Restoration of species-rich limestone grassland communities from overgrown land: the importance of propagule availability

Meelis Pärtel a,∗, Rein Kalamees a, Martin Zobel a, Ejvind Rosén b

a Institute of Botany and Ecology, University of Tartu, Lai 40, EE2400 Tartu, Estonia
b Department of Ecological Botany, Uppsala University, Villavägen 14, S-75236 Uppsala, Sweden

Received 16 September 1997; received in revised form 22 January 1998; accepted 3 February 1998

Abstract

A field experiment was established in the eastern coast of the Baltic Sea to test the relative roles of the availability of propagules and light competition in the restoration dynamics of a former calcareous grassland overgrown by pine (Pinus sylvestris L.). The treatments were: clear-cutting of trees with additional grazing and transplantation of sods from an open grassland with all possible sources of propagules. Species richness and composition were studied on a small-scale during 7 years in the transplanted patches of 20 × 20 cm and in their surroundings of 50 × 50 cm. In the cut and grazed site the species richness increased. Transplantation of sods from an open species-rich grassland did not result in higher richness even in their closest surroundings. In the forest, transplanted patches lost their high species richness by the second year. In the cut and grazed site, transplanted patches remained species-rich, but after 3 years, control patches reached the same level of species richness. In landscapes where former species-rich limestone grasslands are overgrown, but the local species pool has not yet changed, restoration of semi-natural grassland communities does not require the additional input of diaspores of grassland species. Transplantation of sods is potentially important method of community restoration in case of impoverished local species pools. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Alvar; Community management; Dispersal; Grassland restoration; Species pool; Succession; Transplantation

∗ Corresponding author. Tel.: +372 7 441325; fax: +372 7 441272; e-mail: pmeelis@ut.ee

0925-8574/98/$19.00 © 1998 Elsevier Science B.V. All rights reserved.
PII S0925-8574(98)00014-7
1. Introduction

The area of species-rich semi-natural grasslands has decreased considerably during the last decades throughout Europe (Rosén, 1982; Gibson et al., 1987; Bakker, 1989; van Dijk, 1991; Ejrnæs and Bruun, 1995; Kiefer and Poschlod, 1996). Traditional cultural landscapes have been considered to be especially valuable, representing the history of environmentally friendly land-use in Europe over several thousands of years. In most cases species-rich grasslands need continuous management—grazing of suitable intensity or mowing (Rosén, 1982; Gibson et al., 1987). Otherwise, overgrowing by taller species like graminoids, shrubs and trees will eliminate, through light competition, many typical grassland species resulting in considerably lower species richness (Rosén, 1982; Kull and Zobel, 1991; Bobbink and Willems, 1993).

A scientific nature protection study should be based on community ecology experiments (van der Maarel and Kötli, 1996). Experiments to study the restoration of species rich grasslands have been carried out in several countries. Most of them deal with restoration processes on abandoned cultivated land (Gibson and Brown, 1991a,b; Olff and Bakker, 1991; Berendse et al., 1992; Bobbink and Willems, 1993; Hutchings and Booth, 1996; Willems and van Nieuwstadt, 1996). Less work has been done on former grasslands which have been overgrown by shrubs and trees forming a species-poor secondary brushwood. The latter problem has been more actual in the calcareous grasslands of northern Europe, where most of the clearing experiments have been carried out (Laasimer, 1981; Hæggström, 1983; Rosén, 1988; Zobel et al., 1996), but also elsewhere (Kiefer and Poschlod, 1996). Though the importance of long-term studies has been stressed (Rosén, 1995; Bakker et al., 1996b), there is a deficit of long observation series in restored grasslands, which is largely a result of problems with long term funding (Tilman, 1989). Despite the fact that the existing restoration experiments have shown some success, the resulting ‘restored communities’ are mostly far from being real ‘ancient’ grasslands, the development of which will probably take centuries not only in abandoned fields (Gibson and Brown, 1991b) but also in overgrown areas (Kiefer and Poschlod, 1996; Zobel et al., 1996). Aerts et al. (1995) concluded that heathland restoration requires the active introduction of \textit{Calluna vulgaris} (L.) Hull propagules. Restoration of a species rich grassland requires the immigration or introduction of propagules of a large number of species. The importance of different diaspore sources during restoration succession is mostly unknown. The studies of the seed banks of grazed and overgrown alvar grassland communities have shown that although the seed bank may be important for very early successional stages (Kiefer and Poschlod, 1996) or for populations of certain species (Willems, 1988), its overall importance as a seed source for species rich community restoration is negligible (Bakker et al., 1996a; Bekker et al., 1997; Kalamees and Zobel, 1997). There are very few studies of the seed rain in calcareous grasslands. Poschlod (1993), Jackel and Poschlod (1994), Kiefer and Poschlod (1996) were able to trap mainly the seeds of ruderal species, bushes and trees. Recently, the importance of seed dispersal by sheep has been described (Fischer et al., 1996). Though there is no
doubt that the results of community restoration depend a great deal on the local species pool (Pärtel et al., 1996), the presence of a diaspor does not inevitably mean that it will germinate and establish in particular conditions.

In Estonia, a small country on the eastern coast of the Baltic Sea, alvars—calcareous grasslands on thin soils—were quite widespread until the middle of this century (Laasimer, 1965, 1981). After that the changes in land use were drastic—grazing of animals ceased in many places. Today only a fraction of the grasslands remain and only a few are still grazed. In 1990, a field experiment was established to study the possibilities of restoring a species-rich alvar grassland from land overgrown by Pinus sylvestris L. Clear-cutting of trees and grazing were used as restoration treatments. The results showed that small-scale species richness increased after the improvement of light conditions (Pärtel and Zobel, 1995).

In the present study, we were interested in: (a) the changes in species richness and species composition during the 7 years of restoration management, and (b) whether the availability of diaspor was limiting the increase of richness and shoot density and change of species composition. The transplantation of sods from an open grassland to a community under restoration management was used as an experimental treatment. This means that the contribution of all possible sources of propagules of grassland species (seed bank, rhizomes, seed rain and vegetative dispersal from transplanted plants) were artificially increased. Also, we tried to estimate the role of different seed sources in restoration succession from overgrown land to open grassland.

2. Methods

The study site was located in the coastal zone of western Estonia (58°37′N, 23°35′E) in a former alvar grassland (Pärtel and Zobel, 1995). The initial grassland community belonged to the Filipendula vulgaris—Trifolium montanum association with common species such as Anthyllis vulneraria, Antennaria dioica, Briza media, Festuca ovina, Galium verum, Helictotrichon pratense, Hieracium pilosella, Thymus serpyllum etc. (Laasimer, 1965). Nomenclature of species follows that of the Estonian Flora (Eesti NSV floora, 1959–1984). The grassland had become overgrown with Pinus sylvestris since grazing ceased approximately 40 years ago. The field layer under the trees still contained many species found in grasslands, but it had a significantly lower shoot density and a higher herb canopy. The thickness of the soil layer was 10–12 cm, below that lies a mixture of coarse limestone pebbles. Soil pH was 6.9–7.2 (Kalamees, 1995). The mean standing crop of the field layer in the overgrown area was 116 g and in the open grassland 168 g dry weight per 1 m² (Erikson, 1993). The soil seed bank of the overgrown community contains 22 species (Kalameees and Zobel, 1997).

In 1990 a homogeneous young forest expanded in the area. Two similar adjacent sites of approximately 20 × 20 m were chosen. One was left untouched while in the other site, pines were cut and grazing by sheep was introduced (one ewe and one lamb for 1 week twice a year). From 1994 onwards, grazing was simulated by cutting all above ground vegetation and by disturbing the moss layer.
In 1990 four patches of sod (20 × 20 cm) from an open grassland approximately 100 m away, were transplanted into both sites. Transplanted patches and an area of 50 × 50 cm around each patch were marked with sticks. A similar system of vegetation sampling was used in the study community without transplantation: six control patches of 20 × 20 cm with surrounding areas of 50 × 50 cm. All rooted vascular plant species were recorded from each transplanted and control patch and from their surroundings. Recordings were made in the beginning of July during 7 years, 1990–1996.

Differences from the initial situation (1990) were tested for each following year. The differences between patches or their surrounds with and without transplantation during one year were checked. \( T \)-test was used for the statistics.

The percentage of species in the surrounds of the control patches which belonged to persistent seed bank (Kalamees and Zobel, 1997), and the percentage of wind-dispersed and animal-dispersed species (Hodgson et al., 1995; Poschlod et al., 1996) were calculated for each year. Comparisons between manipulated and non-manipulated sites, as well as between the initial situation and all the following years were carried out. The study plots were compared with the local species pool which was defined as all species in the local landscape unit (approximately 1 km²), consisting of open alvar grasslands and overgrown grasslands of different successional stages.

3. Results

Species richness dynamics are presented in Fig. 1. In the forest, species richness in transplanted patches was higher than in the control only in the first year, afterwards the levels of species richness equalized. There were no differences in species richness in the surrounds of transplanted and control patches. In the cut and grazed area, species richness in the transplanted patches remained constant while in the control patches a continuous increase of the richness was observed. Similar increases in species richness were also observed in the surrounds of both transplanted and control patches.

Species which were not in the initial community in 1990 but which arrived into the surrounds of transplanted or control patches are indicated in Table 1. Each species, which was either present in some of the transplanted patches in 1990, or which was present in the forest soil seed bank is identified. Similarly, the ability to disperse by wind or by animals is also indicated for each species. Nine to ten species arrived in the surrounds of both experimental and control patches in the forest, regardless of whether there was a patch in the centre or not. In the cut and grazed area, 20 and 21 species appeared, respectively.

There were more invading species in the cut and grazed site per year, than in the forest, but the final cumulative number of species per whole series did not differ much.

The percentage of wind-dispersed species in the local species pool was 27 and the percentage of animal-dispersed species were 33. In Fig. 2, the mean percentage of
Table 1
Newly arrived species in the surrounds of transplanted and control patches of 20×20 cm in two sites under different management regimes

| Year of arriving | Forest | Cut + grazed | | | |
|------------------|--------|--------------|------------------|------------------|
|                  | Transplanted | Control | Transplanted | Control |
| 1991             | Astragalus danicus<sup>TR</sup><sup>SB</sup> | (Cerastium holosteoides)<sup>W</sup> | Hieracium pilosella<sup>TR</sup><sup>SB</sup><sup>W</sup>, Anthyllis vulneraria<sup>TR</sup><sup>W</sup>, Linum catharticum<sup>TR</sup><sup>SB</sup><sup>A</sup> | Hieracium pilosella<sup>SB</sup><sup>W</sup>, Anthyllis vulneraria<sup>W</sup>, Cerastium holosteoides<sup>W</sup>, Ranunculus polyanthemos<sup>A</sup> |
| 1992             | Thymus serpyllum<sup>TR</sup><sup>SB</sup> | Polygala amarella<sup>A</sup>, Hieracium praealta<sup>W</sup> | Antennaria dioica<sup>TR</sup><sup>W</sup>, Carex caryophylica<sup>SB</sup><sup>A</sup>, Hypericum perforatum<sup>SB</sup><sup>W</sup>, (Leontodon autumnalis)<sup>W</sup>, Leucanthemum vulgare<sup>TR</sup>, Polygala amarella<sup>A</sup> | Arenaria serpyllifolia<sup>SB</sup><sup>W</sup>, Leucanthemum vulgare, Linum catharticum<sup>SB</sup><sup>A</sup> |
| 1993             | Carlina vulgaris<sup>W</sup>, (Medicago lupulina)<sup>SB</sup> | (Campanula rotundifolia)<sup>SB</sup><sup>W</sup>, Carlina vulgaris<sup>W</sup>, (Medicago lupulina)<sup>SB</sup>, Helictotrichon pubescens<sup>A</sup> | (Campanula rotundifolia)<sup>SB</sup><sup>W</sup>, Astragalus danicus<sup>SB</sup>, (Trifolium pratense)<sup>TR</sup><sup>A</sup> | Trifolium repens<sup>A</sup>, Euphrasia officinalis<sup>W</sup>, Fragaria virginia<sup>A</sup>, Poa compressa, Polygala amarella<sup>A</sup>, Listera ovata<sup>W</sup> |
| 1994             | (Campanula rotundifolia)<sup>SB</sup><sup>W</sup>, Carex caryophyllea<sup>SB</sup><sup>A</sup>, (Linum catharticum)<sup>A</sup>, Listera ovata<sup>W</sup> | (Polygala comosa)<sup>A</sup>, (Trifolium repens)<sup>A</sup> | Campanula rotundifolia<sup>SB</sup><sup>W</sup>, Carex caryophyllea<sup>SB</sup>, (Knautiavulgaris)<sup>A</sup>, Ranunculus bulbosus<sup>SB</sup><sup>A</sup> |
| 1995             | Helictotrichon pubescens<sup>A</sup> | (Ranunculus polyanthemos)<sup>A</sup> | | |
| 1996             | Hieracium praealta<sup>W</sup>, Euphrasia officinalis<sup>W</sup> | Alchemilla vulgaris<sup>A</sup>, Artemisia campestris, Campanula glomerata, Potentilla tabernaemontani, Vicia cracca | Hieracium praealta<sup>W</sup>, Astragalus danicus<sup>SB</sup>, Dactylis glomerata<sup>SB</sup>, Trifolium pratense<sup>A</sup> |
Table 1 (Continued)

<table>
<thead>
<tr>
<th>Year of arriving</th>
<th>Forest</th>
<th>Cut+grazed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Transplanted</td>
<td>Control</td>
</tr>
<tr>
<td>Initial number of species per series</td>
<td>31</td>
<td>37</td>
</tr>
<tr>
<td>Number of invaded spp.</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td>Final number of species per series</td>
<td>40</td>
<td>47</td>
</tr>
<tr>
<td>%TR</td>
<td>22</td>
<td>—</td>
</tr>
<tr>
<td>%SB</td>
<td>56</td>
<td>30</td>
</tr>
<tr>
<td>%W</td>
<td>44</td>
<td>50</td>
</tr>
<tr>
<td>%A</td>
<td>22</td>
<td>40</td>
</tr>
</tbody>
</table>

Abbreviations: TR—species was transplanted into the particular site in 1990, SB—species was found in the local forest seed bank, W—species is wind-dispersed, A—species is animal dispersed. Species in brackets were observed in the particular series only during 1 year. The cumulative numbers of arrived species per site are given. Note that transplanted series had 4 and the control series 6 replicates. Percentages of different types of species dispersal are given—since one species may use different methods to reach a site simultaneously, the sum of percentages is higher than 100%.
wind and animal-dispersed species in the surrounds of the control patches is given. In the forest, the percentage of both dispersal types was lower than the mean for the local species pool and it did not change during the 7 years. In the cut and grazed site, the initial percentages of wind- or animal-dispersed species were similar to that in the forest. Following the start of restoration management, both percentages reached the levels characteristic for the local species pool. In the case of wind-dispersed species, this level was already achieved after the first year while in the case of animal-dispersed species, the level characteristic of the local species pool was reached after 3 years.

The percentage of species which had viable seeds in the local soil seed bank was slightly lower than or equal to the percentage in the local species pool (Fig. 2). However, there were no evident differences between the forest and the cut and grazed area. Also, there were no statistically significant differences between years.

Fig. 1. Left side: dynamics of species richness in transplanted grassland patches of 20 × 20 cm (white columns, n = 4) and similar areas (control patches) of the original community (dark columns, n = 6) during 7 years. Right side: dynamics of species richness in the surrounds of the transplanted patches (50 × 50 cm, white columns) and the control patches (dark columns). Means ± S.E. are given. An asterisk above a column indicates a significant difference from the initial year (1990, t-test, P < 0.05). Underlined year numbers indicate significant difference between transplanted and control series within the same study site (t-test, P < 0.05).
Fig. 2. The mean percentage ± S.E. of wind- and animal-dispersed species, and the percentage of species found in the local forest soil seed bank in the surrounds of the control patches in the forest (squares) and in the cut and grazed site (circles) during 7 years. Significant differences between sites are indicated by the underlining of the respective year, significant differences from the initial value (1990) are indicated by filled symbols ($P < 0.05$). The dashed line indicates the corresponding percentage in the local species pool.

When the species, which newly arrived at the study plots, are considered (Table 1), one can see a few species (*Astragalus danicus*, *Carex caryophyllea*, *Dactylis glomerata*, *Medicago lupulina*) which are present in the seed bank but which lack the ability to disperse effectively by wind or animals. In these cases, one would expect that they originate from the local seed bank.
4. Discussion

In an overgrown alvar grassland, species richness per unit area started to increase when restoration management (cutting of trees and grazing by sheep after that) were initiated. Rapid changes took place during the first 4 years, after that succession slowed. The lack of diaspores was not inhibiting succession from young pine forest to open grassland. Patches of sod from grassland, transplanted into the forest, already lost their high species richness by the following year. Patches, transplanted into a cut and grazed site, kept their high richness, but did not influence even their close surroundings—species richness increased there just as quickly as it did in control plots. The influence of a transplanted sod is evidently stronger if the local species pool has impoverished.

The presence of diaspores may have a significant effect on the restoration of populations of particular species and whole communities (Poschlod and Jordan, 1992; Bobbink and Willems, 1993; Jackel and Poschlod, 1994; Fischer et al., 1996; Willems and van Nieuwstadt, 1996). The different result of the present study may be explained by the nature of the landscape around the study sites. In the strongly fragmented landscapes of Central Europe the increase of species richness under restoration management may be directly dependent on the arrival of diaspores of certain species (Jackel and Poschlod, 1996). In the Northern European countries, where natural and seminatural landscapes spread more or less continuously over large areas, the effect of isolation on species richness is not usually evident (Eriksson et al., 1995). As we noticed earlier (Paërtel and Zobel, 1995), the overgrowing of the former alvar grassland in the current study area by *Pinus sylvestris* significantly reduced species richness per area, but none of the species disappeared totally from the local species pool. Consequently, rapid reimmigration is possible and restoration management does not require additional introduction of diaspores.

The proportion of wind- and animal-dispersed species in the species list was relatively lower in the overgrown area. After the cutting of trees, these proportions increased and reached the levels in the local species pool. One may conclude that dispersal by wind is the most rapid way for species to arrive in sites under restoration management; dispersal by animals becomes important some years after the clear-cutting. Most diaspores travel only short distances (Harper, 1977; Verkaar et al., 1983; McEvoy and Cox, 1987; Poschlod et al., 1996), but the structure of the canopy certainly has an effect on the distance of dispersal. Wind-dispersal is expected to be more efficient in the case of an open canopy. Seed rain may also include ruderals which do not belong to a particular (semi)natural community (Peart, 1989; Skoglund, 1990; Poschlod and Jordan, 1992; Holzapfel et al., 1993; Kiefer and Poschlod, 1996), but their establishment is more probable when there are ‘free’ gaps in the field layer. In our study sites, we did not notice the establishment of any ruderal species, the majority of the invading species were typical for calcareous grassland communities.

Kiefer and Poschlod (1996) found that in a cleared area on an overgrown former calcareous grassland, colonization took place primarily as a result of the germina-
tion of diaspores from the diaspore bank. We expected more species from the bank in the grazed site, since small disturbances by animals may expose the soil surface and activate the seed bank (Graham and Hutchings, 1988). However, our results did not provide any evidence that the seed bank significantly contributes to the increase in the number of species following restoration management since the proportion of species having persistent seed bank did not differ between sites and between years. It is probable that newly appeared individuals of certain species, like some legumes, Carex caryophyllea and Dactylis glomerata originate from the seed bank, but these changes have negligible influence on the level of species richness. We have to agree with previous authors (Thompson and Grime, 1979; Bakker et al., 1996a; Bekker et al., 1997) that limestone grassland species were rather poorly represented in the seed bank of the overgrown grassland and therefore the seed bank cannot be an effective source for the restoration of such grasslands.

As conclusion, the restoration of species-rich calcareous grassland community is successful in landscapes where the local pool of appropriate species is still present. No artificial input of diaspores will be needed. In isolated sites where the species are not any more available, much more efforts are needed to retrieve former grassland and the result is still doubtful. Transplantation of sods from species-rich sites can have a positive effect in these cases.

Acknowledgements

J. Pütsepp, H. Zingel, R. Mändla, M. Suurkask and E. Möls assisted during field work. This research was financed by the Estonian Science Foundation (Grants 2391 and 3280) and the Royal Swedish Academy of Science (for E. Rosén). We would like to thank E. Roosaluste for critical comments on the manuscript.

References

Manag. 41, 171–183.
Institute of Botany and Ecology, University of Tartu. (In Estonian)
Eriksson, Å., Eriksson, O., Berglund, H., 1995. Species abundance patterns of plants in Swedish
Fischer, S.F., Poschlod, P., Beinlich, B., 1996. Experimental studies on the dispersal of plant and
Gibson, C.W.D., Brown, V.K., 1991a. The effects of grazing on local colonisation and extinction during
Gibson, C.W.D., Brown, V.K., 1991b. The nature and rate of development of calcareous grassland in
Graham, D.J., Hutchings, M.J., 1988. A field investigation of germination from the seed bank of a chalk
120, 1–66.
Chapman and Hall, London.
Holzapfel, C., Schmidt, W., Shmida, A., 1993. The role of seed bank and seed rain in the recolonization
Hutchings, M.J., Booth, K.D., 1996. Studies on the feasibility of re-creating chalk grassland vegetation
on ex-arable land. I. The potential roles of the seed bank and the seed rain. J. Appl. Ecol. 33,
1171–1181.
Jackel, A.K., Poschlod, P., 1994. Diaspore production and the influence of the size of diaspore rain in
two calcareous grassland sites. Ber. Inst. Landschafts-Pflanzeno¨kologie Univ. Hohenheim 3, 123–
132.
Jackel, A.K., Poschlod, P., 1996. Why are some plant species of fragmented continental dry grasslands
frequent and some rare? In: Settele, J., Margules, C.R., Poschlod, P., Henle, K. (Eds.), Species
Kalamenees, R., 1995. The seed bank in an Estonian chalk grassland—comparison of different succes-
Kalamenees, R., Zobel, M., 1997. The seed bank in an Estonian calcareous grassland: comparison of
In: Settele, J., Margules, C.R., Poschlod, P., Henle, K. (Eds.), Species survival in fragmented
711–714.
Laasimer, L., 1981. Anthropogenous changes of plant communities and problems of conservation. In:
Pärtel, M., Zobel, M., 1995. Small-scale dynamics and species richness in successional alvar plant
communities. Ecography 18, 83–90.
Pärtel, M., Zobel, M., Zobel, K., van der Maarel, E., 1996. The species pool and its relation to species
J. Ecol. 77, 236–251.


