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The influence that *Picea abies* Karst. and *Fagus sylvatica* L. have on the vitality of *Vaccinium myrtillus* L. in montane mixed forests of central Europe on silicate bedrock

Der Einfluss von Picea abies *Karst. und* Fagus sylvatica *L. auf die Vitalität von* Vaccinium myrtillus *L. in mitteleuropäischen Bergmischwäldern der Montanstufe auf Silikat*

Carl E. Höcke, Juliane Spiegelhalter, Stefanie M. Gärtner and Albert Reif

Abstract

Bilberry (Vaccinium myrtillus *L.*) *is a dwarf shrub with high ecological relevance as habitat and as a food source for many animals in mountain forests of central Europe. This species benefits from conifer forests and declines with an increase of broadleaved tree species in the canopy. The ongoing large-scale conversion from conifer to broadleaved forests may significantly alter the ground vegetation, especially the dominance of a key species such as bilberry. We used morphological indicators to investigate the vitality of bilberry. The first objective was to determine whether the vitality of bilberry is negatively impacted by increasing the proportion of beech* (Fagus sylvatica *L.*) *in Norway spruce* (Picea abies *Karst.*) *forests. The vitality of bilberry was measured by its cover, height, biomass, shoot length and basal diameter. The second objective was to determine whether these changes in bilberry vitality were related to light, canopy cover, soil pH, organic layer mass and tree species.*

The data was collected from three study areas in the southern and central Black Forest. The bedrock consisted of gneiss and granite whereas the stands were either: pure beech, a mixture of beech and spruce or pure spruce. The stands were located adjacent to each other. On all three areas a higher vitality of bilberry was observed under spruce compared to beech. Mixed effect models show that the occurrence of spruce is the most important variable explaining the increase in bilberry biomass. Light had a small positive effect, whereas soil properties had negligible effects and were site specific.

These results are a strong indication of the negative influence that beech has on bilberry in conifer dominated forests. This has to be taken into consideration when developing silvicultural approaches and should be a consideration when making plans for the preservation of habitat for species like capercaillie (Tetrao urogallus *L.*). *This is even more important today because the recent trend in central European forestry is to increase the proportion of beech.*

Keywords: *beech, spruce, bilberry, forest conversion,* Tetrao urogallus*, capercaillie*

Zusammenfassung

Die Heidelbeere (*Vaccinium myrtillus* L.) hat große ökologische Bedeutung im Bereich der montanen mitteleuropäischen Bergmischwälder, unter anderem als Lebensraum und Nahrungsgrundlage für viele Tierarten. Dieser Zwergstrauch wird durch nadelholzreiche Bestände begünstigt. Der heute praktizierte Waldumbau hin zu höheren Laubholzanteilen verändert die Bodenvegetation und insbesondere die Anteile der Schlüsselart Heidelbeere. Auf der Grundlage morphologischer Indikatoren wurde die Vitalität der Art untersucht. Ziele dieser Studie waren:

1. Eine Analyse, inwiefern die Vitalität der Heidelbeere in durch die Fichte (*Picea abies* Karst.) geprägten Wirtschaftswäldern durch einen zunehmenden Anteil an Buche (*Fagus sylvatica* L.) beeinträchtigt wird. Hierzu wurden vitalitätsbezogene Merkmale wie Bodenbedeckung, Wuchshöhe, Biomasse, Sprosslänge und Sprossdurchmesser am Wurzelansatz der Heidelbeere gemessen.

2. war es Ziel, den Einfluss der Lichtversorgung, der Deckung des Kronendaches, des pH-Wertes des Bodens, der organischen Auflage, der bestockenden Baumarten und des Standortes auf die Veränderungen von Morphologie und Vitalität der Heidelbeere zu analysieren.

Hierzu wurden im Südlichen und Mittleren Schwarzwald in drei Untersuchungsgebieten auf Gneiss bzw. Granit die entsprechenden Daten erhoben. In diesen Gebieten grenzten ein Buchenbestand, ein Ökoton mit einer Mischbestockung aus Fichte und Buche (nur in zwei Gebieten), sowie ein Fichtenbestand direkt aneinander.

In allen drei untersuchten Gebieten zeigte sich unter Fichtenbestockung eine wesentlich höhere Vitalität der Heidelbeere. Die Bestockung erwies sich auch in der Analyse unter Verwendung gemischter Modelle als die wichtigste erklärende Variable hinsichtlich eines Anstiegs der Biomasse der Heidelbeere. Licht hatte einen geringen positiven Einfluss, der Einfluss der Bodeneigenschaften war gering und geologiebedingt standortsspezifisch.

Somit konnte gezeigt werden, dass das Auftreten von Buche in fichtendominierten Wäldern sich stark negativ auf die Heidelbeere auswirkt. Dies gilt es bei waldbaulichen Planungen zu berücksichtigen, beispielsweise wenn es um Planungen zum Schutz beerstrauchreicher Lebensräume und der von ihnen abhängigen Arten geht, darunter auch das Auerhuhn (*Tetrao urogallus* L.). Dies ist auch insofern von großer Bedeutung, da gerade heute in der mitteleuropäischen Forstwirtschaft eine Zunahme der Buche in nadelholzgeprägten Wäldern befürwortet und praktiziert wird.

Schlüsselwörter: Buche, Fichte, Heidelbeere, Waldumbau, *Tetrao urogallus*, Auerhuhn

1 Introduction

Vaccinium myrtillus L. (bilberry) is a dwarf shrub common on acidic sites in coniferous forests and heath lands throughout temperate and boreal European forests and in north western and central forests of Asia. In southern Europe and along the Black Sea, bilberry is limited to higher elevations (e. g. Ritchie 1956, Coudon & Gégout 2007). Many studies have pointed out the ecological relevance of this species as habitat, as food for wildlife and for biodiversity (e. g. Atlegrim 1991, Storch 1993, Baines et al. 1994, Welch et al. 1994, Suter et al. 2002, Melis et al. 2006). It is considered a crucial habitat element for the endangered capercaillie (*Tetrao urogallus* L.) particularly where bilberry cover is highly variable as in central Europe (Schroth 1991, Storch 1993), the Pyrenees (Quevedo et al. 2006) and Scotland (Baines et al. 2004). As a result bilberry cover is an important factor in habitat models and management plans for capercaillie and other species of the grouse family (*Tetraoninae*) (e. g. Storch 2002, Baines et al. 2004, Bollmann et al. 2005, Parlane et al. 2006, Quevedo et al. 2006, Braunisch & Suchant 2007, Kvasnes & Storaas 2007, Stettler & Christen 2010).

The understory of Norway spruce (*Picea abies* Karst.) forests often consists of a dense carpet of bilberry (*Vaccinium myrtillus*). It has been observed that under a single European beech (*Fagus sylvatica* L.; from now on called “beech”) when found in a spruce forest or in the ecotone between spruce and beech forests, this bilberry carpet often abruptly declines. Although this phenomenon is obvious and common, it has not yet been studied. In this study we investigate and discuss possible reasons for this phenomenon.

The impact of beech on this important species for wildlife is interesting considering that since the 1970s in central Europe there has been ongoing conversion of conifer monocultures to mixed-wood forests with a higher broadleaved tree component (e. g. Fritz 2006, von Teuffel et al. 2005). Conversion has been linked to changes in soil ecological processes (Gruselle 2009, Berger et al. 2002) as well as in forest ground vegetation (e.g. Augusto & Ranger 2003, Gärtner & Reif 2004, Weckesser & Schmidt 2007, Denner & Schmidt 2008). There is strong evidence that bilberry becomes less abundant and decreases in cover as the proportion of beech in conifer stands increases (Gärtner & Reif 2005, Weckesser & Schmidt 2007). This could be due to a change in light or soil chemistry or due to the addition of beech leaf litter acting as a physical barrier to bilberry establishment (Koreleff 1954, Gregory 1966, Williams et al. 1990, Simard et al. 2003).

In temperate forests optimal light conditions for bilberry are semi-shade with at least 10 % of the above canopy light, but rarely full sunlight (Ellenberg 2001). In Scotland the light optimum was found to lie between 20 (Hester et al. 1991b) and 35 % (Parlane et al. 2006) of the above canopy light. Two studies in northern Europe found light to be an important factor in the abundance of bilberry and that in low light conditions it was replaced by other dwarf shrubs (Karlsson 1989) or herb species (Kuusipalo 1983). Fertilisation experiments in southern Finland showed that light was more important than nutrients for the ecological optima of bilberry and *Vaccinium vitis-idaea* L. (Mäkipää 1999).

Therefore our hypothesis was that the decline of bilberry under beech could be due to reduced light transmittance. But tree species also modify soil chemistry which could also have an impact on the performance of bilberry. Long-term N-deposition generally results in a decline of bilberry and other Ericaeous species and an increase in abundance and cover of nutrient demanding and nitrophilous species (e. g. Röder et al. 1996, Bernhardt-Römermann et al. 2007, Strengbom & Nordin 2008). However, there is some experimental evidence suggesting that bilberry and other Ericaeous species like *Vaccinium vitis-idaea* remain unaffected and even benefit from N-deposition on sites where the soil nutritional status is less than bilberry´s optimum. Bilberry declined only when N-deposition affected moderately rich or rich sites (Kellner & Märshagen 1991, Kellner 1993, Mäkipää 1999). Liming practises affect bilberry dominated forest vegetation in a way that is similar to N-deposition in that there is an increase in nutrient demanding species and nitrophytes with a corresponding decrease in species typically on acidic sites. The vegetation changes are caused by direct damage or increased competition and are more pronounced on poor sites (Schornick 1990, Kraft et. al. 2003). There is evidence that the effects of liming and N-deposition interact positively (Kraft et al. 2003, Reif et al. 2014) however the effects seem to be site specific and depend on dosage. Becker et al. (1992) attributed the vegetation changes on a site, 20 years after it was fertilized, to be the result of additional Ca; but not due to additional N or P. Overall, liming effects on bilberry-dominated vegetation can last for more than four decades (Schornick 1990). As for the addition of N, liming or fertilisation with calcium or phosphorus on sites less than optimal for bilberry could produce a slight increase in its cover (Schornick 1990, Hester et al. 1991b, Kraft 1999, Mäkipää, 1999, Jandl et al. 2000, Höcke 2006), while on richer sites, the effects were the opposite (Schornick 1990, Becker et al. 1992, Werner 1995, Zoldan 1997, Kraft 1999, Misson et al. 2001, Schmidt 2002). The negative effects increase with increasing amounts of lime and the same is expected with the addition of Mg, K, P and N (Mitscherlich & Moll 1962, Schornick 1990, Kraft 1999, Höcke 2006). Furthermore, experiments have shown that bilberry takes up calcium from solutions preferentially, which seems to be an adaptation to extremely acidic and base poor sites (Ingestad 1973).

In this study we aimed

1. to test the hypothesis that the vitality of bilberry (*Vaccinium myrtillus*) expressed by the variables cover, height, biomass, shoot length and basal diameter are negatively affected by an increase of beech cover in spruce forests.

2. we hypothesize that these changes can be attributed to variations in light, canopy cover, the proportion of beech and spruce in the canopy, soil pH, and the mass of the organic layer.

Our study was carried out in three areas with gneiss and granite bedrock in the south-central Black Forest of Germany.

2 Material and methods

2.1 Study areas

We selected three areas situated in the montane belt on the western side of the south-central Black Forest using GIS-based stand data (ArcView 3.2, ESRI, Redlands, CA, USA) provided by MLR Baden-Württemberg (2009a). Within each area, Norway spruce and beech stands separated by a narrow ecotone were selected. Additionally, the stands had to be more than 100 years old and have only a single tree layer. The topography and soil conditions were similar (Aldinger et al. 1998, MLR Baden–Württemberg 2009b). We looked for beech and Norway spruce stands where bilberry was the dominant species in the herb layer under both canopies. Minor difference in bilberry cover adjacent to the ecotone between the stands with different tree species mixture did not influence the area and stand selection. The bedrock for the area "Märchenwald" (M), 47°50'18'' North, 7°51'18'' East, 1230 m a. s. l., and "Schauinsland"(**S**), 47°54'47'' North, 7°54'44'' East, 1190 m a. s. l., consisted mainly of prevariscan gneiss and migmatites while for the area "Rohrhardsberg" (R), 48°07'26'' North, 8°08'22'' East, 1080 m a. s.l., it was granite (Geyer & Gwinner 1991). All soils were acidic cambisols with local podsolisation (Aldinger et al. 1998).

The mean annual air temperature ranges between 4.5 and 6.5 °C and the annual precipitation between 1550 and 1700 mm (Fiedler 1995). The potential natural vegetation is forest dominated by beech (*Fagus sylvatica*) and fir (*Abies alba* Mill.), with maple (*Acer pseudoplatanus* L.) as a minor species (Aldinger et al. 1998, Reidl et al. 2013). Norway spruce (*Picea abies*) is assumed not to be a component of the potential natural vegetation. The species was planted in the study area, but does occur naturally on bog margins and on boulder slopes, and above ca. 1300 m a. s. l. in zonal forest (Ludemann 2006, Reidl et al. 2013). According to the data from the closest monitoring station around 45 kg of airborne nitrogen per hectare per year were deposited under the spruce canopy in the areas S and M, and 20 to 30 kg N ha^{-1} yr^{-1} in area R. We assume that N-deposition was higher under spruce because their evergreen needles can intercept N particles (comb effect) year round (Hug et al. 2005).

2.2 Sampling design, data assessment and biomass estimation

In each pure Norway spruce and beech area we established 10 quadrats measuring 2 by 2 m with the sides aligned north-south and east-west. The plots were arranged in a systematic grid separated by a minimum of 10 metres. Each quadrat centre was a minimum of 10 m from the ecotone. In the S and M areas we systematically placed an additional 10 quadrats in the ecotone. These quadrats were located under beech and Norway spruce mixed-woods and positioned equidistant from the pure beech and spruce stand boundaries. No plots were put in the ecotone at area R due to a local disturbance caused by logging roads.

To avoid the edge effect we kept a minimum of 10 m away from adjacent stands and 2 m away from skid trails. Because our interests lay in the influence of the canopy, the quadrats with tree regeneration and those that had dead wood on the ground covering > 10 % were systematically moved 2 m north, and if the criteria for placing a quadrat was still not met, the quadrat was moved another 2 m east. Within each quadrat three 20 by 20 cm subquadrats with a distance of 50 cm from the quadrat centre to subquadrat centre were selected randomly along three of the four cardinal directions.

In each quadrat we determined the average height (HeV) of the bilberry carpets in 5 cm classes by measuring dominant heights. The percent cover (CoV) within each plot was estimated. Additionally, we determined the arithmetic mean of the shoot length of the three largest shrubs (SLVmax) and the three largest basal diameters (BDVmax) out of all the bilberries for each plot.

We modelled the biomass of bilberries on the 2 by 2 m quadrats (BMVmod) using a linear regression function. It was developed with the variables HeV (cm), CoV (as fraction) (cf. Kuusipalo 1983) and dry biomass (g/m²) assessed as aggregates on the three subquadrats for each quadrat. The product of height (cm) by cover (percentage) was selected as one variable because it represents a measure of volume. For the regression model we used 59 plots. We achieved a normal distribution for the variables way using a square root transformation (Shapiro-Wilk-test $p > 0.05$). Further assumptions of linear regression like linearity and homoscedasticity were met. The following linear regression model was derived using the software Statistica 6.0 (StatSoft, Inc. 1994–2001):

$$BMVmod^{0,5} = 2.84 + 3.46 \cdot (HeV \cdot CoV)^{0,5}$$

We tested this model globally with a corrected coefficient of determination of $r^2 = 0.86$ ($n = 59$, $df = 57$) with an ANOVA ($p < 0.01$) and the constant ($c = 2.84$; SE 0.58) and B ($B = 3.46$; SE 0.19; ß =0.05) with t-tests ($p < 0.01$). A test of the accuracy of this model on sub-quadrat level ($n = 80$) did not give significantly different values for the observed biomass in g/m² (mean = 134.4, SE = 16.2) against modelled biomass (mean = 133.3, SE = 14.9) as tested with a Mann-Whitney-*U* test ($p = 0.41$). Observed and modelled biomass on the sub-quadrat level ($n = 80$) was highly and significantly correlated (Spearman's $R = 0.97$; t-test $p < 0.01$).

We sampled the dry mass of the organic layers including the Oi, Oe and Oa in the three sub-quadrats. The organic material was weighed when fresh and then again after it was dried at 55 °C until no further weight loss could be detected. Mineral soil samples were collected from the upper 5 cm of each sub-quadrat. The three soil samples taken from each quadrat were well mixed. Fifteen ml of each sample was mixed with 20 ml 0.01 molar $CaCl_2$ solution and left to rest for two hours after which the soil solution pH was measured with a WTW® "pH 300i/Set" electrode.

Tab. 1: Correlation matrix of Spearman's rank correlation (n = 80) for variables of estimated and measured site characteristics and vitality indicators of *Vaccinium myrtillus* L. * p < 0.05, ** p < 0.01 t-test significance level.

Tab. 1: *Korrelationsmatrix der Spearman Rangkorrelationen (n = 80) der geschätzten und gemessenen Standortsparameter und Vitalitätsindikatoren (Variablen) von* Vaccinium myrtillus *L. * p < 0.05, ** p < 0.01, T-Test- Signifikanzniveau.*

n = 80	cover spruce[a]	cover beech[a]	canopy cover[a]	direct light[b]	diffuse light[b]	total light[b]	pH mineral soil	mass organic layer	height[c]	shoot length[c]	stem diameter[c]	cover[c]	biomass[c]
cover spruce[a]	-	-0.73**	0.09	0.00	0.10	0.04	-0.15	0.04	0.46**	0.48**	0.44**	0.65**	0.62**
cover beech[a]	-0.73**	-	0.54**	-0.23*	-0.39**	-0.33**	0.10	0.02	-0.58**	-0.60**	-0.57**	-0.67**	-0.69**
canopy cover[a]	0.09	0.54**	-	-0.19	-0.34**	-0.27*	-0.14	0.21	-0.25*	-0.25*	-0.25*	-0.21	-0.25*
direct light[b]	0.00	-0.23*	-0.19	-	0.63**	0.93**	0.19	-0.19	0.00	0.00	-0.03	0.05	0.06
diffuse light[b]	0.10	-0.39**	-0.34**	0.63**	-	0.84**	0.31**	-0.33**	0.19	0.21	0.13	0.29**	0.31**
total light[b]	0.04	-0.33**	-0.27*	0.93**	0.84**	-	0.28*	-0.28*	0.08	0.01	0.04	0.15	0.17
pH mineral soil	-0.15	0.10	-0.14	0.19	0.31**	0.28*	-	-0.77**	-0.07	-0.12	-0.19	0.08	0.07
mass organic layer	0.04	0.02	0.21	-0.19	-0.33**	-0.28*	-0.77**	-	0.03	0.07	0.14	-0.20	-0.15
height[c]	0.46**	-0.58**	-0.25*	0.00	0.19	0.08	-0.07	0.03	-	0.95**	0.91**	0.81**	0.89**
shoot length[c]	0.48**	-0.60**	-0.25*	0.00	0.21	0.01	-0.12	0.07	0.95**	-	0.95**	0.82**	0.88**
stem diameter[c]	0.44**	-0.57**	-0.25*	-0.03	0.13	0.04	-0.19	0.14	0.91**	0.95**	-	0.77**	0.82**
cover[c]	0.65**	-0.67**	-0.21	0.05	0.29**	0.15	0.08	-0.20	0.81**	0.82**	0.77**	-	0.98**
biomass[c]	0.62**	-0.69**	-0.25*	0.06	0.31**	0.17	0.07	-0.15	0.89**	0.88**	0.82**	0.98**	-

a tree layer, b percentage above canopy light, c of *Vaccinium myrtillus* L. on 2m · 2 m plots.

For each 2 by 2 m quadrat we estimated the horizontal projection of the canopy cover (10 percent classes) for Norway spruce, beech and the total canopy cover. From the centre of each quadrat, from one metre in height, we took a hemispherical photo taken when the sky was homogenously overcast (Nikon Coolpix® 8400; fisheye converter Nikon FC-E9, option "fisheye" as a 300 dpi, 3264–2448 pixel picture in jpeg format, oriented north and levelled). The hemispherical photos were processed according to Brunner (1998). The direct and diffuse light was calculated with the program hemIMAGE (Brunner 1998). The first and last day of the vegetation period was estimated with values from Fiedler et al. (1995) which gave us a vegetation period from April 20 to October 20 (areas M, S) and from April 15 to October 20 for area R.

2.3 Data analysis

Shapiro-Wilk test of all parameters (n = 80) indicated a normal distribution only for mineral soil pH in $CaCl_2$. As neither logarithmic nor root transformation (log (1+x), $x^{0,5}$, $x^{0,2}$) improved this condition we used non-parametric statistics. We chose Spearman's rank correlation to test the relation between all environmental variables and the response variables for the vitality of bilberry. We tested differences between groups globally with a Kruskal-Wallis *H*-test and in the case of significance, pair wise with the Mann-Whitney-*U*-test using the software Statistica 6.0 (Statsoft 1994-2001).

A Principal Component Analysis (PCA) to visualize the relationship between the variables and plots using CANOCO 4.52 (ter Brak & Smilauer 2003) applying a standardisation to the response variables was done. Supplementary z-transformed variables were projected into the PCA as vectors.

To get a better insight into the cause-effect-relation, we constructed a set of alternative models to estimate bilberry biomass as a function of multiple explanatory variables. We developed four models based on the hypothesis that beech is responsible for the decline in bilberry biomass. Two models including the estimated cover of beech in the plots and the other two models including the proportion of beech as a factor (fSpecies, Tab. 1) described the stand type from no beech (pure spruce stand: fSpecies1), to a mix between beech and spruce (fSpecies3) to the pure beech stand type (fSpecies2). As additional explanatory variables we included those variables which were not intercorrelated (R < +/- 0.5) and selected. In the case of correlated variables, the one with the highest correlation coefficient with bilberry biomass was selected. The most parsimonious models included only the beech cover estimate (beech) or the stand cover type (fSpecies) and as a random affect the study area (fArea). The two more complex models also included the pH of the organic material (pH) and the estimate of the percentage of above canopy light (PACLtot). The full stand type model also included the estimate of canopy cover (totCover, Tab. 1).

Mixed effect models were used to account for the lack of variance heterogeneity between the three study areas and the nested sampling design. To develop the models we used the function 'lme' in the 'nlme' package, version 3.1-97 (Pinheiro et al. 2010) within R version 2.12.1 (R Development Core Team 2010) with the study area as a random variable. To evaluate the models we used the information theoretic framework (Burnham & Anderson 2002, Anderson 2008). The evaluation of the models was performed using the R package "AICcmodavg" version 1.13 (Mazerolle 2010). The second order Akaike´s Information criterion (AICc) for small samples was applied to evaluate the different models (Burnham & Anderson 2002). Additionally, we calculated two more measures to compare the models: the first one was delta AICc which measures the difference of each model relative to the best model. The second measure for the strength of evidence of each model was the Akaike weight which indicated the probability that the model was the best among the whole set of candidate models (Burnham & Anderson 2002). Akaike weights are calculated as the ratio of the delta AICc of a given model relative to the whole set of models.

The magnitude of the effect of each explanatory variable on the response variable was assessed with an estimated average across all models. To conduct the model averaging, the estimate (i. e. the regression coefficient) of each of the variables for each model was weighted by the Akaike weights

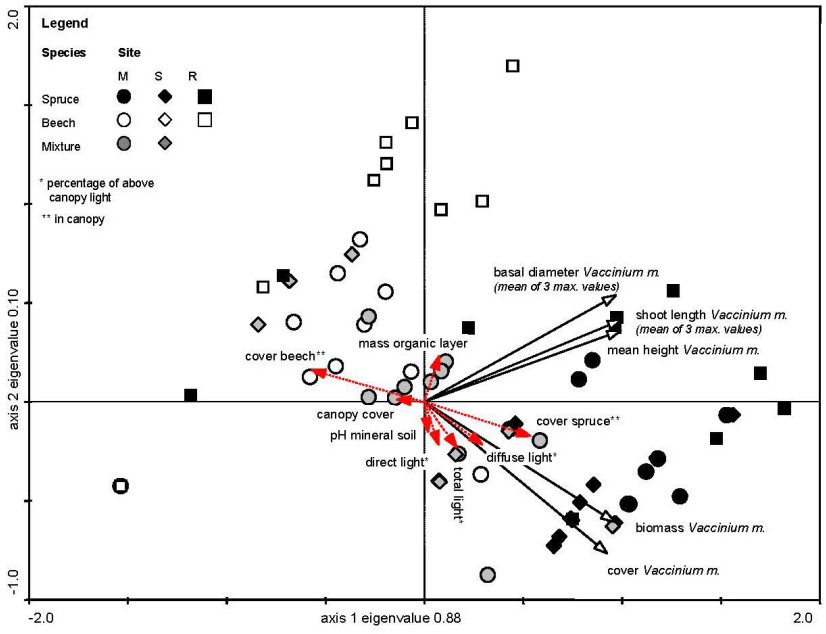

Figure 1

Fig. 1: *Vitality indicators of* Vaccinium myrtillus *L. (solid vectors) and supplementary factors (dotted vectors) for the plots grouped by research area and tree species composition in a PCA ordination (symmetric biplot, species scores divided by standard deviation, correlation matrix).*

Abb. 1: Vitalitätsindikatoren von *Vaccinium myrtillus* L. (durchgezogene Vektorpfeile) und erklärende Faktoren (gepunktete Vektorpfeile) der Probeflächen, gruppiert nach Gebieten und Baumartenzusammensetzung in einer PCA-Ordination (symmetrischer Biplot, mit Bezug auf die Standardabweichung, Korrelationsmatrix).

(Mazerolle 2006). The precision of the estimation (SE) of the model average estimate was calculated in the same way.

3 Results

3.1 Bilberry vitality in relation to spruce and beech overstory

We observed a decrease in bilberry growth for all vitality indicators along the gradients from pure spruce to ecotone to pure beech stands in all three areas (Fig. 1, Fig. 2). Under Norway spruce canopy, the vitality of bilberry was significantly higher than under beech canopy. The quadrats next to the ecotone, between Norway spruce and beech (areas M and S) were intermediate in vitality (Fig. 2). The cover (CoV) and biomass (BMVmod) of bilberry differed more distinctly between the spruce and beech stands compared to the height parameters (HeV, SLVmax) and stem diameter (BDVmax). The differences in cover and biomass of bilberry between the ecotone quadrats compared to the quadrats in the pure beech and spruce stands were significant for the two areas (Fig. 2). This was confirmed by the results of rank correlations (Tab. 1) and the PCA (Fig. 1): among the vitality parameters cover and biomass of bilberry showed the highest correlations with spruce in the canopy (Spearman's R = 0.98), while the other parameters had a weaker correlation (Spearman's R between 0.77 and 0.96). The highest biomass (BMVmod) and cover (CoV) of bilberry was found under Norway spruce on the areas M and S with values for each of more than 300 g/m² BMVmod and more than 80 % of CoV, while the values on area R (spruce) were a little lower with ~ 270 g/m² BMVmod and ~ 60 % CoV (Fig. 2). Under mixedwood canopies (only areas M, S) the BMVmod and CoV decreased significantly to about 50 % (Fig. 2).

We found the lowest values of biomass BMVmod and cover CoV of bilberry under pure beech canopy. This decrease, compared to spruce was approximately fourfold on area M and on area R only ~ 15 % of the biomass and ~ 12 % of the cover could be found. In study area S, quadrats under beech canopy had no bilberry – the small amount of BMVmod is an artefact of the regression model. In the beech area of S, outside of the quadrats, a few scattered bilberry plants were observed. The two parameters height (HeV) and mean shoot length of the three longest shoots SLVmax were strongly correlated (Tab. 1, Spearman's R = 0.95) and do not differ much between the three areas under the spruce canopy (HeV ~ 22–25.5 cm, SLVmax ~ 39–42 cm). The decrease of HeV and SLVmax along the spruce/beech gradient was high – almost 50 % – however was not (R) statistically significant on all areas due to a high variability (Fig. 2). Similar results were found for the mean of the three thickest basal diameters (BDVmax, Fig. 2), which is an indication of the age of the ramets (Flower-Ellis 1971, p 13). The thickest diameters (~ 5 mm) were found under spruce at areas M and S.

3.2 The influence of light on the vitality of bilberry

In this study we found no statistical evidence that light plays a significant role in the vitality of bilberry:

1. The light conditions were quite different within each area and with different tree species in the canopy (Fig. 3), and the vitality of bilberry was clearly related to tree species (Fig 2). In areas M and R the spruce quadrats received more light than did the mixed-wood and beech quadrats, while on area S the beech quadrats got the most light followed by spruce and spruce/beech mixed-wood quadrats. The spruce quadrats in area M had the most radiation reaching the ground (~ 23 % total light, Fig. 3), followed by the beech quadrats on area S (~ 18 %); the remaining areas received around 11 to 15 % of the total light reaching the canopy (Fig. 3).
2. We found only very little evidence for a relationship between light supply and the vitality parameters of bilberry (Tab. 1): Only diffuse light was weakly correlated with bilberry biomass. Also, the interpretation of the PCA did not indicate there was a strong relevance of light and canopy cover on the vitality attributes of bilberry because the vectors for the light parameters were almost vertical with the vectors for the vitality of bilberry (Fig. 1).

Looking only at the pure spruce quadrats excluding the influence of beech (Tab. 3), there was only a weak correlation between diffuse light with BMVmod (Spearman's R = 0.4). The other light and vitality indicators were not correlated.

3.3 Soil effects on the vitality of bilberry

We found no indication that soil pH had an influence on the vitality of bilberry. Thus, there were no significant correlations between any vitality indicators and soil pH, neither for the complete dataset (Tab. 1) nor for the pure spruce quadrats (Tab. 2). The medians of the soil pH (Fig. 4) varied from 3.08 (beech quadrats at area R) to 3.70 (beech quadrats at area M) indicating acidic conditions and low base saturation in the iron buffer range (Scheffer et al 2002). We found no statistical evidence for a relationship between mineral soil pH and tree species cover (Tab. 1). At study area S, soil pH was significantly higher for the beech quadrats compared to the spruce and mixedwood quadrats, whereas at area M the differences were not significant, and at area R the spruce quadrats had a significantly higher soil pH. On the areas M and S, on the gneiss bedrock, the soil pH was a little higher (3.40–3.74) compared to area R on granite (3.08–3.25) (Fig.4). The weight, thickness and structure of the organic layers appear to be rather specific for each area and there was no indication of any influence by tree species because there were no significant differences (Fig. 4) and no correlations with the cover of the particular tree species (Tab. 1). The mass of the organic layer was strongly correlated with lower soil pH (Spearman's R = -0.77, Tab. 1) and additionally by a comparison of the dry weight means of the organic layer and the medians of the soil pH (Fig. 4) for the particular stands. Area R, with the lowest soil pH values, had the highest mass for organic layers (3887 g/m² in beech quadrats; 4096 g/m² in spruce quadrats), while in area M, with the highest soil pH, the mass of the organic layer ranged between 424 and 712 g/m². In area S, soil pH and the mass of the organic layer was intermediate. Even though there were big differences in the organic layers on the spruce quadrats between the three areas, the vitality indicators of bilberry remained similar (Fig. 4).

3.4 Model of bilberry vitality

The results in Tab. 3 indicate that model 1, including only stand type as a factor (fSpecies) with an Akaike weight of 0.68 was the best of the four candidate models. Only the first two models (including fSpecies) had a reasonable level of

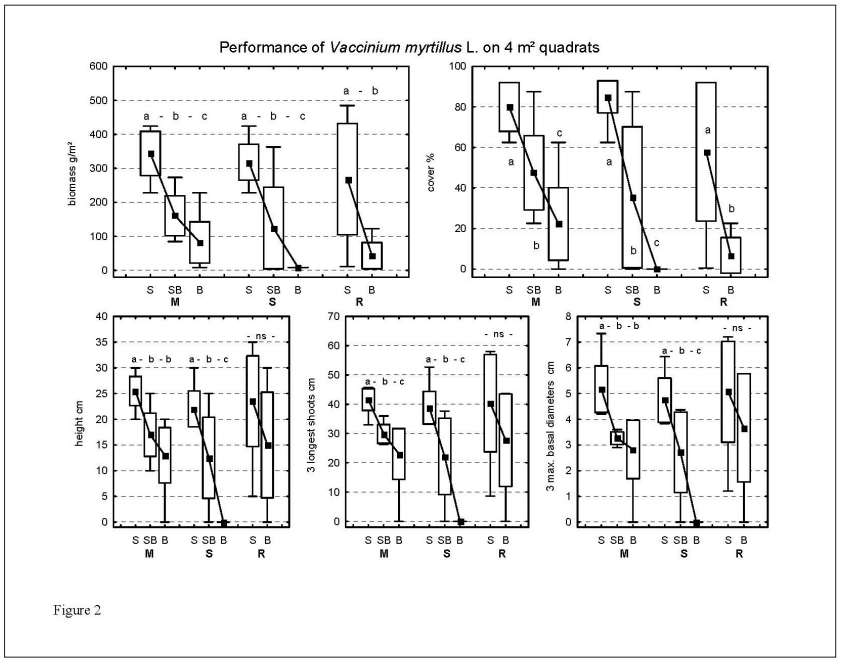

Fig. 2: *Arithmetic mean, standard deviation, minimum and maximum (n = 10) of vitality variables of* Vaccinium myrtillus *L. on 2 m · 2m plots grouped by area (M, S, R) and tree species composition (S = spruce, B = beech). Different letters indicate significant differences p < 0.05 within each site (sites M, S, global Kruskal-Wallis H-test, if significant and site R, pair wise tested with Mann-Whitney-U-test).*

Abb. 2: Arithmetische Mittel, Standardabweichungen, Minima und Maxima (n = 10) der Vitalitätsindikatoren (Variablen) von *Vaccinium myrtillus* L. auf 2 m x 2 m großen Probeflächen, gruppiert nach den Gebieten M, S, R sowie der Baumartenzusammensetzung (S = Fichte, B = Buche). Unterschiedliche Buchstaben zeigen jeweils signifikante Unterschiede p < 0.05 innerhalb jedes Gebiets (für das Gebiet M, S allgemeiner Kruskal-Wallis H-Test, wenn signifikant;für das Gebiet R paarweiser Mann-Whitney-U-test).

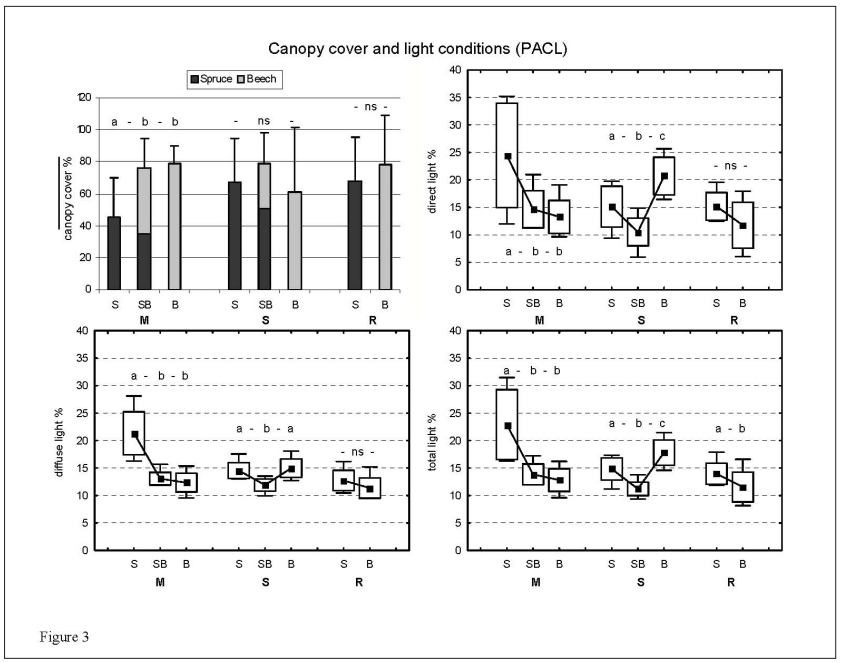

Fig. 3: *Arithmetic mean, standard deviation, minimum and maximum (n = 10) of canopy cover and direct, diffuse and total light grouped by area (M, S, R) and tree species composition (S = spruce, B = beech). Different letters indicate significant differences p < 0.05 within each site (sites M, S, global Kruskal-Wallis H-test, if significant and site R, pair wise tested with Mann-Whitney-U-test).*

Abb. 3: Arithmetische Mittel, Standardabweichungen, Minima und Maxima (n = 10) der Deckung des Kronendaches sowie der direkten, diffusen, indirekten und totalen Einstrahlung, gruppiert nach den Gebieten M, S, R sowie der Baumartenzusammensetzung (S = Fichte, B = Buche). Unterschiedliche Buchstaben zeigen jeweils signifikante Unterschiede p < 0.05 innerhalb jedes Gebiets (für das Gebiet M, S allgemeiner Kruskal-Wallis H-Test, wenn signifikant; für das Gebiet R paarweiser Mann-Whitney-U-test).

support (Delta i < 10) as a rule of thumb a delta < 2 suggests substantial evidence for the model (Tab. 3). The simple model (fSpecies) was 2.1 times more likely to be the best model than model 2 (fSpecies + totCover + PACL_total + pH) based on the evidence ratio (0.6773/0.3221). But the weight of the simple model was wi > 0.90 (Burnham & Anderson 2002), therefore it is not recommended that the conclusions should be based only on the best model. Looking not only at the models, but also at the individual variables (Tab.4), we recognized that the cover type pure beech (fSpecies2) and also the mixture of beech and spruce (fSpecies3) had a high negative impact on the biomass of bilberry compared to the baseline cover type pure spruce (fSpecies1 – not in the model because it is a factor and treated as a baseline). Also a slightly higher pH seemed to have a positive effect on bilberry biomass, but it has to be taken into consideration that there was a high

Tab. 2: *Spearman's rank correlations for light and soil parameters of estimated and measured site characteristics and vitality variables of* Vaccinium myrtillus *L. for all plots under spruce canopy (n = 30) * p < 0.05, ** p < 0.01 t-test significance level.*

Tab. 2: Spearman's Rangkorrelationen der Licht- und Bodenparameter der geschätzten und gemessenen Standortsparameter und Ausprägung charakteristischer Eigenschaften (Variablen) von *Vaccinium myrtillus* L. für alle Probeflächen unter Fichte (n = 30) * p < 0.05, ** p < 0.01, T-Test- Signifikanzniveau.

n = 30	**height[c]**	**shoot length[c]**	**basal diameter[c]**	**cover[c]**	**biomass[c]**
canopy cover[a]	-0.20	-0.12	-0.08	0.13	-0.08
direct light[b]	0.15	0.02	0.08	0.17	0.22
diffuse light[b]	0.35	0.24	0.17	0.33	0.40
total light[b]	0.25	0.13	0.11	0.25	0.30
pH mineral soil	0.28	0.30	0.21	0.26	0.30
mass organic layer	0.07	0.14	0.15	-0.24	-0.07

a tree layer, b percent above canopy light, c of *Vaccinium myrtillus* L. on 2m · 2 m plots.

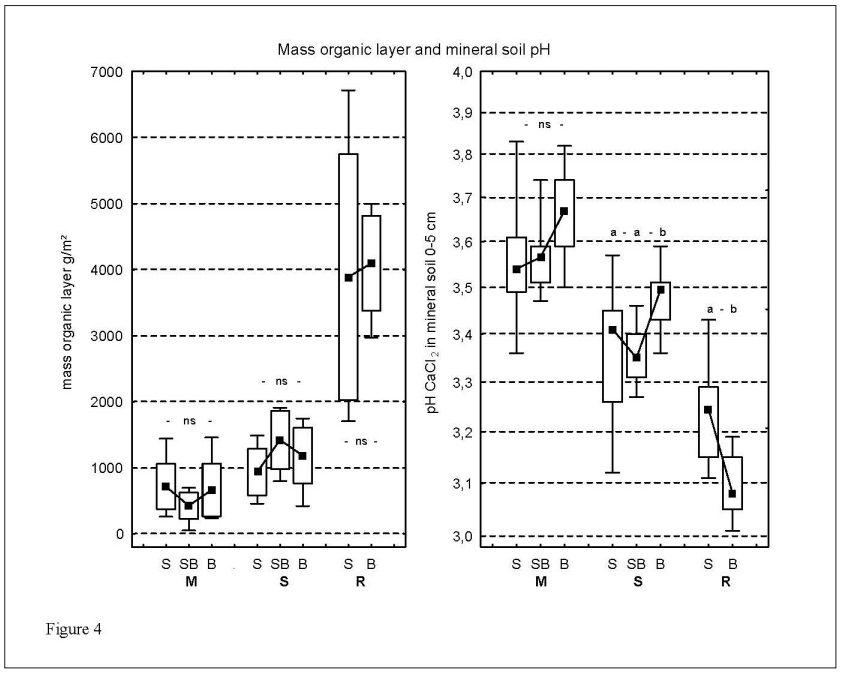

Fig. 4: *Arithmetic mean, standard deviation, minimum and maximum (n = 10) of mass of the organic layer and median, 25 % and 75 % quartiles of soil pH in CaCl2 0–5 cm mineral soil grouped by area (M, S, R) and tree species composition (S = spruce, B = beech). Different letters indicate significant differences p < 0.05 within each site (sites M, S, global Kruskal-Wallis H-test, if significant and site R, pair wise tested with Mann-Whitney-U-test).*

Abb. 4: Arithmetische Mittel, Standardabweichungen, Minima und Maxima (n = 10) der Masse der organischen Auflage sowie Mediane, 25 % und 75 % Quartile des pH-Wertes im mineralischen Oberboden (0 – 5 cm Tiefe), gemessen in CaCl2, gruppiert nach den Gebieten M, S, R sowie der Baumartenzusammensetzung (S = Fichte, B = Buche). Unterschiedliche Buchstaben zeigen jeweils signifikante Unterschiede p < 0.05 innerhalb jedes Gebiets (für das Gebiet M, S allgemeiner Kruskal-Wallis H-Test, wenn signifikant; für das Gebiet R paarweiser Mann-Whitney-U-test).

Tab. 3: *Candidate models to estimate bilberry biomass, including the value of the maximised log-likelihood function (Max. log), the number of estimated parameter (K), Model selection criterion (AICc), the differences compared to the best model (Delta i), and the Akaike weights (weight i).*

Tab. 3: Modelle zur Schätzung der Biomasse der Heidelbeere, einschließlich Angaben zur maximierten log Wahrscheinlichkeitsfunktion (Max. log), der Anzahl geschätzter Parameter (K), der Wert zur Entscheidung für ein Modell (AICc), die Differenzen zum Vergleich mit dem besten Modell (Delta i), und das Akaike Gewicht (weight i).

model nr.	model	max. log (LL)	K	AICc	Δ_i	weight $_i$
1	tree species type	-468	5	947	0.00	0.68
2	tree species type + canopy cover + total PACL + pH mineral soil	-465	8	949	1.48	0.32
3	cover beech	-488	4	985	37.40	0.00
4	cover beech + total PACL + pH mineral soil	-486	6	986	38.53	0.00

K: Parameter count includes intercept and variance.

Tab. 4: *Parameter estimate (regression coefficients) and standard error by model and the multimodel averages based on AICc.*

Tab. 4: Parameterschätzung (Regressionskoeffizienten) und Standardfehler im Modell sowie die Mittelwerte des Multi-Modells, basierend auf AICc.

model	model ranking	intercept (SE)	cover beech	tree species type 2 (beech)	tree species type 3 (mixture)	canopy cover	PACL[b] total	pH mineral soil
tree species type[a]	1	310.06 (18.53)		-265.54 (21.44)	-172.44 (24.53)			
tree species type + canopy cover + total PACL + pH mineral soil	2	-112.31 (169.94)		-269.45 (22.74)	-176.98 (27.25)	0.24 (0.35)	0.66 (2.46)	117.04 (50.77)
cover beech	3	259.70 (21.60)	-2.55 (0.32)					
cover beech + total PACL + pH mineral soil	4	-11.61 (233.33)	-2.39 (0.33)				4.13 (2.86)	60.07 (69.46)
Model average (unconditional SE)			-2.49 (0.33)	-266.8 (21.95)	-173.91 (25.52)	0.24 (0.35)	0.66 (2.46)	117.04 (50.77)

Unconditional SE: not restricted to a single best model but based on the whole set of models, a the category defined by tree species in the canopy, b percentage above canopy light.

initial variability. The other variables seemed to have a very low effect but could be either positive or negative.

4 Discussion

With our results we could confirm our first hypothesis and show that bilberry (*Vaccinium myrtillus*) clearly performs better under spruce than beech forest and that in the ecotone its vitality was intermediate. Regarding the second hypothesis,our analyses show that soil pH, humus and light parameters either had low or no considerable effects on the vitality of bilberry.

4.1 Impact of environmental factors modified by the tree species on the vitality of bilberry

We hypothesized that one reason for the tree species effect on the vitality of bilberry could be the different light conditions in the understory. But we found no clear statistical evidence for light as an important factor for the observed abrupt decline of bilberry under beech. However, there is some positive evidence that (diffuse) light affected the vitality of bilberry in our study (Tab. 1, Tab. 2). One reason for this could be that we only studied the effects of light within a very narrow light gradient under closed forest. Although there was not a high variability between our plots, our results were in accordance with Nielsen et al. (2007). However, when wider light gradients were considered, the result was a positive relationship between relative light transmittance and bilberry cover (Weckesser 2003). Other authors also stress the importance of light for bilberry vitality: in Germany (Ellenberg 2001), Scotland (Hester et al. 1991b, Parlane et al. 2006) and particularly in northern forests (Kuusipalo 1983, Karlsson 1989, Mäkipää 1999).

We found no clear trend that showed an impact of soil pH, or the mass of the organic layer on the vitality of bilberry. The two variables were highly negatively correlated, site specific and more related to the geological substrate, but not to the dominant tree species. Contrary to our findings, other central European studies report that soil in spruce forests was more acidic and had higher accumulations of humus compared to beech (Teuscher 1985, Lücke & Schmidt 1997, Augusto et al. 2003, Weckesser 2003, Jansen et al. 2005, Podrázský & Vieweg 2005). In agreement with our findings were those of Gruselle (2009). She found no pattern in the mineral soil pH and other soil chemical properties related to an overstory of either spruce, beech or a mixture of the two over a broad range of sites in the Black Forest and the Swabian Jura. Although beech litter and organic layers tended to have higher base saturation percentage, the conclusion was that on these acidic sites beech played only a minor role as a base ion pump (Gruselle 2009). Mareschal et al. (2010) found that even fine soils under spruce had a higher pH but a lower CEC compared to beech.

Generally bilberry occurs on forest soils with low pH, but its ecological response may change over large geographic distances and between climatic regions (cf. relative site constancy). Under boreal conditions the competition is different compared to temperate forests because the evergreen dwarf shrubs *Calluna vulgaris, Empetrum nigrum* and *Vaccinium vitis-idaea* have higher vitality under a shorter vegetation period and on the most acidic and N-poor sites. A reason for this could be that bilberry has higher nutrient demands because of its deciduous nature (Salemaa et al. 2008). When considering only deciduous forests with oak and beech, bilberry was found to be limited to the most acidic sites along a pH gradient from podsols to cambisols in southern Sweden (Brunet et al. 1996). But on sites dominated by Norway spruce, the pH of the humus was found not to have any great influence on bilberry vitality while an increased amount of N in humus showed a negative effect (Nielsen et al. 2004).

Many studies point out that forest liming and fertilisation result in a decrease of bilberry abundance and/or cover due to an increase in competition from herbs (e. g. Schornick 1990, Becker 1992, Kellner 1993, Höcke 2006, Strengbom & Nordin 2008). However, there is some evidence that the addition of N and calcium on poor sites, those nutritionally below the optimum required by bilberry, have either no or even a slightly positive effect on bilberry (e.g. Schornick 1990, Hester et al. 1991b, Kellner & Mårshagen 1991, Kraft 1999, Mäkipää 1999, Höcke 2006).

We conclude that the soil chemical properties at our sites match conditions close to the optimum for bilberry. It is likely that a broader fertility gradient, indicated by changing C/N-ratios, would reveal additional effects on the vitality of bilberry.

4.2 Bilberry vitality in relation to spruce and beech

The overall result of our assessment, examining the factors potentially influencing bilberry vitality, revealed that the most important factor was the tree species in the canopy layer. This general finding, that bilberry vitality is different in spruce and beech stands, was also observed in previous studies (Lücke & Schmidt 1997, Gärtner & Reif 2005, Weckesser & Schmidt 2007) but bilberry occurs naturally in oak and beech forests where the soil pH is low (Brunet et al. 1996, Godefroid et al. 2005). On the other hand, Ewald (2000) found that in montane mixed forests of the calcareous Alps, bilberry cover depended on soil quality rather than on canopy composition. Our assumption that the vitality of bilberry under the two tree species would be related to soil chemistry and light environment was not confirmed. Thus, we suggest that specific conditions linked to beech overstory are responsible for the abrupt decline of bilberry vitality under beech (see also Ewald et al. 2014).

One possible reason is that on acidic, nutrient-poor sites beech forms dense mats of roots in the upper soil layers which – in combination with the other factors of low light supply and litter fall – eliminates all vascular plants on the ground ("F a g e t u m n u d u m"). Another possible reason is that broadleaf litter, due to its physical and chemical properties, has a negative influence on the ground vegetation layer (Sydes & Grime 1981a, Facelli & Pickett 1991, Xiong & Nilsson 1999, Barbier et al. 2008): Leaf litter has been reported to be a physical barrier for conifer seedlings (Koreleff 1954, Gregory 1966, Williams et al. 1990, DeLong et al. 1997, Simard et al. 2003). An important property of successful forest understory species might be the ability of their shoots to penetrate leaf litter (Sydes & Grime 1981) however this ability might not be so decisive for bilberry as it is a perennial dwarf shrub. Compacted snow has been shown to have a negative effect on conifer seedlings (Gregory 1966, DeLong et al. 1997) and is therefore likely to be the case with bilberry. This could explain the absence of bilberry under the deciduous beech trees where snow cover accumulates.

Also the chemical properties of beech litter might contribute to the low vitality of bilberry. Beech litter tends to have more base cations compared to spruce litter (e. g. Gruselle 2009). Koojman & Cammeraat (2010) suggest that the low species richness/diversity of beech forests compared to other broad-leaved forests is related to their relatively recalcitrant litter and conclude that litter quality is an important factor controlling the ecosystem. Additionally, there could be allelopathic effects of *Fagus* litter. The litter of the closely related American Beech (*Fagus grandifolia* Ehrh.) was found to be responsible for the reduced growth of *Acer saccharum* Marsh. seedlings in a greenhouse experiment (Hane et al. 2001). Kuiters & Sarink (1986) showed that dried litter of *Fagus sylvatica* contains 35 to 38 times more water soluble phenolic compounds compared to *Picea abies*; namely 40–44 % of beech litter phenols are cinnamonic acids known to inhibit plant growth. Thus, European beech litter compounds might also be a factor in the decline of bilberry observed in our study. Interestingly, many studies report an allelopathic effect for bilberry and other dwarf shrubs because when their leaf extracts where applied, they affected the germination and early development of some tree species (for example Norway spruce e. g. Jäderlund et al. 1996, 1997, Mallik & Pelissier 2000). Chemical compounds in beech litter could have a negative effect on bilberry directly or indirectly through impacts on mycorrhiza (e. g. Souto et al. 2000). This aspect of *Fagus sylvatica* litter has not yet been very well studied even though it might reveal interesting insights into functional relationships in beech forests.

4.3 The impact of forest management – historic and current

Throughout Europe, including the Black Forest, many pastures and fields have been converted to forests in the last 200 years (Manegold 2007, Bode 2005, Hug 2000). Historically, all of our study sites, although forests today, were probably once pastures. If browsing pressure was low, bilberry might have benefited from the pastures. This has been shown to be the case on pastures that experienced low browsing intensity in the southern Black Forest (Bode 2005). Bilberry seems to have a relatively high tolerance to the browsing of red deer (Baines et al. 1994, Hegland et al. 2005, 2010, Melis et al. 2006) and recovers rapidly following intense browsing by sheep (Pigott 1983). In the Vosges Mountains in France high abundances of bilberry were only found in forests which formerly were pastures (Koerner et al. 1997). In the Southern Black Forest Manegold (2007) found significantly less bilberry in forests established after 1950 on former pastures while all other former land use categories like forests, pastures and meadows afforested before 1900 show higher abundances today.

At our Märchenwald site (M**)** the beeches have crooked stems because during early growth they were browsed by cattle. This particular site shows the best bilberry vitality out of all our beech sites; it could have formerly been a pasture and then abandoned. Bilberry vitality has also been reported to increase after clear cutting by Nielsen et al. (2007) who go on to stress the importance of clear cutting for the maintenance of the species in intensively managed forests in southern Norway.

There are many good reasons to increase the deciduous tree species component in conifer dominated forests (e. g. Fritz 2006, von Teuffel et al. 2005). However, it is important for the management of species habitats, e. g., capercaillie (*Tetrao urogallus* L.), to control the proportion of beech because a minimum of 15–20 % cover of bilberry is suggested for capercaillie habitats (Schroth 1991, Baines et al. 2004).

4.4 Conclusions

We were able to show that beech overstory has a strong negative influence on the vitality of bilberry while neither light, soil pH, nor the mass of the organic layer could explain this decline. We considered the physical properties of beech litter and eventually its allelopathic effects as the most likely explanation. We see our results as a sound base for further research on bilberry. In field and greenhouse experiments the effects of leaf litter, fertilisation and light have to be separated.

Today there are many good reasons to increase the stability of conifer dominated forests by introducing other tree species (e. g. Fritz 2006; von Teuffel et al. 2005). In regions where fir occurs naturally (*Abies alba*) its promotion would have many advantages compared to beech because it is evergreen, sheds its needles continuously, and is associated with conifer mycorrhiza. A high proportion of fir would continue the existing habitat tradition of conifer-rich mountain regions. This is particularly important on the “boreal” boundary of species and habitats in times of climate change (Hampe & Petit 2005). It is important for the management of species habitats, e. g., capercaillie (*Tetrao urogallus* L.), to control the proportion of beech because a minimum of 15–20 % cover of bilberry is suggested for capercaillie habitats (Schroth 1991, Baines et al. 2004).

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Adress of authors:

Dr. Carl E. Höcke, MSc Juliane Spiegelhalter, Dr. Stefanie M. Gärtner (corresponding author), Prof. Dr. Dr. h.c. Albert Reif
Chair of Site Classification and Vegetation Science
Institute of Forest Sciences
Faculty of Environment and Natural Resources
Albert-Ludwigs-University Freiburg
Tennenbacher Straße 4
79085 Freiburg, Germany

E-Mail-adresses:
Dr. Carl E. Höcke, E-Mail: carl.hoecke@gmx.de
Juliane Spiegelhalter, E-Mail: j_spiegel@web.de

Dr. Stefanie M. Gärtner, Corresponding author,
Tel.: +49 761 203 3672;
Fax: +49 761 203 3781
E-Mail: stefanie.gaertner@waldbau.uni-freiburg.de

Prof. Dr. Dr. h.c. Albert Reif
E-Mail: albert.reif@waldbau.uni-freiburg.de