a]					
Lepidozia reptans	19 0.1±<0.1	5 <0.1	37 0.3±0.1	18 0.1±<0.1	
Lophocolea heterophylla	9 <0.1	10 <0.1	37 0.1±<0.1	14 <0.1	
Cephalozia lunulifolia	2 <0.1	5 <0.1	23 0.1±0.1	3 <0.1	
Lophozia ventricosa	0 0.0±0.0	22 0.1±0.1	8 0.1±<0.1	2 <0.1	
Ptilidium ciliare	3 <0.1	0 0.0±0.0	5 <0.1	6 0.1±<0.1	*
Lophocolea bidentata	0 0.0±0.0	9 <0.1	6 <0.1	4 <0.1	
Ptilidium pulcherrimum	0 0.0±0.0	5 <0.1	3 <0.1	1 <0.1	
Cephalozia leucantha	0 0.0±0.0	0 0.0±0.0	16 <0.1	11 <0.1	**
Vascular plants[a]					
Vaccinium myrtillus	16 0.1±0.1	30 0.3±0.1	22 0.4±0.2	32 0.1±0.1	
Deschampsia flexuosa	13 0.1±0.1	17 0.1±0.1	25 <0.1	16 <0.1	
Oxalis acetosella	12 <0.1	22 0.2±0.1	29 <0.1	32 <0.1	
Picea abies	6 <0.1	7 0.1±0.1	0 0.0±0.0	2 <0.1	
Dryopteris dilatata	2 <0.1	0 0.0±0.0	7 <0.1	8 <0.1	
Galium saxatile	0 0.0±0.0	7 <0.1	5 <0.1	2 <0.1	
Calamagrostis villosa	0 0.0±0.0	5 0.1±<0.1	3 <0.1	19 <0.1	*
Trientalis europaea	0 0.0±0.0	0 0.0±0.0	12 <0.1	25 0.1±<0.1	**

Footnotes Table 4.3:

[a] Rare species (one or two structure types, <10% frequency) - Old-growth forest: *Trapeliopsis flexuosa*; *Plagiothecium laetum*. - Secondary forest: *Cladonia coniocraea*, *Lecanora filamentosa*, *Lecanora saligna*, *Mycoblastus sanguinarius*, *Parmelia saxatilis*, *Parmelia* spec., *Parmeliopsis hyperopta*, *Stranguspora* spec., *Trapeliopsis flexuosa*; *Barbilophozia lycopodioides*, *Calypogeia azurea*, *C. muelleriana*, *Cephaloziella hampeana*, *Dicranum scoparium*, *Hypnum cupressiforme*, *Mylia taylorii*, *Dicranum montanum*, *Orthotrichum* spec.

[b] Kruskal-Wallis test results for differences in cover: * $P<0.05$, ** $P<0.01$, *** $P<0.001$

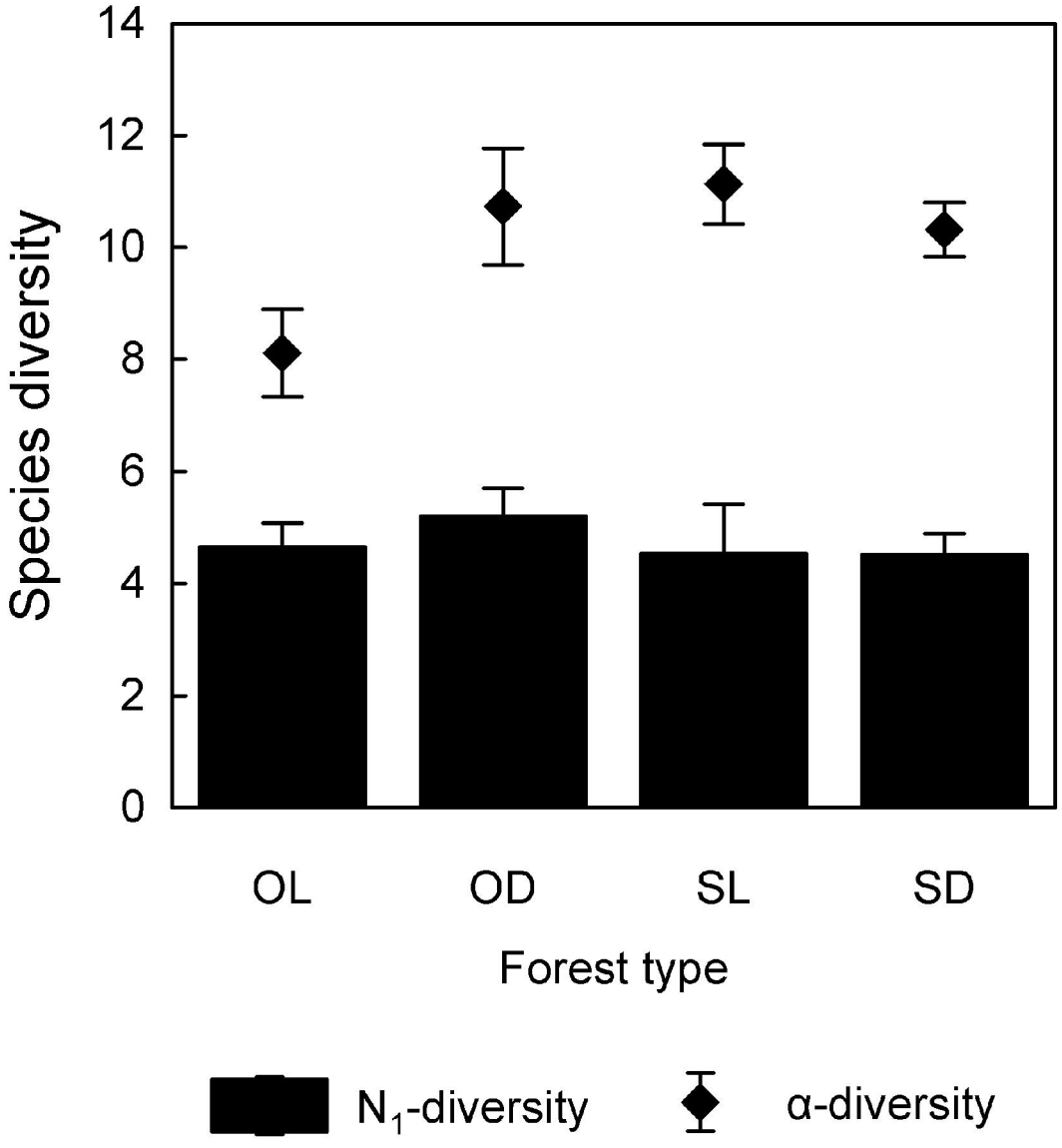

Fig. 4.5 N_1- and α-diversity of epiphyte vegetation in the in the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees)

4.4 Discussion

In contrast to our expectations, plant diversity in the old-growth forest was not higher than in the adjacent secondary forest, although the latter had newly established on a former bog, i.e. represents the first forest generation on non-forest soil. This applied to all studied components of the vegetation, namely the vascular and cryptogamic plants of the ground as well as epiphytes on live trees and standing deadwood. This result shows that in the case of montane spruce forests, a period of 215 years was sufficient for vascular plants, bryophytes and lichens to colonize the newly established stand. The contrasting history of the two neighboring stands with more than up to 200-year old trees, with the one stand being an old-growth forest with long-standing habitat continuity and the other stand being successional to a non-forest ecosystem, can be assumed to be a quite unique setting in Central Europe. Tree age in both forests is far beyond the rotation age of managed spruce forests (MOOG & BORCHERT 2001, HILMO et al. 2009).

Since the old-growth stand exhibited no higher plant diversity than the secondary forest, the conclusion can be drawn that forest continuity beyond a time span of 200 years is not determinative for the present composition of the ground and epiphyte vegetation in the studied mountain spruce forest. The uniqueness of the situation in the studied spruce stands unfortunately implies that no replicate sampling on the stand or the landscape levels was feasible. Therefore, the question arises to which extent the results from our case study from the Harz Mountains National Park can be generalized.

A key factor that most likely has promoted the colonization of the newly established forest since 1796 is the proximity to the old growth stand. It has been substantiated repeatedly in the published literature that short distance to the next old forest is beneficial for the colonization of newly afforested sites. Such examples have been found both for the ground vegetation (BRUNET & VON OHEIMB 1998, BOSSUYT et al. 1999, SINGLETON et al. 2001) and cryptogamic epiphytes (BUCKLEY 2011). Dispersal limitations of many forest species are the main cause behind this relationship (HILMO & SÅSTAD 2001, TAKAHASHI & KAMITANI 2004). Species saturation during the recolonization of new forest sites varies between regions and ecosystems. While many forest plants can colonize nearby newly afforested sites within 100 years (NORRIS 1987, BRUNET et al. 2000), other species need several centuries, as, for instance, shown for liverworts in boreal *Picea mariana* forests, where the maximum species

diversity was reached after 275 years (FENTON & BERGERON 2008). Isolated forest patches within arable land or grassland-dominated landscapes do not reach the plant species diversity of old-growth forests even after several centuries (ROSE 1976, NAGAIKE 2012).

Though the studied old-growth forest has probably never been harvested, it was not exempted from any human impact. During the second half of the 20th century, the upper Harz Mountains were, like many high elevation forests in Central and Eastern Europe, exposed to high atmospheric loads of SO_2 (HAUCK et al. 2012a). The SO_2 pollution was shown to have strongly influenced the epiphytic lichen vegetation in the Harz Mountains (HAUCK & RUNGE 1999; HAUCK et al. 2002). After the dramatic reduction of the SO_2 emissions in Central Europe, soils and vegetation are presently recovering from the former SO_2 load and the resulting acidification (HAUCK et al. 2011, 2012a). The SO_2 pollution has surely caused the extinction of some epiphytic lichens from the upper Harz Mountains (HAUCK 1996) and might also have reduced the species richness of bryophytes, but had probably little effect on the vascular plant vegetation (WINNER & BEWLEY 1978). Therefore, it is likely that the pool of epiphyte species was reduced compared to the preindustrial level. This clearly limits the generalizability of our results; forest ecosystems which are undisturbed not only relating to forest management, but also with respect to air pollution might respond more sensitively to habitat continuity than the forest studied by us.

Certain site factors differing between the studied old-growth and the secondary forest had remarkably little effect on the vegetation. These differences included the lower concentrations of exchangeable K, Ca and Mg in the soil of the secondary forest on the exploited bog, than in the soil prevailing in the old-growth forest (Table 4.1). These observations are strongly supported by studies in boreal forests on drained bogs, where differences in nutrients were found not to be closely correlated with differences in forest ground vegetation either (WESTMAN & LAIHO 2003). Except the differences in the aforementioned elements, the content of C in the upper soil did not significantly differ from the secondary forest, indicating a convergence of the former (organic) bog soil to the natural forest mineral soil. Similar concentrations of N may be due to high atmospheric N-input in the study area (BÖHLMANN et al. 2005).

Furthermore, the mean tree diameter of live trees was higher in the old-growth than the secondary forest, but did not cause higher epiphyte diversity in the former, though a

correlation between tree diameter and species diversity has been substantiated in other studies both for epiphytic bryophytes and lichens (MEŽAKA et al. 2008, HAUCK et al. 2012b). Lower canopy closure in the plots with dead trees in the old-growth forest than in the other plots, and in the secondary forest in particular, may explain some of the minor variation in the vegetation that was observed between the plot types, which was also supported by the results of the NMDS, indicating differences in the ground vegetation between stands of live and dead trees. The lower cover of bryophyte species in the ground vegetation of plots with dead trees in the old-growth forest than in the other stand types might be attributable to relatively slight differences in microclimate resulting from variation of the canopy closure (MA et al. 2010). These differences might also have caused the higher frequency of liverworts *Cephalozia leucanta* and *Ptilidium ciliare* on tree trunks of the secondary forest than the old-growth stand.

Though the study of managed spruce plantations was not part of the present investigation, it is well documented in the literature that they differ from both the studied old-growth and secondary forest stands by their considerably lower diversity of epiphytes (PETERKEN et al. 1992). Recent studies of the epiphytic lichen and bryophyte diversity in 80 to 140-year old spruce plantations of the Harz Mountains were published by GÜNZL (1999) and HAUCK (2000) and showed a lower species diversity than in the more than 200-year old stands of the present study. Structural features that cause the higher diversity with increasing tree age include the increasing availability of thick-stemmed deadwood and large-diameter trees, which offer a higher diversity of microhabitats, such as deep furrows, cavities or inclined trunks (HUMPHREY 2005, FENTON & BERGERON 2008, DITTRICH et al. 2013). The scarcity of such structural features in managed forests has caused the extinction of many epiphyte species in Central Europe, which is, for example, estimated to be as high as ca. 30 % of the epiphytic lichen flora in broadleaved forests of north-western Germany (HAUCK et al. 2012c). The ground vegetation is strongly influenced by light availability. Herb and moss layer of the forests studied are similar to that of 200-year old, selectively logged spruce stands in the Harz Mountains, whereas the understorey vegetation in dense, dark plantations is much sparser (NIEDERSÄCHSISCHES UMWELTMINISTERIUM 1992, DAMM 1994).

4.5 Conclusions

More than 200 years of unmanaged development of the secondary spruce forest were sufficient to achieve the same diversity of vascular and cryptogamic plant species in the ground vegetation and of epiphytes on trees as was found in the nearby old-growth forest. Thus, we had to reject our hypothesis that forest continuity acts independently of, and additive to, tree age on diversity. This does not disprove that an independent habitat continuity effect exits on spruce stands <215 years in age. Comparison with published works from other regions suggests that our results are representative for cases where secondary forests have established in proximity to old-growth forests. Here, the age of the tree individuals of the actual tree generation is more crucial for shaping the vegetation than stand continuity across different tree generations. However, our results are not transferable to isolated secondary forests in open landscapes with long distances to relevant diaspore sources.

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Chapter 5

Small increase in substratum pH causes the dieback of one of Europe's common lichens, *Lecanora conizaeoides*

Markus Hauck, Philipp I. Otto, Sebastian Dittrich, Mascha Jacob, Claudia Bade, Inken Dörfler and Christoph Leuschner

Annals of Botany **108: 359–366.**

Abstract

Backgrounds and Aims *Lecanora conizaeoides* was until recently western and central Europe's most abundant epiphytic lichen species or at least one of the most common epiphytes. The species is adapted to very acidic conditions at pH values around 3 and high concentrations of SO_2 and its derivatives formed in aqueous solution, and thus spread with increasing SO_2 deposition during the 19th and 20th centuries. With the recent decrease of SO_2 emissions to nearly pre-industrial levels within 20 years, *L. conizaeoides* declined from most of its former range. If still present, the species is no longer the dominant epiphyte, but is occurring in small densities only. The rapid spread of the *L. conizaeoides* in Europe from an extremely rare species to the probably most frequent epiphytic lichen and the subsequent rapid dieback are unprecedented by any other organism. The present study aimed at identifying the magnitude of deacidification needed to cause the dieback of the lichen.

Methods The epiphytic lichen diversity and bark chemistry of montane spruce forests in the Harz Mountains, northern Germany, were studied and the results were compared with data recorded with the same methods 13–15 years ago.

Key Results *Lecanora conizaeoides*, which was the dominant epiphyte of the study area until 15 years ago, is still found on most trees, but only with small cover values of ≤1%. The bark pH increased by only 0.4 pH units.

Conclusions The data suggest that only slight deacidification of the substratum causes the breakdown of the *L. conizaeoides* populations. Neither competitors nor parasites of *L. conizaeoides* that may have profited from reduced SO_2 concentrations are likely causes of the rapid dieback of the species.

Key words: Acidity, air pollution, bark chemistry, epiphytes, *Lecanora conizaeoides*, lichen-forming fungi, substratum pH, sulfur dioxide.

5.1 Introduction

Though species of lichen-forming fungi may have large ranges, they are rarely as frequent within their distribution limits as are 'frequent' species of vascular plants. This is at least true for the density of localities, whereas the density of individuals is hardly comparable between organisms that differ so much in their size and biology as lichens and vascular plants. One of the rare exceptions of a lichen-forming fungus with very high densities of both inhabited locations and individuals was, until recently, the ascomycete *Lecanora conizaeoides*, which forms a lichen symbiosis together with the green alga *Trebouxia simplex* (HAUCK et al. 2007).

The range of *L. conizaeoides* includes the oceanic to subcontinental parts of Europe with a few occurrences in coastal areas of North America (LAGRECA & STUTZMAN 2006). In areas of western and central Europe, which were exposed to high acidic air pollution during the 20th century (Fig. 5.1), *L. conizaeoides* was, if not the most common, at least among the most common epiphytic lichen species (WIRTH 1993). In large parts of its range, *L. conizaeoides* was found in almost every tree stand and on nearly every tree. The abundance of the lichen was clearly correlated with the deposition of acidic sulfurous air pollutants (HAWKSWORTH & ROSE 1970, BATES et al. 1996). Therefore, *L. conizaeoides* experienced an enormous spread during the 19th and 20th centuries with increasing SO_2 emissions. The extent of this spread depended on the pollutant load and thus varied between regions. In England, the initial point of global industrialization, *L. conizaeoides* was first noticed in the mid-19th century (HAWKSWORTH et al. 1973). Near London, *L. conizaeoides* already formed a universal cover of tree trunks and branches (PAULSON & THOMPSON 1913). In northern Germany, *L. conizaeoides* was widespread and locally abundant in the early 20th century, but was not found by ERICHSEN (1933) in the higher elevations of the Harz Mountains, the study area of the present work, in 1930, where the species became probably abundant in the 1950s (H. Ullrich, pers. comm.). In the 1950s, *L. conizaeoides* was already the most frequent epiphytic lichen of northern Germany (ERICHSEN 1957, KLEMENT 1958). At that time, it was still rare in less polluted parts of southern Germany, but spread a decade later (WIRTH 1985).

With the reduction of SO_2 emissions in the late 20th century (VESTRENG et al. 2007), *L. conizaeoides* declined from most areas of Europe as rapidly as it had spread before. For England and southern Germany, such a dieback of *L. conizaeoides* was documented for the 1980s and 1990s (WIRTH 1993, BATES et al. 2001). In England, BATES et al. (2001)

established a decrease of the covered substratum area by the species from up to 80 to 0% within 10 years. The rapid changes of the abundance of *L. conizaeoides* in Europe from a very rare species to the most common epiphytic lichen and afterwards from an extremely common species to a rare one demand an explanation. There is no doubt that the high tolerance to acidic sulfurous solutions with pH values as low as 3.0, which is far beyond the acidity tolerance of most other lichens, explains the spread of *L. conizaeoides* with increasing air pollution (HAUCK et al. 2001a, LAGRECA & STUTZMAN 2006). The superhydrophobic thallus surface, which inhibits much of the acidic solution from soaking the thallus, is thought to be the main cause of the tolerance (SHIRTCLIFFE et al. 2006, HAUCK et al. 2008). Moreover, the production of the extracellular depsidone fumarprotocetraric acid is apparently a prerequisite for the high acidity tolerance of *L. conizaeoides* (HAUCK et al. 2009a, b). The apparently outstanding vagility of *L. conizaeoides* and its photobiont also seems to be significant for the rapid spread of this lichen symbiosis (HAUCK et al. 2007). However, while the mechanisms causing acidity tolerance are largely known, no mechanistic explanation for the recent dieback of *L. conizaeoides* with decreasing acidic pollutant load exists.

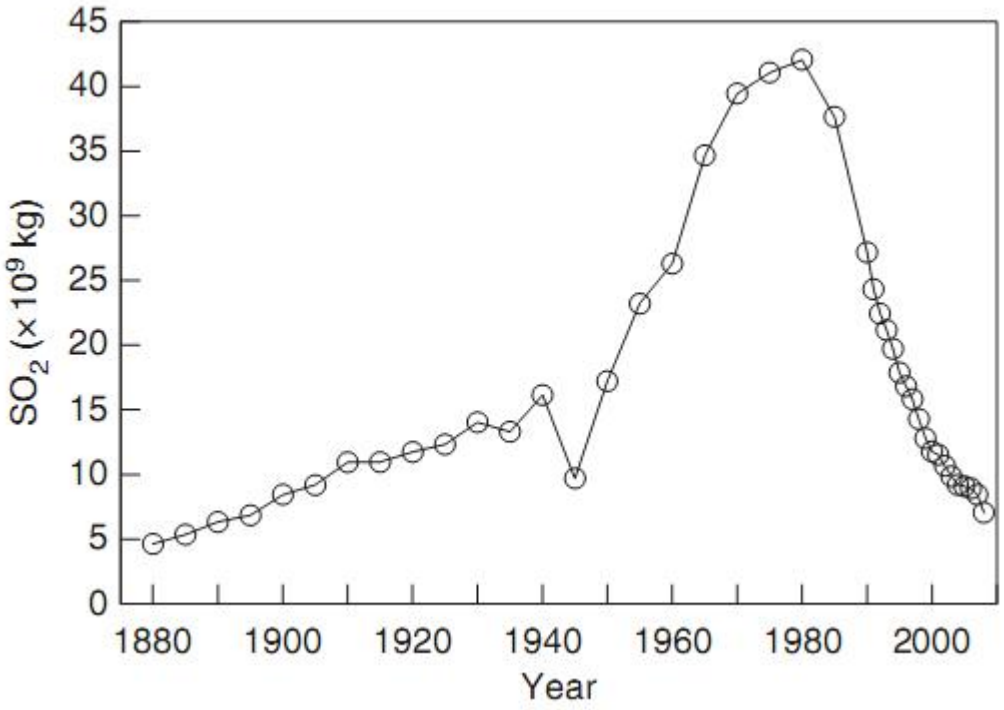

Fig. 5.1 Sulfur dioxide emissions in Europe (excluding Russia) from 1880 to 2008 (after MYLONA 1996; EUROPEAN ENVIRONMENT AGENCY, unpubl. res.).

Two research questions arise in this context. (1) How strong was the change in the environmental pH conditions to cause the dramatic dieback of *L. conizaeoides*? (2) What kind

of physiological mechanism makes *L. conizaeoides* not only tolerant of, but even dependent on, acidity? In the present work, we focused on the first of these questions, as the extent of the pH change has to be known to search for ecophysiological explanations. Since the decline of *L. conizaeoides* from a dominant species to a very rare one, or the extinction at a given place, can happen within short time scales (e.g. ≤5 years in southern Germany, WIRTH 1993), we tested the hypothesis that only a slight decrease of acidity may cause the decline of *L. conizaeoides*. Components which are relevant to the chemical environment of a lichen include the substratum, precipitation, fog and gases (FARMER et al. 1991). Our study is based on the measurement of pH values of aqueous suspensions of tree bark, as the chemical traits of the substratum underlie a lower short-term variation than that of precipitation (HAUCK 2000).

Furthermore, bark samples were analysed for element concentrations to check whether chemical parameters other than the pH itself may have been altered due to the reduced pollutant load and thereby potentially affected the abundance of *L. conizaeoides*. The measurements, which were recorded from montane spruce forests of the Harz Mountains, northern Germany are compared with 13–15 year old data from the same study area. *Lecanora conizaeoides* was the dominant epiphyte on spruce in the Harz Mountains from the 1960s to the 1990s. In the 1990s, virtually all spruce trees were inhabited by *L. conizaeoides*. In a study including .200 spruce trees, all of them were colonized by *L. conizaeoides* and the species reached a cover of up to 80% on individual tree trunks (HAUCK 2000).

5.2 Material and methods

Study area

The study was conducted in montane forests of Norway spruce (*Picea abies*) in the Harz Mountains, northern Germany. Recent data were collected in 2010 on Mt Brocken (51 847′ N, 10 838’E) at 1000 m and compared with data from the same forest of 1997 (published in HAUCK et al. 2002) and from the Acker-Bruchberg ridge (51 845’ to 51 846’N, 10 827’ to 10 828’E) at 800 m from 1995 (HAUCK et al. 2001a, HAUCK & RUNGE 2002). The Harz Mountains are the highest mountain range in northern Germany with elevations up to 1142 m (Mt Brocken) and are primarily formed of acidic Paleozoic rocks. At elevations between 800 and 1142 m, annual mean temperature varies between 3 and 6 °C and precipitation ranges

from 1500 to 1600 mm. The prevailing winds come from the southwest and west; fog events and long-lasting snow cover are common. Norway spruce is native to the Harz Mountains at the studied altitudes.

Soil pH

The pH of aqueous soil suspensions of 10 g dry weight (d.wt) of soil in 20 mL of deionized water was determined in the upper soil (at 5 to 10 cm) from 25 randomly selected sample points in 2010 and compared with data from 12 sample points of 1997 (HAUCK et al. 2002). The mean pH values in 2010 amounted to 3.6±0.0 inH_2O and 3.0±0.0 in KCl, which exceeds the pH values published by HAUCK et al. (2002) by approx. 0.4 pH units. Those pH values amounted to 3.2±0.1in H_2O and 2.6±0.1 in KCl. Recording epiphytic lichen data, bark sampling and chemical analysis A total of 90 mature spruce trees was sampled in 2010 in an area of 20 ha. All living spruce trees with a minimum diameter at breast height of 15 cm and all snags with at least some bark left at the trunk around the breast height level were sampled on 26 plots of a size 10 m × 10 m. These plots were available from a forest inventory and biodiversity study and covered different stages of the natural dynamics cycle in the spruce forest ecosystem. Therefore, the sample trees can be assumed to represent an unbiased collective of the forest trees in terms of the cover of *L. conizaeoides* Nyl. ex Crombie and bark acidity. The number of sample trees on the 10 m × 10 m plots amounted to 3.9+0.3, with a maximum of seven trees per plot. Since living and dead conifers are known to differ in their bark chemistry and in the cover of *L. conizaeoides* (HAUCK 2005), the vitality status of the trees was recorded to enable a separate data evaluation for living and dead trees.

In total, 53 living trees and 37 snags were sampled. Epiphytic lichen vegetation was recorded from the trunk of every sample tree at a height of 0–2 m above the ground. Cover of the individual epiphytic lichen species, including *L. conizaeoides*, was estimated as a percentage. The nomenclature of lichen species is based on WIRTH et al. (2011). Bark was sampled from each sample tree from a standard exposure (i.e. western exposure at a height of 100–200 cm above the ground) to be consistent with former studies of our group (HAUCK et al., 2001a, 2002). Epiphytes were carefully removed from the bark surface with a wire brush before sampling. Bark samples were dried at 105 8C and homogenized in a swing mill using an insert that is free from metal abrasion. The bark powder was used to determine the C and N concentrations using a C/N analyser (Vario EL III, Elementar Analysensysteme, Hanau,

Germany). Bark pH was measured with an MP 120 pH meter with electrode InLab 413 (Mettler-Toledo, Greifensee, Switzerland) in suspensions with deionized water (25 mL per g d. wt) shaken for 24 h before the measurements (pH [H_2O]). After acid digestion with 65% HNO , the total concentrations of potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), aluminium (Al), manganese (Mn), zinc (Zn), copper (Cu), phosphorus (P) and sulfur (S) were analysed with ICP-OES using an Optima 5300DV (Perkin Elmer, Waltham, MA, USA).

Reference data of lichen cover from 1995 to 1997 were collected from 14 living trees and six snags from Mt Brocken (HAUCK et al., 2002) and 115 living trees and 25 snags from the Acker-Bruchberg ridge (HAUCK et al. 2001a, HAUCK & RUNGE 2002). Data of bark pH and element content were available for 100 living trees and 20 dead trees from the Acker-Bruchberg ridge, but not from Mt Brocken. Epiphytic lichen data and bark chemistry characteristics were principally studied with the same methods as in the present work, though metal concentrations were studied with AAS (SpectrAA 30 Varian, Mulgrave, Victoria, Australia) instead of ICP-OES.

Statistics

Arithmetic means+s.e. are presented throughout the paper. All data were tested for normal distribution with the Shapiro-Wilk test. Significance of differences in vegetation and bark chemistry data, which were not normally distributed, was tested with the Kruskal–Wallis test. These analyses were calculated with SAS 6.04 software (SAS Institute Inc., Cary, NC, USA). Detrended correspondence analysis (DCA) was applied to study differences between different tree collectives in variation of epiphytic lichen abundance. Canonical correspondence analysis (CCA) was used to relate site factors to the variation of epiphytic lichen cover on the tree trunks. The significance of correlations between epiphytic lichen data and environmental parameters was tested with a Monte Carlo permutation test with 999 iterations. Species occurring on < 10% of the sample trees were excluded from the CCA. DCA and CCA were calculated with the program PC-Ord 4.01 (MjM Software, Gleneden Beach, OR, USA).

5.3 Results

Bark chemistry

The pH of aqueous bark suspensions increased by 0.4 units on living trees and by 0.25 on dead trees from the 1990s to 2010 (Table 5.1). The bark of dead trees was less acidic than that of living trees in both sampling periods. However, the pH difference between the bark of dead and living trees became smaller; it diminished from 0.3 to 0.1 pH units. The tree bark was richer in N, K and Mg in 2010 than in the 1990s, whereas the S and Fe concentrations of bark and even more the Fe/Mn ratio were lower in 2010 than 15 years earlier.

Epiphytic lichen diversity

Trees clearly differ in their epiphytic lichen vegetation between 2010 and the mid-1990s. In the DCA, releves from today and the 1990s form two distinct groups along the first axis (Fig. 5.2). This matches with the decline of *L. conizaeoides* (the most frequent epiphyte in the releve s of the 1990s) from the 1990s to 2010 (Fig. 5.3A). On living trees, the mean cover of *L. conizaeoides* on the lower 2 m of the trunks decreased from, respectively, 36±1% (Acker-Bruchberg ridge, 1995) or 26±3% (Mt Brocken, 1997) to 1±0% (Mt Brocken, 2010). On dead trees, *L. conizaeoides* covered a lower proportion of the trunk surface already in the 1990s (Acker-Bruchberg, 20±2%; Mt Brocken, 17±4%) and decreased to 0.5±0.1% in 2010. Despite the low cover values, *L. conizaeoides* was still present on 94% of the living trees and 60% of the dead trees in 2010. In the 1990s, the species occurred on all sample trees.

Only four lichen species besides *L. conizaeoides* exceeded a mean cover of 5% in at least one site (Fig. 5.3). *Hypogymnia physodes* decreased in a similar way to *L. conizaeoides*, but started from much lower cover values in 1990s than the latter. Characteristic of *H. physodes* is the higher cover on dead trees than on living trees, which is in contrast to the behaviour of *L. conizaeoides*. The mean cover of three of these species, namely *Cladonia digitata*, *C. polydactyla* and *Lepraria jackii*, increased from the 1990s to 2010. In contrast to *L. conizaeoides*, which prefers the middle stem, those three species usually colonize the trunk from its base upwards. The total of lichen species per sample trees was always higher on dead trees than on living ones, but remained largely stable between the years (Fig. 5.3F). While differences in the epiphytic lichen vegetation caused the separation of living trees and snags

into two groups along the second axis of the ordination diagram in the 1990s, living and dead trees clustered in a single scatter plot in 2010 (Fig. 5.2). In the 1990s, the influence of tree vitality was higher than that of the site, since living trees from either site clustered in one scatter plot, as did the dead trees in another scatter plot.

Table 5.1 Element concentrations (in µmol g^{-1} d wt; in the case of C, mmol g^{-1} d. wt) and pH of spruce bark collected from trunks at 1.5 m height in the Harz Mountains in 2010 and 1997 (Mt Brocken; B2010, B1997) as well as 1995 (Acker-Bruchberg ridge; A1995).

	B2010		B1997		A1995	
	Living trees	Snags	Living trees	Snags	Living trees	Snags
pH	3.60±0.02	3.71±0.06	-	-	3.18±0.01	3.46±0.06
N	306±6	333±17	-	-	164±17	496±37
P	5.59±0	7.93±0.89	-	-	6.92±0.22	12.3±0.9
S	14.7±1.3	14.2±0.9	-	-	17.1±0.4	21.0±1.9
C	41.9±0.1	42.0±0.2	-	-	44.1±0.1	43.9±0.2
K	10.8±1.9	18.8±3.2	9.91±1.18	13.5±2.3	6.67±0.43	8.04±1.18
Ca	143±6	147±12	164±16	201±30	124±5	163±12
Mg	6.29±0.33	11.3±1.2	5.26±0.29	9.26±1.46	5.67±0.27	10.3±1.1
Fe	1.76±0.13	1.15±0.11	6.29±1.12	6.24±1.10	8.23±0.34	4.98±0.69
Mn	1.30±0.08	1.75±0.17	1.44±0.11	1.79±0.13	1.67±0.07	2.06±0.26
Fe/Mn	1.58±0.14	1.17±0.35	4.90±0.89	3.53±0.67	6.25±0.51	4.79±1.51
Al	4.74±0.30	4.30±0.34	-	-	6.74±0.29	4.90±0.81
Zn	1.15±0.06	1.56±0.14	1.71±0.25	2.51±0.51	1.66±0.09	3.58±0.20
Cu	0.09±0.01	0.08±0.01	0.16±0.01	0.14±0.01	0.19±0.01	0.10±0.01

Kruskal–Wallis test results (referring to the data of 1995 and 2010 where all parameters were measured) for all parameters $P < 0.001$. Number of sample trees (alive/dead): A1995, 100/20; B1997, 14/6; B2010, 59/31.

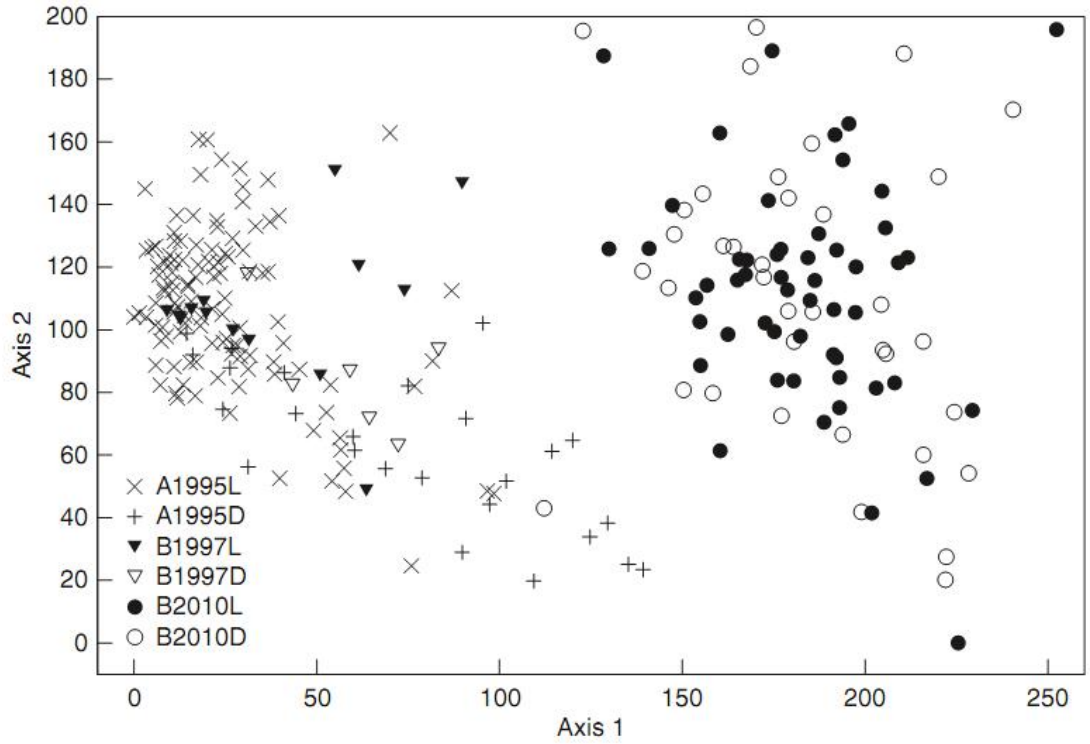

Fig. 5.2 DCA ordination of *Picea abies* from the Harz Mountains (n = 250) depending on epiphytic lichen cover on the lower trunk at 0–2 m above the ground (34 species). Trees from different points in time (1995, 1997, 2010), sites (A, Acker-Bruchberg ridge; B, Mt Brocken) and status (L, alive; D, dead) are plotted with different symbols. Total variance in species data: 1.56. Eigenvalues: 0.57 (axis 1), 0.16 (axis 2). Length of gradient: 2.52 (axis 1), 1.97 (axis 2).

Results of the CCA show that the decrease in cover of *L. conizaeoides* and the increase of *C. digitata*, *C. polydactyla* and *L. jackii* is correlated with increasing pH and Ca, Mg and K concentrations, but decreasing Fe of the bark (Table 5.2). This result is supported by the results of bivariate correlation analyses as exemplarily shown for the cover of *L. conizaeoides* plotted against the pH (Fig. 5.4). The results of the CCA, which includes all species growing on .10%of the sample trees irrespective of their cover, also show that *Hypocenomyce caradocensis* and *Lecanora filamentosa* declined together with *L. conizaeoides*, whereas the cover of *Hypocenomyce scalaris* and *Platismatia glauca* increased similarly to the more dominant species *C. digitata*, *C. polydactyla* and *L. jackii*. The observed decline of *H. physodes* (Fig. 5.3D) was correlated neither with the change of pH nor with the mentioned metal concentrations (Table 5.2).

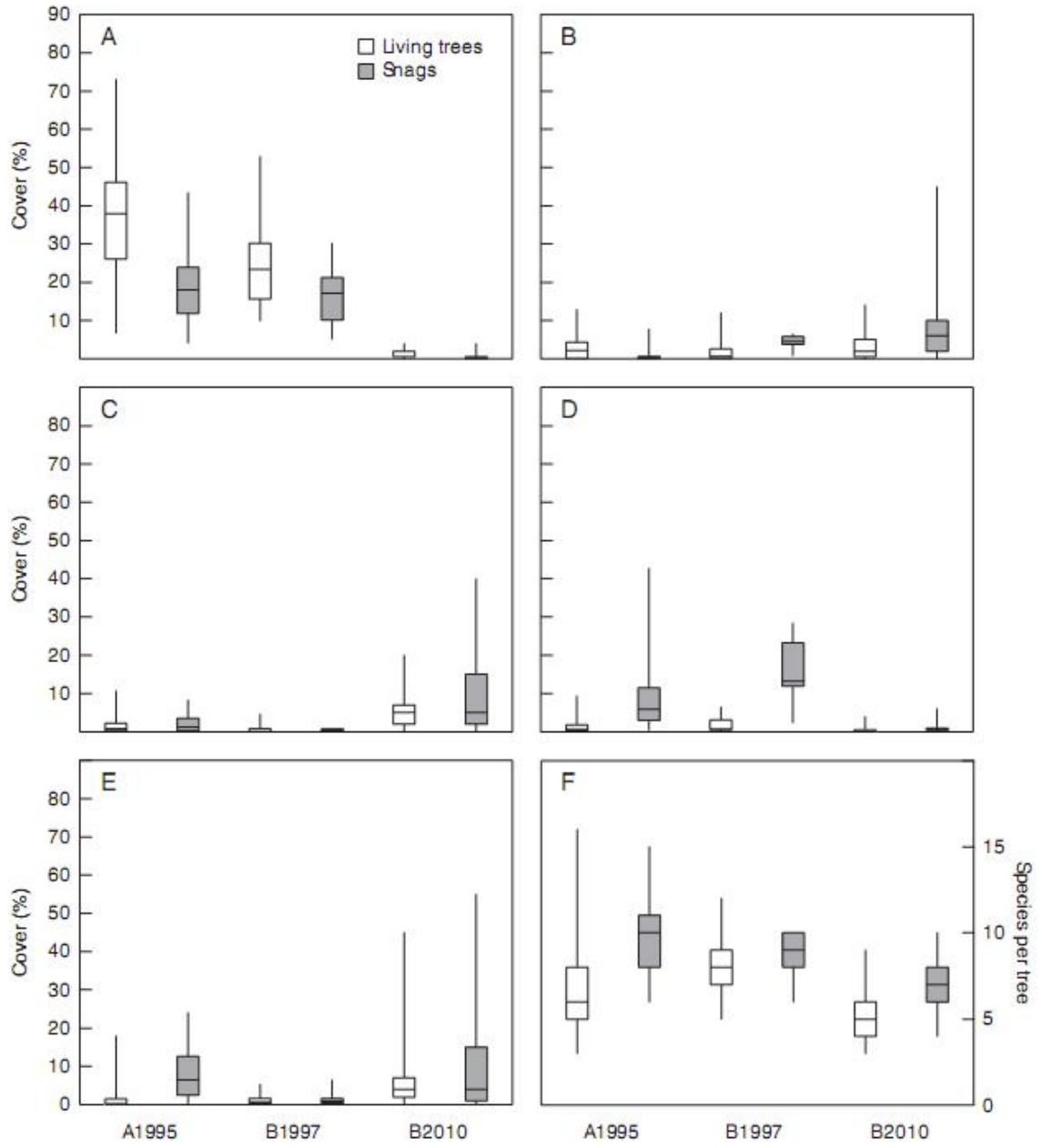

Fig. 5.3 (A–E) Cover of epiphytic lichen species on the lower 2 m of *Picea abies* trunks including all species which exceed cover values of 5% at one or more sites: (A) *Lecanora conizaeoides*, (B) *Cladonia digitata*, (C) *C. polydactyla*, (D) *Hypogymnia physodes*, (E) *Lepraria jackii*. (F) Number of lichen species per tree. Sites: A, Acker-Bruchberg sampled in 1995; B, Mt Brocken sampled in 1997 and 2010. Data from living trees and snags are displayed separately, as indicated. Columns show medians as well as 25% and 75% quartiles, whereas bars indicate absolute minima and maxima. Kruskal–Wallis test results for differences between means of data represented by different columns (all $P < 0.001$): (A) $x^2 = 188.2$, (B) $x^2 = 33.8$, (C) $x^2 = 81.7$, (D) $x^2 = 72.9$, (E) $x^2 = 91.9$, (F) $x^2 = 69.2$. Number of sample trees (alive/dead): A1995, 115/25; B1997, 14/6; B2010, 53/37.

5.4 Discussion

Change in bark chemistry

In a period of only 15 years, the spruce bark has responded with decreased acidity to the recently reduced deposition of acidic sulfurous air pollutants in central Europe. The increase of the pH by 0.4 units matches well with the increase of the pH in the upper soil and suggests that bark pH might be used as a surrogate for assessing the progress of soil acidification and deacidification. The recently reduced SO_2 deposition already results in decreased S content of the bark. The concentrations of Mg and K typically increase along with the pH in biotic and abiotic surfaces with cation adsorption, including bark, living plant tissues lacking an intact cuticle, and soil (FINZI et al. 1998, SCHMULL & HAUCK 2003a). The lower concentrations of Fe and Mn in the bark in 2010 than in the 1990s is probably due to reduced availability from the presently less acidic soil (RÖMHELD 1987). The increased N content of bark indicates the accumulation of airborne N (BÖHLMANN et al. 2005).

Table 5.2 Axis 1 scores in CCA of all species (n ¼ 13) growing on 10% of sample trees (n = 210)

Species	CCA score
Hypocenomyce caradocensis	–1.040
Lecanora conizaeoides	–0.820
Lecanora filamentosa	–0.801
Hypogymnia physodes	–0.066
Parmeliopsis ambigua	–0.042
Mycoblastus fucatus	0.224
Cladonia pyxidata s.l.	0.027
Pseudevernia furfuracea	0.219
Cladonia digitata	0.954
Platismatia glauca	1.109
Lepraria jackii	1.285
Cladonia polydactyla	1.375
Hypocenomyce scalaris	2.115

Positive scores are positively correlated with the pH (r = 0.58) and concentrations of Ca (r = 0.75), S (r = 0.67),Mg (r ¼ 0.65) and K (r = 0.53), and are negatively correlated with the concentration of Fe (r = –0.63) in bark ($P \leq 0.001$ for correlations between species and bark chemistry parameters in a Monte Carlo test with 999 permutations).

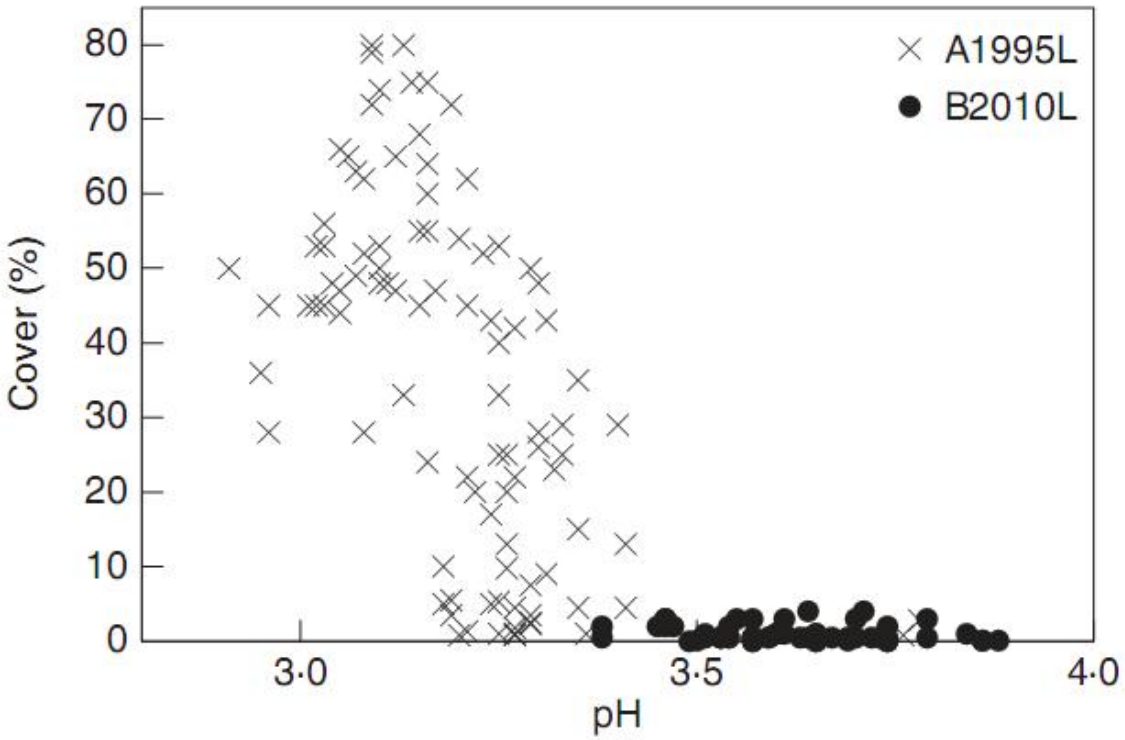

Fig. 5.4 Cover of *Lecanora conizaeoides* vs. the pH of aqueous bark suspensions (pH [H_2O]) at the lower 2 m of living *Picea abies* trunks at the Acker-Bruchberg ridge in 1995 (A1995L; 100 sample trees) and Mt Brocken in 2010 (B2010L; 53 sample trees).

Changes in epiphytic lichen cover and relationships to bark chemistry

Though *L. conizaeoides* was by far the most dominant epiphyte in the Harz Mountains during the 1990s, it is a rare species today, which, however, still occurs on most spruce trees but in very low cover values. The rapid dieback of *L. conizaeoides* agrees with recent observations obtained from other areas in western and central Europe (WIRTH 1993; BATES et al. 2001). Since the earlier spread of *L. conizaeoides* was repeatedly shown to be the result of the acidification of precipitation and the substratum and perhaps elevated S concentrations (WIRTH 1985, BATES et al. 1996, HAUCK et al. 2001b), it is plausible to assume that the continent-wide dieback of *L. conizaeoides* is caused either by the reduction in the deposition of acids or by that of SO_2 to nearly to pre-industrial levels, which coincide with the dieback or precede it (Fig. 5.1). The high tolerance of *L. conizaeoides* to a broad range of microclimatic conditions (WIRTH 1985) supports this assumption and makes a detrimental effect of global warming on the species unlikely. While this reasoning is well established (BATES et al. 2001), the magnitude of pH increase sufficient to cause the decline of *L. conizaeoides* was unknown

so far. The present results suggest that an increase in the substratum pH by only 0.4 units was sufficient to cause the breakdown of the *L. conizaeoides* populations in the study area.

The putative inhibitory effect of a small increase in the pH from 3.2to3.6 is more difficult to explain than damage due to increasing acidity. A large decrease in acidity (i.e. an increase of several pH units) can cause Fe and P deficiency in lichens (PAUL et al. 2009). That Fe or P deficiency has resulted from the slight pH increase observed in the present study is more than doubtful. The reduced total Fe content of bark should be more significant to the Fe nutrition of the lichen than the direct pH effect on the efficacy of *L. conizaeoides* for Fe uptake. Field data of BATES et al. (2001) and HAUCK et al. (2001b), who independently described optimum curves for the dependence of *L. conizaeoides* cover on the supply with inorganic S, suggest that not only acidity itself, but also acidity combined with high S concentrations controls the abundance of this species. Thus the reduced total S content of the spruce bark could exert an additional unfavourable effect on *L. conizaeoides*. MASSARA et al. (2009) concluded from spraying experiments with different concentrations of bisulfite that the pH rather than the S supply controls the abundance of *L. conizaeoides*; however, as the pH was not manipulated independently of the bisulfite concentration, this conclusion is not completely convincing. The results of LAGRECA & STUTZMAN (2006), who found *L. conizaeoides* on conifer bark of low pH in an area of eastern North America which was never exposed to SO_2 pollution comparable with that in Europe, are more supportive of the hypothesis that SO_2 and its derivatives formed in aqueous solution themselves are less significant for the vitality of *L. conizaeoides* than the pH itself.

Factors other than bark chemistry might also be responsible for the dramatic dieback of the former common and widespread species *L. conizaeoides*. Competition by other epiphytes was obviously of sub-ordinate significance for the dieback of *L. conizaeoides*, as most lichen species, which spread between the 1990s and 2010, including *Cladonia* spp., *L. jackii* and *H. scalaris* prefer the trunk base.

Lecanora conizaeoides, a characteristic inhabitant of the middle stem, mostly leaves empty bark surfaces after its decline which are largely devoid of epiphytes. This observation from the Harz Mountains parallels results of WIRTH (1993) from southern Germany. An interaction of atmospheric chemistry and the population dynamics of the lichenicolous

basidiomycete *Athelia arachnoidea*, which is a widespread parasite of *L. conizaeoides* (GILBERT 1988), was probably not the cause of the decline of this lichen in the Harz Mountains, as *A. arachnoidea* was never common in the upper elevations of this area. Thus, our field study provides evidence that the population dieback of *L. conizaeoides* was indeed caused by changes in the physicochemical site conditions and was not due to competing lichens.

It is remarkable that the lichen *H. physodes* decreased simultaneously with *L. conizaeoides*,as *H. physodes* preferred the spruce trees with the highest pH values and lowest S content in bark and stemflow during the 1990s (HAUCK 2003). The susceptibility of *H. physodes* to acidic sulphurous solutions is the reason why this species was formerly more frequent on dead or dying trees than on healthy trees, as the dense foliage of the latter intercepts more protons and S compounds from the atmosphere (HAUCK & RUNGE 2002, HAUCK 2003). The known sensitivity of *H. physodes* to acidity suggests that other factors are responsible for the present decline. Among these factors are the increased Mn/Fe ratio in the bark and the increased N deposition. Both high Mn/Fe ratios and high NO_3^- concentrations were experimentally shown to damage *H. physodes* at ambient concentration ranges (SCHMULL et al. 2002, HAUCK et al. 2003).

Interestingly, SCHMULL et al. (2002) and SCHMULL & HAUCK (2003b) found the cover of *H. physodes* and other species to decrease with increasing Mn/Fe ratio in spruce bark and with increasing NO_3^- concentration in stemflow water in a spruce–fir forest of eastern North America. This dependency was found when the SO_2 deposition was already largely reduced and the pH (H_2O) values of the bark ranged at moderate values between 3.4 and 4.0. In the Harz Mountains, high correlation coefficients were found in multiple regression analyses for models explaining the variation in the cover of *H. physodes* with the concentrations of S and NO_3^- in stemflow using the data of the 1990s (HAUCK & RUNGE 2002, HAUCK et al. 2002). At that time, however, the influence of S concentrations on lichen abundance clearly exceeded that of NO_3^- concentrations. Decreasing abundance of *H. physodes* along with the decline of *L. conizaeoides* was also found in England (BATES et al. 2001). *Platismatia glauca*, a species which resembles *H. physodes* in terms of acidity tolerance, is fairly tolerant to moderate N pollution (PALMQVIST & DAHLMAN 2006). In contrast to *H. physodes*, *P. glauca* became more abundant between the 1990s and 2010 (Table 5.2).

With decreasing acidic pollutant load of the atmosphere, the chemical composition of the bark becomes increasingly similar in trees with large or small amounts of foliage, or dead trees. In the 1990s, the contrasting epiphytic lichen diversity on living and dead or dying trees was attributed to the reduced interception of substances from the atmosphere in the canopy with declining needle mass (HAUCK & RUNGE 2002, HAUCK 2003). This explains the existence of the separate clusters of living and dead trees in the DCA (Fig. 5.2). HAUCK (2005) already showed that this separation diminished when areas with low atmospheric pollutant load were studied. Today, living trees and snags form a single cluster in the DCA in the Harz Mountains, suggesting that the epiphytic lichen vegetation of living and dead trees became more alike due to the decreased acidic sulphurous deposition. This higher similarity of the epiphytic lichen vegetation between living and dead trees today than in the 1990s is a post-hoc confirmation of the hypothesis by HAUCK & RUNGE (1999) and HAUCK (2003) explaining the high epiphytic lichen diversity in forests affected by acidic air pollution with differences in stemflow chemistry and not with microclimate.

5.5 Conclusions

The highly acidophytic lichen *L. conizaeoides* showed a dramatic decrease in abundance in the Harz Mountains from the most dominant epiphyte to a rare species within only 15 years. Our analysis suggests that this decline is attributable to a slight increase of substratum pH by only 0.4 pH units. Competition due to the expansion of less acidity-tolerant epiphytes or increased infestation with lichenicolous fungi can be ruled out as playing a crucial role in the dieback of *L. conizaeoides* in the area. Other lichen species increased with decreasing acidic sulfurous air deposition, but these species (e.g. *Cladonia*, *Lepraria* spp.) prefer the lower parts of the trunk which were never the main habitat for *L. conizaeoides*. Increased Mn/Fe ratios and the continuing atmospheric deposition of N seem to be the key chemical site factors in these spruce forests after the reduction of atmospheric SO_2 levels in the 1990s. Due to the dieback of *L. conizaeoides*, the epiphytic lichen vegetation of living and dead spruce trees is today more similar to each other than it was in the 1990s, when this species dominated the bark of the living trees.

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Chapter 6

Lichen substance concentrations in the lichen *Hypogymnia physodes* are correlated with heavy metal concentrations in the substratum

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Abstract

Lichen substances (i.e. lichen-specific carbon-based secondary compounds) are known to be involved in the uptake and immobilization of metal ions, though the biochemical mechanisms of this interaction are largely unexplained. Previous research on potential effects of lichen substances on heavy metal uptake and tolerance mostly focused on lichens in heavily polluted areas with exceptionally high metal concentrations. In the present study, we aimed at gathering information as to whether lichen substances might be involved in the fine-tuning of metal uptake even at not or low-polluted sites. Therefore, we studied lichen substance concentrations in the epiphytic lichen *Hypogymnia physodes* and metal concentrations in its substratum in a montane spruce forest of Germany. *H. physodes* produces two depsides and five depsidones, which had been shown to be involved in metal homeostasis, namely in Cu and Mn uptake, in previous laboratory experiments. The amount of lichen substances increased with increasing heavy metal concentration in the substratum, though the latter varied only in the range of a few μmol g^{-1} between the sample trees. Variability of lichen substance concentrations in *H. physodes* within the individual trees was low. Among the different lichen substances of *H. physodes*, the amount of the depsidone physodalic acid relative to the total of lichen substances was most closely correlated to the concentrations of Cu and Mn in the substratum, whereas the amount of the depsidone 3-hydroxyphysodic acid decreased both with increasing concentrations of these two metals and physodalic acid. Thus, our data suggest that lichen substances contribute to metal homeostasis not only in heavy metal-rich habitats, but also at not or low-polluted sites where the lichen substances apparently help to maintain constant intracellular metal concentrations despite of spatially varying availabilities of metal ions.

Key words: Depsides, depsidones, physodalic acid, metal homeostasis, heavy metals, bark chemistry

6.1 Introduction

While the diversity of lichen substances has been explored for more than a century, resulting in the characterization of more than 800 compounds (HUNECK & YOSHIMURA 1996; HUNECK 2001), research on the biological functions of lichen substances is much younger. One interesting trait of lichen substances is their apparent role in metal homeostasis. After some early evidence substantiating the putative interaction of lichen substances with metals by the formation of complexes (SYERS 1969, ENGSTROM et al. 1980, PURVIS et al. 1987, 1990), UV spectroscopic studies and sporadic X-ray diffractic analyses showed that the formation of complexes of metal ions with lichen substances is widespread (TAKANI et al. 2002, HAUCK et al. 2009a, 2010a, b). Studies with lichen species in the laboratory revealed that individual lichen substances can either promote or inhibit the uptake of metal ions. Thereby, lichen substances can apparently facilitate lichens to grow at nutrient-poor sites (HAUCK et al. 2009b) or constitute heavy metal tolerance (HAUCK 2008).

One of the best studied lichen symbioses in terms of metal homeostasis is the foliose *Hypogymnia physodes*, a lecanoralean ascomycete associated with the coccoid green alga *Trebouxia* and widely distributed as an epiphyte of acidic bark and wood in temperate and boreal forests. This lichen produces two depsides and up to five depsidones (MOLNÁR & FARKAS 2011). Laboratory experiments with lichen thalli with or without their natural content of lichen substances showed that the lichen substances in *H. physodes* selectively inhibit the intracellular uptake of Cu^{2+} and Mn^{2+} from solution, but do not affect that of Fe^{2+} or Zn^{2+} (HAUCK 2008). Experiments on the influence of isolated lichen substances on the adsorption of metal ions at the cation exchange sites of cellulose filters suggested that the inhibition of Cu^{2+} and Mn^{2+} uptake is primarily due to the depsidone physodalic acid (HAUCK & HUNECK 2007).

Concentrations of Cu^{2+} and Mn^{2+} in bark or stemflow have been repeatedly shown to be negatively correlated with the abundance of *H. physodes* in the field (HAUCK et al. 2001; SCHMULL et al. 2002). High concentrations of both Cu^{2+} and Mn^{2+} can cause membrane damage and chlorophyll degradation and inhibit the reproduction in *H. physodes* (MIKHAILOVA & SCHEIDEGGER 2001, HAUCK & PAUL 2005). Hence, the evolution of a mechanism that reduces the uptake of Cu^{2+} and Mn^{2+} into the lichen would be a selective advantage for *H. physodes*. This is especially relevant in the case of Mn^{2+}, as high

concentrations are often a limiting factor for epiphytic lichens in boreal and temperate forests (HAUCK & PAUL 2005, PURVIS et al. 2008). However, both Cu^{2+} and Mn^{2+} are essential micronutrients, which can occur at very low concentrations in precipitation and tree bark, which are the main sources for metal ions in epiphytic lichens. Therefore, the constitutive expression of efficient inhibitors for Cu^{2+} and Mn^{2+} uptake would indeed favor the lichen at sites with high availability of these metals, but would exclude it from sites with low Cu^{2+} and Mn^{2+} availability. The result would not be the broadening of the ecological niche of the lichen, but merely a shift towards substrata with increased Cu^{2+} and Mn^{2+} availability. A species might also benefit from an obligatory dependence on substrata which are toxic for other species due to reduced competition, but such a strategy is risky, as the sudden shortfall of the pollutant may lead to the extinction of the species, as was currently observed with the SO_2-tolerant lichen *Lecanora conizaeoides* in large parts of Western and Central Europe (HAUCK et al. 2011).

Since *H. physodes* is a very successful and widespread species in the northern hemisphere, we looked for evidence that the production of lichen substances, which are capable of reducing the intracellular uptake of Cu^{2+} and Mn^{2+} in this lichen, might be inducible by high concentrations of these ions. There is at least some indication in the literature that the production of lichen substances could be inducible by heavy metals. BIAŁOŃSKA & DAYAN (2005) found increased concentrations of physodalic acid in thalli of *H. physodes* transplanted to industrial areas, where among others Cd, Cr, Ni, Pb, Zn and S were emitted. Though these authors did not attempt to provide a physiological explanation for their findings, their results clearly suggest that the production of physodalic acid is affected by element concentrations in the environment. PAWLIK-SKOWROŃSKA & BAČKOR (2011) measured higher concentrations of the depside lecanoric acid in *Hypocenomyce scalaris* and the depsidones fumarprotocetraric acid in *Cladonia furcata* at a mining site heavily polluted with Pb and Zn compared to a control site. However, although both the studies of BIAŁOŃSKA & DAYAN (2005) and PAWLIK-SKOWROŃSKA & BAČKOR (2011) are suggestive of the inducibility of lichen substance formation by external metal concentrations, they provide no information as to whether the production of certain compounds is only a stress response to exceptionally high concentrations of heavy metals at highly polluted sites or if lichen substances play a role in the 'everyday' fine-tuning of metal homeostasis in lichens even at sites with low availability of heavy metals.

To obtain information that may help answering this question, we correlated metal concentrations in tree bark with the concentration of lichen substances in the epiphytic lichen *Hypogymnia physodes* from a montane spruce forest of Germany, which is not exposed to a local pollution source. Assuming that lichen substances are involved in the control of metal uptake not only at strongly heavy metal-polluted sites, the hypotheses were tested that (1) the concentration of lichen substances varies with the metal concentrations of the substratum and (2) lichen substance concentrations vary less between lichen thalli from the same tree than from different trees (with different metal concentrations in the bark). Since the studies of BIAŁOŃSKA & DAYAN (2005) as well as HAUCK & HUNECK (2007) suggested that physodalic acid might be involved in metal homeostasis more strongly than other compounds and since high concentrations of Cu^{2+} and Mn^{2+} are known to damage *H. physodes*, (3) the more specific hypothesis was tested that the concentration of physodalic acid increases with the concentration of Cu^{2+} and Mn^{2+} in the substratum.

6.2 Material and methods

Field work

The study was conducted in montane forests of Norway spruce (*Picea abies* (L.) H. Karst.) in the Harz Mountains, northern Germany. Samples were collected in an unmanaged old-growth forest on Mt. Brocken (51°47' N, 10°38' E) at 1000 m a.s.l. in August 2011. The Harz Mountains are the highest mountain range in northern Germany with elevations up to 1142 m (Mt. Brocken) and are primarily formed of acidic paleozoic rocks. At elevations between 800 and 1142 m, annual mean temperature varies between 3 and 6 °C and precipitation ranges from 1500 to 1600 mm yr^{-1}. The prevailing winds come from southwest and west; fog events and long-lasting snow cover are common. Norway spruce is native to the Harz Mountains at the studied altitudes.

The study species *Hypogymnia physodes* (L.) Nyl. is a widespread species in the upper Harz Mountains, which occurs on most mature spruce trees. We randomly selected 90 mature spruce trees and included all of these trees into the study where >1 % of the lower trunk surface was covered with thalli of *H. physodes*. That way, 31 sample trees with *H. physodes* were selected. All lichen samples were collected from the west-facing aspect of the trees at a

height of 1.5 to 1.9 m above the soil level. On ten randomly selected trees, thalli of *H. physodes* were additionally sampled at a height of 0.8 to 1.5 m and 1.9 to 2.2 m above the ground to study the variation of the lichen substance concentrations within the lichens growing on the same tree. At the height of 1.5 to 1.9 m above the soil level, a bark sample was collected and cleared of epiphytes after the sample of *H. physodes* had been taken.

Chemical analyses

The dry thalli of *H. physodes* from each collection were submersed into acetone four times each for 10 min. The efficacy of the acetone treatment at removing the lichen substances from *H. physodes* amounts to c. 90 % (HAUCK 2008). The HPLC analysis principally followed the procedures described by GEYER (1985) and FEIGE et al. (1993). The method is based on a reverse-phased column and gradient elution. Measurements were carried out with an Agilent 1100 HPLC system (Agilent Technologies, Böblingen, Germany) including a binary pump, a Eurospher 100-5 C18 column (Macherey-Nagel, Düren, Germany) and a diode array detector. Solvents used included methanol and 1 % ortho-phosphoric acid (FEIGE et al. 1993). Absorbance was measured at λ = 245 nm. Acetone extracts were filtered with acetone-resistant PTFE membrane filters (0.45 µm) before the analysis.

Lichen substances known from *H. physodes* include the cortical depsides atranorin and chloroatranorin as well as the medullary depsidones physodic, 3-hydroxyphysodic and physodalic acids in major concentrations and protocetraric and 2'-*O*-methylphysodic acids in minor concentrations (HUNECK & YOSHIMURA 1996, MOLNÁR & FARKAS 2011). Isolates of atranorin, chloratranorin as well as physodic and hydroxyphysodic acids from the lichen substance collection S. Huneck (formerly IPB Halle, Germany) were used as reference samples. The retention times of these substances were found to be 44.6 min (atranorin), 46.4 min (chloratranorin), 36.7 min (physodic acid) and 31.1 min (3-hydroxyphysodic acid). A signal at 33.0 min in the chromatograms of the lichen extracts (Fig. 1) could be identified as physodalic acid with the help of published analyses of *H. physodes* extracts (BIAŁOŃSKA & DAYAN 2005, MOLNÁR & FARKAS 2011). Signals that were likely to represent protocetraric and 2'-*O*-methylphysodic acids were not found without relevant reference samples. Since we had no reference sample available for physodalic acid, a substance which was of major interest for our study, we generally abstained from establishing calibration curves, but limit

data presentation to the specification of the signal area (of absorbance units). Since a diode array detector was used, the relative amounts can only be compared within the same substance, because potential substance-specific differences in UV absorption limit the comparability of signals between substances. Nevertheless, the proportion of the individual lichen substances to one another was assessed by expressing the signal area of the individual substance relative to the total signal area of all analyzed lichen substances of the relevant sample.

Bark samples were dried at 105 °C and homogenized in a swing mill using an insert that is free from metal abrasion. Bark pH was measured with an MP 120 pH meter with electrode InLab 413 (Mettler-Toledo, Greifensee, Switzerland) in suspensions with deionized water (25 ml per g dry weight) shaken for 24 h before the measurements (pH [H_2O]); afterwards KCl was added in an excess concentration to measure the pH (KCl) value. After acid digestion with 65 % HNO_3, the total concentrations of Mn, Cu, Fe, Zn, K, Ca, and Mg were analyzed with ICP-OES using an Optima 5300DV (Perkin Elmer, Waltham, Massachusetts, USA).

Arithmetic means ± standard errors (SE) are presented throughout the paper. All data were tested for normal distribution with the Shapiro-Wilk test. Variation of the lichen substance concentrations between and within the individual sample trees was analyzed with a two-way analysis of variance (ANOVA). Correlations between the concentrations of lichen substances and metals in the substratum were studied by calculating Pearson's product moment correlation coefficients. The statistical analyses were computed with SAS 9.13 software (SAS Institute Inc., Cary, North Carolina, USA.).

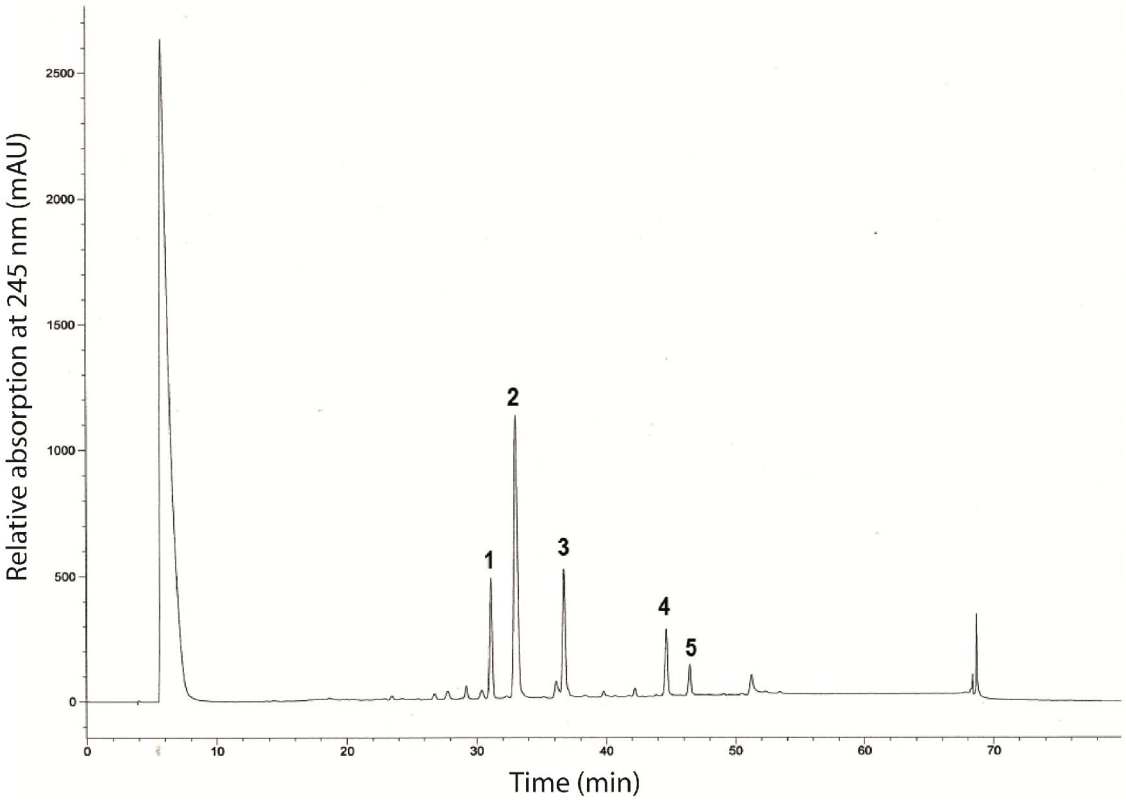

Fig. 6.1 HPLC chromatogram of *H. physodes* acetone extract containing (1) 3-hydroxyphysodic acid, (2) physodalic acid, (3) physodic acid, (4) atranorin, (5) chloratranorin.

Statistics

6.3 Results

The variation of lichen substance concentrations in *H. physodes* was clearly higher between the thalli from different trees than in thalli from the same tree (Table 6.1). Two-way ANOVA showed that the effect of the sample tree could explain nearly the whole variation of lichen substance concentrations, whereas within-tree variation was insignificant (Table 6.2). The signal areas of the three depsidones physodalic, physodic and 3-hydroxyphysodic acids were positively correlated with one another, as were the signal areas of the two depsides atranorin and chloratranorin (Table 6.3). The signal areas of the two depsides were positively correlated with the signal areas of physodic and physodalic acids, but not with that of 3-hydroxyphysodic acid. A different pattern of correlations between the amounts of lichen substances was found, when the signal areas were expressed in percent of the total signal area of all lichen substances in the relevant sample. In this case, the relative amount of 3-hydroxyphysodic acid was negatively correlated with that of the two other depsidones, physodalic acid and physodic acids, as well as with that of the two depsides, atranorin and

chloratranorin (Table 6.3). The relative amount of both depsides was positively correlated with each other and with the relative amount of physodic acid.

Table 6.1 Signal areas (±SE) of five lichen substances, depsides (atranorin, chloratranorin) and depsidones (physodic, 3-hydroxyphysodic, physodalic acids), in thalli of *H. physodes* collected at three different heights (0.8 to 1.5 m, 1.5 to 1.9 m, 1.9 to 2.2 m above the ground) from ten spruce trees.

Tree No.	Atranorin	Chloratranorin	Physodic acid	Hydroxyphysodic acid	Physodalic acid
1	1356±18	470±9	3645±20	5845±20	7887±19
2	805±10	323±3	3561±26	6333±42	9269±50
3	3236±20	765±5	5127±24	4095±42	12476±61
4	2003±18	654±13	4382±57	5407±4	10781±188
5	1252±21	506±5	4003±4	5371±24	10110±24
6	2314±15	747±14	4227±27	8111±92	10004±106
7	1672±18	704±1	4079±31	6370±58	7038±39
8	1934±6	740±1	4204±3	4128±5	7016±11
9	3620±11	1043±24	5185±20	2417±11	7074±11
10	3978±15	1537±3	4904±4	4197±7	13906±3

Table 6.2 Results of two-way ANOVA quantifying the effect of the sample tree and the replicate sample per tree on depside and depsidone amounts in *H. physodes*.

	Total (df=11)			Tree (df=9)		Replicate (df=2)	
	R^2	*F*	*P*	*F*	*P*	*F*	*P*
Atranorin	1.00	2587	<0.001	3161	<0.001	0.97	0.40
Chloratranorin	1.00	795	<0.001	971	<0.001	5.08	0.02
Physodic acid	1.00	266	<0.001	325	<0.001	1.34	0.29
Hydroxyphysodic acid	1.00	900	<0.001	1100	<0.001	1.86	0.18
Physodalic acid	1.00	605	<0.001	739	<0.001	1.91	0.18

Table 6.3 Pearson correlation coefficients (r) for the relationship between the amounts of the individual lichen substances (A: signal area; B: percent of signal area related to the total signal area of all lichen substances) in *H. physodes*. Error levels (*P*) are given in brackets.

	Chloratranorin	Physodic acid	Hydroxyphysodic acid	Physodalic acid
A:				
Atranorin	**0.88 (<0.001)**	**0.66 (<0.001)**	0.03 (0.84)	**0.54 (<0.001)**
Chloratranorin		**0.66 (<0.001)**	0.00 (0.99)	**0.58 (<0.001)**
Physodic acid			**0.48 (0.003)**	**0.76 (<0.001)**
Hydroxyphysodic acid				**0.60 (<0.001)**
B:				
Atranorin	**0.83 (<0.001)**	**0.44 (0.007)**	**-0.73 (<0.001)**	0.03 (0.87)
Chloratranorin		**0.41 (0.01)**	**-0.79 (<0.001)**	0.21 (0.23)
Physodic acid			**-0.41 (0.01)**	-0.31 (0.07)
Hydroxyphysodic acid				**-0.61 (<0.001)**

Table 6.4 Metal concentrations (in µmol g^{-1} dry weight, ±SE) and pH of spruce bark collected from trunks (*N*=31) at 1.5 m height in the Harz Mountains.

	Concentration/pH
Cu	0.08±0.01
Mn	1.27±0.06
Fe	1.86±0.18
Zn	1.18±0.07
Total heavy metals	4.32±0.19
K	8.27±1.00
Ca	134±8
Mg	6.55±0.74
pH (H_20)	3.62±0.03
pH (KCl)	2.95±0.03

The bark of the spruce trees inhabited by *H. physodes* was acidic with a mean pH (H_2O) of 3.6 (Table 6.4). Fe, Mn, and Zn were the most highly concentrated heavy metals in the bark, while Cu occurred at very low concentrations. The total amount of lichen substances (deduced from the total signal area in the chromatogram) increased with increasing content of heavy metals (Cu, Fe, Mn, Zn) in the substratum, though the total heavy metal concentration varied only in the range of a few µmol g^{-1} (Fig. 6.2). The signal area of physodalic acid was significantly correlated with the concentrations of Fe, Mn, and Zn in the substratum (Table 6.5). Furthermore, the signal areas of physodic and 3-hydroxyphysodic acids increased with

increasing Fe content of the bark, as did the signal areas of atranorin and chloratranorin with the Mn content and of chloratranorin with the Zn content.

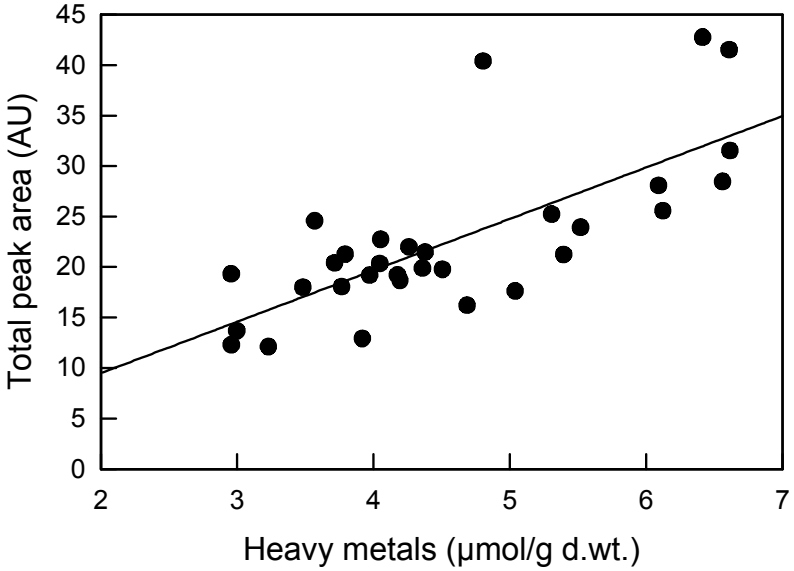

Fig. 6.2 Total signal area of lichen substances in *H. physodes* in the HPLC chromatograms versus the content of heavy metals (Cu, Fe, Mn, Zn) in the substratum (r = 0.74, $P<0.001$, $y = -685 + 5090x$).

Table 6.5 Pearson correlation coefficients (r) for the relationship between heavy metal concentrations in the substratum and the amount of lichen substances (A: signal area; B: percent of signal area related to the total signal area of all lichen substances) in *H. physodes*. Error levels (*P*) are given in brackets.

	Atranorin	Chloratranorin	Physodic acid	Hydroxyphysodic acid	Physodalic acid
A:					
Cu	0.14 (0.45)	0.14 (0.44)	0.15 (0.42)	-0.21 (0.26)	0.29 (0.11)
Mn	**0.35 (0.05)**	**0.44 (0.01)**	0.30 (0.10)	-0.03 (0.86)	**0.45 (0.01)**
Fe	0.25 (0.18)	0.23 (0.21)	**0.36 (0.05)**	**0.42 (0.02)**	**0.49 (0.006)**
Zn	0.34 (0.06)	**0.38 (0.04)**	0.27 (0.10)	0.03 (0.88)	**0.36 (0.05)**
B:					
Cu	0.09 (0.62)	0.10 (0.61)	-0.06 (0.75)	-0.46 (0.009)	**0.68 (<0.001)**
Mn	0.17 (0.36)	0.26 (0.15)	-0.19 (0.30)	-0.34 (0.06)	**0.46 (0.009)**
Fe	-0.03 (0.86)	-0.05 (0.78)	**-0.41 (0.02)**	0.09 (0.64)	0.12 (0.50)
Zn	0.15 (0.42)	0.18 (0.34)	-0.17 (0.37)	-0.20 (0.29)	0.25 (0.17)

When the signal areas were expressed in percent of the total signal area of all lichen substances, increasing relative amounts of physodalic acid were found with the concentrations

of Cu and Mn, whereas the relative amount of 3-hydroxyphysodic acid decreased with increasing Cu and Mn concentrations (Table 6.5). The content of Fe in the substratum decreased with increasing proportion of physodalic acid in the total lichen substance totals.

6.4 Discussion

The high variation of the content of lichen substances in thalli of *H. physodes* between different trees combined with the low variation of lichen substance concentrations within the individuals of *H. physodes* growing on the same tree suggest that the production of lichen substances is strongly influenced by the environment. This conclusion agrees with studies of gradients of solar irradiation where increasing concentrations of UV- and visible light-absorbing lichen substances were found with increasing average photon flux densities (BJERKE & DAHL 2002, NYBAKKEN et al. 2007). The correlation with the heavy metal concentrations of the substratum (which naturally vary within a forest stand because of variations in soil chemistry or the canopy exposure to the atmosphere) supports the hypothesis that the biosynthesis of lichen substances also responds to the availability of these metals. This finding agrees with reports of elevated lichen substance concentrations at strongly heavy metal-polluted sites (PAWLIK-SKOWROŃSKA & BAČKOR 2011) as well as with the experimental result that thalli of *H. physodes* with or without their natural content of lichen substances differ in the intracellular uptake of heavy metals from solution (HAUCK 2008).

The closest correlation with heavy metal concentrations was found with the amount of physodalic acid. This is in line with increased concentrations of this depsidone in thalli of *H. physodes* in industrial compared to remote areas (BIAŁOŃSKA & DAYAN 2005) and with the observation that isolates of physodalic acid were more active in influencing the adsorption of metal ions at cation exchange sites of cellulose filters than physodic acid, atranorin and protocetraric acid (HAUCK & HUNECK 2007). The negative correlation of the signal area of physodalic acid relative to the total signal area of all lichen substances with the corresponding values of 3-hydroxyphysodic and physodic acids suggests that the two latter substances could be partly converted into physodalic acid under the presence of high heavy metal concentrations. BIAŁOŃSKA & DAYAN (2005) also found decreasing concentrations of 3-hydroxyphysodic acid with increasing physodalic acid content of *H. physodes*. The closest correlations of the signal area of physodalic acid related to the total signal area of lichen

substances were found with the Cu and Mn concentrations of the substratum. This correlation is likely to be causal, as the lichen substances of *H. physodes* are known to control the intracellular uptake of these metals in this lichen (HAUCK 2008).

In contrast to 3-hydroxyphysodic and physodic acids, physodalic acid has neighboring aldehyde and hydroxyl moieties at one of the benzol rings of the molecule. This structure was considered to be crucial for metal complex formation in depsidones by PURVIS et al. (1987, 1990). Thus, it seems likely that physodalic acid is increasingly formed with increasing exposure to heavy metals to immobilize potentially toxic excess amounts of these metals. The detailed mechanisms how lichen substances and their complexes with metal ions contribute to metal homeostasis are largely unknown and require more research.

6.5 Conclusions

Our results are suggestive of a potential role of lichen substances, and of physodalic acid in particular, in controlling the uptake of heavy metals in lichens not only at sites with exceptionally high concentrations of these metals (e.g. rock formations with naturally high metal concentrations, mining sites), but even in not or moderately polluted ecosystems with low or moderate availability of heavy metals. With the present work and previous studies, more and more evidence has been accumulated that the complex formation of lichen substances with metal ions plays a key role in this process. However, the detailed mechanisms of the control of metal uptake by lichen substances have still to be elucidated.

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Chapter 7

Significance of over-mature and decaying trees for carbon stocks in a Central European natural spruce forest

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Abstract

Old-growth forests are important stores for carbon as they may accumulate C for centuries. The alteration of biomass and soil carbon pools across the development stages of a forest dynamics cycle has rarely been quantified. We studied the above- and belowground C stocks in the five forest development stages (regeneration to decay stage) of a montane spruce (*Picea abies*) forest of the northern German Harz Mountains, one of Central Europe's few forests where the natural forest dynamics have not been disturbed by man for several centuries. The over-mature and decay stages had the largest total (up to 480 Mg C ha^{-1}) and aboveground biomass carbon pools (200 Mg C ha^{-1}) with all biomass C stored in dead wood in the decay stage. The soil C pool (220–275 Mg C ha^{-1}, 0-60 cm) was two to three times larger than in temperate lowland spruce forests and remained invariant across the forest dynamics cycle. On the landscape level, taking into account the frequency of the five forest development stages, the total carbon pool was approximately 420 Mg C ha^{-1}. The results evidence the high significance of over-mature and decaying stages of temperate mountain forests not only for conserving specialized forest organisms but also for their large carbon storage potential.

Key words: climate change, boreal forest, forest biomass, growth dynamics, primary forest, coarse woody debris, *Picea abies*, Harz Mountains

7.1 Introduction

The earth's forests with an extension of approximately 42 million km^2 store about 45 % of the global terrestrial carbon (BONAN 2008). Recent studies found both net ecosystem and net biome productivity to be predominantly positive in temperate, boreal, and tropical forests of young to old age (15 to >200 years) (LUYSSAERT et al. 2008, 2010), showing that forests can act as carbon sinks in large parts of the forest dynamics cycle. The productivity of mature trees typically declines with age (RYAN et al. 1997), which suggests that forests should sequester less carbon beyond the age of maximum growth (ZHOU et al. 2006). This view has been questioned by SCHULZE et al. (2009) and DOLMAN et al. (2010) who provided some evidence that old-growth forests may take up more carbon than formerly expected.

Beside forest age, forest management (including deforestation) has a large influence on the global carbon cycle with deforestation accounting for approximately 18% of the global CO_2 net release to the atmosphere (IPCC 2007). In forests intensively exploited for timber, both the biomass and soil C stocks generally decrease with increasing forest management intensity (SCHULZE et al. 1999; YANAI et al. 2003). This aspect is highly relevant for Europe's forests which have been subjected to a variety of management impacts during the past centuries or sometimes even millennia (CIAIS et al. 2008; ELLENBERG & LEUSCHNER 2010). These anthropogenic disturbances included not only timber harvest, but also litter raking, fuel wood collection, and wood pasture. A likely consequence are unbalanced soil carbon stocks, reduced soil fertility, and often decreased wood biomass stocks in many contemporary stands as compared to old-growth forests (GLATZEL 1999).

Unmanaged old-growth forests have a more diverse stand structure and harbor more deadwood than managed forests (CHATTERJEE et al. 2009). Natural stand dynamics proceed from a phase with abundant offspring to a stage with rapid height growth and canopy expansion to late stages with over-mature and finally decaying trees. Over-mature trees and deadwood with large diameters are usually absent from managed temperate forests. Their conservation may reduce timber yield, but these old trees are of high value for biodiversity conservation by providing habitats for numerous specialized organisms, including hole-nesting birds, bats, xylophagous insects, fungi, lichens, and bryophytes that are rare or absent from the earlier development stages (SCHIEGG 2000; ÓDOR et al. 2006; HILMO et al. 2009).

The objective of this study was to examine the significance of over-mature and decaying forest patches for the carbon storage in biomass (live and dead) and soil of a coniferous mountain forest ecosystem. We conducted a case study in a montane spruce forest ecosystem on Mt. Brocken, Germany, which was spared from intense forest management for centuries and thus represents one of central Europe's rare examples of a forest with natural stand dynamics and all different development stages being present in a mosaic of forest patches (STÖCKER 1997). We used this study object to test the hypotheses that stages with predominantly over-mature and decaying trees are characterized by (1) higher above-ground and (2) higher soil carbon stocks, assuming a positive effect of an increasing amount of deadwood and of long periods without forest management on the carbon transfer from biomass to the soil.

7.2 Methods

Study area and sample plot selection

The study was conducted on the eastern slope of Mt. Brocken, the highest peak of the Harz Mountains (1142 m a.s.l.) in northern Germany, at 900 – 1,000 m a.s.l. (51° 47' N, 10° 38' E) in an old-growth spruce forest (*Picea abies* (L.) H. Karst.) of 300 ha size. This forest stand was part of a protected hunting ground for deer, bears, wolves and lynxes of the nobility and clergy since the early Middle Ages (ca. 800 - 1500 AD, SCHADE 1926), and logging and forest pasture were prohibited (JACOBS 1871, 1878). Because of its restricted accessibility, the forest also has never been exploited for charcoal production during the long-lasting medieval mining period in the Harz Mountains (KORTZFLEISCH 2008). The oldest spruce trees in the forest are over 280 years old (HAUCK et al. 2012a). The climate of Mt. Brocken is characterized by an annual precipitation of 1,600 mm (including 192 mm of snow), an annual mean temperature of 2.9°C (1961-1990), and 306 fog days per year (GLÄSSER 1994). Parent rock material is granite; soils are Stagnic Cambisols and, more locally, Leptic Cambisols, and Histic Planosols. The typical humus form is mould.

The studied forest includes the full spectrum of development stages in a forest dynamics cycle. Five structurally defined development stages were distinguished following STÖCKER (1997) (see Table 1). In each stage, five plots of 10 m x 10 m were established. Due to the limited size of the old-growth stand, it was not possible to select the sample plots with a

completely randomized design. However, the plots of a given development stage were more or less evenly spread over the forest area to avoid clumping of replicate plots in certain sections of the forest.

For extrapolating to the landscape level, we quantified the frequency of the five development stages in the whole study area of 300 ha. We chose four transects following the 925, 950, 975, and 1000 m contour lines and assigned the forest at intervals of 20 m distance to the five development stages defined in Table 7.1. Patches showing within a 10-m radius of the sample point the structural characteristics of two development stages were assigned by 50% to these two stages (this approach was necessary at 5 % of the sample points). Bogs and forested scree fields were excluded from this calculation. The percental frequency values of the five stages were averaged over the four transects and extrapolated to the entire forest.

Table 7.1 Structural attributes of forest development stages in old-growth upper-montane spruce forests on Mt. Brocken (following the classification by STÖCKER 1997, modified).

	Regeneration	**Initial**	**Climax**	**Overmature**	**Decay**
Number of stems	low-high, increasing	very high, decreasing	high, stagnating	high, decreasing	medium-low, decreasing
Canopy cover	low, steadily increasing	medium-high, gap closure	high, gap closure	decreasing, gaps	medium-low, decreasing
Deadwood	remains from decay phase	small-sized wood debris	low, increasing	increasing in canopy layer	only dead trees
Height structure	Very few mature trees	heterogeneous structure	low variance in tree height	low variance in tree height	disintegration of canopy layer
Age structure	saplings dominate	medium-sized trees, low variance	big-medium-sized trees, low variance	big trees, low variance	big dying trees, groups of saplings
Tree vitality	very high	high	stagnating-decreasing	low	low, dieback
Tree regeneration	abundant	low, partly suppressed	very low, suppressed	low, partly suppressed	starting in groups

Determination of aboveground biomass and carbon stocks

The height of all trees with a diameter at breast height (dbh) greater than 7 cm was measured with a Vertex IV sonic clinometer and T3 transponder (Haglöf, Långsele, Sweden). The dbh was recorded with diameter measurement tapes at a resolution of 0.5 mm. The height and

diameter above buttresses (dab) of all spruce seedlings and saplings (dbh < 7 cm) were measured with a folding rule and a caliper. Furthermore, the length and diameter of the standing deadwood and the coarse woody debris with a minimum diameter greater than 2 cm were measured.

Species-specific allometric biomass equations established in mountain spruce forests of Bohemia (Czech Republic) (ČERNÝ 1990) were used to estimate the total aboveground biomass of all living trees with a dbh greater than 7 cm. Aboveground tree biomass (B_A, in kg) was obtained from the expression

$$B_A = 0.11975 \times (D^2 \times H)^{0.81336} \quad (1)$$

where D is the diameter at breast height including bark (in cm) and H is the tree height (in m). The equation was established at trees in three 57-, 78- and 106-year-old even-aged spruce stands at elevations of 540-630 m a.s.l. growing under comparable climatic and edaphic conditions as exist at our study site. Nevertheless, we are aware that published allometric equations generally face limitations when transferred to other sites, introducing possible errors in the calculated aboveground biomass figures (ROCK 2007). Consequently, we discuss the biomass data with care. The seedling biomass (B_S, in kg) was estimated after Chen (1997) with the equation

$$B_S = a + bH + cD \quad (2)$$

with a = -2.726, b = 0.120, and c = 0.658. A carbon concentration of 0.504 kg_C kg_{wood}^{-1} was assumed for calculating the amount of stored carbon from the biomass estimates (MUND et al. 2006). All biomass data refer to dry weight determined at 105 °C.

A decay class was assigned to every piece of coarse woody debris following HOLEKSA (2001) as defined in Table 7.2. Eight decay classes of logs and snags with a minimum diameter greater than 2 cm and length greater than 1 m were distinguished. The deadwood volume (V, in m^3) was obtained with the equation $V = \pi r^2 l$ with r is the radius, and l is the length (cm). The volume of a few almost square-shaped tree stumps was calculated assuming the shape of a cuboid. We used the wood density in these eight decay classes as measured by MERGANIČOVÁ & MERGANIČ (2010) and a carbon concentration of 0.504 kg_C kg_{wood}^{-1} (MUND et al. 2006) to obtain the biomass and carbon stocks of all deadwood objects.

Table 7.2 Characteristics of the decay classes of snags and logs (following the classification by Holeksa 2001, modified). Wood densities for each decay class from MERGANIČOVÁ & MERGANIČ 2010).

Class	Wood density (kg m^{-3})	Surface	Penetration by sharp objects	Profile of fallen logs	Shape of trees and stumps
I	394	smooth	-	round	thin twigs and remaining needles present
II	357	smooth	surface bends	round	twigs breaking off
III	321	crevices of few mm depth	to 1 cm	round	parts of crown still present
IV	284	crevices of 0.5 cm depth	to 3 cm	round	loss of crown, few side branches remain
V	248	crevices 1 cm deep, thick wood pieces tear off from surface	to 5 cm	round	unstable stem, collapsing trees
VI	211	thick pieces tear off from sides	solid pieces only in the centre	round	broken-off stumps
VII	175	entire log with crevices of several cm depth, high vegetation cover	through	flattened	broken-off stumps, deep crevices, cavernous or filled by litter
VIII	138	almost completely covered with bryophytes, lichens and vascular plants	through	irregular, elevated above ground	stumps almost completely covered by vegetation, irregular shape

Soil sampling and chemical analyses

Soil was sampled from four depths (0-10, 10-20, 20-40, 40-60 cm) in a soil profile in the center of each plot (25 plots in total). The litter layer was removed before sampling. At 40–60 cm depth, we could take samples only from a few plots owing to high stone content; these subsoil values, therefore, are discussed with care. Three samples per layer were taken with steel cylinders (100 cm^3) for the analysis of C and N concentrations and salt-extractable cation concentrations on a volume basis. Bulk density and water content of the cylinder samples were calculated after measuring fresh and dry weight (105°C, 48 h). The stone content was obtained for each soil depth from volumetric and gravimetric measurements (steel cylinder samples), but was only visually assessed in the field in the subsoil. The carbon content was calculated for each soil layer from the measured C concentration, soil bulk density and the stone content.

The pH was measured in suspensions of fresh soil samples in H_2O or 1N KCl after 24 h with a MP 120 pH meter and an InLab 413 electrode (Mettler-Toledo, Greifensee, Switzerland). For calculating base saturation, the concentrations of K, Na, Mg, Ca, Al, Fe and Mn in 5 g of fresh soil extracted with $BaCl_2$ (100 ml, 2 N) were measured with ICP-OES (Optima 5300 DV, Perkin Elmer, Waltham, Massachusetts, USA). Dry soil samples (70°C, 48 h) were pulverized with a disc mill and the total concentrations of C and N were measured with a CN analyzer (Vario EL III, Elementar Analysensysteme, Hanau, Germany).

Statistical analyses

Arithmetic means ± standard errors are presented throughout the paper. Significant differences of residuals of a one-way analysis of variance (ANOVA) for stand structure parameters, biomasses and carbon stocks were tested for the five development stages. Pairwise comparisons between the different stages were made with Student's t-test. All data of model residuals were tested for normal distribution with the Shapiro-Wilk test and for homogeneity of variances with the Levene test. The carbon stocks in the different soil layers, which were not normally distributed, were tested with the Kruskal-Wallis test. All statistical tests were done with R 2.14.1 (R Development Core Team, Vienna, Austria) software at a significance level of $P \leq 0.05$.

7.3 Results

Aboveground biomass and carbon stocks

The highest number of living trees exceeding a dbh of 7 cm was found in the initial stage (B), although standing deadwood was scarce (Table 7.3). Standing deadwood was even scarcer in the climax stage (C), but started to increase in the over-mature stage (D) to a maximum in the decay stage (E) with a mean value of 460 dead stems ha^{-1} and a standing deadwood mass of 390 Mg ha^{-1} (Tables 7.3, 7.4). The density of standing dead trees was only reduced to a small extent from the decay stage (E) to the regeneration stage (A) of the next forest generation (Table 7.3). However, because the height of the snags was strongly declining from stage E to A, the standing deadwood biomass was strongly reduced (Table 7.4). Lying trunks and other lying coarse woody debris were more evenly distributed over the stages; their biomass pool ranged from 15 Mg ha^{-1} in the decay stage (E) to 41 Mg ha^{-1} in the over-mature stage (D) (Table 7.4).

The total aboveground carbon stocks, calculated as the sum of the carbon stocks of living trees with a dbh greater than 7 cm, tree seedlings and saplings, and the standing and lying deadwood, increased with proceeding stand development. The lowest carbon stocks were found in the regeneration (A) and initial (B) stages with significantly smaller biomass stocks and biomass carbon pools than in the over-mature (D) and decay (E) stages, where the aboveground biomass reached approximately 400 Mg ha^{-1} and the aboveground carbon stock was about 200 Mg C ha^{-1} (Figure 7.1). The contribution of deadwood to the total biomass carbon pool was almost 100 % in the regeneration (A) and decay (E) stages, and decreased to 6 % in the climax stage (C) (Table 4). In over-mature (D) forest patches, 20 % of the aboveground carbon was stored in deadwood with most of it located in the standing deadwood. The contribution of lying deadwood to the aboveground carbon stock was highest in the regeneration (A) and initial (B) stages.

Table 7.3 Stand structure and soil properties (0-20 cm) of the five development stages (n=5). Given are means and standard error. Different letters indicate significant differences between the forest development stages. [1)] Trees with diameter at breast height (dbh) > 7 cm.

	Regeneration	**Initial**	**Climax**	**Overmature**	**Decay**
Canopy closure (%)	82 ± 1.4ab	91 ± 0.8a	90 ± 0.3a	85 ± 0.6a	74 ± 1.0b
Living trees[1]					
Stem density (N ha^{-1})	40 ± 40a	960 ± 289b	480 ± 66ab	380 ± 37ab	-
Basal area (m² ha^{-1})	0.2 ± 0.2a	14.0 ± 4.8a	70.5 ± 5.4b	72.6 ± 7.8b	-
Mean tree height (m)	3.2	6.6 ± 0.2a	22.5 ± 1.4b	22.3 ± 0.8b	-
Mean dbh (cm)	7.6	12.4 ± 0.6a	43.2 ± 3.3b	48.6 ± 1.3b	-
Seedlings					
Seedling density (N ha^{-1})	10240 ± 1031b	2640 ± 337a	1380 ± 530a	3120 ± 1203a	2160 ± 717a
Mean seedling height (cm)	70 ± 12ab	124 ± 37a	64 ± 34ab	38 ± 5.7b	34 ± 2.3b
Mean root collar diameter (cm)	1.3 ± 0.2a	2.2 ± 0.5a	1.3 ± 0.6b	1.0 ± 0.1a	0.9 ± 0.1a
Standing deadwood and stumps					
Stem density[1)] (N ha^{-1})	425 ± 170ab	200 ± 91ab	125 ± 25b	320 ± 58ab	460 ± 60a
Basal area (m² ha^{-1})	49.3 ± 14.6a	32.5 ± 13ab	5.1 ± 2.2b	24.4 ± 6.5ab	96.7 ± 7.9c
Mean snag height (m)	2.3 ± 0.9a	1.2 ± 0.4a	1.8 ± 1.1a	3.3 ± 0.7a	8.9 ± 2.4b
Mean dbh (cm)	31.4 ± 7.1ab	24.9 ± 7.3ab	13.9 ± 4.1a	21.7 ± 3.1ab	44.6 ± 6.5b
Soil properties					
C/N ratio	19.5 ± 0.7a	20.2 ± 1.7a	21.6 ± 2.1a	19.4 ± 1.1a	19.0 ± 1.0a
Soil C concentration (%)	23.1 ± 5.4a	31.8 ± 5.9a	26.5 ± 5.1a	22.9 ± 5.7a	27.6 ± 5.4a
Bulk density (g cm^{-3})	0.8 ± 0.13a	0.6 ± 0.03a	0.8 ± 0.07a	0.7 ± 0.06a	0.7 ± 0.06a
Base saturation (%)	39.2 ± 7.0a	41.6 ± 8.0a	38.6 ± 7.3a	41.8 ± 5.5a	35.3 ± 3.9a
pH_{H2O}	3.8 ± 0.06a	3.6 ± 0.24a	3.8 ± 0.03a	3.6 ± 0.11a	3.7 ± 0.06a
pH_{KCl}	3.4 ± 0.07a	3.3 ± 0.22a	3.2 ± 0.06a	3.1 ± 0.13a	3.3 ± 0.08a

[1] Trees with diameter at breast height (dbh) > 7 cm.

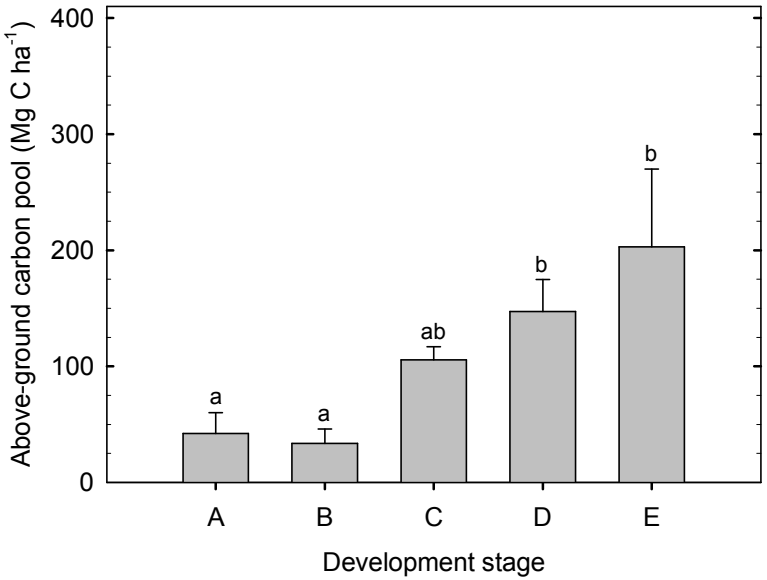

Fig. 7.1 (above) Total above-ground (living trees, tree regeneration, deadwood) carbon stocks (Mg ha^{-1}) in five development stages (A = regeneration, B = initial, C = climax, D = overmature, E = decay stage). Given are means and standard error of *N* = 5 plots. Significant differences between the development stages are indicated with lower-case letters.

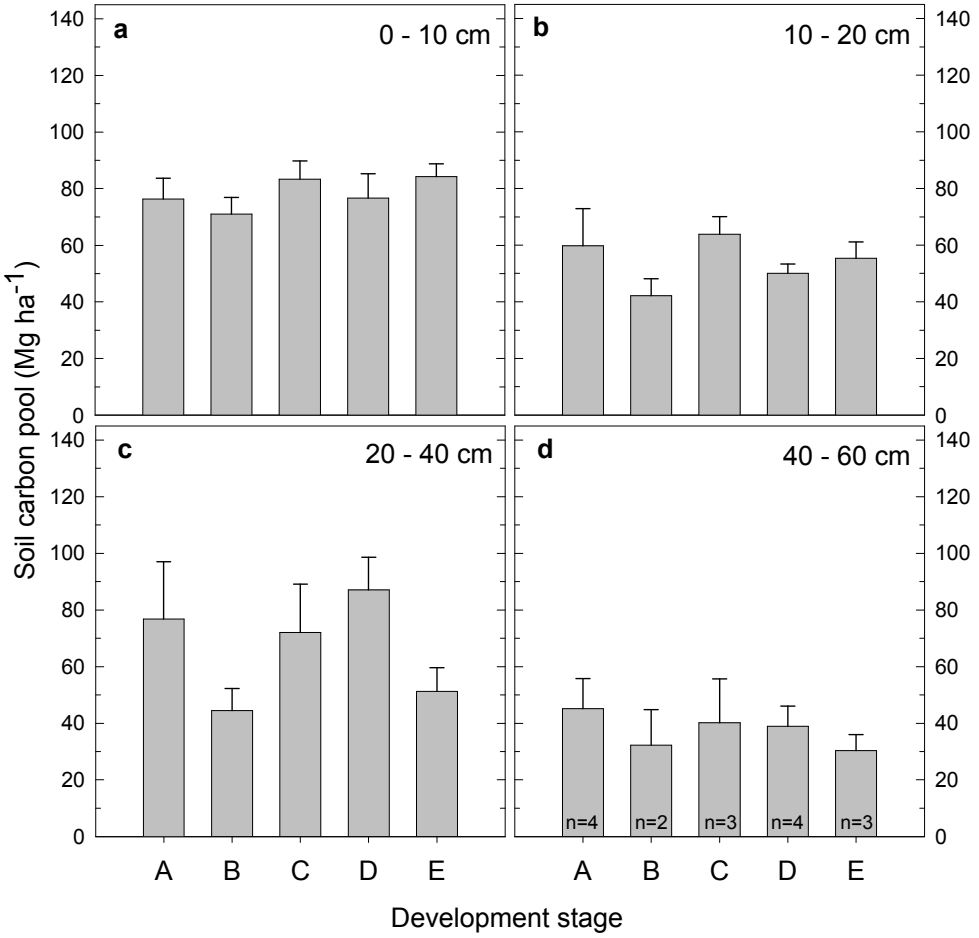

Fig. 7.2 (right) Soil carbon stocks (Mg ha^{-1}) in different soil layers (0-10, 10-20, 20-40, 40-60 cm) in the five development stages (A = regeneration, B = initial, C = climax, D = overmature, E = decay stage). Given are means and standard error of *N* = 5 plots. For the 40-60 cm layer n is indicated in each bar (reduced replicate number due to high bedrock surface).

Soil carbon stocks

The soil physical and chemical properties showed no significant differences between the five development stages for all analyzed parameters (Table 7.3). The soil texture of all plots was similar and dominated by sand and silt (sand 52%, silt 36%, clay 12%; data not shown). The mean soil profile depth to the bedrock surface was 54 cm. The soil carbon stocks did not differ between the development stages in any soil depth (Figure 7.2). All topsoils had high concentrations of SOC due to a tendency to the formation of shallow Histosol profiles (40 % C of the total dry mass at 0–10 cm, 15 % at 10 – 20 cm). The SOC content decreased to 8.5 % at 20-40 cm depth and 3 % at 40–60 cm. The highest carbon stocks (ca. 140 Mg C ha^{-1}) were found in the upper soil (0–20 cm); the stores were about 70 Mg C ha^{-1} at 20–40 cm and 40 Mg C ha^{-1} at 40–60 cm. This adds up to profile totals of around 250 Mg C ha^{-1}.

Ecosystem carbon stocks

On the landscape level, the over-mature (D) and decay (E) stages were over-represented in the studied forest; together they occupied approximately 66 % of the total area (Table 7.5). These two stages had very high total ecosystem carbon stocks between 450 and 485 Mg C ha^{-1} that sum up to 90 Gg C in the whole area of 300 ha, whereas the regeneration (A) and initial (B) stages together contributed only with around 15 Gg C to the total carbon stock of the studied forest (Tables 7.4, 7.5). The mean weighted total carbon pool per hectare of the study area calculated from Table 5 is 422 Mg C ha^{-1}, and thus close to the ecosystem carbon pool of the over-mature stage (Table 7.4).

Table 7.4 Biomass and carbon pools of the different above- and below-ground compartments.

	Regeneration	Initia	Climax	Overmature	Decay
Living trees					
Biomass (Mg ha^{-1})	0.33 ± 0.33a	42 ± 16a	339 ± 30b	328 ± 42b	-
Carbon pool (Mg C ha^{-1})	0.17 ± 0.17a	21 ± 7.8a	171 ± 15b	165 ± 21b	-
Seedling biomass					
Biomass (Mg ha^{-1})	0.14 ± 0.02a	0.06 ± 0.01b	0.01 ± 0.01c	0.02 ± 0.01c	0.02 ± 0.01c
Carbon pool (Mg C ha^{-1})	0.07 ± 0.01a	0.03 ± 0.01b	0.01 ± 0.00c	0.01 ± 0.00c	0.01 ± 0.00c
Standing deadwood					
Mass (Mg ha^{-1})	55 ± 34a	17 ± 10a	4.0 ± 2.8a	57 ± 30a	388 ± 132b
Carbon pool (Mg C ha^{-1})	28 ± 17a	8.6 ± 5.0a	2.0 ± 1.4a	29 ± 15a	195 ± 66b
Decay class	5.4 ± 0.9a	4.6 ± 1.2a	5.1 ± 1.1a	3.2 ± 0.4a	3.6 ± 0.8a
Lying deadwood					
Mass (Mg ha^{-1})	28 ± 8.9a	23 ± 9.2a	19 ± 5.5a	41 ± 17a	15 ± 6.1a
Carbon pool (Mg C ha^{-1})	14 ± 4.5a	11 ± 4.6a	9.6 ± 2.8a	20 ± 8.6a	7.7 ± 3.1a
Decay class	4.9 ± 0.3a	4.7 ± 0.4a	5.0 ± 0.3a	4.9 ± 0.5a	4.2 ± 0.4a
Ecosystem C pool					
Above-ground C pool (Mg C ha^{-1})	42 ± 18a	41 ± 15a	183 ± 16ab	214 ± 34b	203 ± 67b
SOC pool (0-60 cm) (Mg C ha^{-1})	241 ± 37a	223 ± 18a	276 ± 44a	265 ± 19a	221 ± 16a
Total	**291 ± 21ab**	**252 ± 28a**	**464 ± 35bc**	**453 ± 19bc**	**485 ± 79c**

Table 7.5 Carbon pools and distribution of the five different development stages on the landscape level.

	Regeneration	Initial	Climax	Overmature	Decay
Frequency of each development stage (%)	8.4	10.3	14.9	39.1	27.3
Area of each development stage (ha)	25	31	45	117	82
Landscape above-ground C pool (Mg C 300ha^{-1})	1,066	1,276	8,158	25,144	16,627
Landscape SOC pool (Mg C 300 ha^{-1})	6,068	6,895	12,319	31,097	18,105
Total landscape C pool (Mg C 300ha^{-1})	**7,134**	**8,170**	**20,477**	**56,242**	**34,732**

7.4 Discussion

In this old-growth mountain spruce forest, the ecosystem carbon pool varied nearly by a factor of two across the different stand development stages, increasing from 250-290 Mg C ha^{-1} in the regeneration and initial stages to 450-485 Mg C ha^{-1} in the over-mature and decay stages. Thus, our measurements indicate that the forest C pool experiences a cyclic variation with an amplitude of around 200 Mg C ha^{-1} in the approximately 300 year-long forest dynamics cycle (Stöcker 1997) of this mono-specific coniferous forest. This variation is nearly entirely caused by tree age-dependent alteration in the aboveground live and dead biomass fractions, whereas the SOC pool showed no significant trend across the five development stages. The very high biomass and ecosystem C pools in the over-mature and decay stages are primarily the consequence of the low decay rate in the cold and wet environment of the studied mountain forest close to the alpine timberline with 5 months snow cover and a mean annual temperature close to 3°C (GLÄSSER 1994). With the death of all spruce trees until the end of the over-mature stage, 170-190 Mg C ha^{-1} are transferred to the fraction of standing deadwood and are fully decomposed not before the end of the regeneration stage in the next forest generation. In a subalpine spruce forest of the Carpathians with a similar climate as in our study area, spruce snags and logs had a mean residence time of 47-63 years (volume-based calculation) or 71-113 years (log number-based calculation) (HOLEKSA et al. 2008). The continuous persistence of deadwood across subsequent tree generations is a characteristic feature of temperate high-elevation and boreal (high-latitude) forests and distinguishes them from forests in warmer climates at lower elevation and latitude (ZIELONKA 2006, VANDEKERKHOVE et al. 2009).

The stable SOC pool during the roughly 300 years of a spruce forest dynamics cycle agrees with the results obtained from other studies in coniferous forests (for example, PEICHL & ARAIN 2006; BRADFORD et al. 2008). This contrasts with the review of PREGITZER & EUSKIRCHEN (2004), who found the highest SOC stocks in the oldest stand age classes along chronosequences in the earth's main forest biomes; in the boreal forest, these authors assumed the SOC pools to be twice as high in mature than young stands. However, GLEIXNER et al. (2009) re-analyzed the tree age-SOC relationship in temperate coniferous forests with a data set solely consisting of studies with chronosequence data and found no increase, but rather an insignificant trend for a SOC decrease, with increasing age. We explain the lack of significant changes in the SOC pool during the forest development cycle in our study with the low temperature and the absence of stages with high radiation transmission to the forest floor as they may result from stand-level disturbance. In the

studied forest, even the decay and regeneration stages reached a canopy closure of 74 and 80%, respectively, partly due to the high density of standing deadwood. Therefore, development stages with warmer soil and reduced (more favorable) soil moisture conditions, which could promote decomposer activity, are lacking in this cold and moist environment. The positive effect of the generally low temperature on the size of the SOC pool is well demonstrated by the 2-3 fold larger soil C pool in this high-elevation old-growth spruce forest (220–275 Mg C ha^{-1} at 0-60 cm) as compared to managed lowland spruce forests in Germany (ca. 50–70 Mg C ha^{-1} at 0-30 cm, OEHMICHEN et al. 2011; 80-100 Mg C ha^{-1} at 0-90 cm; WÖRDEHOFF et al. 2012). Another reason for the high SOC pools is most likely the long forest continuity at Mt. Brocken which is not found in most lowland spruce stands. Centuries of SOC accumulation in a climate with a tendency for carpet bog formation may well result in soil C stocks greater than 200 Mg C ha^{-1}.

Our estimates of the aboveground live biomass pool are much higher in their maximum at the climax stage (>170 Mg C ha^{-1}) than averages given for boreal coniferous forests (for example, GOWER et al. 1994; PREGITZER & EUSKIRCHEN 2004; BRADFORD et al. 2008; KEITH et al. 2009). Even when the landscape-scale mean of the Mt. Brocken forest is considered (c. 92 Mg C ha^{-1}), this figure is still considerably higher than the mean of 73 Mg dry mass (c. 36 Mg C ha^{-1}) given by GOWER et al. (1994) for 58 boreal pine stands or the average of 61 Mg dry mass ha^{-1} for Eurasian and American boreal forests reported by JARVIS et al. (2001). This difference is probably mainly attributable to the higher summer temperatures and longer growing season in the temperate Harz Mountains than in most parts of the boreal zone. In addition, stand-replacing fires, which are characteristic for many parts of the boreal forest zone (BERGERON & HARPER 2009), are virtually absent from the Mt. Brocken spruce forests. Consequently, the basal area is high with greater than 70 m^2 ha^{-1} in the climax and over-mature stages of this forest, associated with a continuing accumulation of live biomass in the aging trees (see SCHULZE et al. 2009). In this forest, rare stand-level disturbance is mostly a consequence of insect calamities and windthrow. Another factor that needs consideration is nitrogen. In Europe and parts of eastern North America, decades of high N deposition are thought to be a main cause of large increases in forest productivity and biomass stocks as were observed in the past 50 years (NABUURS et al. 2003; BOISVENUE & RUNNING 2006). CIAIS et al. (2008) estimated that the biomass carbon stocks in European forests have increased by a factor of 1.8 during this period. This must also have influenced the high-elevation spruce forests on Mt. Brocken. In fact, dendrochronological records showed a pronounced increase in the radial stem growth of spruce in the studied forest during the last 10-15 years (HAUCK et al. 2012a), which should have increased the biomass

stocks. This suggests that the average tree biomass may not be in a long-term equilibrium in this old-growth forest, independent from biomass fluctuations due to stand dynamics. Nevertheless, the total (live and dead) aboveground biomass carbon pools of the late forest development stages (ca. 200–215 Mg C ha^{-1}) are already high in comparison to Central European lowland spruce plantations despite the cooler climate. Typical biomass figures of such managed stands are in the range of 110-140 Mg C ha^{-1} at maturity (70-140 years old; ELLENBERG & LEUSCHNER 2010; OEHMICHEN et al. 2011) which is roughly 40 % less than is present in the over-mature and decay stages of the natural mountain spruce forest. Finally, it must kept in mind that the allometric equations used for calculating aboveground biomass were established in managed age-class spruce forests and not derived from natural forests; this may have introduced a certain bias in the wood mass data of our study.

When assessing the value of old-growth forests with high carbon density in biomass and soil with respect to their potential of reducing CO_2 emissions, it has to be kept in mind that managed forests produce commercial wood for products that can lower carbon emissions from fossil fuels when they are substituting other products that are produced with more energy input. For example, RÜTER (2011) and ROCK & BOLTE (2011) calculated for the German forest sector that 1 Mg of carbon in wood removed from the forest may replace on average 1.1–1.35 Mg of carbon emissions from fossil fuel sources. If the wood is left to decay in the forest, net emissions of C are the carbon stored in the respective piece of wood plus these forgone replacements. Thus, high wood biomass stores per se are not a good argument for protecting old-growth forests. However, the montane spruce forest on Mt. Brocken stores (as an average across all five stages) roughly 35% of the C in AGB and 65% in the soil. Harvest most likely will considerably reduce the soil C storage for several decades and this loss is probably as large as, or greater than, the CO_2 emission reduction achieved when harvested wood substitutes other products with higher associated CO_2 emission. This underscores the positive impact of this mountain spruce forest on the regional carbon budget.

Our study demonstrates the high significance of patches with over-mature and decaying trees for carbon storage in Central European natural coniferous forests, a result which is probably transferable to other mountain forest ecosystems in the temperate zone. The conservation value of old and decaying trees for protecting specialized taxa of forest biodiversity is already well established (ÓDOR et al. 2006; HAUCK et al. 2012b; DITTRICH et al. 2013). The present study quantifies the important role of over-mature and decaying forest development stages for

ecosystem carbon storage that has rarely been examined in a landscape-scale context. Our results support the view that the decay stage at the end of a forest dynamics cycle with the breakdown of the stand does not decrease, but rather increase, ecosystem carbon storage, because the SOC store remains high and the biomass reduction occurs only after a considerable lag phase in the regeneration and initial phases of the next forest generation. This may be a characteristic of natural forests in cool and moist climates where large forest fires are rare and biomass reduction after break-down or disturbance occurs more gradually. The findings should be an additional incentive to protect the over-mature and decay stages of mountain forests with high SOC stores.

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Chapter

8

Synopsis

8.1 Key lessons learnt

The present study clearly indicates the importance of over-mature and decay stages for the plant diversity in unmanaged forests with natural forest development. This particularly accounts to the diversity of epiphytes on trees, which rely on large, over-mature and dead trees occurring in the late successional stages. The vegetation on lying deadwood was even more diverse in early development stages, whereas the ground vegetation diversity was not significantly affected by natural forest dynamics.

The importance of over-mature and decay stages for plant diversity in natural forests

The results of this study have strongly emphasized the importance of over-mature and decay stages for the richness, turnover and evenness of the forest vegetation, especially for epiphytes on trees. Much more than the species richness, the species turnover of the epiphyte vegetation in the decay stage was different from all other forest development stages (chapter 2). The significance of the late forest development stages for epiphytes is mainly due to the presence of large, over-mature and dead trees. The canopy cover, and microclimatic conditions seem to be less important than the range of different microhabitats provided by large, over-mature trees (KUUSINEN & SIITONEN 1998, HAUCK et al. 2006, LARRIEU & CABANETTES 2012.). Furthermore, the presence of large, old trees in unmanaged forests is more significant to the epiphyte diversity than the forest continuity. In a comparative study, the epiphyte diversity was very similar between the investigated old-growth forest (> 400 years continuity) and adjacent secondary forest (> 200 years), which were both rich in overmature and decaying trees (chapter 4).

The epiphyte diversity varied across the forest development stages and were markedly different from differently-aged managed forests (FRISVOLL & PRESTØ 1997). While epiphyte diversity in managed forests gradually increases with the stand age, starting from lowest numbers in youngest age classes, the epiphyte diversity in the forest studied was highest in the late development stages, and remained at intermediate level in the regeneration stage (chapter 2). Many epiphytes prevailed on standing deadwood remains present in the regeneration stage The epiphyte diversity on lying deadwood was even highest in the early development stages. This substantiates the existence of a deadwood legacy, meaning that epiphytes can colonize adjacent tree regeneration from dead wood pieces provided by the late development stages (chapter 2). This legacy, documented for several natural forest ecosystems (FRANKLIN et al. 2002),

particularly consists in standing and lying deadwood, maintaining habitat tradition for many cryptogamic epiphytes, while tree seedlings are not yet colonized by epiphytic lichens and bryophytes. Thereby, most of the forest plant species, at least among others, also occurred on lying deadwood, which was continuously provided across all development stages. This underlines the significance of deadwood to the total forest plant diversity (chapter 3). Additional to the general importance of deadwood for numerous organism groups (JONSSON et al. 2005), the study has also outlined some determinants of the diversity of deadwood-inhabiting vegetation. The deadwood size class and grade of decomposition had a much stronger impact on the diversity of bryophytes, lichens and vascular plants growing on lying trunks, than the canopy cover (chapter 3). The importance of coarse woody debris provided by dying trees, which often collapse with advanced decay, was exemplified by the epiphyte diversity. Species numbers reached saturation beyond a trunk diameter of 40 cm and at advanced decay classes (chapter 3). Small woody debris (<10 cm), common in managed forests, was barely colonized by plant species (chapter 3).

As epiphytes on trees as well as on lying trunks well regenerated after declines in single stages (chapter 2), the re-colonization of suitable habitats provided by the ageing and decaying trees and large deadwood pieces was apparently successful. While many epiphytes, particularly bryophytes and lichens are dispersal-limited (HILMO & SÅSTAD 2001), the adjacency of the differently-aged forest patches together with persisting old trees and large deadwood in early successional stages maintains the plant species diversity (JOHANSSON et al. 2012). This has also been shown by the comparison of the neighbouring old-growth and secondary spruce stands (chapter 4), where the species diversity of epiphytes and the ground vegetation have strongly converged within about 200 years. This is contrasting to isolated forests in more fragmented landscapes (BRUNET 2004). Only in small-scale forest mosaics, dispersal-limited plant species of over-mature and decaying stands can colonize younger-aged forest patches within proceeding succession. Immigration of forest plants in more remote sites proceeds much slower (BRUNET & VON OHEIMB 1998). In the forest ground vegetation, particularly vascular plants, many species could also be dispersal-limited, but are more resilient to changes in the forest structure like variations in the canopy cover and stem density. Thus, many species can establish in early successional stages and persist across the whole forest ageing cycle. The documented resilience of the understorey vegetation in old-growth forests (MESSIER et al. 2009) is substantiated by the insignificant variations of the diversity and species turnover in both herb and cryptogam layer of the forest studied (Chapter 2 & 4).

While the species composition of epiphyte vegetation on dead trees in the decay stage was different from the other stages dominated by live trees, due to the presence of some rare bryophytes and lichens, the diversity of epiphytes was not different between live and dead trees. This goes well in line with studies from other lowly-polluted natural forests (HAUCK 2005). Previous studies in the same study site showed a higher richness of epiphytes on dead trees compared to live trees. Due to the lower surface and atmospheric interception of dead trees, the stemflow chemistry had a lower content in SO_4^{2-} and heavy metals, with higher bark pH. Thus, epiphytes were less affected by noxious air-pollution on dead than on live trees (HAUCK et al. 2002). Due to, nowadays, lower air pollution, the vitality of trees increased (HAUCK et al. 2012). The bark pH of the sample trees was slightly higher than in previous studies. Thus, the epiphytic vegetation of live and dead trees partly recovered in this natural forest. This is partly indicated by the decline of the highly acidophytic lichen *Lecanora conizaeoide*s, which is more tolerant for the pollution-induced substrate acidification (chapter 5). Additionally, the species richness was less different than under higher levels of pollution (HAUCK et al. 2002). The lower influence of the tree vitality on epiphytes in natural forests was also shown by biochemical studies (chapter 6). These results suggested a key role of specific lichen substances in metal homeostasis even in the lowly-polluted study site. Thereby, the lichen substance content in *Hypogmnia physodes* was not strongly differing between thalli from the different live and dead sample trees (chapter 6).

Implications for forest conservation and sustainable forestry

Our results emphasize the outstanding importance of the late successional stages in natural forests, which do not occur in managed forests. Overall, the high epiphyte diversity in late successional stages, the deadwood legacy provided by over-mature and decaying stands, and the unique composition of epiphyte vegetation in decaying forests patches corroborate the importance of late successional stages. In contrast, the ground vegetation did not exhibit higher plant diversity or characteristic species in over-mature and decay stages.

Conservation approaches that cease the management of large forests areas, and give way to natural disturbance regimes, are most promising in preserving species richness in forests. Natural forest age dynamics, and with it, the evolvement of over-mature and decaying tree stands is not only beneficial to epiphytic plants, but also to other organisms bound to habitats provided by old, large trees and deadwood (NILSSON et al. 1995, SCHERZINGER 1996, LÕHMUS & LÕHMUS 2011).

Even in managed forest sites or younger afforestations, the retention of solitary old trees and large deadwood objects can partly sustain species diversity (LÕHMUS et al. 2006, BUßLER et al. 2007, DRAPEAU et al. 2009). Modified management practices should include selective cuttings and extended rotations to preserve a minimum of large, old trees (ROLSTAD et al. 2001, LINDENMAYER et al. 2006). With weighing potential economic losses against the gains of biodiversity conservation, the high carbon storage potential in the late successional stages, at least, of high montane spruce forests also has to be included (chapter 7). Therefore, the retention of over-mature and decaying forest patches could both limit biodiversity losses and mitigate global change.

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Summary

Central European forests haven been strongly shaped by human activities since the Neolithic. Most forests lack a near-natural stand structure and large, over-mature trees as well as standing or lying deadwood. Forest management does not admit the evolvement of late successional stages with senescent, live trees or dying and collapsing trees. Numerous studies have pointed on the importance of over-mature and decaying forest patches for specialised forest organisms.

The present study aimed to outline the importance late-successional stages within the framework of natural forest dynamics, for the plant diversity in an old-growth spruce forest (*Picea abies* (L.) Karst.) at Brocken Mountain, Northern Germany. Additional assessments addressed the autecology of epiphytic lichens in a near-natural, lowly-polluted forest environment, and the potential function of over-mature and decaying forest patches for carbon storage. The different investigations were founded in plot-based sampling across the different forest development stages, including both ground and epiphyte vegetation.

The results clearly indicate the high importance of late forest succesional stages for the diversity of epiphytes. While the epiphyte richness on trees in both over-mature and decay stage was much higher, the ground vegetation did not change across the different successional stages. Furthermore, the epiphyte vegetation in the decay stage strongly differed in composition from all the other stages. Some rare species preferably occurred on the dead trees of the decay stages. Furthermore, the late forest development stages provided a deadwood legacy, as large standing and lying deadwood, was present across all forest development stages, enabling epiphyte colonization throughout the whole forest ageing cycle. The presence of old and dead trees was also shown to be more significant than the forest continuity. As the old-growth forest and a neighbouring secondary forest,with both numerous over-mature and dead trees, had widely converged within less than 200 years.

By testing determinants of the epiphyte cover and richness on lying deadwood, highest impact was substantiated for the substrate variables log size and grade of wood decay, with a low impact of the canopy cover. Deadwood was shown to be important to the total forest plant diversity, as many rare species exclusively occurred on deadwood, and many frequent species also occurred on deadwood among other substrates. While small-sized deadwood was barely colonized by epiphytes, large deadwood, provided space for a rich epiphyte vegetation.

Analyses on epiphytic lichens revealed a dramatic decline of the acidophytic species *Lecanora conizaeoides* due to a slight increase in bark pH. Additionally, the epiphyte communities on dead and live trees were shown to be less different than they had been under higher air pollution. Biochemical studies on the lichen *Hypogymnia physodes* showed a high content of lichen substances, regulating metal-uptake even under lower pollution levels. Thereby, variation between lichen samples of live and dead trees was also low.

Over-mature and decay stages were also proven to be characterized by high carbon storage in the soil and biomass. Together with the results on the plant diversity in the late successional stages, the importance of large deadwood pieces and over-mature and dead trees, the importance of over-mature and decay stages in forest is clearly illustrated. Conservation approaches which exclude management from large forest areas and thus admit the evolvement of over-mature and decay stages, will certainly limit biodiversity losses and mitigate global change.

Zusammenfassung

Die Wälder Mitteleuropas wurden seit dem Neolithikum stark durch den Menschen beinflusst. Die meisten Wälder weisen keine naturnahe Struktur mehr auf, es fehlen große, alte Bäume ebenso wie stehendes und liegendes Totholz. Die Fortwirtschaft lässt die Herausbildung später Entwicklungsphasen mit alternden und absterbenden, zusammenbrechenden Baumindividuen nicht zu. Zahlreiche Studien haben jedoch die Bedeutung alter und zerfallender Waldbestände für spezialisierte Waldorganismen gezeigt.

Die vorliegende Studie beabsichtigte, die Bedeutung der späten Sukzessions-Stadien für die Pflanzendiversität im Rahmen der natürlichen Dynamik eines unbewirtschafteten Fichtenwaldes (*Picea abies* (L.) Karst.) auf dem Brocken in Norddeutschland herauszustellen. Zusätzliche Untersuchungen behandelten die Autökologie epiphytischer Flechten in einer naturnahen, wenig belasteten Waldumgebung und das Potenzial alter und zerfallender Waldstadien für die Speicherung von Kohlenstoff. Die verschiedenen Untersuchungen bauen auf Plot-basierte Erhebungen in den verschiedenen Waldentwicklungsstadien auf, und bezogen dabei sowohl die Epiphyten- als auch die Bodenvegetation ein.

Die Ergebnisse zeigen eindeutig die Bedeutung der späten Wald-Sukzessionsstadien für die Diversität von Epiphyten. Während die Artenvielfalt der Epiphyten in Alters- und Zerfallsstadien höher war als in jüngeren Sukzessionsstadien, unterschied sich die Bodenvegetation kaum zwischen den verschiedenen Sukzessionsstadien. Weiterhin unterschied sich die Zusammensetzung der Epiphytenvegetation im Zerfallsstadium deutlich von allen übrigen Stadien. Einige seltene Arten kamen vorwiegend auf den abgestorbenen Bäumen der Zerfallstadien vor. Hier entstehen große stehende und liegende Totholzobjekte, die auch in jüngeren Entwicklungsstadien erhalten bleiben (‚*deadwood legacy'*), und über den gesamten Waldentwicklungszyklus die Epiphytenansiedelung auf Bäumen ermöglichen. Es zeigte sich auch, die Präsenz alter und abgestorbener Bäume wichtiger war als die Kontinuität in der Waldbedeckung. Die Vegetation des studierten Urwaldes und eines benachbarten Sekundärwaldes, die beide viele alte und tote Bäume aufwiesen, hatten sich innerhalb von 200 Jahren stark angenähert.

Untersuchungen der Vegetation des liegenden Totholzes bestätigten einen starken Einfluss der Substrateigenschaften Stammgröße und Holz-Zerfallsgrad. Der Kronenschlussgrad der

Waldbestände hatte hingegen einen geringeren Einfluss. Totholz hat eine hohe Bedeutung für die Waldpflanzen-Diversität. Viele seltene Arten wuchsen ausschließlich auf liegendem Totholz, während viele häufige Arten, neben anderen Substraten, ebenfalls auf Totholz vorkamen. Während kleine Totholzobjekte kaum besiedelt wurden, beherbergten große Totholzobjekte eine artenreichere Epiphytenvegetation. Die höchste Epiphytendiversität wurde jenseits mittlerer Zerfallsgrade erreicht.

Zusätzliche Untersuchungen von epiphytischen Flechten zeigten einen extremen Rückgang der acidophytischen Flechte *Lecanora conizaeoides* bei einer leichten Erhöhung des pH-Wertes der Baumrinden. Zudem zeigte sich, dass die Artenvielfalt der Epiphyten sich weniger zwischen lebenden und abgestorbenen Bäumen unterschied, als es unter höherer Luftverschmutzung. Zusätzlich wiesen biochemische Analysen der Flechten *Hypogymnia physodes* einen hohen Gehalt an Flechtenstoffen nach, die auch bei geringer Umweltbelastung die Aufnahme von Schwermetallen regulieren. Auch hier waren nur geringe Unterschiede zwischen den Proben von den verschiedenen lebenden und abgestorbenen Bäumen festzustellen.

Es wurde außerdem nachgewiesen, dass die Alters- und Zerfallsstadien sich durch eine hohe Kohlenstoffspeicherung in Boden und Biomasse auszeichnen. Zusammen mit den Ergebnissen zur Pflanzendiversität, der Bedeutung der großen Totholz-Objekte sowie alter und abgestorbener Bäume, wurde die Bedeutung der Alters- und Zerfallsstadien klar bestätigt. Schutzmaßnahmen, die auf den Ausschluss der Bewirtschaftung großer Waldgebiete abzielen und damit die natürliche Herausbildung der Alters- und Zerfallsstadien zulassen, können sicher einen Rückgang der Biodiversität begrenzen und die Folgen des globalen Klimawandels abmildern.

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Conference proceedings

DITTRICH, S. & JACOB, M. 2012. Auswirkungen der natürlichen Altersdynamik auf die Pflanzendiversität in naturnahen Fichtenwäldern im Nationalpark Harz. - Interdisziplinärer

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Diploma Thesis: *Vegetationsökologische Untersuchungen in den Restitutionsgebieten "Hammer Schleife" und "Wester Schleife" (Emsland, Nordwestdeutschland)*

1995-2001 Albert-Einstein-Gymnasium Hameln; Graduation: Abitur.

Jobs, services and additional courses

2011 Preaching education – Ev.-luth. Landeskirche Hannovers, Hildesheim

2010 Training on event managment and presentation – Deutscher Evangelischer Kirchentag, Mainz

2007-2008 Scientific assistant – Osnabrück University, Division of Ecology

2001.2002 Alternative civil service - Stadt Bad Münder, field of work: environment

2001 Assistant - RexamGlass, Bad Münder

2001 Seminar on management and communication – Lenze, Hameln