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Interactions of Ecological Factors and Natural Regeneration in an Altimontane Norway Spruce (*Picea abies* (L.) Karst.) Stand

By

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S u m m a r y

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In an altimontane Norway spruce stand in the Julian Alps, Slovenia, the influence of direct and diffuse site factors, ground vegetation, soil and mycorrhiza on natural regeneration was studied in gaps of different size. Norway spruce successfully germinated and survived the first years under slightly open canopies, yet further development was possible only in the gaps. Regeneration success varied within gaps. Microsites within small gap exposed to direct radiation or overgrown by *Polytrichum formosum* were unfavourable for regeneration. Successful regeneration was found in plots with more podzolized soils, higher content of organic matter, sparse forest ground vegetation coverage and more diffuse site factor. Results support the assumption that in the plots with abundant direct site factor, water stress can hinder the germination and regeneration of Norway spruce during the first decade. For this reason we propose to create narrow gaps, with an east-west orientation of their longer axis.

I n t r o d u c t i o n

Silvicultural strategies are developing rapidly in the Alps (SCHEIRING 1996, OTT & al. 1997). Forest ecosystems, which are close to their natural limits

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here and therefore very susceptible to disturbances, face present-day phenomena such as climate change, air and water pollution, expansion of social functions, etc. In addition to new problems, the old ones such as instability of forest stands, cattle grazing and game browsing remain unsolved. The present even-aged structure of forest stands in the Slovenian Alps is the result of the clear-cut forest management system in the past. In addition, Norway spruce has been promoted for centuries to the detriment of other species. Conversion of even-aged stands is a long process (SCHÜTZ 1989, OTT & al. 1997), where natural regeneration is important, since planting cannot replace its vigour and adaptability. Besides this, planting is becoming uneconomical.

Earlier research of natural regeneration in Slovenia's altimontane Norway spruce forests concentrated on competition in the herb layer, interactions in the mycorrhizosphere, conditions in soil strata and micro-relief (HORVAT-MAROLT 1984, ROBIC 1985, ROBIC & al. 1998, URBANCIC & KUTNAR 1998). The role of solar radiation was not examined satisfactorily. The warmth of the upper soil layer, which is significantly affected by direct solar radiation, is an important factor for germination and root development (IMBECK & OTT 1987, BRANG 1996). The solar radiation climate can be efficiently modified by silvicultural measures. Results from different research sites in the Swiss Alps show that, in general, Norway spruce regeneration can survive in the long-term on the northern slopes only in microsites with at least some direct insolation during the vegetation period (IMBECK & OTT 1987, OTT & al. 1991, BRANG 1996, OTT & al. 1997). The purpose of this study was to identify the major factors deterring establishment of tree seedlings in an altimontane Norway spruce stand in the Julian Alps of Slovenia.

Materials

The research site is located on the high Pokljuka plateau on the eastern side of the Julian Alps in Slovenia. Research plots were set in a mature 150-180 year old Norway spruce forest at an altitude of 1200 m (KRAIGHER & al. 1995). The average annual temperature is 3 °C, the annual precipitation 1950 mm. Temperature inversions are frequent because of the dish-shaped relief. The parent material consists of mixed moraine of crystalline and limestone or dolomite, which partially covers limestone laky chalk. Soil conditions on the permanent research plot are highly variable (URBANCIC & KUTNAR 1997). According to international classification (FAO-Unesco 1989), four major soil groups with the following eight soil units were found: Dystric and Ferralic Cambisols, Haplic, Cambic and Carbic Podzols, Eutric Gleysols and Terric and Fibric Histosols. The vegetation on the permanent research plot was classified into two plant communities (URBANCIC & KUTNAR 1996): *Rhytidiadelpho lorei-Piceetum* and *Sphagno-Piceetum* var. geogr. *Carex brizoides*. On the Pokljuka plateau, spruce forests prevail almost completely as a result of severe alpine climate, relief and past forest management. Anthropogenic influences in the past such as charcoal burning, cutting wood and cattle grazing changed the tree species composition from original beech-fir forests to pure Norway spruce stands with only 1 % broad-leaved species and 1 % silver fir.

Methods

In 1997 we systematically arranged 106 research plots in four sampling strata: 25 plots in a closed spruce stand, 15 in a clearing (0.35 ha), 33 in a small gap (0.03 ha) and 33 in a medium gap (0.05 ha). The gaps were over 15 years old and the clearing originated from 1995. The plots were established in a N-S and E-W direction from the centre of strata, in 0.5 m x 0.5 m squares, two metres apart (Fig. 3). Diffuse and direct site factors (potential direct radiation in hours from April to August) according to ANDERSON 1964 were assessed with the horizontoscope (TONNE 1954, SCHÜTZ & BRANG 1995, BRANG 1996). The original method was modified and updated by applying photography and computerised image analysis.

Forest soil was examined in five systematic samples in each plot. Morphological characteristics, thickness of genetic soil horizons and soil types and depths were determined for each core. Quantitative samples of humus strata were collected with a cylindrical core sampler 7 cm in diameter from 3 spots around the centre of each plot. For each sample, values of pH in de-ionised water and in 0.01 M calcium chloride, organic carbon content, humus, total nitrogen and C/N ratio were determined. For the whole permanent research plot, soil was probed using the same procedure in a 20 x 20 m grid and soil samples were taken from representative profiles. Types of ectomycorrhizae were studied in soil cores (274 cm³, 0-20 cm deep). 13 samples were taken from the soil in the closed stand, 17 samples from the small gap and 15 from the clearing. In mycorrhizal samples, all the roots were counted and types of ectomycorrhizae briefly characterised and counted (after AGERER 1987-1998, for descriptions see TROST & al. 1999). Non-turgescer types were placed into a single category of old unidentifiable types and were not taken into account in this interpretation. From these data (data taken from TROST & al. 1999, SIMONCIC & al. 1998, ROBIC & al. 1998) species richness index (d) and Shannon-Weaver Index of Diversity (H) were calculated (after ATLAS & BARTHA 1981, as described by KRAIGHER 1999).

In all plots, cover estimates of ground vegetation were made for all plant species in five vertical layers: moss, lower and upper herb layers, lower and upper shrub layers. The vegetation was surveyed according to eleven classes: cover of plant species from 0 to 5 %, from 6 to 10 %, 11 to 20 %, 21 to 30 %, ..., 91 to 100 %. In the research plots the following data were measured or estimated: number of one-year-old seedlings, number of seedlings up to 10 cm, number of saplings higher than 10 cm. The main composition gradients in the vegetation on the plots inside the small gap were extracted using a principal component analysis (PCA). For the calculation of vegetation diversity in the strata, Shannon index (H) was used (MCCUNE & MEFFORD 1995).

Results

Radiation

Radiation climate in the four analysed strata differed significantly (Fig. 1). The highest values of both components of radiation were measured in the clearing. For the other strata the highest median value of the diffuse site factor was estimated in the medium gap at 27.6 %, followed by the small gap with 21.4 % and the stand with the median value of 18.6 %. The highest values of potential direct radiation, if we disregard the clearing, were obtained in the stand with the median value of 7.7 h, followed by the medium gap with 6.6 h and the small gap with 4.2 h. Median values for potential direct radiation are relatively low, yet variability within the strata is significantly high.

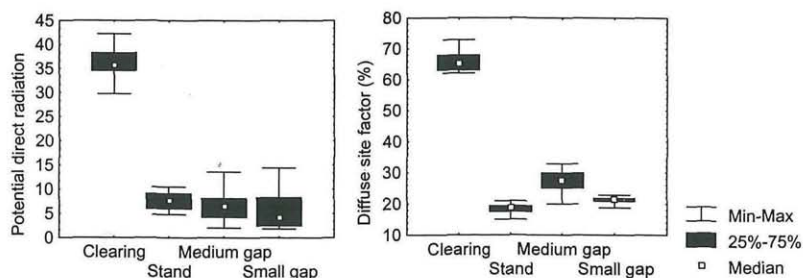


Fig. 1. Distribution of the diffuse site factor (ANDERSON 1964) and potential direct radiation in hours from April to August in the strata on the plots.

Soil properties and mycorrhiza

On the plots, three soil types were determined according to the Slovenian classification: Dystric Cambisols, Brunipodzols and Podzols. Their nine lower pedo-systematic units formed as many as 47 combinations of soil conditions in 106 plots. Therefore, soil types were divided into five groups with respect to signs of podzolization: from group one - non podzolized soil (no signs of podzolization were found on 5 cores) to group five - strongly podzolized soil (signs of podzolization were found in all cores and at least in one core up to the stage of strong podzol). The soils were less podzolized in the medium gap and clearing (mode = 3), followed by the stand (mode = 4). The highest proportion of strongly podzolized soils was found in the small gap (mode = 5).

The median values of root tips per sample were highest in the clearing (in total 24,715 in 15 samples) and in the stand (in total 23,920 in 13 samples). In the small gap, the median value of root tips was lower (in total 11,978 root tips in 17 samples), and so also was the variability of samples. The percentage of non-mycorrhizal root tips was similar in all the strata (1 % in the clearing and in the stand and 3 % in the small gap), yet there was a higher proportion of vital types of ectomycorrhizae in the stand (47 %), followed by the small gap (28 %) and the clearing (18 %) (Fig. 2a).

In the stand and in the small gap 22 types were separated in total, only four of which have been described previously to the species level. The others were preliminarily described (eight types as described by TROST & al. 1999) or linked to the type to which most characteristics corresponded, but not all. These were preliminarily assigned the name with a tilde. From these data biodiversity indexes were calculated (by KRAIGHER 1999) as follows: in the stand the species richness (d) was 4.69, in the small gap 2.56, and in the clearing 1.88; The Shannon-Weaver index of diversity (H) in the stand was 2.23, in the small gap 1.52, and in the clearing 1.48. Therefore, the diversity in the forest soils was opposite to the diversity in the ground vegetation cover (see 4.1.3.). However, because of the high diversity below ground, further investigation using molecular tools is needed for interpretation of the distribution of types of ectomycorrhizae and other parameters.

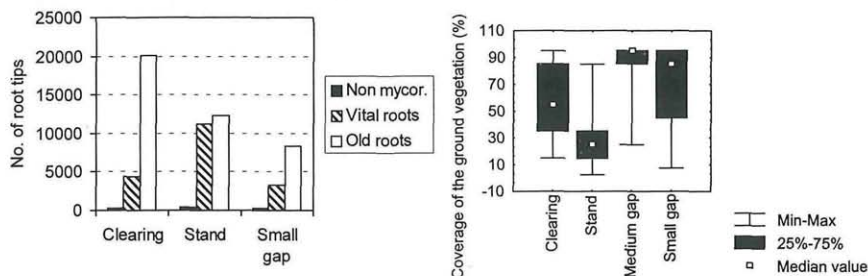


Fig. 2. (a) Number of non-mycorrhizal, vital and old root tips in the strata. (b) Ground vegetation cover including Norway spruce regeneration in the strata.

Forest ground vegetation

The median value of ground vegetation cover in the plots varied from 25 % in the stand through 55 % in the clearing to 85 % and 95 % in the small and medium gaps, respectively (Fig. 2b). Under the canopy of the spruce stand extremely few plant species were found. The total number of plant species did not essentially differ in the clearing and the medium gap, but there were changes in the combination of species and in the cover of individual species. In particular there was vigorous cover by herbs in the gaps. Cover by Norway spruce in forest ground vegetation was lowest in the stand and increased from the clearing to the small gap and to the medium gap. The Shannon index values, calculated for individual strata, showed relatively low diversity, less than 1.5. The index showed an increase in diversity from the spruce stand ($H = 1.078$) to the small gap ($H = 1.714$), where it was maximum. In the medium gap ($H = 1.422$) the amount of diversity decreased again because of extreme domination of Norway spruce in the ground vegetation. In the clearing the index values were also low ($H = 1.168$).

Norway spruce regeneration

After a partial seed year of Norway spruce in 1996, enough one-year-old seedlings for successful regeneration developed in the closed stand and partially in the small gap (Table 1). In the medium gap the number of one-year-old seedlings was low, since the cover of older regeneration was already dense. Considering the work on Norway spruce seed production and distribution by VELTSISTAS 1980 and HOHENADL 1981, we can presume that low germination rates in the clearing are mainly the result of unfavourable conditions for germination (e.g. water stress) rather than a lack of seeds.

Table 1. Median values and maximum numbers of Norway spruce plants in the plots (expressed in thousands per hectare) according to strata and developmental phase.

	Stand (N=25)		Medium gap (N=33)		Small gap (N=33)		Clearing (N=15)	
	Median	Max	Median	Max	Median	Max	Median	Max
One-year-old seedlings	360	3400	0	440	120	2240	0	120
Seedlings	560	5240	0	1760	160	4720	80	320
Saplings	0	0	160	480	0	880	0	760

The largest proportion of plots without germinated seedlings was found in the medium gap (64 %), followed by the clearing (53 %), the small gap (33 %) and the closed stand (12 %). The results for the medium gap were anticipated, since it was already covered with advanced Norway spruce regeneration. Yet the results suggest that the germination process failed in the clearing and partially also in the small gap.

Table 2. Spearman's rank order correlation between variables indicating regeneration success and the direct and diffuse site factors.

Variable	No. of plots	Direct site factor			Diffuse site factor		
		Spearman's.			Spearman's.		
		R	t(N-2)	p-level	R	t(N-2)	p-level
One-year-old seedlings	33	-0.42	-2.60	0.014	0.14	0.81	0.422
Seedlings	33	-0.44	-2.75	0.010	0.14	0.79	0.435
Saplings	33	-0.28	-1.65	0.109	0.39	2.36	0.025

We turned our attention to locate plots with no regeneration (seedlings or saplings) at all. Most of them were found in the small gap (30 %), while in all the other strata their share was 12-14 %. The ground plan of the small gap (Fig. 3) indicated that plots without any regeneration were located in the northern part of the gap, which receives more direct site factor. A similar pattern was observed in the medium gap. When we analysed the relation between the direct and the diffuse site factors and some response variables (Table 2), we found that the direct site factor negatively affected most variables, especially the number of germinated seedlings, while the diffuse site factor influenced saplings positively.

Interactions

In the next stage, the objective was to discriminate forest ground vegetation patterns with similar ecological content and to link them with spruce regeneration patterns and measured ecological variables. A matrix of 12 species of forest ground vegetation in 33 plots inside the small gap was used as input for a principal component analysis. The first three axes accounted for 46.5 % of the total variation of the vegetation cover. For an interpretation of the three axes, species with large factor loadings and with known ecology were selected (Fig. 4). The correlation between factor scores and variables describing soil and radiation properties was analysed using Spearman's rank correlation coefficient (Table 3).

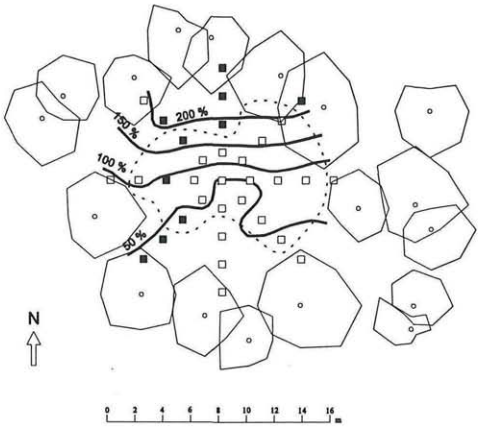


Fig. 3. Ground plan of the small gap with crown projections and a plot design. Black squares mark plots in which no germinated or older Norway spruce seedlings were found. Distribution of potential direct radiation is shown by contour lines. The surface inside the dotted line receives amounts of the diffuse site factor higher than 100 % of the average in the gap.

The first axis (Fig. 4) started with plots with low levels of direct site factor, dense ground vegetation cover and more frequent northern exposure on the right side of the figure, and proceeds to the plots with inverse values of these mentioned factors. The right side of the axis was characterised by *Polytrichum formosum*. The second axis began with plots with low levels of soil podzolization, thicker humus layer, thinner horizon A layer and dense ground vegetation cover. The second axis was negatively correlated with the density of spruce seedlings and saplings (Table 3). The third vertical axis started with plots with a lower content of organic matter in the humus layer, lower C/N ratio, lower pH values, and thinner organic humus subhorizon O_h. The number of spruce seedlings and saplings decreased along the third axis (Table 3).

Table 3. Spearman's rank correlation coefficient expressing correlation between factor scores for three factors obtained from ordination of ground vegetation and variables derived from soil, regeneration and solar radiation analyses in the small gap.

	N	Factor 1		Factor 2		Factor 3	
		Spear. R	p-level	Spear. R	p-level	Spear. R	p-level
Level of podzolization	33	-0.12	0.498	-0.43	0.012	-0.12	0.522
pH in H ₂ O	33	0.30	0.095	0.12	0.518	-0.42	0.014
C/N ratio	33	-0.07	0.691	-0.14	0.428	-0.41	0.017
Ground vegetation cover	33	0.70	0.000	0.50	0.003	-0.01	0.957
One-year-old seedlings	33	-0.12	0.491	-0.64	0.000	-0.61	0.000
Seedlings	33	-0.14	0.449	-0.64	0.000	-0.53	0.001
Saplings	33	-0.08	0.654	-0.57	0.000	-0.47	0.006
Direct site factor	33	-0.49	0.003	0.25	0.165	0.19	0.281
Diffuse site factor	33	-0.00	0.987	-0.13	0.475	-0.22	0.212

In the lower herb layer (PIC_Z2), Norway spruce was located at the right centre of the first axis, on the far right side of the second axis and above the centre of the third axis (Fig. 4). This could be interpreted as a preference for microsites with mean to low direct radiation, high levels of podzolization, mean amounts of forest ground vegetation cover and mean content of organic matter in the humus layer.

From Fig. 4, other ecological groups of plants, with sparse regeneration can be observed. The group composed mostly of *Polytrichum formosum* was especially important, since it forms a very dense carpet. This moss invades gaps after they have been created. Similar results were reported by IMBECK & OTT 1987 and BRANG 1996. For all plots in the four strata we found a negative correlation between the cover of *Polytrichum formosum* and the density of germinated and older seedlings with Spearman's $r = -0.46$ and -0.42 , respectively.

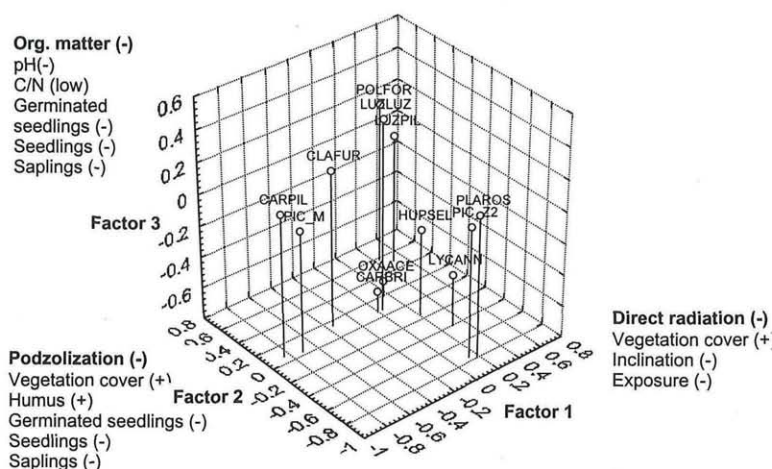


Fig. 4. Principal components analysis (Rotation: Varimax normalized) of species composition in the small gap. Plot of factor loadings with characterisation. Each point was given an abbreviated Latin species name.

Discussion

The results demonstrate that Norway spruce can successfully germinate and survive the first years under a slightly open stand. Further development of regeneration is possible only by the creation of gaps. In the small gap, the development of seedlings was highly variable inside the gap. Parts of the gaps exposed to direct site factor and parts overgrown by a dense carpet of *Polytrichum formosum* were especially unfavourable for regeneration. Abundant regeneration was found in plots with more podzolized soils, sparse ground vegetation cover, more organic matter content in the humus layer and more diffuse site factor. Survival of shaded ectomycorrhizal trees has been shown to depend on mycelial networks, and that

different types of ectomycorrhizae have a different role in nutrient acquisition and translocation (SIMARD 1996, LINDAHL & al. 1998). This may explain why natural regeneration of Norway spruce in these plots is highly mosaic: mycorrhizal connections could counteract light and temperature-dependent regeneration, and therefore needs further research. The results indicate that water stress associated with the direct site factor may prevent germination and regeneration within the gaps. This issue should be examined in further research. Other analyses, too, support this hypothesis. For example, the last snow-covered areas of the gaps in the spring coincide with successful regeneration.

In sites, comparable to the studied one, creation of medium size gaps is an appropriate silvicultural method for regeneration of Norway spruce stands, but only after a successful seed year. An even better solution would be first to open slightly the stand and wait for successful germination and then, after a year or two, to create gaps. Successful development of spruce thicket in the medium gap indicates minimum dimensions of the gaps (about 0.05 ha). Results for the clearing suggest that large clearings should be avoided. Because of the evident negative influence of direct radiation on regeneration in the early years, we recommend creating narrow gaps, which are oriented with their longer axis pointing in the east - west direction.

A c k n o w l e d g e m e n t s

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