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Analysis of natural regeneration in declining spruce forests on the Slovak part of the Beskydy Mts.

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Paper deals with regeneration processes in unnatural spruce forest ecosystems in the Beskydy mts. (North-Western Slovakia), declining due to so called “new type of spruce decline”. On 510 sample plots along the transects allocated across the most affected areas, site-related, stand-related data and data about natural regeneration were collected in years 2007–2008. Relations between coverage and vitality of regeneration and main ecological factors were analyzed using multidimensional statistical methods. Results show that declining spruce forests are able regenerate spontaneously, but rather by small-scale dynamics in the gaps and under canopy. When intensive damage and larger new-formed clearings occurred, some unfavorable tendencies in regeneration were indicated. Norway spruce continues to have the highest proportion in regeneration, followed by European beech that expands to a much higher occurrence and coverage than it has in mature stands, Silver fir is present in a lower frequency, but as a steady admixture. The main factors controlling regeneration in general are stand age, canopy closure and the presence of tree species in a mature stand; the influence of other factors seem to be less important and differs between tree species according to their ecological demands.

Keywords: spruce decline, regeneration coverage, regeneration vitality, regression analysis, Beskydy Mts.

Introduction

The presence or absence of natural regeneration predetermines the future of the forest stand. Seedling establishment is a critical life history stage. At this stage, tree survival and growth is most sensitive to the micro-site environment, while light conditions and soil moisture are considered to be the primary limiting resources for tree regeneration (Gray et al. 2005). In shaded forest understorey, only shade-tolerant species can regenerate. The growth of seedlings and saplings that occur in such conditions, as well as the regeneration of light-demanding species, is suppressed until a canopy gap appears (Numata et al. 2006). Therefore, forest regeneration processes frequently depend on the natural disturbance regimes (Whitmore 1984). Usually, the dynamics of forests is distinguished into coarse-scale and fine-scale dynamics (Spies and Franklin 1989), which are in a more recent literature defined as patch and gap dynamics, respectively (Lewis and Lindgren 2000). Although sometimes the terms gap and patch are used as synonyms, the distinction between them has been recognized and described thoroughly in the literature (McCarthy 2001). The main difference between these two types of dynamics is the size of forest openings that appear after a disturbance, while the area of 200 m^2 has been accepted as a border size.

Patches are larger forest openings that result from rapid, at times catastrophic, disturbances causing a discrete spatial pattern (White and Pickett 1985). An exogenous disturbance agent appears at a specific point in time and causes large-scale mortality, which creates a patch. Wind, fire, and insect outbreaks are the primary agents that create patchy openings (McCarthy 2001). The conditions in a patch differ significantly from those in the stand, allowing also light-demanding and pioneer species to regenerate (McCarthy 2001). Hence, shortly after the formation of a patch, tree species diversity is the highest (Spies and Franklin 1989).

Gap dynamics is associated with small or micro-scale disturbance of the forest canopy causing the mortality of individual trees, which subsequently results in small openings in the canopy (McCarthy 2001, Yaroshenko et al. 2001). Although the area of the gaps studied all over the world has varied from 5 m^2 to 2.5 ha, most of the gaps reported in the literature range from 50 to 500 m^2 (Bobiec 2007). The size of the gap depends on the fact whether gaps are formed from single tree or multiple tree falls, on tree size and crown dimensions, and the age of the gap. The gap size for single treefalls normally ranges from 50 to 200 m^2 (McCarthy 2001). Advance regeneration of climax or shade-tolerant species established under the shade of forest canopy prior to small-scale disturtbance, respond to small gaps and take advantage of enhanced light conditions. Spies and Franklin (1989) reported that even the most shade-tolerant species require such gaps in the canopy to survive and grow into the overstorey.

The aim of the paper is contribute to the knowledge on regeneration processes in forest ecosystems after disturbances. Special attention is paid to regeneration potential of Norway spruce and admixed tree species such as European beech, Silver fir and others in unnatural, predominantly spruce forests, which have been in the last years strongly affected by a so called "new type of spruce decline" (Kulla 2006, Jakuš et al. 2008). The problem of Norway spruce decline is new, actually related to the extensive areas of the Beskydy Mts. in Slovakia, the Czech Republic and Poland. Hence, by now there is a lack of relevant findings about the natural regeneration and the succession of affected ecosystems.

Territory of interest

The data for the analyses were collected in the sample plots established along transects allocated across areas strongly affected by spruce decline in the Kysuce and Orava regions in the North-western Slovakia (Fig. 1).

The area of interest belongs to the Western and Central Beskydy Mts., generally characterized by a softly modeled hilly landscape with narrow valleys, and with the orientation of main mountain ridges from the southwest to the northeast. An altitude ranges from about 400 to 1700 m above see level. Geological substratum is palaeogenic flysch, built up from sandstones, slates and claystones. Prevailing soil type is cambisol, with transitions to podzols, planosols and gleysols (in the terms of WRB soil classification). Moderately cold and very wet hilly climate is typical for the region.

According to relevant published sources concerned with tree composition of natural forests in Slovakia (Zlatník 1959, Michalko 1986), pure Common beech and mixed silver fir-beech forests (*Fagus sylvatica*, L., *Abies alba*, Mill.) were in absolute majority before the man arrival on the territory. Spruce could have been present on 10–20% of the area at most, mainly as an admixture species.

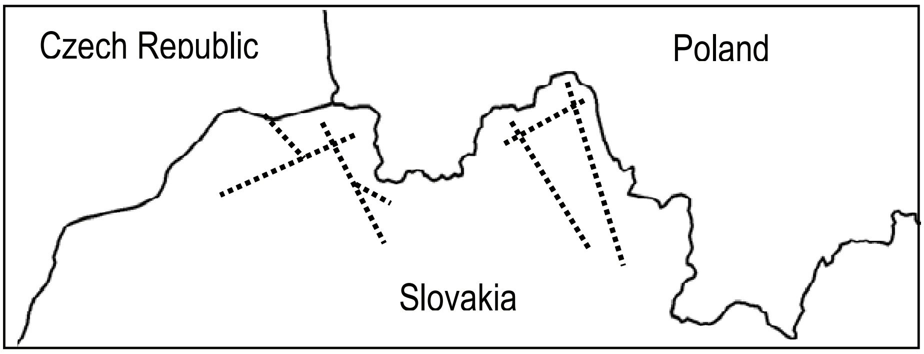

Fig. 1: Territory of interest with the delineated location of the sample transects

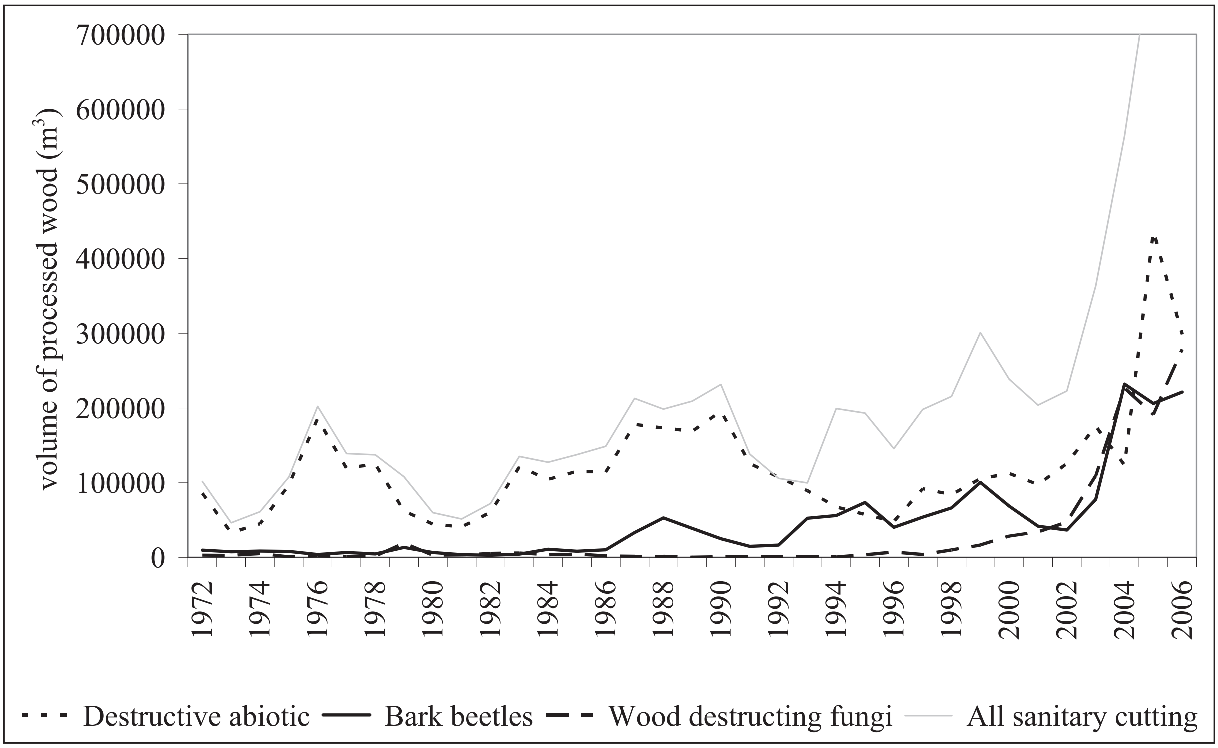

Fig. 2: Time series of annual sanitary cuttings according to summarized data for the territory of interest (districts Čadca, Kysucké Nové Mesto, Námestovo, Tvrdošín, Dolný Kubín)

Current forests are almost without exceptions unnatural. According to the data from the transects, the average tree species composition of the examined forests is as follows: spruce 77%, beech 11%, fir 7%, maple, elm and other valuable broadleaved species 2%; birch, rowan and other pioneer broadleaved species 2%; pine, larch and others less than 1%.

Extensive spruce decline driven mainly by biotic agents-bark beetles (*Scolytidae*) and honey fungus (*Armillaria* sp.), started after year 2002 (Fig. 2). It is characterized by dispersed dieback of individual trees, groups of trees, formation of gaps and consequently patches – large cleaned areas after sanitary cuttings.

Material and methods

Alltogether, 510 sample plots were pre-selected in the forest compartments traversed by the line transects, situated in the direction of the highest variability of site and stand conditions in the areas affected by decline. The centre of the sample plot was determined with GIS tools above the ortho-photo-map from the time period prior to the occurrence of extensive spruce dieback (2002–2003), in representative conditions for the selected compartment. In the field, the pre-selected plot centres were identified by GPS. In each plot, altitude, exposition and slope inclination were measured, and the following data characterising site, mature stand and regeneration were visually assessed in the years 2007–2008:

- Ecological-trophical order according to Buček and Lacina (2000) on a scale: 1 – oligotrophic, 2 – hemioligotrophic, 3 – eutrophic, 4 – heminitrophylic or hemicalcicolic, 5 – nitrophylic or calcicolic.
- Irradiation level gradient according to the measured exposition, on a scale: 1 – N, NE; 2 – NW, E; 3 – W, SE; 4 – SW, S.
- Shape of the terrain on a scale: 0 – straight, indifferent from the point of water and nutrients accumulation, +1 – concave, accumulating shapes, -1 – convex, water and nutrients loosing shapes.
- Vertical structure of a mature stand, expressed as a number of relevant tree layers with a coverage exceeding 10% and a mean dbh higher than 7 cm.
- Naturalness of a mature stand assessed on a scale: 1 – unnatural transformed, 2 – unnatural changed, 3 – seminatural, 4 – close to nature, 5 – natural virgin forest.
- Damage class of a mature stand, predefined as: 1 – undamaged stands, keeping closed canopy, even if some individual trees die; 2 – moderately damaged stands, characterized

by the gaps in the canopy caused by tree dieback that on average do not exceed 0.01 ha, or the maximum of 0.02 ha; 3 – strongly damaged stands, characterized by a broken canopy with patches larger than 0.02 ha.

- Total coverage of tree layers and coverage of individual tree species in a mature stand and in regeneration in % of the whole area.
- Vitality of tree species in a mature stand and in regeneration, assessed according to growth dynamics, density and color of assimilatory organs and visible damage symptoms on a scale: 1 – dying; 2 – slight vitality, surviving is questionable; 3 – moderate vitality, surviving is probable; 4 – high, extraordinary vitality.
- Presence of visible damage on regeneration, caused by wild game, cutting activities, and presence of unspecific yellowing without apparent reasons, on a binary scale: 1 – present, 0 – absent.
- Total coverage of ground vegetation and coverage of mosses, grass, herbs and shrubs in % of all area.

The data about the site and the mature stand were visually estimated inside the circle with the radius of approximately 50 meters (approximate area of 0.8 ha), data about regeneration and ground vegetation were visually estimated inside the circle with the radius of approximately 25 meters (approximate area of 0.2 ha) around the plot centre. Finally, the stand age was determined using the data from forest management plans; if the stands were composed of more tree layers, the age was computed as a weighted mean, while the standing timber volume was used as a weight.

Basic statistics for regeneration coverage were computed, the influence of the factor stand damage was analyzed by analysis of variance (ANOVA) with post-hoc comparison of means by Tukey´s HSD test for unequal samples. Multiple influence of all factors on regeneration coverage was assessed by multiple regression using Generalized linear models (GLM) of Statistica 7.0 software. Regarding the observed distribution of regeneration coverage (Fig. 3), Poisson regression was applied with *ln* transformation of a link function. The coverage category was used as a dependent variable with a step of 10% (1: 1–10%, 2: 11–20%, etc.). In order to analyse factor impacts on regeneration vitality, ordinal multinomial regression was performed with *logit* transformation of a link function. The results were interpreted according to the standard procedures used for the evaluation of logistic regression models (Quinn & Keough 2002, Meloun et al. 2005). In addition, a quasi-R^2 as an indicator of explained proportion of all variability in a multidimensional data set by the model, was calculated from the distribution of residuals around the fitted linear function beginning in the origin of the coordinate system (zero point).

Results and discussion

Natural regeneration coverage

Natural regeneration was observed in 92 % of all sample plots. Norway spruce (82%) followed by European beech (65%) were present most frequently. Tab. 1 presents the review of detailed results on basic descriptive statistics.

Markedly lower values of median in comparison with mean indicate a strongly left-sided distribution of observed coverage frequencies, what is also documented in Fig. 3. Most frequent coverage of overall regeneration (when it occurs), expressed by median as more suitable measure in conditions like these, is only about 10%.

Norway spruce, European beech and Silver fir are the main tree species in regeneration, while valuable broadleaved species (maple, elm, lime, and ash tree) as well as other broadleaved are less frequent with lower coverage.

Danielewicz and Zientarski (2004) examined the dynamics of natural regeneration of Norway spruce in the Karkonosze National Park, and stated that in spite of a sudden and a rapid decline of forests in the examined area, the spruce stands seem to be able to regenerate spontaneously. Grassi et al. (2004) found that both Silver fir and Norway spruce were able to utilize favorable conditions created by small and diffuse canopy openings before the actual gap creation. From these two species, fir before-gap regeneration appeared to have a better chance of refilling the gap. Beech is a shade-tolerant species that can recruit also underneath the forest canopy, beech seedlings might have profited from the enhanced light conditions after the canopy openings (Nagel et al. 2006).

Surprisingly, other broadleaved species, such as birch, rowan and alder, were observed in regeneration in a small proportion, although it was expected that these pioneer species would occupy gaps and cleared areas after sanitary cutting in declining stands. Similarly as in our case, Nagel et al. (2006) did not detect higher occurrence of light-demanding tree species on a windthrown plot because of the advance regeneration of shade-tolerant species established underneath the forest canopy taking advantage

Tab. 1: Descriptive statistics on natural regeneration coverage in the studied region, categorized according to tree species and stand damage classes

Tree species	Stand damage class	N	Occurrence (%N)	Mean	Standard deviation	Median	Quantile 25%	Quantile 75%
				Computed from cases when regeneration occurred				
Norway spruce	1	259	80	8.8	12.5	3.9	1.0	10.5
	2	161	80	8.5	12.8	4.0	0.9	9.8
	3	90	93	9.9	12.7	5.0	1.9	12.6
	All classes	510	82	8.9	12.6	4.0	1.0	12.0
Silver fir	1	259	46	2.3	3.9	1.0	0.3	3.0
	2	161	50	4.0	5.6	1.0	0.4	6.0
	3	90	57	3.3	4.7	1.2	0.5	4.0
	All classes	510	49	3.1	4.7	1.0	0.3	3.9
European beech	1	259	59	3.9	6.1	1.3	0.5	4.8
	2	161	71	6.6	9.9	1.8	0.5	10.0
	3	90	71	9.4	14.1	3.1	1.0	12.7
	All classes	510	65	5.9	9.6	1.8	0.5	6.7
Valuable broadleaved	1	259	28	1.9	4.0	0.9	0.2	2.0
	2	161	26	1.6	3.9	0.5	0.3	1.0
	3	90	10	8.0	19.4	0.2	0.2	1.0
	All classes	510	24	2.3	6.4	0.6	0.2	1.5
Other broadleaved	1	259	47	3.3	4.0	1.9	0.8	5.0
	2	161	60	2.3	3.9	0.9	0.4	2.3
	3	90	62	4.4	9.5	1.4	0.6	3.9
	All classes	510	54	3.2	5.6	1.3	0.5	3.9
Regeneration altogether	1	259	88	14.3	15.0	10.0	3.0	20.0
	2	161	93	16.6	16.2	10.0	3.0	25.0
	3	90	100	21.4	20.0	15.0	5.0	30.0
	All classes	510	92	16.4	16.6	10.0	3.0	25.0

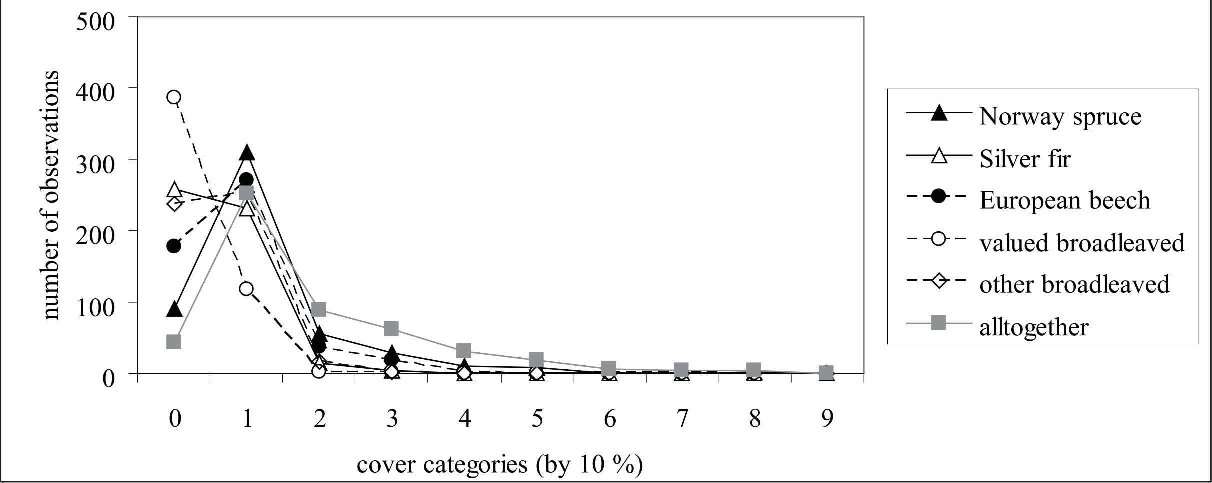

Fig. 3: Distribution of observed main tree species occurrence (as counts) in natural regeneration by coverage categories

of the sudden canopy opening. McCarthy (2001) stated that pioneer species regenerate when light conditions are satisfactory, i.e. when the size of the gap exceeds approximately 200 m². Bobiec (2007) found that birch, rowan, and alder regenerate almost solely in gaps, while in his study the minimum size of the gaps was 250 m². Hence, relatively small proportion of these tree species observed in the regeneration in strongly damaged stands would suggest that the development of these forests follows fine-scale dynamics (see e.g. Spies and Franklin 1989), and that time after a sudden patch formation could be too short for the occupation of clearings by pioneers.

Data in Tab. 1 show some tendencies that the frequency of regeneration occurrence as well as the regeneration coverage increases in more damaged forest stands for spruce, beech and silver fir, but due to the high variability these tendencies are mostly not significant. In mature stands, analysis of variance (ANOVA) for the factor damage class proved significant decrease of spruce coverage due to spruce dieback, and probably naturally lower proportion of beech in damage class 3 (Fig. 4). In addition, the proportion of valuable broadleaved and other broadleaved species in undamaged stands (damage class 1) is significantly higher than in damaged stands (damage class 2, 3), what can indicate a positive effect of broadleaved species on forest resistance against damage. In regeneration, only the coverage of beech regeneration was proved to be significantly higher in damaged stands (damage class 2 and 3) than in undamaged stands, in spite of the lower presence of beech in mature stands of this category.

Considering the literature review, this could results from several factors. Except of mentioned advanced regeneration of beech underneath the forest canopy, higher proportion of beech regeneration can be caused also by more frequent mast years that were observed by Övergaard et al. (2007) in Southern Sweden. These authors also suggest that nitrogen deposition can also act as a fertilizer that has a positive impact on beech regeneration.

Fig. 5 shows the principle of the evaluation of the influence of multiple ecological factors on regeneration. The intensity of the influence is evaluated by Wald statistic, computed for each factor as a square of ratio of an estimated linear b_i coefficient and its standard deviation - $(b_i/s_{bi})^2$. Statistical significance of the factor influence is reported by p-value expressing the confidence level of t-test for Wald statistic. Two significance levels are used in this study. When p-value is lower then 0.05, the influence is statistically significant, and when p-level is between 0.05 and 0.20, the influence is insignificant but considered to be an important trend. The signs of b_i coefficients determine the sense of the influence. Tab. 2 presents the results of Poisson regression interpreted as described above.

Stand age and canopy closure are the most important factors controlling regeneration in general. Regeneration coverage significantly in-

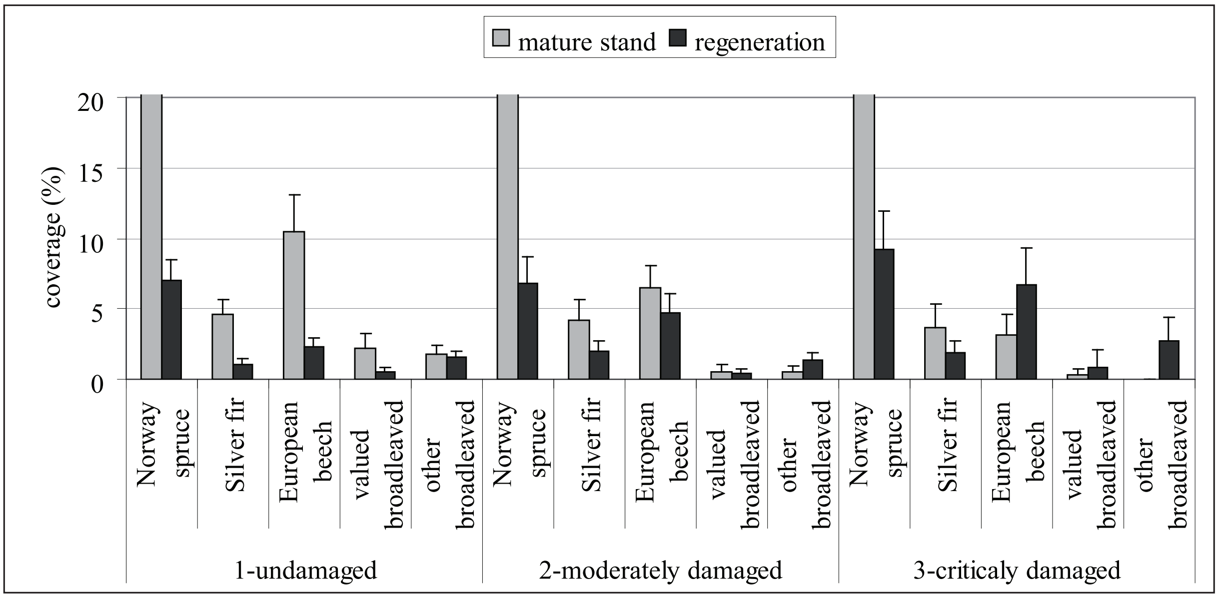

Fig. 4: Average tree species coverage in natural regeneration according to stand damage classes, compared with tree species coverage in mature stands (abscissa expresses standard error of mean at 95 % confidence level, overlapping data of mature Norway spruce coverage are 54.8±3.0 % for undamaged, 54.6±2.6 % for moderately damaged and 38,4±3,4 % for critically damaged stands)

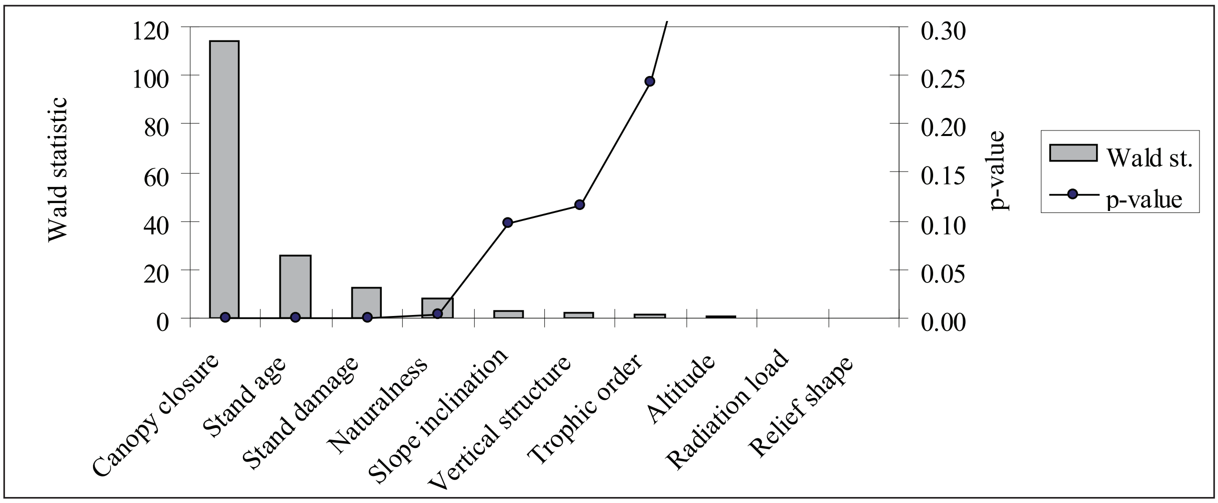

Fig. 5: Influence of selected factors to overall extent of natural regeneration (all tree species), assessed by the test of Wald statistic

creases in older stands with more open canopy. The positive correlation of tree species presence in mature stands with their coverage in regeneration is logical. No significance detected for spruce is due to the generally high proportion of this species in the mature stands, which is not limiting its regeneration.

With regard to the aim of this study, the negative influence of stand damage level on regeneration coverage is interesting, which was found significant for spruce, and as a trend also for fir and valuable broadleaved species. Some inconsistencies of these results with the results of ANOVA (Fig. 4) indicate imbalances in data structure, mainly a higher proportion of older stands in damage classes 2 and 3, which increased their means. Age is one of the main factors controlling current decline in the territory of interest, when it increases, the probability of the decline also increases (Kulla 2006). The multiple regression partitioned these effects and revealed that the increase of the damage itself has an unfavorable effect on regeneration coverage of the mentioned tree species. It means, that in more damaged stands regeneration is weaker than in less damaged stands of comparable age, structure and ecological conditions. Beech and pioneer tree species are exceptions, probably due to the reasons discussed above. The positive effect of the vitality of mature spruce trees on spruce regeneration coverage is also a notable finding. Other factors showed to be significant less frequently, and differently according to ecological requirements of individual tree species.

The analysis of the influence of the same factors on ground vegetation coverage proved similar tendencies. More extended coverage tends to be in older stands with open canopies, but not because of the recent damage, in unnatural forests, on mild slopes, northern expositions and at lower altitudes.

The parameters of the goodness of fit of the derived models (Deviance, Pearson chi-square) reach values lower than or close to 1.0 meaning that there is no reason to suppose insufficient fit of the data set by the derived models. On the other hand, the computed values of quasi R^2 are low. Hawkes (2000) reported that regression models have generally low ability to describe complex ecosystems satisfactorily, and suggested a shift towards modeling for exploration and explanation rather than for predictions. Such an approach was also utilized in this study.

Natural regeneration vitality

The results show relatively good vitality of regeneration (between 3 – moderate and 4 – high) with no effect of the damage level of the mature stand for all tree species, except for spruce. The vitality of spruce regeneration is lower on average (between 2 – slight and 3 – moderate), and significantly increases with increase of the stand damage level. However, this is most probably the result of the light limitation by shading of mature stands without or with lower damage (Fig. 6).

The evaluation of the influence of factors on regeneration vitality was performed by the same way as in the case of regeneration coverage (Tab. 3). Ordinal multinomial regression represents a series of binomial logistic regressions for consequent pairs of categories, with the presumption that the factor influence increases or decreases along the gradient expressed by the dependent categorical variable (vitality), what enables to estimate average linear coefficients b_i and Wald statistics for the model series.

Odds ratio refers to the proportion of correctly categorized cases by the derived model from all observations.

The mature stand is the most important factor limiting the vitality of regeneration by shading, water and nutrient competition. The vitality of regeneration of most tree species is positively correlated with the vitality of mature trees. The increasing damage of a mature stand has a negative influence on the vitality of shade-tolerant species (beech, fir), what could be explained by the shock after a sudden canopy opening over advanced and so far shaded regeneration (Tab. 3). The vitality of regeneration was unfavorably influenced by cutting activities, what is manifested mainly for spruce and beech creating the greatest proportion of the regeneration. The important finding is, that relatively lower vitality of spruce regeneration does not seem to be coupled with unspecific yellowing, which could be referred to the new type of spruce decline.

Conclusions

From the analysis of the coverage and the vitality of regeneration in declining unnatural spruce forests in the Slovak part of Beskydy Mts. we obtained the following results:

- Declining forests are able to regenerate spontaneously, but rather via small-scale dynamics with advanced regeneration in the gaps and under canopy (regeneration occurred on 92% of all examined sample plots).
- Norway spruce continues to have the highest proportion in regeneration, followed by European beech that expands to a much higher occurrence and coverage than it has in mature stands, Silver fir is present in a lower frequency, but as a steady admixture.

Tab. 2: Influence of selected site and stand-related factors to extent of natural regeneration and ground vegetation coverage in forest stands, assessed by t-test of Wald (results of Poisson regression)

	Natural regeneration						**Ground vegetation**				
	Altogether	**Norway spruce**	**Silver fir**	**European beech**	**Valuable broadleaved**	**Other broadleaved**	**Altogether**	**Mosses**	**Grass**	**Herbs**	**Shrubs**
Altitude			(+)		-	-	(-)	-			-
Ecological-trophical order		-			+	-	-	-			+
Irradiation level		(-)		(+)			-	-		-	
Relief shape					(-)						
Slope inclination	(-)	-		(+)			-	-	-	(-)	
Vertical structure	(+)	+				(+)	+	-			+
Naturalness	+	(-)		+		(-)	-	-		-	(-)
Canopy closure	-	-	-	-		-	-	-	-	-	-
Stand age	+	+	+	+	+	+	+	+		+	
Stand damage	-	-	(-)		(-)		-	(-)		-	
Tree species presence in stand			+	(+)	+	+					
Tree species vitality in stand		+	(+)								
Sample size (N)	506	506	507	506	508	509	506	506	500	506	504
Deviance (D/df)	0.65	0.60	0.66	0.71	0.57	0.64	1.15	0.70	0.73	1.14	0.65
Pearson chi-square (χ^2/df)	0.66	0.55	0.56	0.54	0.71	0.52	1.10	0.65	0.61	1.14	0.61
Quazi R^2	0.44	0.37	0.27	0.25	0.28	0.14	0.41	0.39	0.31	0.28	0.24

\+ positive influence (increases when increases) significant at 95% confidence level ($p < 0.05$)
(+) positive influence (increases when increases) significant at 80% confidence level ($0.05 < p < 0.20$)
\- negative influence (increases when decreases) significant at 95% confidence level ($p < 0.05$)
(-) negative influence (increases when decreases) significant at 80% confidence level ($0.05 < p < 0.20$)

- The main factors controlling regeneration in general are stand age, canopy closure and the presence of tree species in a mature stand; the influence of other factors seem to be less important and differs between tree species according their ecological demands.
- Increasing stand damage showed to have a negative influence on the coverage of the majority of main tree species, and also on vitality of shade-tolerant species (European beech, Silver fir).
- Contrary to expectation, pioneer tree species had not occupied newly-formed clearing areas promptly, what might signify some problems with spontaneous forest regeneration in conditions of large scale (patch) dynamics.
- The average vitality of regeneration is generally good (moderate to high) for all tree species except Norway spruce, which had a lower vitality (slight to moderate), but not due to the symptoms referred to actual spruce decline, but rather due to the competition of the mature stand.

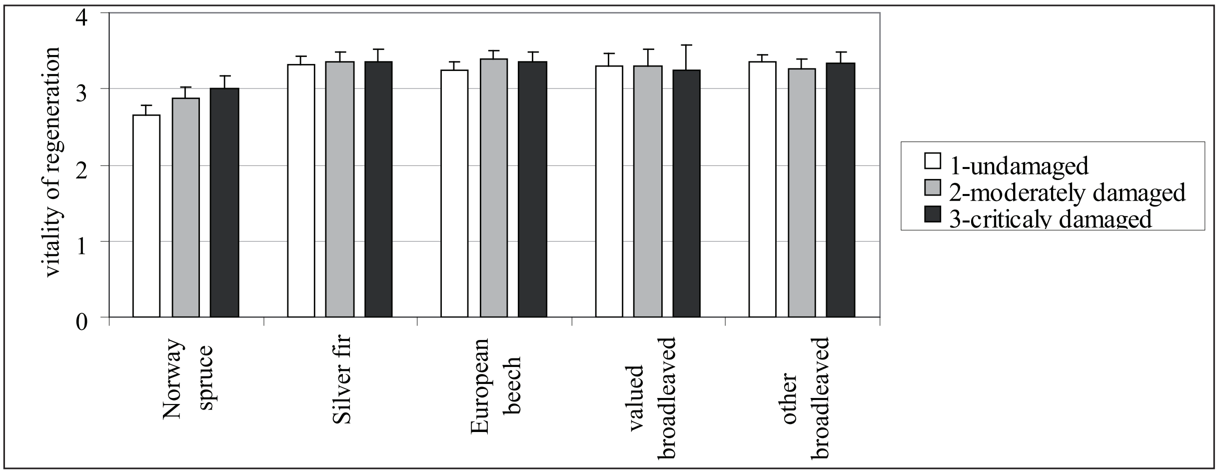

Fig. 6: Average vitality of natural regeneration according to tree species and stand damage class (abscissa expresses standard error of mean at 95% confidence level

Tab. 3: Influence of main limiting factors on vitality of natural regeneration, assessed by t-test of Wald statistics (results of ordinal multinomial regression, interpretation of signs comformable with Tab. 2)

	Norway spruce	**Silver fir**	**European beech**	**Valueable broadleaved**	**Other broadleaved**
Altitude	(+)	-			+
Ecological-trophical order					+
Irradiation level		(+)			
Relief shape			(-)	(-)	
Canopy closure	-	-	-	-	-
Grass, herbs and shrubs cover	+		(+)	-	-
Cutting damage	-	(-)	-		(-)
Game damage	(+)	-		-	-
Unspecified yellowing					-
Species vitality in mature stand	+	+	+	+	
Stand damage class		(-)	-		-
Sample size (N)	424	252	337	127	276
Deviance (D/df)	0.63	0.53	0.49	0.52	0.45
Pearson chi-square (χ^2/df)	0.99	0.90	0.77	0.88	0.83
Odds ratio	65%	64%	63%	64%	68%

On the basis of the obtained results, we recommend for the management of declining spruce forests growing in the territory of interest and in similar conditions:

- Prolong maximally the process of canopy disintegration mainly in younger stands before their fertility to support natural regeneration by small-scale dynamics.
- Recognize of any admixture in spruce regeneration, its support by silvicultural techniques and protection against wild game.
- Sowing or planting of pioneer tree species (birch, aspen) on new-formed clearings to improve conditions for regeneration (natural or artificial) of shade tolerant tree species before expansion of ground vegetation.

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