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Establishment of *Picea abies* seedlings in a central European mountain grassland: an experimental study

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Abstract. Secondary meadows in the Krušné hory mountains, central Europe, are not colonized by woody species, although they have been abandoned for half a century and are surrounded by *Picea abies* (Norway spruce) forests. The causes of inhibition of establishment of Norway spruce seedlings in the meadows were tested experimentally. The experiment was started in a masting year to ensure sufficient seed input. Four treatments (vegetation cut; vegetation cut and litter removed; all above-ground biomass and topsoil removed; control) were combined in a factorial design. The effect of browsing, mainly by deer, was assessed by fencing half of the experimental plots. Seedling establishment differed among treatments (all pair-wise differences were significant) but was independent of fencing. In contrast, seedling survival was influenced both by the treatment and fencing. At the end of the second year, only the plots with all biomass and organic topsoil removed supported viable populations of spruce seedlings. Dense herb cover and a thick layer of slowly decaying litter are considered the main factors inhibiting the establishment of woody species.

Keywords: Abandoned meadow; Central Europe; Colonization; Norway spruce; Seedling establishment.

Nomenclature: Rothmaler et al. (1987).

Introduction

Establishment of seedlings of woody plants is a critical step in the succession from open grasslands to woodland. Various factors may potentially inhibit the establishment, such as lack of water, high water-table, fire, toxic substrata, lack of diaspores, browsing, and competition from the herb layer (e.g. Glenn-Lewin et al. 1992; Magee & Antos 1992; Lavertu et al. 1994; Prach 1994). Successful establishment of woody species has been reported frequently, whereas case studies documenting inhibition of woody species encroachment are rather rare (see Pijanovska 1985; Falińska 1991; Facelli & Pickett 1991a; Hill et al. 1995).

In central Europe, many secondary mountain grasslands, both pastures and hay meadows, have been left without management, usually due to various economic reasons. Some of these have gradually been overgrown by woody species, notably *Picea abies* (Norway spruce), the dominant of central European mountain forests above ca. 1000 m a.s.l. (Ellenberg 1988). Moreover, this species has frequently been planted since early 19th century, also at lower altitudes. However, there are large secondary mountain grasslands, abandoned shortly after World War II, where neither *Picea* nor other woody species have established. The Krušné hory Mts. area includes many such grasslands.

Successful establishment of trees in the study area was expected to be inhibited by competition from the compact grass sward. However, other reasons such as a lack of viable diaspores (the area is strongly affected by air pollution) and animal browsing could not be *a priori* excluded. To test the role of herb competition and animal browsing, the experimental destruction of the herb layer was combined with fencing. The experiment was started in the exceptionally abundant masting year of 1992/1993 to ensure sufficient input of diaspores.

Study area

The study was performed in the southwestern part of the Krušné hory (Ore) Mountains, Czech Republic, near the border with Germany, at 840 m a.s.l.; 50°23' N; 12°38' E. The area has a moderately cold climate with a mean annual temperature of 4.5 °C and an annual precipitation of ca. 1100 mm (Böer & Veseck□1975). The substratum consisted of coarse sand and fine gravel, originating from disintegration of the granite bedrock, and was poor in nutrients, with pH of ca. 4.5 (O. Rauch pers. comm.).

The area was originally covered by a mosaic of mountain beech (*Fagus silvatica*) woods and spruce (*Picea abies*) forests. In the 16th century, a small settlement was established which gradually expanded until it had ca. 900 inhabitants (of German descent) by the beginning of the 19th century. The deforested area was ca. 80 ha in size and contained pastures, hay meadows, and small arable fields and gardens surrounding scattered mountain farms. After World War II (1946-1947), the inhabitants were expelled and the whole area was left unmanaged. Nowadays, spruce plantations surround the treeless areas, while other trees native to the area, notably *Acer pseudoplatanus*, *Betula pubescens*, *Fagus silvatica* and *Sorbus aucuparia* are rare.

The experiment was set up in a lower, level part of the grassland area near a small creek, in the vicinity of mature spruce plantations. The vegetation was homogeneous and characterized – before the experiment started – by the following phytosociological relevé (visual cover estimations in %; + = cover < 1%; *r* = one or two small individuals):

Date 20.8.1992; sample plot 10 m × 10 m; level area cover of herb layer 98%, of moss layer 1%; species composition:

Holcus mollis	80%	*Galium harcynicum*	20%
Narduus stricta	5%	*Agrostis capillaris*	+
Deschampsia cespitosa	+	*Polygonum bistorta*	+
Avenella flexuosa	r	*Calamagrostis villosa*	r
Carex brizoides	r	*Carex leporina*	r
Carex nigra	r	*Poa chaixii*	r
Juncus filiformis	r	*Juncus squarrosus*	r
Moss layer:		*Polytrichum juniperinum*	1%

Methods

Four treatments were carried out, each in ten replicates, on experimental plots of 1 m^2:

(1) above-ground biomass cut and removed, litter left in the plot;
(2) above-ground biomass including litter removed;
(3) all vegetation and organic topsoil removed;
(4) control.

One part of the study area was fenced by 2.5 m high wire fence with a dense net near the ground and a loose net above, thereby excluding deer, wild boars, hares and rabbits but not small mammals (rodents). The plots within the fence were not truly independent replications, as the fenced area formed a continuous area (separate fencing of individual plots was impossible for technical reasons).

The experiment was started on the 20th of August, 1992. A massive release of spruce seeds from trees in the surroundings was expected in the early months of 1993. Established seedlings were counted in late August 1993 and 1994.

Data were analyzed by repeated measure ANOVA (von Ende 1993). Seedling numbers were log transformed log (x +1) to achieve normality and homogeneity of variances. After the log transformation, the significance of within subject factors corresponds to differences in seedling establishment, whereas the interaction terms between particular factors and time corresponds to differences in seedling survival. If seedling survival is independent of treatment, then the number of seedlings in a plot in the second year is:

$$N_2 = p\, N_1 \tag{1}$$

where N_1 and N_2 are the numbers of seedlings in a plot in respective years and p is the common probability of survival; thus

$$\log N_2 = \log p + \log N_1 \tag{2}$$

Consequently, if seedling survival is independent of treatment, the factors treatment and time (i.e. survival) are additive, without any interaction; correspondingly, the interaction term reflects the dependence of survival on the treatment.

Results and Discussion

The repeated measure ANOVA (Table 1) shows that the number of established seedlings was significantly affected ($P \leq 0.001$) by the treatments. Separate analysis performed on the data from the first year, followed by

Table 1. Simplified ANOVA table for the univariate repeated measures analysis of log(x + 1) transformed counts of seedlings. DF - degrees of freedom; F - value of test statistics; P - corresponding significance level. SS = Sum of squares; MS = Mean square.

Between treatments					
Source	SS	DF	MS	*F*	*P*
Treatment	19.888	3	6.629	128.678	< 0.0005
Fencing	0.009	1	0.009	0.181	0.673
Error	2.215	43	0.052		
Within treatments					
Source	SS	DF	MS	F	P
Time	38.369	1	38.369	1215.567	< 0.0005
Time × Treatment	3.719	3	1.240	39.276	< 0.0005
Time × Fencing	0.224	1	0.224	7.090	0.011
Error	1.357	43	0.032		

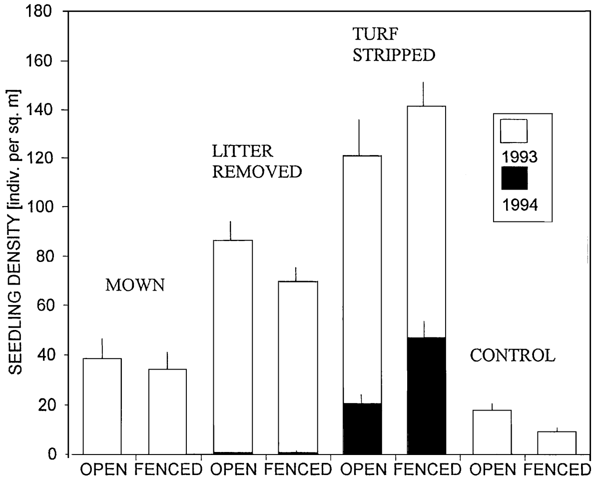

Fig. 1. Average seedling density in plots under various treatments, in the first (1993) and second (1994) year of the experiment. MOWN: above-ground biomass cut and removed, litter left in the plot; LITTER REMOVED: above-ground biomass including litter removed; TURF STRIPPED: all vegetation and organic topsoil removed; CONTROL: untreated control plots. In 1993 the seedling densities differed significantly among treatments (all pairwise comparisons significant at $\alpha = 0.05$) and did not differ significantly between fenced and open plots. In 1994, the differences between fenced and unfenced turf-stripped plots were significant.

multiple comparison of means (Tukey-test), revealed that the differences between all possible treatment pairs were significant ($P < 0.05$). The numbers of established seedlings were not influenced by fencing. Seedling survival from 1993 to 1994 differed between treatments (significant interaction term Treatment × Time; $P < 0.001$) and also between fenced and unfenced plots (significant Time × Fencing; $P < 0.05$). Successful establishment of tree seedlings is evidently inhibited by the compact herb layer (Fig. 1). – The above-ground biomass in a similar vegetation at a nearby site was estimated to be 315 g/m^2 (including 100 g/m^2 standing dead; litter not analyzed) (Lepš et al. 1995).

No seedlings survived until the second season in the untreated control plots and in those plots where only the above-ground biomass was cut and removed. Very few seedlings with low vitality survived in the plots from which the litter was removed. Viable seedlings thus survived only in those plots from which the turf was stripped (Fig. 1). The seedling establishment was thus effectively prevented in the untouched plots and in those that were mown, whereas only severe mechanical disturbance, that destroyed the herb layer, caused the seedlings to survive. All seedlings recorded in 1994 were apparently established in the masting year 1993. Hence it may be suggested that seed input probably does not occur in usual years. High pollution may be responsible for this (Vacek 1981).

Elimination of browsing by large mammals may slightly increase the probability of seedling survival (see Table 1). Although in the present study the sampling units within fenced/unfenced treatments were not true replications, the fact that seedling survival was influenced by fencing whereas establishment was not, suggests the possible effects imposed by browsing.

The results indicate that spontaneous afforestation of the abandoned grasslands cannot be expected unless the turf is opened by disturbance in these and other comparable sites in the Krušné hory (Ore) Mountains. This conclusion corresponds with our observation that the only spontaneous tree establishment in the area was on the ruins of deserted buildings. Blažková (1991), in her phytosociological survey of montane meadows from the area, noted that the composition of herbaceous species changed after cessation of mowing, but she did not observe colonization by trees (see also Hundt 1964). Comparable inhibition of *Picea abies* establishment by a compact herb layer was also reported from Norway (Kielland-Lund 1981).

Comparing the area under study with other similar abandoned mountain meadows or pastures in central Europe, there is high variability in the colonization by woody species (see also Prach 1994). Some grasslands remain without woody species for years, while others are colonized rapidly by shrubs and trees. It is difficult to explain this variability without a large-scale experimental study in a large number of meadows. It seems, however, that the establishment of woody species is particularly inhibited in abandoned mountain grasslands of colder regions with acid and nutrient-poor soils where decomposition of accumulated litter is slow. The present study represents such a case. However, this hypothesis is based on our field experience only – no comparative exact data are available from central Europe – and requires further testing.

Several experimental studies demonstrated that large amounts of litter can both inhibit and stimulate tree establishment (Facelli & Pickett 1991a, b; Facelli 1994; Hill et al. 1995). The negative influence of biomass from surrounding vegetation on tree seedling performance was demonstrated in the experiments of Berkowitz et al. (1995). However, it appeared that biomass, intensity of competition, and the growth of tree seedlings were not consistently related to each other, because abiotic site conditions interfered. Unfortunately, the present study does not enable us to separate the effect of litter on the inhibition of tree establishment from that of the living biomass.

The role of a compact herb layer in preventing establishment of woody species was also demonstrated by Skoglund & Verwijst (1989); De Steven (1991); Magee & Antos (1992) and others. In a compact herb layer, gap formation is often needed for woody species establishment (Pickett & White 1985; Hill et al. 1995). Artificial disturbance can be applied if natural disturbance does not occur. Van der Valk (1992) distinguished several types of barriers that must be removed to make successful colonization of a site by any plant possible, thus providing a 'colonization window' (Johnstone 1986; van der Valk 1992). The present study provides an example of a 'vegetation barrier' to successful colonization. Animal browsing obviously played a minor role, although it must be potentially considered as an important ecological factor in this and other similar cases (e.g. Hill et al. 1995).

It is evident from all above mentioned references that establishment and survival of seedlings of woody species in any particular grassland is subjected to many factors and is hardly predictable by a simple way without properly designed experiments.

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