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Regeneration niches of Norway spruce (*Picea abies* [L.] Karst.) saplings in small canopy gaps in mixed mountain forests of the Bavarian Limestone Alps

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Abstract Natural regeneration measurements are the main silvicultural objective in overaged protective forests of the Bavarian Limestone Alps. While manifold problems with these stands, especially the impact of browsing, are widely recognised, the regeneration niches of Norway spruce (*Picea abies* [L.] Karst.) are insufficiently known. The purpose of this study was to determine favourable combinations of site factors for the development of spruce in small, unfenced canopy gaps, located on *Aposerido-Fagetum caricetosum albae* forest sites. We recorded the occurrence of spruce saplings (as dependent variable) and of six site factors (as independent variables) on 480 0.5 m^2-subplots. In addition, we estimated the coverage of six acid adapted plant species to determine correlations with the humus depth. A binary logistic regression analysis was used to predict the probability of the occurrence of a spruce sapling in dependency of the different site factors. Supported by other studies, we assumed that the supply of solar radiation was adequate for the sufficient regeneration of spruce within the canopy gaps. Other site factors significantly determined the regeneration niches of spruce saplings. More spruce saplings were found near hindrances and on rough surfaces than would be expected from a random occurrence of saplings. These microsite types may have characteristics, especially protection against snow gliding that promotes spruce establishment. A calculated "hindrance index", which accounted for the number, and the distance of surrounding hindrances might be a good specific value to describe the influence of hindrances on steep slopes. The sapling establishment decreased on thin humus layers. Our assumption for the sites was that thick organic layers might represent a good seedbed for spruce. Decayed dead wood was scarce, but was exceedingly favoured by spruce saplings. Results obtained suggest that the natural regeneration establishment of spruce on steep slopes can be successfully influenced by site factors which inhibit the influence of snow gliding. According to a "positive microsite" concept, we recommend for artificial regeneration measurements with spruce, microsites close to hindrances (e.g. stumps, downed trees) and *Vaccinium myrtillus* as a predictor for thick, acid humus layers.

Keywords *Picea abies* · Regeneration niches · Safe sites · Dolomite · Bavarian Limestone Alps

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Introduction

The mountainous regions of the Bavarian Limestone Alps were primarily covered by mixed Norway spruce (*Picea abies* [L.] Karst.)–European Beech (*Fagus sylvatica* L.)–Silver fir (*Abies alba* Mill.) forests, which belonged to the vegetation types *Aposerido-Fagetum caricetosum albae* and *A.-F. c. ferruginea* on moderately dry and moderately fresh sites (Ewald 1997). Since the seventeenth century, well structured, mixed virgin forests were used for salt works and iron smelting by clearcutting and were often replanted with spruce (Zierhut 2003; Meister 1969a). In addition, the increased influence of hoofed game browsing, since the middle of the nineteenth century, has resulted in a substantial decrease of fir and broadleaf species (Bernhart 1990). Currently, many initially mixed forests have been replaced by spruce dominated or pure spruce stands (Meister 1969b).

In many cases, these human influenced secondary forests are characterised by a low tree density (Ammer 1996b) and a high crown transparency, especially on dolomite sites (Ewald et al. 2000; Haupolter 1999). Therefore, many primary public functions of these forests such as avalanche and rockfall protection, soil conservation or flood control are endangered (Kräuchi et al. 2000; StMELF 1997; Meister 1969b). Establishing natural regeneration is the main silvicultural objective in these mostly overaged forests (Rothe and Borchert 2003). In contrast, the continuity of protective functions of the forests are endangered via the absence of natural regeneration. Whilst the regeneration of broadleaf species and fir in the Limestone Alps is seriously hindered by ungulates until this day, spruce is affected to a less extent by browsing (Ammer 1996a). However, the regeneration ecology of spruce—especially the effects of microsites on drier, south facing dolomite slopes—is not sufficiently understood. As a result of the positive influence on the snow cover, spruce is the most important tree species in protective forests (StMELF 1997). Artificial regeneration measurements in reforested areas on dolomite sites are often unsuccessful and planted spruces are characterised by low growth rates combined with inadequate tree nutrition especially for nitrogen and phosphorous. On the other hand, natural regenerated spruces on thick organic layers are in a sufficient nutritional status and show higher growth rates (Baier 2004). In addition, we observed that the spruce natural regeneration within canopy gaps or in clearings after windthrow appeared in clusters.

Early establishment of plant species depends on ‘‘safe sites’’ (Harper 1977) and it is well known that conifer seedlings preferably establish on specific substrates on the highly heterogeneous forest floor (Mori et al. 2004; Brang et al. 2003; Brang 1998; Simard et al. 1998). With small seeds, spruce is more substrate-restricted than other tree species (Knapp and Smith 1982). Beside substrates as a rooting zone, hindrances and/or the surface shapes which restrict the snow movements or decrease the persistence of snow cover are necessary for an unhindered development of spruce regeneration on steep slopes (Kupferschmid-Albisetti 2003; Senn and Schönenberger 2001; Ott et al. 1997; Mößmer et al. 1994).

Various methodologies are in use to measure the spatial distribution of regeneration on a study site. Common indices are the dispersion index according to Bouxin and Gautier and the aggregation index according to Clark and Evans (Ammer et al. 2004). A distance dependent method which provides information about the heterogeneity of the spatial distribution is the zero-area method according to Cox (Ammer et al. 2004; Cox 1971). Currently, the zero-area control method which is based on the Poisson distribution was used to identify unfavourable sites for natural regeneration (Olmez and Yahyaoglu 2004). To account for our observations of clustered spruce saplings, which indicate favourable combinations of site factors for the development of spruce, we used a binary logistic regression analysis: this method allows one to predict the probability of a dependent variable (e.g. occurrence of a spruce sapling) in dependency of different independent variables (e.g. site factors) (Brang et al. 2003; Knoke 2003a).

It is well known that spruce is the strongest light-depending tree species in the mountainous forests of the Bavarian Limestone Alps and therefore the regeneration ecology of spruce is strongly influenced by stand structure like basal area or canopy converge (Ammer 1996b). This study therefore aims at analysing and quantifying the influence of relevant site factors others than light, which have a significant impact on the presence or absence of spruce saplings on the south exposed, steep mountainous slopes of the Bavarian Limestone Alps. Thus, we deduced recommendations for forest practice in order to enhance the regeneration niches (‘‘safe sites’’) for successful natural and/or artificial regeneration of spruce.

Materials and methods

Study sites

In order to insure an adequate and more or less homogeneous supply of radiation, we searched for similar shaped and wide canopy gaps with initial spruce natural regeneration as study sites. In many cases, active

Table 1 Location parameters, tree composition, and soils of the study sites

Forest district/forest stand	Location	Elevation (m asl)	Inclination	Aspect	Tree composition of the mature stand	Soils[a]
X Weiße Valepp/6 Äußerer Stolzenberg a[1]	47°37′50″N, 11°52′10″E	960	25°	SSW	Spruce–beech stand with some maple	Rendzic leptosols, eutric leptosols
X Weiße Valepp/7 Innerer Stolzenberg d[2]	47°37′42″N, 11°52′45″E	950	20°	SSW	Spruce–beech–silver fir stand	Rendzic leptosols, eutric leptosols, chromic cambisols
XVII Lappberg/3 Langenberg a[1]	47°37′12″N, 11°47′07″E	950	25°	SSE	Spruce–beech stand with some silver fir	Rendzic leptosols, eutric leptosols
XVIII Rinneneck/2 Rinneneck d[1]	47°36′19″N, 11°49′40″E	1020	35°	S	Spruce–beech–silver fir stand with some maple	Rendzic leptosols, eutric leptosols
XXIX Sonnberggehäng/1 Sonneneck c[1]	47°37′16″N, 11°41′55″E	870	25°	S	Spruce–beech stand with some maple	Rendzic leptosols, chromic cambisols
XXIX Sonnberggehäng/2 Rothmartelgraben a[1]	47°37′18″N, 11°41′06″E	1,100	30°	S	Spruce–beech–silver fir stand with some maple	Rendzic leptosols, eutric leptosols

regeneration measurements in old protective forests are considered to be detrimental to stand stability. Therefore, it was difficult to find such small cutting areas. After the investigation of different forest districts, we selected six comparable small canopy gaps as study sites in protective forests situated in the area of the forest district Kreuth, near lake Tegernsee (Table 1). The slopes were S-, SSW-, to SSE-exposed and were relatively steep (20–35°). All the soils derived from dolomite (‘‘Hauptdolomit’’), a very pure (low clay mineral content) alpine triassic (Nor) sediment ($CaMg(CO_3)_2$), with a porous bedrock. Hauptdolomit is the main soil forming parent material of the Bavarian–Tyrolian Limestone Alps (Bayerisches Geologisches Landesamt 1981). According to the FAO classification, the soils belonged to the shallow type rendzic leptosols (Buol et al. 1997). In addition, deeper developed chromic cambisols appeared within the sites ‘‘Weiße Valepp’’ and ‘‘Sonnberggehäng’’, which were situated close to the valley. The chromic cambisols derived from loose detritus, which was preferentially deposited at the toe of the slope. Except for the site ‘‘Sonnberggehäng’’, eutric leptosols (humus layers > 15 cm up to 35 cm) were also described.

The ‘‘alpid’’ climate of the northern Alps is cool, with a high annual variation in temperature and high precipitation (Walentowski et al. 2004). The average annual temperature (interpolated according to Fliri 1975) of the study sites varied between 5.5°C (870 m asl) and 4.5°C (1,100 m asl). The average annual precipitation (interpolated according to Enders 1979) varied between 1,812 mm (870 m asl) and 1,922 mm (1,100 m asl), with a clear summer maximum. All forest sites belonged to the vegetation type *Aposerido-Fagetum caricetosum albae* (Ewald 1997).

Spruce was the dominating tree species with various proportions of beech, fir, some Sycamore maple (*Acer pseudoplatanus* L.), several Chess apple (*Sorbus aria* L.) and Yew trees (*Taxus baccata* L.). The estimated ages of the largely even-aged mature forest stands varied within the range of 150–250 years. The isolated, unfenced canopy gaps were east–west orientated and slot-shaped (approximately rectangles along the contour line with 40–60 m length, and 10–20 m width). The canopy openings resulted from irregular, 20- to 30-year-old salvage cuttings probably after bark beetle infestation, and showed initial spruce natural regeneration. Natural regeneration of the other tree species (mainly beech and maple) was frequent within the unfenced gaps, but as a result of hoofed game browsing they seldom obtained the height of saplings (20 cm). Noticeable was the lack of coarse woody debris within the gaps. Due to the older mature stands, coarse, visible decayed woody debris or old stumps (decay class IV and V, according to Sollins 1982) from the former parent forest were scarce. The main structural elements on the forest floor were the stumps of trees harvested for the bark beetle control or for thinning measurements, at which the logs were removed from the sites.

Sampling design

Our sampling design focused on the occurrence of spruce saplings within the canopy gaps. The choice of saplings offered a retrospective view because we were able to clarify the influences of site factors which enable survival from the emergence of seedlings until this later phase of growth. Saplings were defined as spruces higher than the mean height of competing vegetation of 20–200 cm (Brang et al. 2004; Ott et al. 1997).

Within each canopy gap, a representative rectangular plot (50 m long and 10 m wide along the contour line) was chosen in order to sample typical situations for regeneration. Within each plot, 40 0.5 m^2-subplots (shape: circles) were placed systematically (2 rows with a distance of 5 m and a distance of 2.5 m within a row), and all spruce saplings per subplot were counted. This systematic approach resulted in sampling many sites without spruce regeneration. Therefore, we additionally chose a non-systematic, selective survey with 0.5 m^2-subplots (which were placed exactly on microsites with spruce saplings) to characterise sites with spruce saplings. Because of this second approach, we started in the centre of the 50 m×10 m plot and searched for the nearest spruce > 20 cm. Thereafter, we chose the next closest sapling. If more than one spruce > 20 cm occurred, the tallest sapling formed the subplot centre. This procedure was repeated until 40 replicates were obtained per canopy gap. The description of unfavourable sites combined with calculated random subplots for favourable sites is common in ornithology, and enables one to detect important habitat structures for bird species (Sachslehner 1993). With this procedure, we described in total 210 subplots without spruce saplings and 270 subplots with spruce saplings (30 resulted from the systematic approach) over the 6 studied canopy gaps. We collected the data in July and August 2003.

Description of site variables

Within each 0.5 m^2-subplot (with or without spruce saplings), seven site parameters in metric values and nominal scales were recorded. The total coverage of ground vegetation (%) was estimated. The mean thickness [centimetre (cm)] of the organic layer was measured with a humus cube and thick layers with a Pürckhauer-soil-probe. Apart from the humus thickness, we made a note of old, highly decayed stumps in the subplot.

With regard to other studies, we presumed that the hindrances and their distance to the spruce saplings may play an important role for spruce regeneration establishment on steep slopes (Ammer 1990; Gampe 1989). Hegyi (1974) described a ‘‘competition index’’ which considers the number of surrounding trees, the diameter breast height of the central tree and of the neighbour trees and the tree distances. We also accounted for the number of surrounding hindrances, by measuring the nearest vertical distances (cm) between the root collar of the spruce sapling to four hindrances for a maximum distance of 3 m. Hindrances were e.g. stumps, uprooted stumps, rocks and fallen snags. Thereafter, we calculated a "hindrance index" with the formula:

$$H = \sum_{i=1}^{n} \frac{1}{\text{distance}_i + 1};$$

$H=[0;n]$ (n = number of hindrances; distance_i = distance [dm] between the root collar of the spruce sapling, or in subplots without spruce sapling between the circle centre to the hindrance. The more the distance decreases and number of hindrances increase, H increases.

Surface characters for the microsite (= 0.5 m^2-circle of the subplot) and the surrounding macrosite (= 30 m^2-circle) were addressed for an indirect detection of influences on the snow cover. Thus, the pooled categories of relief as terrace/mound (rough surface, low snow movement), channel/even ground (smooth surface, high snow movement), and depression (long snow persistence) were defined (Arbeitsgruppe Standortserkundung 1996).

As mentioned above, we assumed that the supply of radiation within the studied canopy gaps was adequate and not a limiting factor for the regeneration process of spruce. The effects of light on the annual growth rates of the spruces were of minor importance for our study. Thus, we estimated the coverage of saplings by canopy visually to account for situations of whether saplings occurred in the edge of the canopy gap. Visual estimates of canopy coverage can produce large amounts of data quickly, with a high relationship to plant growth (Brandeis et al. 2001). Canopy conditions were classified into three classes: dense (sapling was fully covered under canopy); loose (sapling was at crown edge or in a small gap with at the most one crown diameter); open (gap bigger than one crown diameter).

Acid humus layers are important sources for spruce nutrition under alkaline soil conditions (Baier et al. 2005; Baier 2004; Glatzel 1968). Therefore, we tried to evaluate plant species, which are able to indicate these situations. For our study, we used only plants, with a reaction-number ≤ 3 according to Ellenberg et al. (1991), which are naturally adapted to acid soil conditions. We extracted the six most frequent plant species from the vegetation database BERGWALD with 4,836 recordings, which were conducted in different vegetation types of the mountainous regions of the Bavarian Limestone Alps (Ewald 1997). Our objective was to deduce indicator plant species, which are easy to learn and to apply in forest practise. We used the following plant species in descending order of occurrence in the data set (in parentheses following the species name is the reaction-number/percent of occurrence in data set): *Vaccinium myrtillus* (2/53%), *Maianthemum bifolium* (3/28%), *Melampyrum pratense* (2/23%), *Huperzia selago* (3/21%), *Vaccinium vitis-idaea* (2/18%), *Lycopodium annotinum* (3/17%). And then we estimated the frequency of each plant species (%) per 0.5 m^2-subplot.

Statistical analyses

We decided to use a binary logistic regression analysis method to analyse the "spruce sapling" probability. The binary logistic regression analysis, as a structure searching statistical method, calculates the likelihood of an occurrence of a spruce sapling taller than 20 cm (as the dependent variable) as affected by different independent variables (Backhaus et al. 2003). This method is simple and robust and the SPSS 11.5 (SPSS Inc., Chicago, IL, USA) statistical program provides numerous diagnostical opportunities (RRZN 2001). This analysis is not based on multivariate normal-distributed independent variables and shares with metric and categorical variables (Backhaus et al. 2003). Therefore, the occurrence or absence of spruce saplings in the subplots and the nominal scaled site variables where coded as shown in Table 2. As a result of the dummy coding, the three nominal classes of independent variables were expressed by two new variables (Backhaus et al. 2003). Interdependencies among the independent variables were tested by the existence of correlations, and additionally by a multivariate regression analysis and the corresponding tolerance values ($1-R^2$) (Knoke 2003b). Then, we used the option "stepwise forward" of SPSS to select and introduce only significant ($P \leq 0.05$) variables into the model. Negative parameters of the logit-function reduce the probability of the occurrence of spruce saplings; in contrast positive parameters enhance the occurrence of

Table 2 Definition of classes of the variables used in the binary logistic regression analysis and in the discriminant analysis

Variable classes	Values in the binary logistic and in the discriminant analyses
Dependent variables:	
A spruce sapling occurred in the subplot	1
A spruce sapling did not occur in the subplot	0
Independent Variables:	
Coverage of ground vegetation	Metric
Hindrance index	Metric
Coverage of canopy	Dummy variables
Dense (sapling fully covered by canopy)	1/0
Loose (sapling at crown edge or in a gap smaller than one crown diameter)	0/1
Open (sapling was in a gap bigger than one crown diameter)	0/0[a]
Microsite (0.5 m^2-circle)	Dummy variables
Terrace/mound	1/0
Rib/depression	0/1
Channel/even ground	0/0[a]
Macrosite (30 m^2-circle)	Dummy variables
Terrace/mound	1/0
Rib/depression	0/1
Channel/even ground	0/0[a]
Humus thickness/organic layer	Dummy variables
Up to 3 cm	1/0
3.1–15 cm	0/1
> 15.1 cm	0/0[a]

[a]0/0 acts as reference value for the two new dummy variables

spruce saplings. Odd ratios were calculated to analyse the importance of the independent variables on the spruce sapling probability (Backhaus et al. 2003). Hence, the increase or decrease (depending on the algebraic sign) of the independent variables by one unit increases or decreases the spruce sapling probability by the odd ratio. The likelihood-ratio-test, the Hosmer-Lemeshow-test and the Nagelkerke R^2 were used as quality characteristics of the model (Backhaus et al. 2003; RRZN 2001). The success of classification is also important for the quality of the model. The classification test was carried out on the basis of those observations which were used to estimate the parameters of the model. In order to assess the validity of the model, standardised Pearson's residuals were calculated (Backhaus et al. 2003). They should have an approximate mean of 0 and a standard deviation of about 1 (Knoke 2003a). In order to asses the improvement of the model when additional variables were introduced, the reduction of the −2-log-likelihood-value (−2LL) was estimated (Knoke 2003a).

In a second approach, we used the discriminant analysis within SPSS which arrays a discriminant function on the basis of a linear combination of variables. This method assesses metric and nominal variables with the highest influence for separation of the selected groups (Backhaus et al. 2003). The premises for the discriminant function, multivariate normal-distributed independent variables, were not fulfilled. As a result of this, we used this method only as a supplement to the binary logistic regression analysis, although related results were regarded in support of the binary logistic regression analysis (Knoke 2003b). The standardised coefficients of the discriminant function and their algebraic sign indicated the importance of the independent variables. The quality of the model was estimated with the Wilks' Lambda (RRZN 2001).

To assess the relation between thickness of humus layers and coverage of acid adapted plant species, we used the parameter free Spearman rank correlation (Lozan and Kausch 2004).

Results

Area related results

Table 3 accounts for the 0.5 m^2-subplots in systematic grids of the six stands. The average density of spruce saplings was 4,200 stems/ha (height class 20–200 cm). The mean coverage of ground vegetation over all the subplots was high; however, compared to Ammer (1996b), it was typical for forest gaps in the mountainous regions on limestone. The coefficient of variation of the coverage was comparatively low, which indicates a wide expansion of competing vegetation within the canopy gaps since silvicultural activities 20–30 years ago. Subplots with visible decayed old stumps or with coarse woody debris were scarce. The canopy gaps were characterised by a patchwork of humus types and therefore by a highly heterogeneous humus thickness. Thin humus layers appeared on the two sites with deeper developed chromic cambisols.

Influence of site variables on the occurrence of spruce saplings

Table 4 compares the independent variables of 270 subplots with spruce saplings with 210 subplots without spruce saplings. The data are illustrated in Fig. 1, which scored every row of Table 4 to 100%, and therefore demonstrates the relative distribution of site factors in spruce plots compared to plots without spruce.

Table 3 Number of spruce saplings per ha, variation in coverage of ground vegetation, occurrence of coarse woody debris, and variation of humus thickness on the sites studied

	Spruce saplings (number/ha)	Mean coverage of ground vegetation (variation coefficient) (%)	Occurence of humus types and dead wood (% of occurence in subplots)				Mean humus thickness (variation coeffficient) (cm)
			stumps/coarse woody debris	up to 3 cm	3.1–15 cm	> 15.1 cm	
X Weiße Valepp/6 Äußerer Stolzenberg a[1]	6.000	82 (16)	5	17.1	53.7	29.3	10.1 (75)
X Weiße Valepp/7 Innerer Stolzenberg d[2]	4.000	71 (25)	2.5	35.0	62.5	2.5	4.8 (64)
XVII Lappberg/3 Langenberg a[1]	3.000	64 (27)	2.5	15.0	50.0	35.0	15.9 (96)
XVIII Rinneneck/2 Rinneneck d[1]	3.000	68 (45)	0	27.5	40.0	32.5	11.8 (83)
XXIX Sonnberggehäng/1 Sonneneck c[1]	4.000	61 (38)	0	82.5	17.5	0	2.3 (61)
XXIX Sonnberggehäng/2 Rothmartelgraben a[1]	5.000	66 (44)	2.5	27.5	55	17.5	9.9 (114)
Mean values for all sites	4.200	69 (32)	2.0	34	46.5	19.5	9.1 (113)

Table 4 Occurrence of independent variables in plots with spruce and in plots without spruce

Variable	Occurence in plots	
	With spruce > 20 cm ($n=270$)	Without spruce ($n=210$)
Coverage of canopy (all plots %)	100	100
Dense (%)	37	40
Loose (%)	52	49
Open (%)	11	11
Coverage of ground vegetation (%) (mean/SE)[a]	59.6/26.6	70/23.6
Microsite (0.5 $m^2$2-circle) (all plots %)	100	100
Terrace/mound (%)	55	16
Rib/depression (%)	4	4
Channel/even ground (%)	41	80
Macrosite (30 m^2-circle) (all plots %)	100	100
Terrace/mound (%)	66	43
Rib/depression (%)	10	10
Channel/even ground (%)	24	47
Organic layer (all plots %)	100	100
Stumps/coarse woody debris (%)	9	0
Up to 3 cm (%)	20	37
3.1–15 cm (%)	39	47
> 15.1 cm (%)	32	16
Humus thickness [cm] [mean/SE]	13.8/11.6	8.2/10.3
Hindrance index (mean/SE)	0.18/0.34	0.05/0.17

$n=28$ for plots with spruce and $n=210$ for plots without spruce[a]Only plots with saplings < 30 cm and with only one sapling per plot

The canopy coverage was quite similar in the two groups examined. To minimise repercussive impacts of spruce on the ground vegetation, we selected subplots with only one spruce smaller than 30 cm. As a result of the clustered regeneration, there were only 28 subplots out of the 270 subplots with spruce saplings that represent such a category. According to this selection, the ground vegetation coverage was not as dense in plots with spruce as in plots without spruce (Table 4). Figure 1 illustrates the occupied classes of ground vegetation in which the number of subplots with spruce saplings decreased with an increase of coverage. Most spruces were found on microsites with similar tendencies on macrosites that indicated rough surfaces (terrace/mound). In comparison, smooth surfaces (channel/even ground) were shunned by spruces. Depressions occurred seldom (Table 4) and had no negative effect on regeneration. Thick humus layers were linked to spruce saplings, and subplots with old, decayed stumps were always occupied by spruce saplings (Fig. 1). Altogether, humus was thicker in subplots with spruce compared to subplots without spruce. The classification of the hindrance indices illustrates the preference of spruce to grow close to an obstacle.

For the explanatory model, we used all independent variables, because Spearman correlations were low (Table 5) and the calculated tolerance values (data not shown) of the multivariate regression analyses were continuously greater than 0.2 (Knoke 2003b). The basic statistical characteristics of the stepwise binary logistic regression analysis are given in Table 6. As a result of the non-significant influence on the probability of spruce saplings, the independent variable coverage of canopy was excluded by the model. On the other hand, the P-values of the parameters of the five independent variables—coverage of ground vegetation, nearness to a hindrance (expressed by the hindrance index), humus thickness, microsite and macrosite characters—indicated that these variables included in the model were significant. The slightly decreasing −2LL value following the introduction of a further variable in the model showed that "spruce sapling probabilities" could not be predicted much better if further variables were included. The parameter of the hindrance index, the microsite "terrace/mound" and macrosite "terrace/mound" were positive, and so the spruce sapling probability became greater, as the hindrance index and rough surfaces increased. In addition, the odd ratios indicated that spruce saplings occurred more often near a hindrance (odd ratios 4.35), on the microsite terrace/mound (odd ratio 4.33) and on the macrosite terrace/mound (odd ratio 1.99). In contrast, the parameters of high coverage of ground vegetation and thin humus layers (< 3 cm) were negative. Therefore, the decreasing values of these independent variables led to an increasing probability of spruce sapling occurrence. Because of low odd ratios, these independent variables were of minor importance for the spruce sapling probability compared to a hindrance or the surface of the microsite. The high χ^2 value of 136 at $P<0.0001$ of the likelihood-ratio-test, the high χ^2 value of 6.841 at $P=0.554$ of the Hosmer-Lemeshow-test and the Nagelkerkes R^2 of 0.331 (values should be bigger than 0.2) indicated an adequate fit of the model (Backhaus et al. 2003). With an accurate classification of 72%, the performance and conformance of the model were also considered as well. The validity of the model was tested with Pearson's residuals, which had a mean of −0.006 and a standard deviation of 1.000 (Knoke 2003a). Therefore, there was no reason to exclude subplots to improve our analyses.

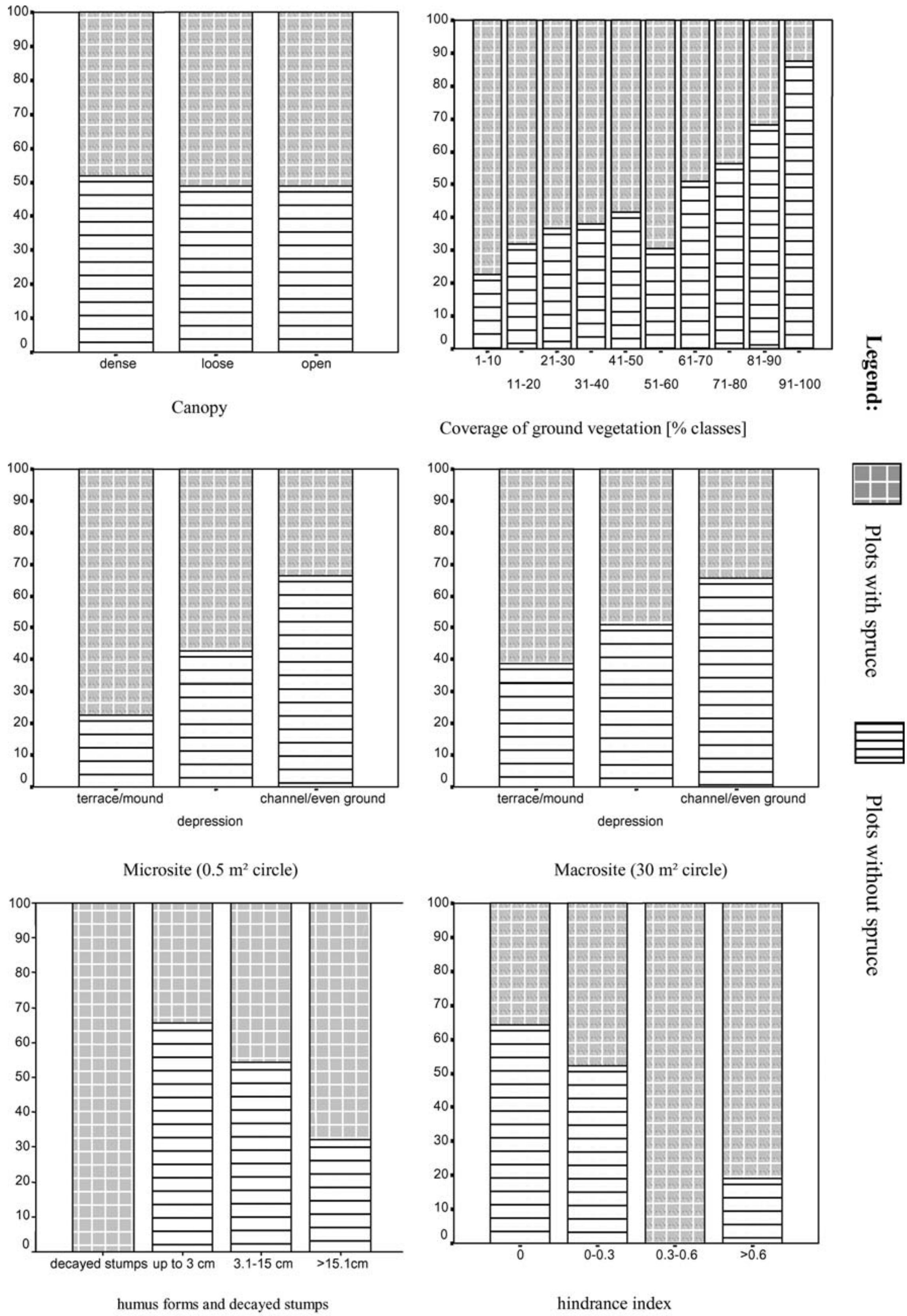

Fig. 1 Percent rates of the total number (y-axis) within each class of independent variable (x-axis) in a comparison of plots with spruce with plots without spruce (each independent variable of Table 4 is set up to 100%)

Table 5 Spearman correlation matrix of independent variables

	Coverage of ground vegetation	Hindrance index	Microsite terrace/mound	Macrosite terrace/mound	Humus thickness < 3 cm
Coverage of ground vegetation	1.000				
Hindrance index	−0.154**	1.000			
Microsite terrace/mound	−0.110*	0.377**	1.000		
Macrosite terrace/mound	0.210**	−0.199**	−0.266**	1.000	
Humus thickness < 3 cm	0.056	−0.191**	−0.176**	−0.102*	1.000

Significance: *$P \leq 0.05$; **$P \leq 0.01$

Table 6 Results of the binary logistic regression analysis for predicting the "spruce sapling" probability and results of the discriminant analysis (total data set $n = 480$)

Variable	Order of affiliation	−2LL after affiliation	Parameter	Standard error of parameters	Odd ratio	*P*-value	Standardised coefficients of the discriminant function[a]
Constant/intercept		577	1.568	0.335	4.800	< 0.0001	–
Coverage ground vegetation	1	544	−0.024	0.005	0.976	< 0.0001	−0.517
Hindrance index	2	535	1.470	0.478	4.353	0.0021	0.304
Humus thickness < 3 cm	3	528	−0.509	0.216	0.601	0.0186	−0.268
Microsite terrace/mound	4	525	1.465	0.245	4.327	< 0.0001	0.633
Macrosite terrace/mound	5	520	0.686	0.226	1.985	0.0300	0.194

Quality characteristics of the model: Likelihood-ratio-test: $\chi^2 = 136$, $P \leq 0.0001$
Hosmer-Lemeshow-test: $\chi^2 = 6.841$, $P = 0.554$; Nagelkerke $R^2 = 0.331$
Success of classification: 72%
[a]Quality characteristics of the model: Wilks' Lambda 0.746, χ^2 138.591, $P < 0.0001$

We used a discriminant function to support the binary logistic regression analysis (Table 6). The high and significant Wilks' Lambda indicated a significant dissociation of the two groups by the discriminant function (Backhaus et al. 2003). The independent variable microsite "terrace/mound" showed a positive effect on the probability of spruce sapling occurrence and had the greatest discriminating impact, followed by a high coverage of ground vegetation which had a negative influence. Humus thickness, hindrance index and macrosite were of lower discriminating importance. According to the discriminant analysis, thin humus layers of < 3 cm also had a negative influence, and high hindrance indices had a positive impact on spruce regeneration. Likewise, the macrosite "terrace/mound" had positive effects. Altogether, the discriminant function pointed to the same positive and/or negative influences of the independent variables on the occurrence of spruce saplings as the results of the binary logistic regression.

Indicator plant species

The relationship between the coverage of the six studied acid adapted plant species and the thickness of organic layers is shown in Table 7. The best indicator for thick organic layers was *Vaccinium myrtillus*. Here, coverage significantly increased with an increasing thickness of the humus layer; however, compared to gramineous ground vegetation (Fig. 2, Table 3), the coverage was still low. The correlations were low for *Lycopodium annotinum* and *Maianthemum bifolium*. The species *Huperzia selago, Vaccinium vitis-idaea* and *Melampyrum pratense* were poor indicators for thick humus layers in

Table 7 Rank correlation coefficients matrix (Spearman's ρ) between thickness of the organic layer in plot and the coverage of selected acid adapted plants

	Coverage (%)					
	Vac. myrt.	Lyc. ann.	Mai. bif.	Hup. sel.	Vac. v.-i.	Mel. syl.
thickness of organic layer [cm]	0.437***	0.257***	0.118**	0.084 (NS)	0.031 (NS)	0.065 (NS)

NS Not significant
***$P \leq 0.001$; **$P \leq 0.01$

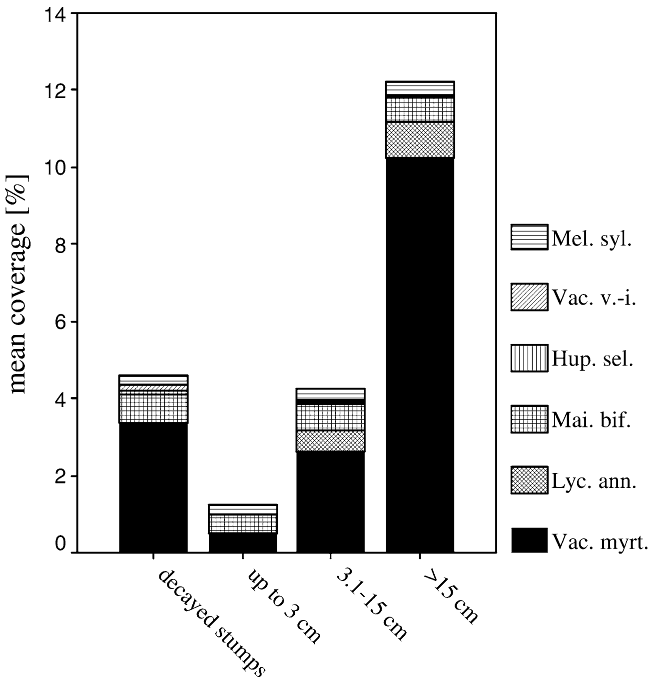

Fig. 2 Mean coverage of acid adapted plants in dependence of the occurence of decayed stumps or the thickness of organic matter

this mountainous region. In addition, *Vaccinium myrtillus* and *Maianthemum bifolium* willingly grew on acid decayed stumps (Fig. 2).

Discussion

Recruitment of spruce strongly depends on ‘‘safe microsites’’ (Ott et al. 1997; Moser 1965). Data presented here indicated that the spatial distribution of spruce saplings establishment was not random and varied among different microsite types (Table 4, Fig. 1). Similar patterns have been found in other studies (Mori et al. 2004; Bauer 2003; Brang et al. 2003; Brang 1998). The binary logistic regression analysis proved that different site factors significantly determined the regeneration niches of spruce saplings (Table 6). These microsite types may have characteristics that promote sapling establishment, whilst others diminish the occurrence of spruces.

Mosandl (1984) demonstrated that selective cuttings (‘‘Femel-cutting’’) in the mixed mountainous forests of the Bavarian Limestone Alps offered adequate solar radiation for a sufficient regeneration of spruce. Contrary to sub-alpine regions in which the importance of direct solar radiation increases, diffuse solar radiation conditions are of significance for spruce regeneration in mountainous forests (Ott et al. 1997). Diaci (2002) proved on comparable sites in Slovenia that diffuse solar radiation in small (0.01–0.05 ha), east–west orientated canopy gaps promoted spruce regeneration. The independent variable for the coverage of canopy was not significant and was excluded by our explanatory model. As was hypothesised for our study sites, we conclude that the supply of solar radiation within the canopy gaps was adequate for spruce regeneration. Therefore, the differences among the recorded subplots were of minor importance for spruce occurrence than the other site factors. However, we have reservations to use this simple method of the visual estimation of the coverage of canopy in such cases with wide light condition gradients (e.g. including closed canopies) and for studies on annual growth rates. Here, exact methods like the fish-eye photography or the horizontoscope are more appropriate to study the effect of solar radiation (Diaci 2002; Ammer 1996b).

Various authors supposed that spruce natural regeneration on steep slopes is hindered by snow gliding (Ammer 1990; Löw and Mettin 1977; Rebel 1922). In reforested areas of the Bavarian Limestone Alps, Gampe (1989) also found widespread damages on artificial regenerated spruces by snow gliding. On the contrary, technical support with artificial hindrances (e.g. snow rakes) advances the survival and growth of coniferous saplings (Mößmer et al. 1994). These findings align with our results that hindrances (e.g. stumps) have a great importance for the recruitment of a new spruce generation. Our calculated ‘‘hindrance index’’, which accounted for the number of hindrances and their distance to a spruce sapling, therefore might be a good specific value to describe the influence of hindrances on steep slopes. The great influence of the shape of a surface on the survival of coniferous saplings was demonstrated on the ‘‘Stillberg’’ site, Switzerland (Brang et al. 2004; Senn and Schönenberger 2001). Likewise our data demonstrated that rough microsites have an important positive impact on the occurrence of spruces. For the south exposed slopes of our study, we believe that the pathogenic fungi *Herpotrichia juniperi* (Duby) Petrak is seldom and therefore of minor importance for spruce establishment, as a result of a short duration of the snow pack (Butin 1989). Spruce seeds, deposited during wintertime in steep environments, are often blown over the frozen snow surface until they encounter a depression that traps them. Close to hindrances, snow melt is enhanced, which naturally creates depressions in the snow pack (Geiger 1961). Therefore, and besides the importance of hindrances to alleviate snow gliding, natural hindrances would be able to act exceedingly well as a seed trap, which might result in an added seedling emergence in the surrounding of hindrances.

Ewald (1997) already demonstrated the great variation in humus thickness of the vegetation type *Aposerido-Fagetum caricetosum albae* (Table 3). The thick humus layers appeared on the sites with shallow rendzic leptosols, and thin humus layers appeared on the two sites with chromic cambisols. That is in accordance with the observations of Bochter (1984), who found that the more the soils became shallower, the more the mightiness of the organic layers over limestone increased. Exposed mineral soil did not occur in our subplots, and most likely depends on disturbances (e.g. windthrow) in these ecosystems. Litter was consequently the most common substrate for germination and thick humus layers led to an increasing probability of spruce sapling occurrence (Table 6). Heavy litter accumulations on the forest floor are often considered to be detrimental to conifer seedling survival because they are prone to drying and prevent the root systems of the seedlings from quickly reaching the mineral soil (Brang 1996, 1998; Greene et al. 1999). Contrary to the above, survival rates and the growth of seedlings increased as the litter accumulation on logs increased (Harmon 1987), and Hanssen (2003) found a positive influence of increasing humus depth on the regeneration of spruce, probably due to shallow soils. The importance of acid organic layers for spruce nutrition increases on alkaline soils, because spruce nutrition is impaired due to low nutrient stocks, and alkaline pH-values that hinder nutrient acquisition in mineral soil horizons (Baier et al. 2005; Krapfenbauer 1969; Glatzel 1968; Zech 1968). Compared to other studies, sapling density was adequate for a sufficient regeneration of the stands (Schönenberger 2002; Ammer 1996b; Löw and Mettin 1977; Mettin 1977). It is known that the number of spruce stems decreases from germination to height of saplings (Bauer 2003; Ammer 1996b; Reif and Przybilla 1995). Due to this, a high number of spruces germinated on the humus layers. We assume that under such adverse mineral soil conditions and due to high precipitation in the Northern Alps, the organic layer might represent a good seedbed.

If highly decayed dead wood occurred in our study, it was occupied by spruce saplings. The importance of rotten logs for spruce regeneration is documented throughout the world (Mori et al. 2004; Brang et al. 2003; Bauer 2003; Simard et al. 1998; Eichrodt 1969). Ott et al. (1997) assumed that due to drought, dead wood on the south slopes is of minor importance. However, in contrast, on shallow alkaline sites, highly decayed dead wood is also of importance for the nutrition of spruce, because seedlings showed a enhanced nutrient uptake and growth compared to mineral soil horizons (Baier et al. 2005). In addition, the water storage capacity increases during decay, and therefore dead wood plays an important role in the availability of water, especially on these dry sites (Laiho and Prescott 2004).

Other microsite types may inhibit successful seedling germination and sapling establishment. Competition of ground vegetation increases under oceanic climate conditions (Ott et al. 1997). Here, the establishment of spruce saplings decreased on subplots with dense gramineous ground vegetation. However, it is difficult to ascertain the original seedbed during seed germination, especially if ground vegetation hindered the early establishment of spruce, or if spruce reduced ground vegetation. We seldom observed spruce seedlings in dense ground vegetation during field work, and according to other studies it is likely that dense, smooth ground vegetation is a serious competitor for the development of spruce seedlings on our sites (Bauer 2003; Diaci 2002).

On acidic soils derived from silicate, *Vaccinium myrtillus* is also considered a competitor for spruce seedling establishment (Bauer 2003; Brang 1996). However, in contrast, Moser (1965) concluded that a loose coverage of *Vaccinium myrtillus* could be beneficial for spruce germination. We believe that the same might be true for our sites with a loose coverage of *Vaccinium myrtillus* on acid humus layers, especially when compared to the high coverage of smooth gramineous competing vegetation. *Vaccinium myrtillus* is adapted on acidic soil conditions, a typical attender of spruce, and a character species of boreal and sub-alpine coniferous forest vegetation types (*Vaccinio-Piceetea*) (Walentowski et al. 2004). Under alkaline soil conditions it is therefore likely that spruce and *Vaccinium myrtillus* prefer the same microsites with acid humus layers as the growing media.

Our results suggest that natural spruce recruitment in protective forests can be influenced by the presence of specific microsites, which impair the influence of snow gliding. Kupferschmid-Albisetti (2003) demonstrated that uncleared snag stands on steep slopes will maintain effective protection for spruce regeneration for decades. Thus, coarse woody debris plays an important role as structural element on the forest floor, and we would therefore recommend that biomass removal is inappropriate, even after bark beetle infestation or storms. This applies to a greater extent, if the low nutrient stocks (especially phosphorous and potassium) of these ecosystems are included in this consideration (Katzensteiner 2003). In accordance with the "positive microsite" concept, we recommend for artificial regeneration measurements with spruce microsites close to hindrances like old stumps or close to cross lying coarse woody debris (StMELF 1997; Schönenberger et al. 1990). In addition, *Vaccinium myrtillus* might be a useful indicator plant species for acid organic layers as beneficial planting sites.

Our presented data were obtained from canopy gaps, in which the competition of spruce with other tree species, especially beech and maple, was reduced by the impact of ungulates. The effects of different site factors should therefore be evaluated for situations with competition of the tree species. Until the seventeenth century, most of the forests were unaltered virgin forests with the proportion of the main tree species being 45% spruce–30% beech–25% fir (Meister 1969a). Therefore, the regeneration ecology of the other important tree species, especially fir and beech, in dependency of microhabitats should be examined in future research. For this purpose artificial seed experiments in small canopy gaps of pure spruce stands with different ecological conditions (e.g. aspect) could be a promising approach to deduce practical applications for the re-establishment of mixed mountain forests.

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