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Impact of the admixture of European beech (*Fagus sylvatica* L.) on plant species diversity and naturalness of conifer stands in Lower Saxony

*Auswirkungen der Einbringung von Buche (*Fagus sylvatica *L.) auf die Artendiversität und Naturnähe von Nadelholzbeständen in Niedersachsen*

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Abstract

The promotion and extension of continuous cover mixed stands with a simultaneous reduction of conifer-monocultures play a major role in current silvicultural practices in Central Europe. It is assumed that the admixture of the natural dominant beech (Fagus sylvatica) *in pure non site-specific conifer stands automatically indicates better conditions in terms of nature conservation and forest management. To test this hypothesis three different conifer-beech-comparisons of pure and mixed stands in Lower Saxony are studied, analysing plant species diversity and naturalness of understorey vegetation as one important indicator for the ecological status of forests. Each comparison includes pure coniferous stands* (Picea abies, Pinus sylvestris, Pseudotsuga menziesii)*, mixed coniferous-beech-stands, and pure beech stands on similar acidic mineral soils where the potential natural vegetation will be an oligotrophic beech forest (L u z u l o - F a g e t u m). The age of stands varies between 50 and 150 years. To specify tree species influence on site conditions and vegetation, the study also includes light climate and soil data of the stands.*

It is observed that, with regard to all comparisons, the admixture of beech reduces plant species diversity but increases naturalness of the stands. The intensity of beech admixture effects differs. While in Scots pine stands the impact of admixed beech is very noticeable, with the mixed stands being nearly identical with pure beech stands, the species change in Douglas-fir and Norway spruce stands proceeds more slowly.

Assuming that the status in nature conservation and forest management is improving with increasing plant species diversity and increasing naturalness, the results of this study show a contrary development on a stand scale, as the potential natural vegetation of the L u z u l o - F a g e t u m is in its self very species poor on vascular plants.

Keywords: *Understorey vegetation,* L u z u l o - F a g e t u m, Picea abies, Pinus sylvestris, Pseudotsuga menziesii, *humus accumulation, light, pH-value, nature conservation*

Zusammenfassung

Die Förderung und Ausweitung von Mischwäldern bei gleichzeitiger Reduktion reiner Nadelholz-Bestände spielt aktuell eine große Rolle im mitteleuropäischen Waldbau. Gemeinhin wird angenommen, dass die Beimischung der standortsgemäßen Buche (*Fagus sylvatica*) in standortsfremden Nadelholz-Monokulturen die Bedingungen im Sinne des Naturschutzes und der Forstwirtschaft verbessert. Diese Hypothese wird auf der Grundlage von drei unterschiedlichen Nadelholz-Buchen-Versuchsreihen geprüft. Im Mittelpunkt steht dabei die Bodenvegetation als wichtiger und sensitiver Indikator für den ökologischen Zustand von Wäldern. Jede Versuchsreihe umfasst reine Nadelholz-Bestände (*Picea abies, Pinus sylvestris, Pseudotsuga menziesii*), Nadelholz-Buchen-Mischbestände und reine Buchen-Bestände auf sauren Mineralböden, auf denen von Natur aus nährstoffarme Buchenwälder (L u z u l o - F a g e t u m) vorherrschen würden. Das Alter der Bestände variiert zwischen 50 und 150 Jahren. Schwerpunkte der Analyse sind die Artenvielfalt und Naturnähe der Bodenvegetation. Um den Einfluss der Baumarten auf den Standort und die Vegetation zu bewerten, werden die Licht- und Bodenverhältnisse der Bestände charakterisiert.

Es zeigt sich, dass mit der Beimischung der Buche in allen Versuchsreihen die Pflanzenartenvielfalt abnimmt und die Naturnähe zunimmt. Unterschiedlich ist dabei die Intensität der Veränderungen. Zwischen den Kiefern-Buchen-Mischbeständen und den Kiefern-Reinbeständen bestehen sehr deutliche Unterschiede im Aufbau der Bodenvegetation, so dass die Mischbestände den Buchen-Reinbeständen bereits sehr ähnlich sind. In den Douglasien- und Fichten-Versuchsreihen vollzieht sich der Artenwechsel vergleichsweise unauffällig und kontinuierlich. Wenn man davon ausgeht, dass der naturschutzfachliche und waldbauliche Status sich sowohl mit zunehmender Phytodiversität als auch bei zunehmender Naturnähe verbessert, so zeigen diese Ergebnisse auf Bestandesebene eine gegenläufige Entwicklung, da das in der Region der potenziell natürlichen Vegetation entsprechende L u z u l o - F a g e t u m von Natur aus sehr artenarm an Gefäßpflanzen ist.

Schlüsselwörter: Bodenvegetation, L u z u l o - F a g e t u m, *Picea abies, Pinus sylvestris, Pseudotsuga menziesii,* Humusakkumulation, Licht, pH-Wert, Naturschutz

1 Introduction

In the 19th century in many parts of Central Europe there was widespread reforestation on degraded soils with non-autochthonous coniferous tree species, such as Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*). These species were favoured because they were easy to establish and to manage, and because these fast growing species appeared to provide a solution to significant timber shortage at this time (Spiecker 2003). Driven by a similar motivation for fast growing and high yielding timber crops, non-native

Douglas-fir (*Pseudotsuga menziesii*) has also been introduced into many parts of Central Europe more recently (Kowarik 2010, Kownatzki et al. 2011).

Today the use of these fast growing monocultures is still very common, but it is intensely debated because of their potential instability and their negative impacts on biodiversity (Spiecker 2003). A high level of biodiversity is thought to increase ecosystem stability, at least with respect to the diversity of overstorey tree species (Schütz 2001, Scherer-Lorenzen et al. 2005, Röhrig et al. 2006, Barbier et al. 2008, Paquette & Messier 2011). Large-scale conversion of the existing even-aged coniferous stands into continuous cover mixed stands is recognised as a solution to improve forest ecosystem stability and biodiversity. The main broadleaved tree species used in many forest conversions at present is European beech (*Fagus sylvatica*), which is one of the dominant native tree species of Central European forests (Bohn & Neuhäusl 2000/2003).

Many studies have found unfavourable effects of conifer plantations on vegetation, humus, soil etc. when compared to pure broadleaf stands (Norway spruce: Zerbe 1994, Hüttl & Schaaf 1995; Douglas-fir: Knoerzer et al. 1996, Marques & Ranger 1997; Scots pine: Zerbe et al. 2000, Augusto et al. 2002). Fewer studies have explicitly considered how conifer-broadleaf mixtures influence biodiversity or site conditions (Spruce/beech: Lücke & Schmidt 1997, Matthes 1998, Leitl 2002, Gärtner 2003, Engelhard & Reif 2004, Grodzińska et al. 2004, Schmidt et al. 2004; Douglas-fir/beech: Vor & Schmidt 2006; Pine/beech: Schmidt et al. 2004, Vor & Schmidt 2006, Denner & Schmidt 2008). The main objective of these studies is often the analysis of biodiversity. The discussion of the results in context with naturalness or ecosystem functions is mostly lacking.

It is assumed that stands of native forest trees automatically entail a higher naturalness of the associated biotic communities (Fritz 2006, Reif & Walentowski 2008). However, at least regarding understorey vegetation of managed mixed forests, this assumption is lacking scientific proof. Our study compares plant species composition, species diversity, and occurrence of forest species of pure coniferous, mixed coniferous-beech, and pure beech stands in Lower Saxony, based on two similar studies by Weckesser (2003) and Budde (2006). To enable a better understanding for the underlying mechanisms, light, humus morphology, and soil acidity are also compared. The aim of this study is to find answers to the following questions:

1. Are plant species diversity and naturalness influenced by the admixture of beech to coniferous plantations?
2. Does a site factor change by the admixture of beech to coniferous stands which then might explain a change in understorey vegetation?

The results and discussion will show how these ecological interactions are influenced by the admixture of beech in coniferous stands and, whether they are as favourable as assumed in terms of silviculture and nature conservation.

2 Material and methods

2.1 Research area

The study sites are located in two separate areas of Lower Saxony (north-western Germany). These are within the Solling Mountains and the Pleistocene regions of Lower Saxony. The Solling Mountains belong to the mountain ranges of southern Lower Saxony (forest growth zone "Mitteldeutsches Trias-Berg- und Hügelland", Gauer & Aldinger 2005) and rise to 528 m above sea level. The research area is characterized by a humid, sub-montane to montane climate (latitude: 51°40' N–51°50'N, longitude: 9°26'E–9°44'E, elevation: 300–450 m NN, annual precipitation: 915–1,030 mm, mean annual temperature: 7.3–7.8°C, Gauer & Aldinger 2005). The parent rock of the Solling plateau is red sandstone covered with loess. Therefore the main soil type is an acid silty loam cambisol (FAO classification) with a high content of aluminium but a good water supply (Weckesser 2003, with further details and maps of the research area and investigated stands).

Investigations in the Pleistocene regions cover a much wider geographic range, including three different forest growth zones. The northernmost part is the coastal area of Lower Saxony (forest growth zone "Niedersächsischer Küstenraum", latitude: 53°24' N–53°29'N, longitude: 9°00'E–9°20'E, elevation: 0–75 m NN, annual precipitation: 715–840 mm, mean annual temperature: 8.4–9.0°C, Gauer & Aldinger 2005). Following a climatic gradient from the Atlantic northwest to the more sub-continental affected southeast, the west-central lowlands of Lower Saxony (forest growth zone "Mittelwestniedersächsisches Tiefland", latitude: 52°33' N–53°18'N, longitude: 8°30'E–9°40'E, elevation: 75–150 m NN, annual precipitation: 650–810 mm, mean annual temperature: 8.5–9.3°C, Gauer & Aldinger 2005) have a slightly lower annual precipitation and a higher mean annual temperature. Finally, at the end of the climatic gradient the eastern lowlands of Lower Saxony (forest growth zone "Ostniedersächsisches Tiefland", latitude: 52°39' N–53°28'N, longitude: 9°45'E–10°40'E, elevation: 30–170 m NN, annual precipitation: 560–810 mm, mean annual temperature: 8.1–9.1°C, Gauer & Aldinger 2005) are situated. The entire Pleistocene region is formed by glacial sedimentary deposits resulting in sandy soils partly covered with loess. The main soil type is the fresh sandy podsol-cambisol (FAO classification) with low base saturation and not influenced by a high groundwater table (Budde 2006, also with further details and maps of the research area and investigated stands).

The potential natural vegetation in both regions would be the Luzulo-Fagetum (Gerlach 1970, Heinken 1995, Ellenberg & Leuschner 2010). In the Middle Ages at the latest natural beech forests have been largely replaced by arable fields and meadows on more fertile soils, and by heathlands and pastures on less fertile soils. Remaining forests have been grazed and managed for the production of fuel wood and charcoal. Around 200–250 yrs. ago the devastated areas were converted into large monocultures of conifer (Gerlach 1970, Kremser 1990). While Scots pine is at least considered native in a few parts of the lowlands (Hesmer & Schroeder 1963, Heinken 1995), Norway spruce is not in regard to the Solling Mountains (Firbas 1952, Schmidt-Vogt 1987). Present-day forest stands are still dominated by these conifer species. Scots pine covers 27–45 % of the total forest area in the three investigated growth zones of the lowlands, while in the Solling Mountains Norway spruce occupies approximately 60 % of the forested area (Gauer & Aldinger 2005). Since the Second World War there is a tremendous increase in planting of exotic Douglas-fir mainly caused by decreasing prices of Douglas-fir seeds and saplings (Kownatzki et al. 2011). Current forest planning allots up to 10 % of the forest area for long-term Douglas-fir silviculture in Lower Saxony, mainly in mixture (Kleinschmit 1991, Kowarik 2010).

2.2 Sampling methods and analysis

In both study areas pure coniferous and beech stands were compared with mixed stands. One study delivers vegetation data on Norway spruce with beech in the Solling Mountains (Weckesser 2003), the other on Douglas-fir with beech, and Scots pine with beech in the Pleistocene lowlands (Budde 2006). To enable a better comparison within the two studies, 20 plots (400 m^2) of each stand type (Solling Mountains: pure spruce, pure beech, spruce/beech mixture, Lowlands: pure pine, pure Douglas-fir, pure beech, pine/beech mixture, Douglas-fir/beech mixture) have been selected for this analysis. Criteria for the selection of stands included stand age (> 50 and < 150 years), canopy cover of > 50 % and, in mixed stands, the proportions of the beech-conifer mixture was restricted to a coverage of at least 40 % coverage for either tree species. The wide range of stand age is due to the fact, that some tree species, like Douglas-fir, reach high productivity and maturity more early than other. Furthermore, many of the Douglas-fir stands have been established not before the Second World War (Kownatzki et al. 2011). To minimize influence of stand age on results, chosen stands should be more or less in their optimum of tree layer coverage and wood productivity. All plots were situated in managed forests, but no management activities took place in the last three years prior to the start of field research.

Vegetation was assessed within the 400 m² plots in tree (≥ 5 m height), shrub (woody plants: 0.5–5 m height), herb (woody plants: < 0.5 m, all ferns, grasses, herbs), and moss layer at the peak of the vegetation period (June, July). Visual estimates of the percentage cover of each of the species present were recorded in each of these different strata (Dierschke 1994). The nomenclature for vascular plants followed Wisskirchen & Haeupler (1998) and for the bryophytes Koperski et al. (2000).

Alpha-diversity was calculated for each study plot including all species in the herb and moss layers. Degree of naturalness was assessed by species occurring only in the herb layer using a method developed by Schmidt et al. (2003): this method provides an affinity value for every species for different forest habitats. The relative proportions of these so-called forest species as well as the non-forest species in each plot is used as an indicator of naturalness. Facilities and limits of this approach are discussed by Schmidt et al. (2004) and Schmidt & Schmidt (2007).

Any differences in vegetation species composition between study plots were calculated and visualized by Detrended Correspondence Analysis (DCA) with Pc Ord (McCune & Mefford 1999). Additionally, two different indices were applied to illustrate vegetation similarity between pure and mixed stands: For a qualitative approach the Sørensen coefficient (Sørensen 1948, cited by Dierschke 1994), based on the presence-absence relationship between the number of species of two stand types and the total number of species. For quantitative purposes the percent similarity index was used (Czekanowski 1909, cited by Goodall 1973), based on constancy (number of relevés within one stand type in which a given species occurs, Dierschke 1994). Both DCA and similarity indices include all species of the herb and moss layer.

The relative irradiance was measured on homogeneously clouded days directly above the herb layer with PAR sensors (type Licor S190). 36 (lowlands) and 40 (Solling) measurements per plot (each lasting two seconds) have been related to continuous data recorded at a reference outside the forest (Heinken 1995). For measuring the thickness and soil acidity of the humus layer 12 soil samples (25 x 25 cm by using a metal frame) were taken per plot. In the lowland plots humus samples were separated into O_L (organic litter layer) and O_F/O_H (decomposing organic layer) horizons while in the Solling plots the humus layer was not separated. For pH analysis in KCl, all 12 fresh samples of each plot were combined to form a mixed sample.

Because the investigated stands appeared to be very diverse and heterogeneous, tests for a normal distribution of the data failed. Accordingly, the non-parametric Kruskal-Wallis test was applied for the comparison between the forest types. The level of significance was set at p ≤ 0.05. Statistical analyses were done using Statistica 6.1 (StatSoft, Inc. 2004).

3 Results

3.1 Vegetation structure and diversity

Results are always shown in separate comparisons according to the three coniferous tree species. Concerning percentage cover of vegetation layers (Tab. 1) all three comparisons coincide more or less in their results. Highest coverages of tree layer are found in the pure beech stands, accompanied by low coverages of ground vegetation. In pure conifer stands the relations are vice-versa (exception: herb layer of Norway spruce stands).

Within the Douglas-fir and Scots pine comparisons an evident influence of admixture of beech to coniferous species exists. Percentage covers of bryophytes and herbs show an obvious depression in mixed stands that do not differ significantly from pure beech forests. In contrast to this, the coverage of the moss layer in mixed stands of spruce and beech is as high as in pure spruce stands.

In each of the three types of pure coniferous stands, a higher species diversity of herbs and mosses was found than in pure beech forests (Fig. 1). Nevertheless, admixture of beech to coniferous species does not necessarily have a negative influence on plant species diversity as mean species numbers

	Tree layer (%)				Shrub layer (%)				Herb layer (%)				Moss layer (%)			
	Mean	±SE	*(Median)*		Mean	±SE	*(Median)*		Mean	±SE	*(Median)*		Mean	±SE	*(Median)*	
Douglas-fir																
Douglas fir	77,8	2,2	*(77.5)*	a	1,1	0,5	*(0.1)*	a	31,0	6,7	*(23.8)*	a	30,5	5,0	*(22.5)*	a
Mixed	89,8	2,4	*(91.3)*	b	0,8	0,3	*(0.1)*	a	6,6	2,1	*(1.7)*	b	1,9	0,9	*(0.2)*	b
Beech	94,4	1,5	*(96.3)*	b	0,2	0,1	*(0.0)*	a	15,6	6,8	*(0.3)*	b	0,2	0,0	*(0.1)*	b
Norway spruce																
Spruce	72,5	1,0	*(73.8)*	a	0,0	0,0	*(0.0)*	a	8,3	1,7	*(4.8)*	a	7,9	1,3	*(5.1)*	a
Mixed	77,5	1,4	*(75.6)*	a	1,3	0,5	*(0.0)*	a	16,5	3,3	*(13.0)*	a	5,9	1,0	*(5.0)*	a
Beech	85,5	1,4	*(87.5)*	b	0,1	0,0	*(0.0)*	a	11,1	2,8	*(8.4)*	a	0,5	0,1	*(0.3)*	b
Scots pine																
Pine	58,0	1,2	*(57.5)*	a	4,9	1,9	*(2.0)*	a	96,1	1,0	*(97.5)*	a	72,0	5,3	*(78.8)*	a
Mixed	94,0	1,4	*(96.3)*	b	0,6	0,3	*(0.0)*	b	7,0	3,1	*(0.3)*	b	0,7	0,3	*(0.1)*	b
Beech	94,4	1,5	*(96.3)*	b	0,2	0,1	*(0.0)*	b	15,6	6,8	*(0.3)*	b	0,2	0,0	*(0.1)*	b

Tab. 1: Coverage of vegetation layers (n = 20, plot size = 400 m²). Means that do not share the same letter differ significantly (Kruskal-Wallis test, p < 0.05).

Tab. 1: *Deckungsgrade der Vegetationsschichten (n = 20, Aufnahmefläche = 400 m²). Kleinbuchstaben kennzeichnen signifikante Unterschiede zwischen den Mittelwerten (Kruskal-Wallis-Test p < 0.05).*

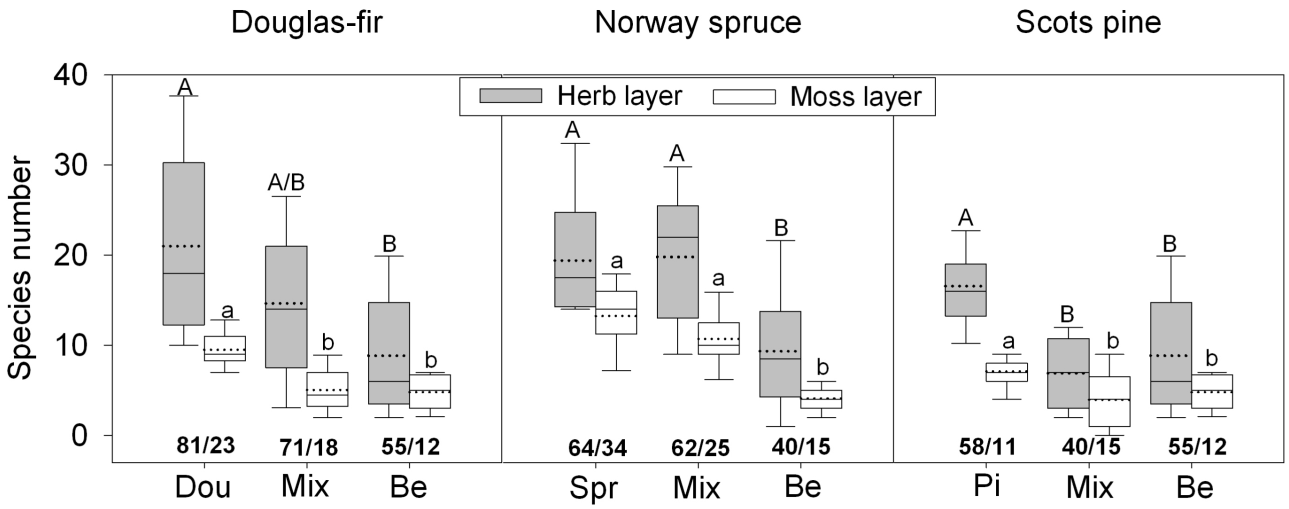

Fig. 1: Species number per plot (400 m², n = 20) for herb and moss layer, including all species. The solid line indicates median, the dotted line mean value, n = 20. Figures below the box plots show cumulative species richness in each stand type. Means that do not share the same letter differ significantly (Kruskal-Wallis test, $p < 0.05$).

Abb. 1: *Zahl der Arten in der Kraut- und Moosschicht pro Aufnahmefläche (400 m², n = 20). Die durchgezogene Linie bezeichnet den Median und die gepunktete den Mittelwert. Die Ziffern unterhalb der Boxplots geben die kumulative Artenvielfalt für jeden Bestandestyp wieder. Unterschiedliche Buchstaben kennzeichnen signifikante Unterschiede (Kruskal-Wallis-Test, p < 0.05).*

in mixed stands of beech and spruce (20 herbs, 13 mosses) do not differ significantly from numbers found in pure spruce stands (19 herbs, 11 mosses). In contrast to this, species diversity in mixed forests of pine and beech (7 herbs, 5 mosses) is as low as in pure beech stands (9 herbs, 5 mosses). Furthermore, in mixed stands of Douglas-fir and beech the herb layer diversity (15) has an intermediate position between the pure stands (Douglas-fir 21, beech 9) whereas the number of moss species is as low as in the pure beech stands.

Cumulative species richness in each stand type (Fig. 1) corroborates these findings. While mixed stands of spruce and beech, with a total of 62 herbs show a similar diversity to pure spruce stands (64) concerning the herb layer, mixed stands of Douglas-fir and beech have an intermediate position (both herb with 71 species and moss layer with 18 species). As for the Scots pine comparison mixed stands even present the lowest diversity in the herb layer (40).

3.2 Naturalness

For comparison of biological diversity, which is one of the main aims of nature conservation, it is important not only to determine α-diversity for the different stand types, but it is rather necessary to differentiate between plants that are typical for a certain habitat and which are not. Following the “list of vascular forest plant species” of Schmidt et al. (2003) in the Lowlands (Douglas-Fir, Scots pine) over 50 % of the species in the herb layer are plants growing predominantly in forests, summarized as “Category 1” (Fig. 2). As for the Solling sites (Norway spruce) ratios of forest plants (Cat. 1) and plants which are not predominantly linked to forest (Cat. 2) are just the other way around. Not even the beech stands in the Solling Mountains reach a percentage of 40 % forest plants.

If the comparisons are viewed with respect to the influence of beech on coniferous stands, there is always an increasing percentage of typical forest plants with the admixture of beech. In relation to Norway spruce and Scots pine, this beech effect is much clearer than in Douglas-fir, whereas the shifting in the Scots pine stands is mainly a result of a changing proportion of regenerating tree species. On the other hand, it must be taken into consideration that according to the absolute number of species (Fig. 2) both categories show decreasing trends from pure conifer to pure beech stands, simply because species diversity is decreasing in general (see previous chapter).

3.3 Similarity

In the Douglas-fir and Norway spruce comparisons, composition of vegetation in mixed stands has a greater similarity with coniferous stands than with beech stands (Tab. 2). However, mixed stands with pine and beech have a greater affinity towards pure beech stands than towards pure pine stands. Similarity is actually lowest between mixed stands and pure pine stands. This suggests an absolute dominance effect of beech trees in the mixed stands.

Tab. 2: Similarity coefficients based on presence-absence (Sørensen-index, calculated following Dierschke 1994) or constancy (percent similarity-index, calculated following Dierschke 1994) of all species of the herb and moss layer within each stand type.

Tab. 2: *Ähnlichkeitskoeffizienten (Sørensen-Index: Vorkommen/Nicht-vorkommen; Percent similarity-Index: Vorkommen mit Berücksichtigung der Stetigkeit, jeweils unter Anwendung der Formeln bei Dierschke 1994) unter Einschluss aller Arten der Kraut- und Moosschicht innerhalb eines Bestandestyps.*

Douglas-fir			Norway spruce			Scots pine		
			Sørensen					
	Be	Mix		Be	Mix		Be	Mix
Mix	66.7		Mix	60.6		Mix	60.7	
Dou	69.0	72.5	Spr	58.6	72.4	Pi	60.3	53.2
			Percent similarity					
	Be	Mix		Be	Mix		Be	Mix
Mix	66.6		Mix	55.1		Mix	60.8	
Dou	53.2	66.9	Spr	47.1	74.9	Pi	42.1	38.3

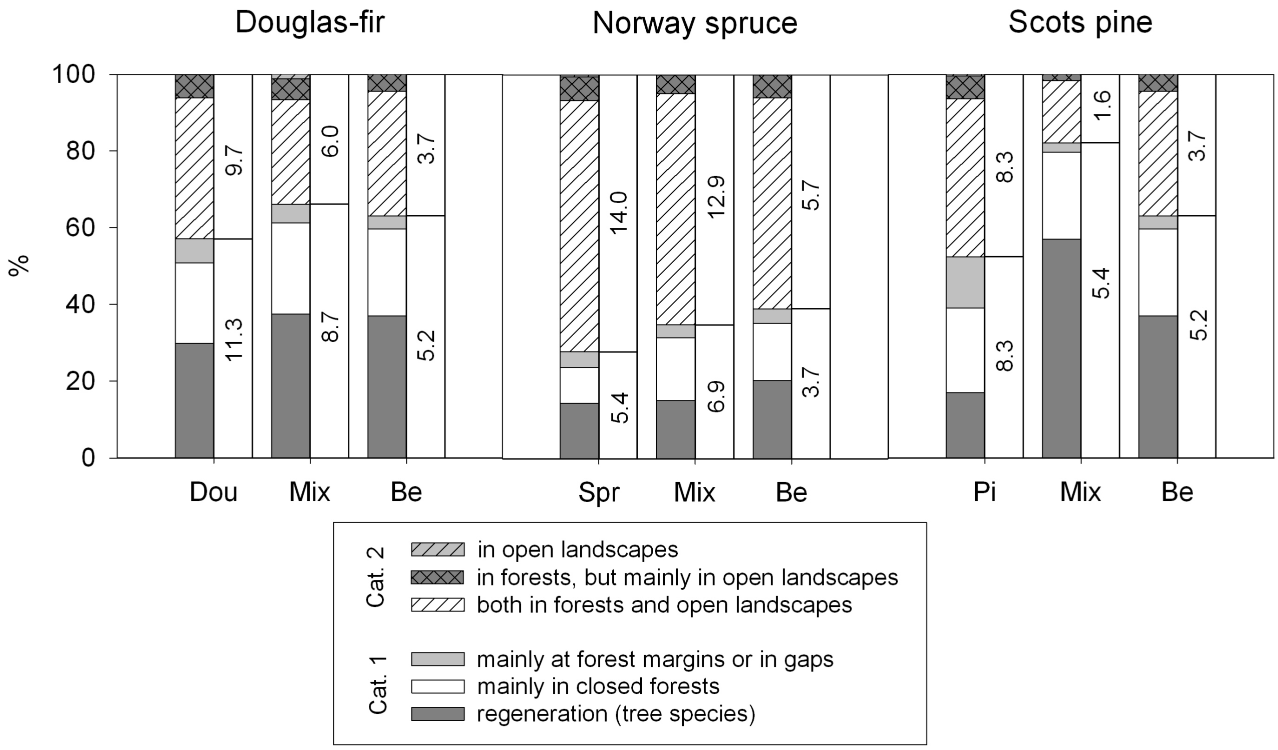

Fig. 2: Percentages of forest plants (herb layer, all species) based on means of qualitative analysis of vegetation relevés (n = 20, plot size = 400 m²). Figures beside the bars show mean absolute numbers of species per plot relating to categories 1 and 2.

Abb. 2: *Qualitatives Waldartenspektrum der Krautschicht in den verschiedenen Bestandestypen (n = 20, Flächengröße 400 m²). Die Ziffern neben den Balken geben die mittleren Artenzahlen pro Fläche für die Kategorien 1 und 2 wieder.*

The qualitative interpretation with Sørensen (1948, cited by Dierschke 1994) as well as the percent similarity index (Czekanowski 1909, cited by Goodall 1973) generally indicate high similarities between the stand types, nearly always more than 50 %. Luzulo-Fagetum could therefore be understood to form the potential natural vegetation even in most of the studied pure coniferous stands. Differences between both indices occur when pure beech stands are considered. For all three comparisons they show about the same similarity towards the mixed stands and towards the pure coniferous stands in terms of the Sørensen coefficient. When the frequency of species occurrence in the stand types is included (percent similarity index) similarity towards mixed stands is clearly higher than towards pure coniferous stands, especially concerning the pine stands.

If coverage of species is considered, similarity of stand types shows a quite distinct pattern referring to the ordination diagram (Fig. 3). The first axis (eigenvalue 0.34 and length of gradient 2.98) separates corresponding pure beech stands from pure coniferous stands, with the mixed stands always showing an intermediate position.

Beech and pine stands show the greatest distance in regard to species composition. Most differentiating species in the herb layer, serving as main variables for the first axis, are *Fagus sylvatica* with a strong positive correlation (r = 0.62) and *Deschampsia flexuosa* (r = -0.76) or *Vaccinium myrtillus* (r = -0.73) with a negative correlation. All differentiating species with a negative correlation have a high frequency and coverage in the pure pine stands (Tab. 3 Appendix). Table 3 also shows that within the comparison of pure coniferous stand – mixed stand – pure beech stand a qualitative change of the species pool does not take place. Almost all plant species occurring in pure beech stands are also found in the mixed and pure coniferous stands enriched by species typical to coniferous forests (e. g. *Vaccinium myrtillus, Trientalis europaea, Dicranum scoparium*) and forest gaps (e. g. *Epilobium angustifolium, Rubus spec.*).

Another influencing factor which is worked out by the ordination is the site dependency. The second axis (eigenvalue 0.23 and length of gradient 2.56) clearly differentiates the stands from the Solling region from those in the lowland region. But also a more compact arrangement is visible within the Solling stands, which points at more homogenous stands compared to the Lowland stands. This may be a matter of tree species (Norway spruce), but it is more likely that this effect is caused by the different geographic extent of the two study sites.

3.4 Light climate, humus accumulation and soil acidity

The main environmental variables affecting vegetation are light and soil. In order to reduce soil variables, only the humus accumulation and pH-values of the organic layer are analysed as the most representative factors.

In all of the three comparisons relative irradiance measured on the forest floor was very low in beech stands (2.1 % and 2.8 %) and differs significantly from pure conifer stands (Fig. 4). Within the conifer stand types, maximum irradiance values are found in the pine stands, presenting a mean value of 25.3 %. For the mixed stands a strong impact of beech on the light climate is obvious in the admixture with Douglas-fir as well as with pine. With relative irradiance values of 3.5 % (Douglas-fir-beech) and 2.1 % (Scots pine-beech) they do not show significant differences to the pure beech forests. In contrast to this, relative irradiance in mixed stands of spruce

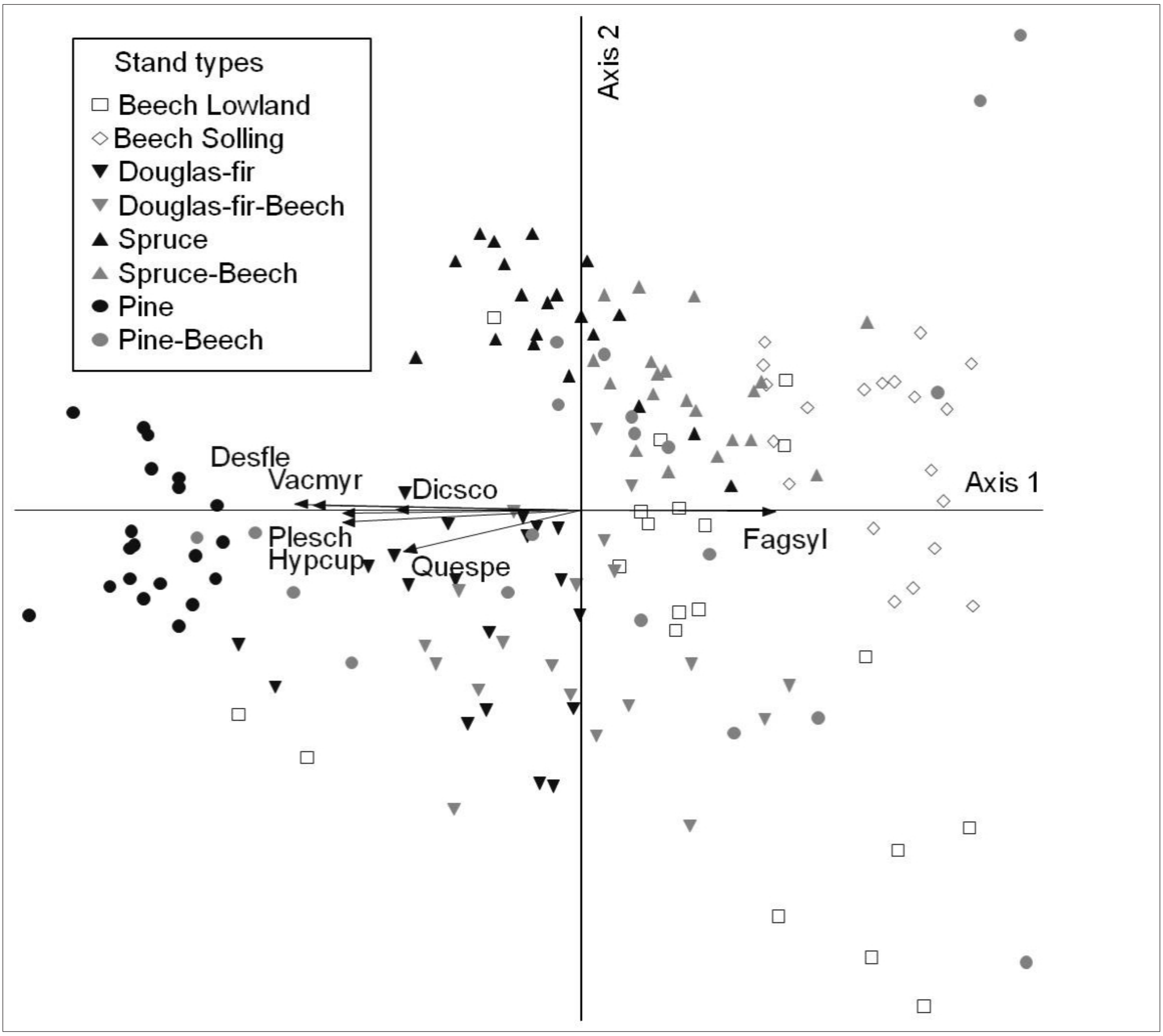

Fig. 3: Ordination diagram based on DCA of plots (plot size = 400 m²) in different stand types. Cover of species was squareroot-transformed. Arrows indicate the most important species according to a Pearson correlation coefficient r ≥ 0.60, Desfle: *Deschampsia flexuosa*, Dicsco: *Dicranum scoparium*, Fagsyl: *Fagus sylvatica*, Hypcup: *Hypnum cupressiforme* (includes *H. jutlandicum* in the lowlands), Quespe: *Quercus* spec., Plesch: *Pleurozium schreberi*, Vacmyr: *Vaccinium myrtillus*.

Abb. 3: *DCA-Ordinationsdiagramm der Aufnahmen (Aufnahmefläche 400 m²) in den verschiedenen Bestandestypen. Der Deckungsgrad wurde einer Wurzeltransformation unterzogen. Pfeile zeigen die wichtigsten Arten mit einem Pearson-Korrelationskoeffizienten r ≥ 0.60. Desfle:* Deschampsia flexuosa*, Dicsco:* Dicranum scoparium*, Fagsyl:* Fagus sylvatica*, Hypcup:* Hypnum cupressiforme *(im Tiefland einschließlich* H. jutlandicum*), Quespe:* Quercus spec.*, Plesch:* Pleurozium schreberi, Vacmyr: Vaccinium myrtillus.

and beech (5.9 %) does not differ significantly from the values measured in the pure spruce stands (5.6 %).

In each of the three comparisons, the humus layer is thickest in the mixed stands (Fig. 4). In the Douglas-fir comparison, the lowest humus accumulation is found in the conifer stands, whereas in the Norway spruce comparison, humus accumulation is at its lowest in the pure beech stands. Within the Scots pine comparison, pure stands do not differ from each other. Generally, humus accumulation in the Solling Mountains does not exceed a depth of 6 cm, whereas all plots in the lowlands are at least 5 cm deep (pure Douglas-fir) and in most stand types about 8 cm. With a depth of nearly 12 cm, the mixed stands of Scots pine and beech have the greatest accumulation of all the stands.

Compared to pure beech forests, the three pure conifer stand types are generally characterized by lower pH values in the humus layer (Fig. 4). pH-values in the Solling Mountains are generally lower, on average 3.0 in the pure spruce stands, up to 3.7 in the pure beech stands. In the lowlands, beech stands show pH-values of nearly 4 (O_F/O_H-horizon) and at least 3.6 in the conifer stands. Mixed stands, especially with spruce and Douglas-fir, show a greater affinity with pure conifer stands than with beech stands. In the O_L-horizon a considerable influence of the beech litter on soil acidity can be shown only for the mixed stands with Scots pine, as pH-values do not differ from those measured in pure beech plots. In the O_F/O_H-horizon this effect is not obvious.

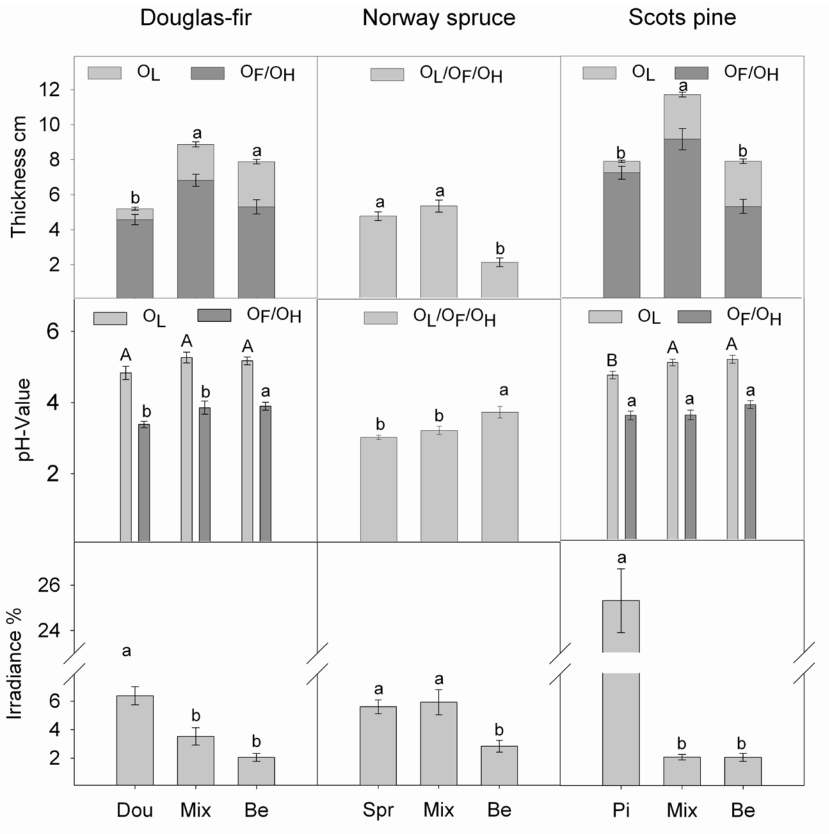

Fig. 4: Thickness and pH-value (KCl) of the litter layer (O_L), decomposed humus layer (O_F/O_H), and relative irradiance for the herb layer. n = 20 except for the Solling site (soil data: Spr 13, Mix 8, Be 16, irradiance: Spr 13, Mix 14, Be 16) and irradiance in the lowlands (Dou 11, Dou-Be 11, Be 9, Pi 9, Pi-Be 14), plot size = 400 m²; means that do not share the same letter differ significantly (Kruskal-Wallis test, $p < 0.05$).

Abb. 4: *Mächtigkeit und pH-Wert (KCl) der Humusauflage (unzersetzte Streuschicht O_L), zersetzte Humusauflage (O_F/O_H)) und relativer Lichtgenuss der Krautschicht. n = 20 mit Ausnahme der Flächen im Solling (Bodendaten: Fi 13, Fi-Bu 8, Bu 16, Licht: Fi 13, Fi-Bu 14, Bu 16) und der Lichtdaten im Flachland (Dgl 11, Dgl-Bu 11, Bu 9, Kie 9, Kie-Bu 14), Flächengröße 400 m². Unterschiedliche Buchstaben kennzeichnen signifikante Unterschiede (Kruskal-Wallis-Test, p < 0.05).*

4 Discussion

Questions about the improvement of the status for nature conservation and forestry by admixture of beech in coniferous stands are, strictly speaking, questions about how ecological interactions meet the aims of silviculture or nature conservation. Both agree on fundamental assumptions concerning the preservation of biological diversity and increasing naturalness of forests. Although the connection between diversity and ecosystem functions is not yet known in detail (Schulze & Mooney 1993, Loreau et al. 2002, Scherer-Lorenzen et al. 2005, Leuschner et al. 2009), it is a commonly held opinion, that biodiversity increases ecosystem stability (Sukopp & Trepl 1987, Führer 2000, Schmidt 2006, Paquette & Messier 2011). Changes in forest tree species composition and structure inevitably lead to changes in the biodiversity of forest-dwelling species. A meta-analysis by Paillat et al. (2010) shows that diversity of some taxa is more affected by forest management than others. Our study only highlights one component, the understorey vegetation with vascular plants and soil-dwelling bryophytes, well aware that results may be different if including species like epiphytic lichens, fungi, birds or insects.

4.1 Diversity and naturalness

The results generally show a decreasing species diversity from conifer stands towards beech stands. Clear gradients of diversity, in comparable Scots pine admixtures, are also found by Schmidt et al. (2004) or Vor & Schmidt (2006). Comparisons of the diversity of Douglas-fir stands with mixed stands or beech stands are rare and results are varying depending on the research area and site conditions. While studies from Zerbe (1999) in the Spessart Mountains coincide with the present results, Knoerzer & Reif (1996) observed the opposite in the Black Forest. Both studies only compared pure stands of Douglas-fir with beech. Vor & Schmidt (2006), who compared pure Douglas-fir with mixed stands, found no significant differences concerning diversity. As for the Norway spruce comparison, the influence of beech on diversity is often not considerable until the beech fraction is clearly dominant (Leitl 2002). Plant species numbers, as well as coverage of vegetation layers, of mixed and pure spruce stands in the Solling Mountains do not differ significantly. Nevertheless, other authors were able to observe clear relationships where mixed stands always have a medium position (Lücke & Schmidt 1997, Matthes 1998, Engelhard & Reif 2004, Schmidt et al. 2004, Barbier et al. 2008).

As far as naturalness of herb layer is concerned, in Douglas-fir and Scots pine comparisons the highest percentage of typical forest plants is reached in the mixed stands. Only the Norway spruce comparison shows a continuous relative increase of typical forest species from pure spruce over mixed up to pure beech stands. Lücke & Schmidt (1997), Leitl (2002), Gärtner (2003) and Schmidt et al. (2004) also found in their vegetation studies an increasing naturalness with increasing beech fraction. But, similarly to the results of the present study, Lücke & Schmidt (1997) point out that the absolute number of forest species is decreasing with an increasing beech fraction. Based on the potential occurrence of plant species in close-to-nature beech forests Schmidt et al. (2004) also confirm a continuous increase of naturalness with the conversion of Scots pine stands into beech stands.

The claim for both more diversity and more naturalness often means a conflict on a local scale in regions where one would expect the Luzulo-Fagetum to be the potential natural vegetation. These forests show very low numbers of plant species in general and therefore, diversity increases due to enrichment or conversion with non site-specific tree species. Relationships between increasing number of plant species and anthropogenic influence have been noticed by several authors. Weckesser (2003) and Fritz (2006) describe increased species diversity of artificial coniferous forests as a direct effect of human impact. The studies of Detsch (1999), Oheimb et al. (1999), Schmidt (1999, 2005), Westphal (2001) and Schmidt & Schmidt (2007) as well as a meta-analysis on European forests (Paillet et al. 2010) document higher vascular plant species diversity in managed forests compared with unmanaged forests.

Diversity does not necessarily mean naturalness, depending very much on the spatial scale used (Anders & Hofmann 1997, Standovár et al. 2006). Hence Fritz (2006) points out, that for the postulation of more diversity it is important to observe a wider area than only one stand. At the landscape level, the conflict between diversity and naturalness recovers because of different stand types. At least concerning the gamma-diversity of this study, defined as cumulative species richness per stand type, naturalness and diversity remain contrary. To mix different stand types with a clearly distinct naturalness may not be convincing in this context.

With regard to higher naturalness, it is important to differentiate between natural and artificial diversity (Dierssen & Kiehl 2000, Schmidt et al. 2003). Therefore mixed forests should be promoted first of all to their natural habitats, e. g. the transition zone between broadleaves and conifers in mountainous areas. Furthermore, mixed forests are also important regarding the uncertainty of future climate trends and the long-term perspective which is necessary for stand conversion. Considering economical aspects, Lüpke & Spellmann (1999) highlight the positive impact of beech on pure spruce stands, because beech is less sensitive to environmental disturbances and therefore reduces economic risks. Even so, an absolute exclusion of spruce would result in noticeable profit cuts because of the higher productivity of spruce (Pretzsch & Schütze 2005).

4.2 Similarity and site conditions

While plant species diversity and naturalness show more or less consistent trends for all three comparisons, with a decreasing diversity and an increasing naturalness due to admixture of beech, similarity highlights the differences between them. Both the admixture with Douglas-fir and Norway spruce seem to change species composition relatively slowly, with the mixed stands still having a higher similarity towards the pure coniferous than the pure beech stands. For Norway spruce this is confirmed by Leitl (2002) and Fritz (2006). In contrast, mixed stands with pine and beech are scarcely distinguishable from pure beech stands, which means that Scots pine stands are ecologically more sensitive to conversion with beech. In this regard, Schmidt (2007) refers to European beech as an “Ecosystem engineer” because physical and chemical site conditions change strongly by replacing coniferous trees with European beech. However, a qualitative change of the species pool does not take place. Almost all species occurring in pure beech stands are also found in the mixed and pure coniferous stands enriched by typical species of coniferous forests. This could be understood that not only tree species composition itself is an important factor for understorey species composition, but also the homogenous site conditions characterizing the Luzulo-Fagetum as potential natural vegetation. Augusto et al. (2003) even found a lower impact from tree species on understorey vegetation in comparison with the impact from site conditions and silvicultural management. In fact there is no consensus about the effect of different tree species on understorey vegetation (Lücke & Schmidt 1997, Ewald 2000, Augusto et al. 2002, 2003). On the one hand, every tree species produces typical light conditions which are more or less independent from silvicultural management (Mitscherlich 1981, Messier et al. 1998, Hagemeier 2002, Frech 2006, Mölder et al. 2008, Ellenberg & Leuschner 2010). On the other hand, light conditions at stand level are highly influenced by silvicultural impacts, which again may be typical for each tree species. In Lower Saxony, the silviculture follows the guidelines of the LÖWE program (Long term program for ecological-orientated forest management, Niedersächsische Landesforsten 2011). This means that harvesting methods do not differ between stand types because trees are always single-tree- or group-selected. Differences therefore can arise due to stand structure, which mainly depends on stand history. Investigated beech stands often have a more differentiated age distribution because they have been naturally regenerated for some decades while conifers were planted and even-aged. Likewise, top soil quality is affected by the tree species, especially acidification through conifer trees (Spruce: Zerbe 1994, Hüttl & Schaaf 1995, Lücke & Schmidt 1997; Douglas-fir: Marques & Ranger 1997). Humus accumulation (Fischer et al. 2002, Kautz & Topp 1998) and C/N-ratio (Lücke & Schmidt 1997, Zhong & Makeschin 2004) change as well with the introduction of deciduous trees into conifer stands. Forest management also has been shown to influence soil fertility (Augusto et al. 2002). However, even if the use of harvesting machines is more common in conifer stands than in beech stands, there should not be any difference in soil disturbance because the machines should stay on strictly defined skidding tracks.

The effect of beech introduction on understorey vegetation in pure conifer stands is therefore indirectly measurable in terms of light and soil conditions. Light conditions clearly play a major role, especially concerning coverage of understorey vegetation, e. g. Weisberg et al. (2003) found a greater influence from light conditions on coverage than on plant species diversity.

5 Conclusion

To address the issue of the improvement of conifer stands through beech, first of all it is important to declare objectives concerning their status for nature conservation and forestry. Assuming that these objectives are promotion or preservation of a natural diversity, measured by the potential natural vegetation of the Luzulo-Fagetum, beech clearly has a positive impact on artificial conifer forests. Depending on the conifer tree species, the effects are different. While mixed stands of pine and beech are hardly distinguishable from pure beech stands, in terms of species diversity or vegetation structure, mixed spruce-beech stands show a higher similarity towards pure spruce stands. Douglas-fir-beech stands range in between, with a greater similarity to the pure beech stands.

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Appendix / Anhang

Tab. 3: Plant species of herb and moss layer (*: *Hypnum cupressiforme* includes *H. jutlandicum* in the lowland stands). Absolute frequency (F) and coverage (C, mean %, 0.0 = ≤ 0.05 %), n = 20, plot size = 400 m². r = Pearson correlation with the first order axis of the DCA matrix. Only species reaching r ≥ 0.33 or at least a frequency of ten in one stand type are included.

Tab. 3: *Arten der Kraut- und Moosschicht(*: im Tiefland wurden* H. cupressiforme *und* H. jutlandicum *zusammengefasst). Absolute Häufigkeit (F) und Deckungsgrad (C, prozentuales Mittel, 0.0 = ≤ 0.05 %), n = 20, Aufnahmefläche = 400 m². r = Pearson-Korrelation mit der 1. Achse der DCA-Matrix. Nur Arten mit r ≥ 0.33 oder einer Häufigkeit von mindestens 10 in einem Bestandestyp wurden berücksichtigt.*

	Douglas-fir						Norway spruce						Scots pine						
	Dou		Mix		Be		Spr		Mix		Be		Pi		Mix		Be		r
Herb layer	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	
Predominantly in conifer stands																			
Deschampsia flexuosa	**17**	0.9	**12**	0.2	**5**	1.0	**19**	2.3	**17**	3.3	**5**	0.0	**20**	43.8	**7**	0.1	**5**	1.0	-0.76
Vaccinium myrtillus	**19**	1.2	**8**	0.0	**-**	-	**18**	1.7	**14**	0.2	**-**	-	**20**	48.8	**7**	4.0	**-**	-	-0.73
Dryopteris carthusiana	**6**	0.0	**8**	0.0	**4**	0.0	**10**	0.0	**17**	0.0	**8**	0.0	**20**	0.8	**5**	0.0	**4**	0.0	-0.49
Sorbus aucuparia	**19**	0.1	**15**	0.0	**6**	0.0	**20**	0.0	**20**	0.0	**8**	0.0	**15**	0.1	**11**	0.0	**6**	0.0	-0.48
Dryopteris dilatata	**20**	12.7	**17**	2.8	**10**	0.0	**20**	1.2	**19**	0.6	**11**	0.0	**19**	1.4	**5**	0.2	**10**	0.0	-0.35
Quercus spec.	**12**	0.0	**8**	0.0	**6**	0.0	**3**	0.0	**2**	0.0	**-**	-	**19**	0.1	**10**	0.0	**6**	0.0	-0.60
Rubus idaeus	**11**	6.6	**10**	1.1	**2**	0.0	**13**	0.0	**12**	0.5	**8**	0.6	**19**	15.2	**3**	0.0	**2**	0.0	-0.42
Galium saxatile	**7**	0.0	**3**	0.0	**-**	-	**19**	0.2	**16**	0.1	**-**	-	**12**	0.5	**-**	-	**-**	-	-0.33
Epilobium angustifolium	**8**	0.0	**1**	0.0	**2**	0.0	**17**	0.1	**12**	0.0	**1**	0.0	**13**	0.0	**1**	0.0	**2**	0.0	-0.38
Trientalis europaea	**11**	0.2	**6**	0.0	**-**	-	**15**	0.1	**4**	0.0	**-**	-	**16**	1.0	**1**	0.0	**-**	-	-0.52
Pseudotsuga menziesii	**15**	0.1	**11**	0.0	**1**	0.0	**-**	-	**-**	-	**-**	-	**-**	-	**-**	-	**1**	0.0	-0.17
Agrostis capillaris	**5**	0.0	**1**	0.0	**1**	0.0	**15**	0.0	**10**	0.3	**8**	0.0	**3**	0.0	**-**	-	**1**	0.0	0.09
Rubus fruticosus agg.	**13**	0.1	**5**	0.0	**4**	0.0	**3**	0.0	**9**	0.1	**3**	0.0	**12**	0.5	**4**	0.0	**4**	0.0	-0.44
Pinus sylvestris	**2**	0.0	**1**	0.0	**2**	0.0	**-**	-	**-**	-	**-**	-	**10**	0.0	**-**	-	**2**	0.0	-0.51
Calluna vulgaris	**1**	0.0	**-**	-	**-**	-	**-**	-	**-**	-	**-**	-	**10**	0.1	**-**	-	**-**	-	-0.48
Frangula alnus	**6**	0.0	**7**	0.0	**3**	0.0	**-**	-	**1**	0.0	**-**	-	**10**	0.0	**4**	0.0	**3**	0.0	-0.47
Betula spec.	**10**	0.0	**5**	0.0	**3**	0.0	**1**	0.0	**-**	-	**-**	-	**6**	0.0	**-**	-	**3**	0.0	-0.41
Ceratocapnos claviculata	**8**	0.2	**3**	0.1	**2**	0.0	**-**	-	**-**	-	**-**	-	**8**	0.5	**2**	0.0	**2**	0.0	-0.44
Predominantly in beech stands																			
Fagus sylvatica	**8**	0.0	**20**	0.3	**19**	3.1	**8**	0.0	**19**	2.2	**20**	7.1	**-**	-	**18**	0.4	**19**	3.1	0.62
Indifferent																			
Luzula luzuloides	**-**	-	**-**	-	**-**	-	**17**	0.0	**20**	0.6	**16**	0.7	**-**	-	**-**	-	**-**	-	0.38
Carex pilulifera	**19**	0.2	**12**	0.0	**13**	0.0	**19**	0.1	**20**	0.0	**14**	0.1	**5**	0.0	**1**	0.0	**13**	0.0	0.12
Oxalis acetosella	**10**	6.8	**9**	1.4	**2**	2.3	**10**	1.8	**17**	7.5	**12**	2.3	**1**	0.0	**6**	0.3	**2**	2.3	0.28
Athyrium filix-femina	**4**	0.2	**-**	-	**-**	-	**6**	0.1	**15**	0.0	**3**	0.0	**-**	-	**1**	0.0	**-**	-	0.14
Juncus effusus	**7**	0.0	**3**	0.0	**1**	0.0	**8**	0.0	**12**	0.0	**8**	0.0	**1**	0.0	**-**	-	**1**	0.0	0.11
Cardamine flexuosa	**4**	0.0	**1**	0.0	**2**	0.0	**8**	0.0	**10**	0.0	**4**	0.0	**-**	-	**-**	-	**2**	0.0	0.21
Prunus serotina	**3**	0.0	**7**	0.0	**2**	0.0	**-**	-	**-**	-	**-**	-	**2**	0.0	**3**	0.0	**2**	0.0	-0.31
Moss layer																			
Predominantly in conifer stands																			
*Hypnum cupressiforme**	**19**	8.9	**15**	0.5	**11**	0.0	**10**	0.5	**18**	0.0	**11**	0.0	**20**	26.6	**11**	0.1	**11**	0.0	-0.69
Pleurozium schreberi	**13**	0.1	**-**	-	**-**	-	**6**	0.0	**3**	0.0	**-**	-	**20**	29.7	**2**	0.0	**-**	-	-0.69
Dicranum scoparium	**20**	0.2	**8**	0.1	**14**	0.0	**16**	0.3	**16**	0.1	**1**	0.0	**18**	2.7	**12**	0.1	**14**	0.0	-0.61
Plagiothecium laetum var. *curvifolium*	**-**	-	**-**	-	**-**	-	**13**	1.1	**19**	0.1	**1**	0.0	**-**	-	**-**	-	**-**	-	-0.13
Eurhynchium praelongum	**17**	5.0	**6**	0.0	**1**	0.0	**8**	0.0	**4**	0.0	**1**	0.0	**11**	0.7	**-**	-	**1**	0.0	-0.30
Lophocolea bidentata	**1**	0.0	**1**	0.0	**-**	-	**9**	0.3	**-**	-	**-**	-	**15**	0.1	**2**	0.0	**-**	-	-0.46

Scleropodium purum	**11**	1.5	**1**	0.0	**-**	-		**-**	-	**-**	-	**-**	-		**10**	4.4	**-**	-	**-**	-		-0.42
Predominantly in beech stands																						
Pseudotaxiphyllum elegans	**-**	-	**-**	-	**2**	0.0		**-**	-	**3**	0.0	**9**	0.0		**-**	-	**-**	-	**2**	0.0		0.36
Indifferent																						
Polytrichum formosum	**20**	6.3	**17**	0.5	**15**	0.1		**20**	3.3	**20**	5.0	**19**	0.4		**17**	1.6	**12**	0.3	**15**	0.1		-0.12
Herzogiella seligeri	**1**	0.0	**2**	0.0	**4**	0.0		**14**	0.1	**20**	0.1	**1**	0.0		**-**	-	**7**	0.1	**4**	0.0		0.14
Brachythecium rutabulum	**15**	7.8	**9**	0.6	**13**	0.0		**15**	0.2	**19**	0.3	**9**	0.0		**18**	7.5	**9**	0.2	**13**	0.0		-0.35
Mnium hornum	**13**	1.4	**11**	0.0	**13**	0.0		**10**	0.5	**15**	0.1	**5**	0.0		**-**	-	**3**	0.0	**13**	0.0		0.10
Atrichum undulatum	**13**	0.1	**7**	0.0	**8**	0.0		**5**	0.0	**6**	0.0	**5**	0.0		**-**	-	**3**	0.0	**8**	0.0		0.18