

Cryptogams in calcareous grassland restoration: perspectives for artificial vs. natural colonization

– Michael Jeschke –

Abstract

Cryptogams form a large part of dry grassland plant species richness. As a frequently used tool in grassland restoration, hay transfer is known to transfer cryptogam species. This might result in cryptogam stands differing from those achieved by natural succession. To assess hay transfer as a medium for cryptogam restoration, I analysed species composition of cryptogams in the hay of dry grasslands in Southern Germany, how fast they establish, and how fast they colonize adjacent plots. Cryptogam samples from hay showed species combinations similar to those of the mown sites and large shoot numbers to be present in the hay. Even low-growing and rare species were found in the hay. Hay receptor sites showed larger pleurocarpous moss and fruticose lichen patches than comparable sites without hay transfer, indicating earlier arrival of viable diaspores at the receptor sites. For acrocarpous mosses that colonize new sites by spores, no differences in turf size between succession and restoration plots were found. This shows that species transferred by hay have a distinct advantage over species that have to arrive at newly opened sites by natural means, i.e. many years later. The colonization from small restoration sites into adjacent areas without hay transfer proceeds with moderate speeds of about 1 to 2 m per year, probably with wind drift as the most important dispersal agent. Abundant cryptogam species including most pleurocarpous mosses and some *Cladonia* species rarely producing spores will be greatly enhanced by hay transfer. Nevertheless, the facilitation of pleurocarpous mosses may be detrimental to acrocarpous moss and epigeaic and saxicolous lichen species diversity, which should be considered in dry grassland restoration. I suggest a combination of different restoration measures in a mosaic pattern to create suitable conditions for a maximum of cryptogam species.

Zusammenfassung: Kryptogamen bei der Renaturierung von Kalkmagerrasen: Perspektiven für künstliche Ansiedlung gegenüber natürlicher Besiedlung

Kryptogamen bilden oft einen erheblichen Anteil der Phytodiversität von Magerrasen. Durch die bei der Renaturierung von Magerrasen inzwischen regelmäßig angewandte Übertragung von Mahdgut werden auch viele dieser Kryptogamen auf neue Flächen verbracht. Dies kann zu Beständen führen, die sich deutlich von durch natürliche Sukzession entstandenen unterscheiden. Um die Eignung von Mahdgutübertragung zur Erhaltung von kalkmagerasentypischen Kryptogamenarten festzustellen, wurde zunächst die Artenzusammensetzung des Mahdguts eines süddeutschen Kalkmagerrasens erfasst. Dann wurden die Ansiedlung und das Wachstum der Arten auf den neuen Flächen ermittelt. Schließlich wurde die Ausbreitung der Arten von den neu angesiedelten Beständen in die Umgebung untersucht. Die Kryptogamenfraktion des Mahdguts zeigte eine ähnliche Zusammensetzung wie die gemähten Bestände. Sie wies eine hohe Anzahl von Moosstängeln und Flechtenthalli sowie deren Fragmenten auf, darunter auch niedrigwüchsige und seltene Arten. Insgesamt wurden 59 % der auf der Fläche gefundenen Arten im Mahdgut nachgewiesen. Mahdgut-Rezeptorflächen zeigten größere Lager von pleurokarpen Moosen und Flechten als Sukzessionsflächen, was auf eine frühere Ankunft der Arten bei Mahdgutübertragung hinweist. Akrokarpe Moose, die sich vorwiegend über Sporen ausbreiten, zeigten hingegen keine Unterschiede in der Lagergröße. Durch die Mahdgutübertragung werden also im Mahdgut enthaltene Arten gefördert, was andere Arten benachteiligen kann. Die anschließende Ausbreitung der Arten in die angrenzenden Flächen geht mit ca. 1 bis 2 Metern pro Jahr voran, wobei der Wind den mutmaßlichen Hauptausbreitungsfaktor darstellt. Durch Mahdgutübertragung werden insgesamt häufige Kryptogamenarten mit vorwiegend vegetativer Ausbreitung gefördert, d. h. viele pleurokarpe Moose und einige *Cladonia*-Arten. Diese Förderung von raschwüchsigen pleurokarpen Moosen kann allerdings eine verringerte Diversität von Erdflechten und akrokarpen Moosen bewirken. Daher empfehle ich eine streifenweise Kombination verschiedener Renaturierungstechniken, um möglichst viele Kryptogamenarten zu erhalten.

Keywords: Bryophyte, diversity, dry grassland, hay composition, hay transfer, succession, topsoil removal.

1. Introduction

Calcareous grasslands are characterized by their high species richness (POSCHLOD & WALLIS DE VRIES 2002, DENGLER 2005) and are an essential habitat for many endangered plant species (WILLEMS 2001). Cryptogam species may account for a large part of dry grassland species richness (up to 46%, Jeschke, unpublished data), especially on small spatial scales (DENGLER 2005, INGERPUU et al. 2005, JESCHKE & KIEHL 2006a).

However, calcareous grasslands have strongly declined in their extent during the last 150 years, with only some fragments remaining (WILLEMS 2001, POSCHLOD & WALLIS DE VRIES 2002). Therefore, restoration projects have been initiated to newly create or enlarge existing calcareous grasslands to provide habitats for endangered species (BAKKER & BERENDSE 1999, PFADENHAUER & MILLER 2000, WALKER et al. 2004). High nutrient levels of restoration sites can be reduced by topsoil removal in order to provide appropriate habitat conditions for low-productivity dry grassland species (KIEHL et al. 2003).

Since many dry calcareous grassland cryptogam species are dispersed mainly by shoot or thallus fragments (ANDERSON et al. 1982, VAN TOOREN et al. 1990, KETNER-OOSTRA et al. 2006, PAULIUK et al. 2011), they have difficulty colonizing new sites (VAN TOOREN et al. 1990). Hay transfer has proven to generate stands with a high rate of characteristic species, at least for vascular plants (KIRMER & MAHN 2001, KIEHL et al. 2006). Hay transfer does not only disperse vascular plants but also cryptogam species (KIRMER & MAHN 2001, JESCHKE & KIEHL 2006a, EICHBERG et al. 2010), and should therefore be a suitable measure to establish new grasslands with high cryptogam species richness.

However, as vegetation data from two calcareous grassland sites show, species composition and texture of the cryptogam layer differed between restoration sites and adjacent ancient grassland plots (JESCHKE & KIEHL 2006a, b). This may be an effect of hay composition and the colonization potential of the transferred species.

To assess hay transfer as a means of cryptogam restoration, it is necessary to know which cryptogams are present in the hay, how fast they establish, and how fast established stands colonize adjacent sites. Therefore, this study aims to quantify the number of macroscopic diaspores in the hay of a nature reserve rich in cryptogam species and determine dispersal distance and arrival time for semi-dry grassland cryptogam species in order to better understand dry grassland restoration dynamics in the cryptogam layer.

2. Study area

This study was carried out in the nature reserves “Garching Heide” (Germany, 48° 17' N, 11° 39' E) and “Kissing Heide” (Germany, 48° 17' N, 10° 57' E) in Southwest Germany. The semi-dry grassland vegetation of the two sites belongs to the *Cirsio-Brachypodium* Klika et Hadac in Klika 1948 and the bryophyte community *Abietinellum abietinae* Stodiek 1937 (cf. NEUMAYR 1971, MARSTALLER 2009). The dry grasslands of the *Garching Heide* are considered as *Pulsatillo-Caricetum humilis* Gauckler 1938, the cryptogam layer by the main bryophyte communities *Tortelletum inclinatae* Stodiek 1937 and *Abietinellum abietinae* Stodiek 1937 and, in open microsites, the epigeaic lichen community *Toninio-Psoretum decipientis* Stodiek 1937.

Between 1991 and 1993 (Garching Heide) and in 1995 (Kissing Heide), fields adjacent to the nature reserves were converted into calcareous grasslands by removal of the nutrient-rich topsoil and transfer of fresh diaspore-containing hay from the nearby nature reserve (for detailed information confer KIEHL et al. 2006). The topsoil was removed down to the nutrient-poor C-horizon consisting of calcareous gravel and silt. Other restoration sites near Garching Heide had received hay directly after ploughing, without soil removal. Another field adjacent to the nature reserve was abandoned in 1959 and in this article is referred to as former arable field.

3. Methods

3.1. Vegetation data and hay composition

I used vegetation data from 4-m² plots recorded between 2003 and 2008 to calculate mean species diversity and mean cover of the cryptogam groups present in the study areas Garching Heide and Kissinger Heide.

In August 2011, hay samples were collected from the nature reserve and the former arable field (succession since 1959) in the Garching Heide. As the mown hay was immediately removed for large-scale restoration measures, patches of hay remaining at the mown site were used for hay sampling. At each grassland, five 1-dm³ samples (manually compressed hay collected in a 1 litre plastic container) of hay containing cryptogams were collected at randomly selected plots. Bryophyte and lichen shoots and fragments were extracted from the hay and shoot numbers as well as dry weight of each species recorded. Fragments and shoots were categorized in three categories: intact shoots, larger fragments with at least one branching, and non-branched fragments larger than 10 mm in length. Fragments shorter than 10 mm were less abundant, difficult to determine to species level and therefore excluded. *Cladonia* species were soaked before disentangling to minimize fracturing of the podetia.

3.2. Colonization potential

In 2009, the maximum diameters of bryophyte wefts and turfs (terminology of growth forms follows MÄGDEFRAU 1982) and of fruticose and foliose lichen thalli were recorded on 10 topsoil removal sites near the two nature reserves. Seven sites had received hay transfer at different times in the past (6, 14, 16 and 18 years previously) and three sites were left open to be colonized by the surrounding grasslands (9, 29 and 64 years previously). On each site, the three largest patches of 6 xerophytic grassland species – if present – were recorded. For rounded thalli or bryophyte mats, wefts and turfs, the diameter was measured, for more or less rectangular patches, length and width was recorded. Only homogenous patches which showed no signs of merging were used.

Furthermore, in December 2008, the colonization distances of the bryophytes *Tortella tortuosa* and *Ditrichum flexicaule* from topsoil removal plots ($n = 4$) which had received raked cryptogam material from the nearby nature reserve in October 2003 were recorded. These two species had previously been absent from the restoration sites, and their colonization distances were not influenced by competition because the plots were free of vegetation. Along transects to the north, east, south and west, species presence or absence was recorded (one hundred 5 cm × 5 cm subplots per 0.5 m distance), giving an abundance percentage for each 50 cm transect section. Transects started in the centre of the receptor plot, and minimal distance is shown, i.e. distance “0” gives the 50 cm section from the receptor plot border outwards. Recording was stopped when three successive 50 cm sections were free of the observed species.

3.3. Data analysis

Area and associated diameter were calculated from the cryptogam data. For each bryophyte or lichen species and management (hay transfer vs. succession), linear correlations with time since topsoil removal were calculated (Pearson's *R*). Differences between colonization ranges were tested with Mann-Whitney *u*-tests. Nomenclature follows FRAHM (2011) for mosses, NEBEL & PHILLIPPI (2005) for liverworts, and WIRTH et al. (2010) for lichens.

4. Results

4.1. Cryptogam species composition of the donor grasslands

Topsoil removal plots showed a greater number of lichen species and were therefore significantly higher in overall species numbers ($p < 0.05$, Fig. 1a). Saxicolous and other lichens (including epigaic and foliose lichens) were restricted to topsoil removal plots. In plots without topsoil removal, pleurocarpous mosses were the most important cryptogam group in terms of species diversity and cover percentage (Fig. 1a, b). Acrocarpous mosses played a minor role, except on the old topsoil removal site and in the ancient grasslands of the Garching Heide.

Lichen species from the German Red List of endangered species were almost exclusively found on topsoil removal plots, with the exception of *Cladonia rangiformis*. These included

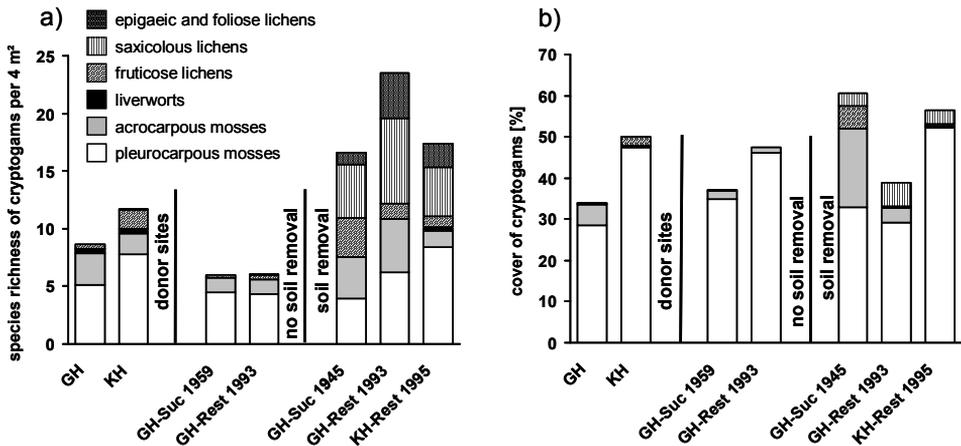


Fig. 1: a) Species numbers and b) cover of six cryptogam groups of ancient grasslands (donor sites, nature reserve), restoration grasslands after hay transfer (Rest, restored grassland), and successional grassland (Suc, successional grassland; Suc 1959 = former arable field). GH = Garching Heide, KH = Kissinger Heide. In addition the year of restoration/beginning of succession is given.

Abb. 1: a) Mittlere Artenzahlen und b) mittlere Deckung verschiedener Pflanzengruppen in alten (Spenderflächen, Naturschutzgebiete), durch Mahdgutübertragung neu angelegten (Rest, renaturierter Magerrasen) und durch Sukzession entstandenen (Suc) Kalkmagerrasen. (GH = Garching Heide, KH = Kissinger Heide, MG = Merishausener Gräte). Zusätzlich ist das Jahr der Renaturierung bzw. der Beginn der Sukzession angegeben.

most epigaic lichen species found (e.g. *Psora decipiens*, *Toninia sedifolia*, *Placidium squamulosum*), and many fruticose species (*Cladonia rangiformis*, *C. symphylicarpa*, *Cetraria islandica*, *Peltigera rufescens*). On some species-rich plots (max. number of species – vascular plants, bryophytes, lichens – on 4 m²: 65 compared to an average of 37 in the nature reserve “Garching Heide”), a cryptogam synusia with the liverworts *Frullania tamarisci*, *Barbilophozia barbata* and *Lophocolea bidentata*, *L. heterophylla* and *L. minor* was recorded. *Frullania tamarisci* is one of two endangered bryophytes found (the other is *Rhytidium rugosum*), showing a high cover at the small patches of open soil where it occurs. These stands are relatively open and have a comparatively high cover of *Carex humilis* and *Dicranum polysetum*.

4.2. Cryptogam species composition of the hay

Ten 1-dm³ (one litre) hay samples from the grassland sites contained ten pleurocarpous mosses, three acrocarpous mosses, one liverwort (the endangered *Frullania tamarisci*), and two *Cladonia* species (Fig. 2). Ten bryophyte and one lichen species of the donor sites were absent from the hay. These consisted of five small species growing directly on soil (*Bryum argenteum*, *B. caespiticium*, *Ceratodon purpureus*, *Syntrichia ruralis*, *Weissia brachycarpa*), four liverworts (*Barbilophozia barbata*, *Lophocolea bidentata*, *L. heterophylla*, *L. minor*), one saxicolous lichen (*Verrucaria nigrescens*) and the acrocarpous moss *Rhodobryum ontariense*. These species had all been found only once or twice in very small quantities, except for *Weissia brachycarpa*.

Although the composition of the five samples from each site varied, dry weight and shoot numbers of the encountered species differed even more between the nutrient-poor nature reserve and the nutrient-rich former arable field. Dry weight of the cryptogam fraction from one litre of hay ranged from 321 to 6734 mg, corresponding with 106 to 1624 shoots and fragments, respectively. For most species, fragments at least 10 mm long as well as larger, branched fragments were more abundant than complete shoots. Unbranched fragments below 10 mm length did only appear in large moss and *Cladonia* species, mainly

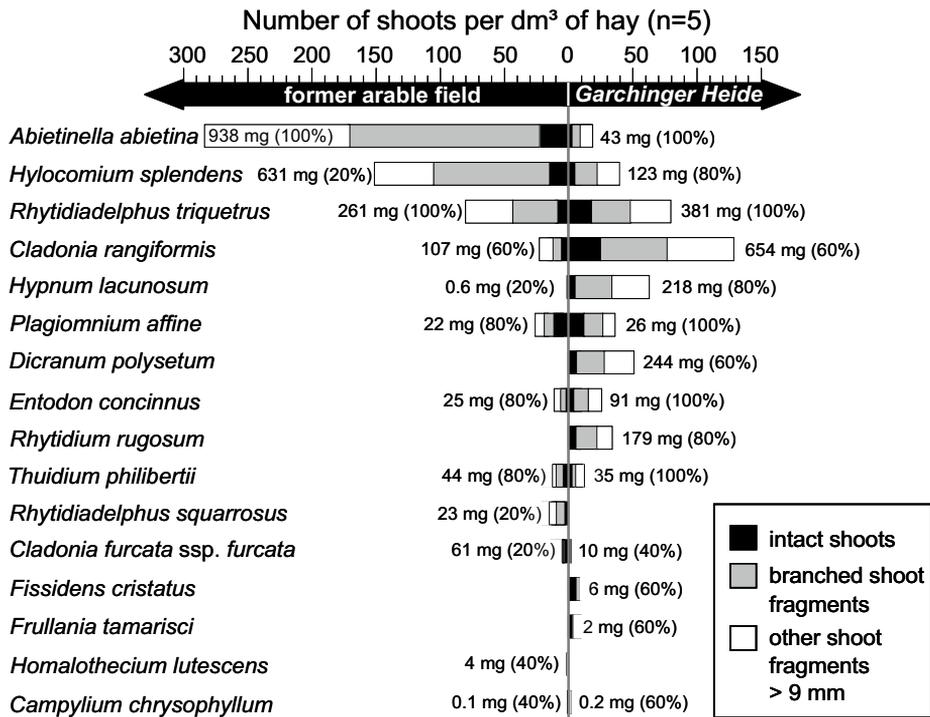


Fig. 2: Shoot and fragment number (> 9 mm, bars), constancy (percentage) and dry weight (numbers, in mg) of bryophyte and lichen species per 1 dm³ of dry hay from the nature reserve and an adjacent former arable field (n = 5). (a = acrocarpous moss, p = pleurocarpous moss, l = liverwort, f = fruticose lichen).

Fig. 2: Spross- und Fragmentzahl (> 9 mm, Balken), Stetigkeit (Prozentangaben) und Trockengewicht (Zahlen, in mg) von 16 Kryptogamen pro 1 dm³ Heu aus der Garching Heide bzw. einem angrenzenden renaturierten Kalkmagerrasen (n = 5). (a = akrokarpes Laubmoos, p = pleurokarpes Laubmoos, l = Lebermoos, f = Strauchflechte).

due to breakage when separating them from the hay. They were in all samples much less abundant than larger fragments. The ubiquitous semi-dry grassland species *Abietinella abietina*, *Rhytidiadelphus triquetrus*, *Plagiomnium affine*, *Entodon concinnus* and *Thuidium assimile* were present in all or most of the samples, often in large numbers. The former arable field yielded large numbers of fragments from the pleurocarpous mosses *Abietinella abietina*, *Hylocomium splendens* and *Rhytidiadelphus triquetrus*. In the hay from the ancient grassland *Rhytidiadelphus triquetrus* also showed high fragment numbers, but samples from this site also contained many shoots from dry grassland species, including *Cladonia rangiformis*, *Hypnum lacunosum*, *Dicranum polysetum* and *Rhytidium rugosum*. Against expectations, even low-growing and rare bryophytes like *Fissidens dubius* and *Frullania tamarisci* were frequently found (in 3 out of 5 samples) in the hay derived from the ancient grassland.

4.3. Effects of hay transfer

Especially the pleurocarpous mosses (*Abietinella abietina*, *Hypnum lacunosum*, *Rhytidium rugosum*) and fruticose lichens (*Cladonia furcata*, *C. rangiformis*) present in the hay were able to colonize hay receptor sites in a relatively short time (Fig. 4, see also Fig. 3), whereas most acrocarpous mosses and epigeaic lichens were not found at the hay receptor sites.



Fig. 3: Clones of the pleurocarpous mosses *Rhytidium rugosum* (above the scale) and *Abietinella abietina* (below the scale) on a topsoil removal site (1993) which had received hay from the adjacent Garchinger Heide. Length of scale is 40 cm. (Photo: M. Jeschke, 2009).

Abb. 3: Bestände der pleurokarpen Moose *Rhytidium rugosum* (oberhalb des Zollstocks) und *Abietinella abietina* (unterhalb des Zollstocks) 16 Jahre nach Oberbodenabtrag und Mahdgutbehandlung nahe der Garchinger Heide. Ein Zollstocksegment misst 20 cm. (Foto: M. Jeschke, 2009).

No pleurocarpous moss and no fruticose lichen were present on the nine year old successional site even though a cryptogam-rich site was directly next to it. Pleurocarpous moss and fruticose lichen individuals on the 29 year old successional site were smaller than on most hay transfer sites, despite the lower age of the latter sites. In contrast, *Tortella inclinata*, which was rarely transferred by hay transfer, but readily produce sporogons, showed no strong differences in turf size between hay transfer and successional sites. Similar results were found for *Ditrichum flexicaule* which was only present at one hay transfer site.

Some species were able to build very large mats: A stand of *Cladonia symphycarpa*, a species not shown in Fig. 4 because it was only present on sites without hay transfer, covered an area of 8 m × 6.5 m on the 64 year old succession site. Stands of *Cladonia rangiformis*, *C. pyxidata* and a turf of *Ditrichum flexicaule* also reached diameters of more than 3 m on the same site. Although these stands were more or less homogenous, they were not included in Figure 4 because they may consist of merged individuals.

4.4. Colonization from the receptor plots

On topsoil-removal sites with low vascular plant cover, many of the introduced cryptogam species colonized the surroundings of cryptogam receptor plots established in 2003. For the xerophytic acrocarpous bryophytes *Tortella tortuosa* and *Ditrichum flexicaule*, the highest dispersal distances detected after five years were 11.5 m and 9 m to the east, respectively. Colonization distances for these species from plot centre to the east were significantly higher ($p < 0.05$, $n = 4$) than distances to south and north (Fig. 5). This trend was visible for all cover percentage classes shown in Fig. 5.

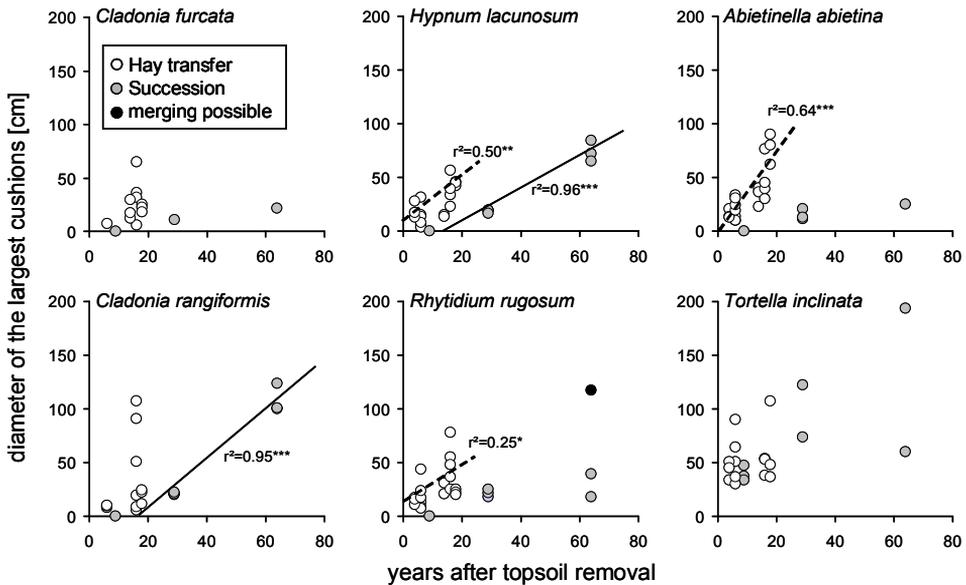


Fig. 4: Diameter of the largest wefts, mats and turfs of six cryptogam species in relation to the time since topsoil removal on sites with hay transfer (white dots; dashed lines) and without hay transfer (grey dots; full lines). Only significant Pearson correlations are shown; $p < 0.05$: *, $p < 0.01$: **, $p < 0.001$: ***).

Abb. 4: Durchmesser der größten Polster von sechs Kryptogamenarten in Abhängigkeit von der Zeit seit der Renaturierung durch Bodenabtrag. Dargestellt sind Sukzessionsflächen (graue Kreise, ganze Linien) und Mahdgutübertragungsflächen (weiße Kreise, unterbrochene Linien) sowie signifikante lineare Korrelationen (Pearson-Korrelationen; $p < 0,05$: *, $p < 0,01$: **, $p < 0,001$: ***).

5. Discussion

5.1. Species composition

Topsoil removal in combination with hay transfer led to high cryptogam species numbers after short time intervals (see Fig. 1a). This combination was shown to be necessary to create sites suitable for xerophytic vascular plant communities (*Pulsatillo-Caricetum humilis*) and associated xerophytic cryptogam communities (*Toninio-Psoretum*, *Tortelletum inclinatae*) on nutrient-rich soils (RÖDER et al. 2006, JESCHKE & KIEHL 2006a, b, JESCHKE 2009). Only on sites with free microsites and low vegetation less competitive species of all plant groups can occur (RYSER 1990, GIGON & LEUTERT 1996). If cryptogam species grow with low competitive pressure by vascular plants, large mats and wefts can be built up which have been shown to inhibit vascular plant colonization (JESCHKE & KIEHL 2008).

The observed liverwort synusia with *Frullania tamarisci* is probably restricted to more humid microsites with low competition by pleurocarpous mosses and moderate vascular plant cover. *Frullania tamarisci* is rarely recorded in calcareous grasslands, but the encountered synusia seems to be characteristic for the patches of the nature reserve "Garchinger Heide" with the highest species diversity.

5.2. Hay transfer

Many vascular plant species growing in semi-dry grasslands can be successfully transferred to newly restored sites by hay transfer (KIEHL et al. 2006). All pleurocarpous moss species occurring in the nature reserve are also brought to newly restored sites with hay transfer (Fig. 2), and many of them show rapid growth (Fig. 4). From the 16 cryptogam species encountered in the hay, only the *Cladonia* species are known to produce spores in

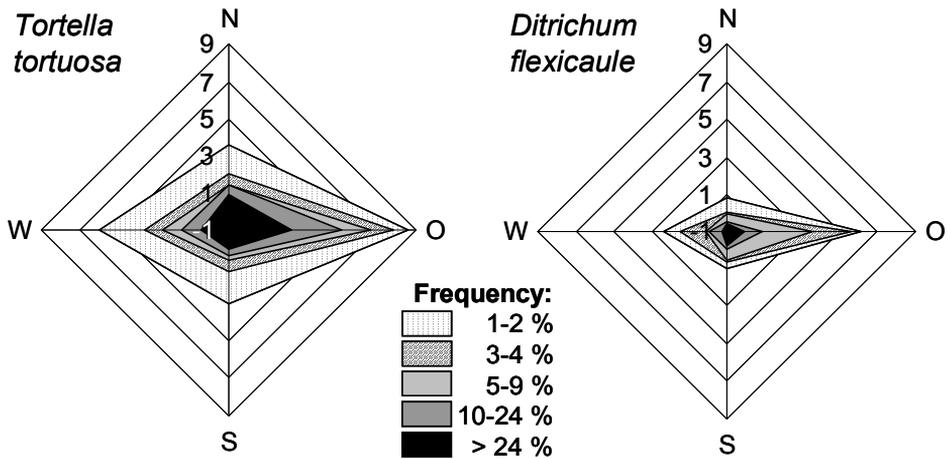


Fig. 5: Colonization range ($n = 4$) of two xerophytic bryophyte species transferred by raked material, which only appeared in or near receptor plots. Shown is the mean frequency per 0.5-m 'intervals' from the border of the receptor plots to 9 m (figure corners) along the main directions (–1 m: centre of receptor plot).

Abb. 5: Ausbreitungsdistanz ($n = 4$) von zwei durch Rechgut übertragenen xerophytischen Moosarten, die nur auf den Empfängerflächen auftraten. Dargestellt ist die mittlere Frequenz je 0,5 m Streckenabschnitt entlang der Himmelsrichtungen ausgehend vom Rand der Spenderfläche (–1 m: Mitte der Empfängerfläche).

the area. In contrast, all of the acrocarpous mosses that were absent from the hay regularly build spores in the area. Most of the pleurocarpous mosses that form the main part of cryptogam cover (see Fig. 1) and cryptogam biomass (JESCHKE & KIEHL 2006) have therefore to rely on fragment dispersal to colonize new sites. Many of these pleurocarpous mosses of the *Abietinellum* are regarded as typical for old grassland sites (NEUMAYR 1971). Other authors also emphasize that these species rarely or never sporulate and thus very likely are strongly limited in their dispersal (VAN TOOREN et al. 1990, FRAHM 2001, KETNER-OOSTRA et al. 2006).

Present dry grasslands are often isolated (BENDER et al. 2005, BUTAYE et al. 2005) because effective means of connection e.g. by transhumance with sheep or cattle have decreased dramatically in most regions (POSCHLOD & WALLIS DE VRIES 2002, POSCHLOD et al. 2005). The role of sheep for bryophyte and fruticose lichen dispersal has recently been shown by PAULIUK et al. (2011). Hay transfer helps these species to overcome dispersal limitations if natural dispersal agents like large herbivores are absent (see Fig. 4). The hay composition shown in Fig. 2 also shows that even rare and very small species (most stems of *Fissidens dubius* are shorter than 10 mm and fixed to the ground by rhizoids) previously thought to be unable to be transferred by hay transfer are nevertheless present in the hay.

Survival and regeneration of bryophyte species from transferred shoots or fragments will be strongly dependent on weather and site conditions that can cause very high mortality (GUNNARSSON & SÖDERSTRÖM 2007, COLE et al. 2010, GRAF & ROCHEFORT 2010). In contrast to the small and rare species, most pleurocarpous mosses are present at the mown sites in huge amounts (0.6 to 2.9 t dry mass/ha, see also JESCHKE & KIEHL 2006a). Even though the sampling procedure of the hay (only hay containing cryptogams was collected) does not allow calculating actual fragment numbers per mown area and year, rough estimates would be about 1,000 to 10,000 fragments per square meter.

In contrast to PAULIUK et al. (2011), who found mostly short fragments below 10 mm in the fleece and hooves of sheep, we encountered almost exclusively longer fragments between 10 and 150 mm. Branched species, often with creeping stems (all pleurocarpous mosses, *Cladonia* sp., *Plagiomnium* and *Frullania*) as well as species with squarrous leaves (e.g.

Dicranum polysetum) will be fixed to the vascular plant hay and transferred with it to receptor plots. *Cladonia* podetia had to be soaked to remove them from the grass stems present in the hay without fracturing. A hint to the differences in favourable cryptogam traits for transfer by sheep or by mown hay is *Plagiomnium affine*, which was absent in sheep fleece (PAULIUK et al. 2011), but quite abundant in the mown hay analysed in our study (see Fig. 2), even though it was abundant in both areas. Small acrocarpous mosses will be underrepresented in the hay as they are either not gathered by mowing or lost during the transfer of the hay to receptor sites.

5.3. Colonization and dispersal

Pleurocarpous mosses transferred by hay transfer can build fast-growing mats and wefts from single stems (MILLER & AMBROSE 1976, MÅLSON & RYDIN 2007), which, together with *Cladonia furcata* and *C. rangiformis*, can cover patches of some square meters in five to ten years and complete restoration sites in less than 20 years (field observations in the Garching Heide and Kissinger Heide). Open microsites in the cryptogam layer will be used up by pleurocarpous mosses before pioneer species, such as epigeic lichen species, will be able to arrive (cf. JESCHKE & KIEHL 2006b). Pleurocarpous moss mats can also inhibit the colonization of topsoil removal sites by vascular plant species, as a previous experiment in the same area has shown (JESCHKE & KIEHL 2008).

The only cryptogams present on the nine year old topsoil removal plot were *Tortella inclinata* and some saxicolous lichens, which all regularly produce spores. As many pleurocarpous mosses and *Cladonia* sp. were present less than 1 m away from the site, the difficulties in colonization are obvious.

Low-growing species (i.e. growing shorter than 4 cm above ground) rarely producing spores will be underrepresented in the hay and therefore reach the restoration sites only in small numbers. If they have a chance to establish on open soil or gravel, some dominant species (e.g. *Ditrichum flexicaule*, *Tortella tortuosa*) are able to compete with pleurocarpous mosses and *Cladonia* species, as the 64 year old topsoil removal site shows (see JESCHKE & KIEHL 2006a, b). In our study, the colonization ranges of two acrocarpous moss species (Fig. 5) showed that the receptor plots served as starting points for the colonization of a new habitat (cf. BOWKER 2007). Colonization was achieved by turf fragments loosened by disturbance. These turfs take some time (sometimes years) to become fixed to the ground and to grow in diameter, before part of the turf can once more be loosened by disturbance (JESCHKE & KIEHL, in preparation).

Maximum colonization distances per year were about one to two metres. The higher colonization distances of *Tortella tortuosa* and *Ditrichum flexicaule* to the east may indicate the influence of the main wind direction (wind from southwest and west) on the dispersal of loose moss shoots and turfs. HEINKEN (1999) showed dispersal distances below one metre for lichen thallus fragments 15 days after trampling, with single thalli up to 10 m away. These dispersal distances rely on fragments, which are produced by disturbance, e.g. trampling or mowing. In undisturbed habitats, fragments are rarer, as the complete absence of cryptogams relying on fragment dispersal on the nine year old successional site shows.

The loose turfs transferred to the receptor plots are of course more readily dispersible than “rooted” turfs fixed to the ground by rhizoids, but loose turfs are abundant at any site with even light disturbance. Cryptogam colonization distances by fragments on undisturbed sites will therefore vary greatly and will entirely depend on natural fragmentation of the cryptogams and small events of disturbance.

5.4. Consequences for nature conservation

As no restoration measure is solely able to create sites that are suitable for all species groups, a combination of different measures on different sections of a restoration site would be the best solution. Hay transfer is an adequate method of transferring the majority of vascular plant species and pleurocarpous mosses, and – if present – liverwort species.

To avoid the side effects of hay transfer, hay transfer in patches in combination with other means of diaspore transfer, e.g. using raked material, could be used. This method is suitable to transfer acrocarpous moss and epigaic lichen species as well as some xerophytic vascular plants (JESCHKE & KIEHL, in preparation). The latter method can also be used on sites that are not regularly mown, like many dry grassland sites.

Acknowledgements

The Heideflächenverein e.V. managed the sites and supported valuable information about management details. I am also thankful to Kathrin Kiehl, Thomas Becker, Sonja Jeschke, Laura Sutcliffe and Thilo Heinken for critically reading the manuscript.

References

- ANDERSON, D. C., HARPER, K. T. & RUSHFORTH, S. R. (1982): Recovery of cryptogamic soil crusts from grazing in Utah winter ranges. – *J. Range Manag.* 35: 355–359. Denver, Colo.
- BAKKER, J. P. & BERENDSE, F. (1999): Constraints in the restoration of ecological diversity in grassland and heathland communities. – *Trends Ecol. Evol.* 14: 63–67. Amsterdam.
- BENDER, O., BÖHMER, H.-J., JENS, D. & SCHUHMACHER, K. (2005): Analysis of land-use change in a sector in Upper Franconia (Bavaria, Germany) since 1850 using land register records. – *Landsch. Ecol.* 20: 149–163. The Hague.
- BOWKER, M. A. (2007): Biological soil crust rehabilitation in theory and practise: An underexploited opportunity. – *Restor. Ecol.* 15: 13–23. Malden, Mass.
- BUTAYE, J., ADRIENS, D. & HONNAY, O. (2005): Conservation and restoration of calcareous grasslands: a concise review of the effects of fragmentation and land management on plant species. – *Biotechnol. Agron. Soc. Environ.* 9: 111–118. Gembloux.
- COLE, C., STARK, L. R., BONINE, M. L. & MCLETCHIE, D. N. (2010): Transplant survivorship of bryophyte soil crusts in the Mojave desert. – *Restor. Ecol.* 18: 198–205. Malden, Mass.
- DENGLER, J. (2005): Zwischen Estland und Portugal – Gemeinsamkeiten und Unterschiede der Phyto-diversitätsmuster europäischer Trockenrasen. – *Tuexenia* 25: 387–405. Göttingen.
- EICHBERG, C., STORM, C., STROH, M. & SCHWABE, A. (2010): Is the combination of topsoil replacement and inoculation with plant material an effective tool for the restoration of threatened sandy grassland? – *Appl. Veg. Sci.* 13: 425–438. Oxford.
- FRAHM, J.-P. (2001): *Biologie der Moose*. – Spektrum Akademischer Verlag, Heidelberg: 357 pp.
- (2011): Kommentierte Liste der Laubmoose Deutschlands. – *Arch. Bryol.* 79: 1–51. Bonn.
- GIGON, A. & LEUTERT, A. (1996): The dynamic keyhole-key model of coexistence to explain diversity of plants in limestone and other grasslands. – *J. Veg. Sci.* 7: 29–40. Uppsala.
- GRAF, M. D. & ROCHEFORT, L. (2010): Moss regeneration for fen restoration: Field and greenhouse experiments. – *Restor. Ecol.* 18: 121–130. Malden, Mass.
- GUNNARSSON, U. & SÖDERSTRÖM, L. (2007): Can artificial introductions of diaspore fragments work as a conservation tool for maintaining populations of the rare peatmoss *Sphagnum angermanicum*. – *Biol. Conserv.* 135: 450–458. Amsterdam.
- HEINKEN, T. (1999): Dispersal patterns of terricolous lichens by thallus fragments. – *Lichenologist* 31: 603–612.
- INGERPUU, L., LIIRA, J. & PÄRTEL, M. (2005): Vascular plants facilitated bryophytes in a grassland experiment. – *Plant Ecol.* 180: 69–75. Dordrecht.
- JESCHKE, M. (2009): Artendiversität von Gefäßpflanzen und Kryptogamen in Kalkmagerrasen und die Auswirkungen von Renaturierungs- und Pflegeverfahren. – *Laufener Spezialbeitr.* 2009(2): 103–112. Laufen.
- & KIEHL, K. (2006a): Auswirkung von Renaturierungs- und Pflegemaßnahmen auf die Artenzusammensetzung und Artendiversität von Gefäßpflanzen und Kryptogamen in neu angelegten Kalkmagerrasen. – *Tuexenia* 26: 223–242. Göttingen.
- & KIEHL, K. (2006b): Vergleich der Kryptogamenvegetation alter und junger Kalkmagerrasen im Naturschutzgebiet „Garching Heide“. – *Ber. Bayer. Bot. Ges.* 76: 221–234. München.
- & KIEHL, K. (2008): Effects of a dense moss layer on germination and establishment of vascular plants in newly created calcareous grasslands. – *Flora* 203: 557–566. Jena.
- KETNER-OOSTRA, R., VAN DER PEIJL, M. J. & SYKORA, K. V. (2006): Restoration of lichen diversity in grass-dominated vegetation of coastal dunes after wildfire. – *J. Veg. Sci.* 17: 147–156. Uppsala.
- KIEHL, K., THORMANN, A., PFADENHAUER, J. (2003): Nährstoffdynamik und Phytomasseproduktion in neu angelegten Kalkmagerrasen auf ehemaligen Ackerflächen. – *Angew. Landschaftsökol.* 55: 39–71. Bundesamt für Naturschutz, Bonn.

- , THORMANN, A. & PFADENHAUER, J. (2006): Evaluation of initial restoration measures during the restoration of calcareous grasslands on former arable fields. – *Restor. Ecol.* 14: 148–156. Malden, Mass.
- KIRMER, A. & MAHN, E. G. (2001): Spontaneous and initiated succession on unvegetated slopes in the abandoned lignite-mining area of Goitsche, Germany. – *Appl. Veg. Sci.* 4: 19–27. Uppsala.
- MÄGDEFRAU, K. (1982): Life-forms of bryophytes. – In: SMITHS, A. J. E. (Ed.): *Bryophyte ecology*: pp. 45–58. Chapman and Hall, London.
- MÄLSON, K. & RYDIN, H. (2007): The regeneration capabilities of bryophytes for rich fen restoration. – *Biol. Conserv.* 135: 435–442. Amsterdam.
- MARSTALLER, R. (2009): Die Moosvegetation des Naturschutzgebietes „Muschelkalkhänge zwischen Lieskau, Köllme und Bennstedt“ bei Halle (Sachsen-Anhalt) – *Mitt. Florist. Kart. Sachs.-Anhalt* 14: 3–32. Halle (Saale).
- MILLER, M. G. & AMBROSE, L. J. H. (1976): Growth in culture of wind-blown bryophyte gametophyte fragments from Arctic Canada. – *Bryologist* 79: 55–63. Washington, DC.
- MÜLLER, F. & OTTE, V. (2008): Verzeichnis und Rote Liste der Moos- und Flechtengesellschaften Sachsens. – Sächsisches Landesamt für Umwelt und Geologie, Dresden: 132 pp.
- NEBEL, M. & PHILIPPI, G. (Eds.) (2005): Die Moose Baden-Württembergs. Band. 3: Spezieller Teil *Bryophyta: Sphagnopsida, Marchantiophyta, Anthocerotophyta*. – Ulmer, Stuttgart: 487 pp.
- NEUMAYR, L. (1971): Moosgesellschaften der südlichen Frankenalb und des Vorderen Bayerischen Waldes. – *Hoppea* 29: 1–364. Regensburg.
- PAULIUK, F., MÜLLER, J. & HEINKEN, T. (2011): Bryophyte dispersal by sheep on dry grassland. – *Nova Hedwigia* 92: 327–341. Stuttgart.
- PFADENHAUER, J. & U. MILLER (2000): Verfahren zur Ansiedlung von Kalkmagerrasen auf Ackerflächen. – In: PFADENHAUER, J., FISCHER, F. P., HELFER, W., JOAS, C., LÖSCH, R., MILLER, U., MILTZ, C., SCHMID, H., SIEREN, E. & WIESINGER, K. (Eds.): *Sicherung und Entwicklung der Heiden im Norden von München*. *Angew. Landschaftsökol.* 32: 37–87. Bundesamt für Naturschutz, Bonn.
- POSCHLOD, B., BAKKER, J. & KAHMEN, S. (2005): Changing land use and its impact on biodiversity. – *Basic Appl. Ecol.* 6: 93–98. Jena.
- & WALLIS DE VRIES, M. F. (2002): The historical and socioeconomic perspective of calcareous grasslands – lessons from the distant and present past. – *Biol. Cons.* 104: 361–376. Amsterdam.
- RÖDER, D., JESCHKE, M. & KIEHL, K. (2006): Vegetation und Böden alter und junger Kalkmagerrasen im Naturschutzgebiet „Garching Heide“ im Norden von München. – *Forum Geobot.* 2: 24–44. Würzburg.
- RYSER, P. (1990): Influence of gaps and neighbouring plants on seedling establishment in limestone grassland. – *Veröff. Geobot. Inst. Eidgenöss. Techn. Hochsch., Stift. Rübel ZÜR.* 104: 71 pp. Zürich.
- VAN TOOREN, B. F., ODÉ, B., DURING, H. J. & BOBBINK, R. (1990): Regeneration of species richness in the bryophyte layer of Dutch chalk grasslands. – *Lindbergia* 16: 153–160. Lund.
- WALKER, K. J., STEVENS, P. A., STEVENS, D. P., MOUNTFORD, J. O., MANCHESTER, S. J. & PYWELL, R. F. (2004): The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. – *Biol. Conserv.* 19: 1–18. Amsterdam.
- WILLEMS, J. H. (2001): Problems, approaches, and results in restoration of Dutch calcareous grassland during the last 30 years. – *Restor. Ecol.* 9: 147–154. Malden, Mass.
- WIRTH, V. (1995): *Flechtenflora*. – Ulmer, Stuttgart: 661 pp.
- , HAUCK, M., VON BRACKEL, W., CEZANNE, R., DE BRUYN, U., DÜRHAMMER, O., EICHLER, M., GNÜCHTEL, A., LITTERSKI, B., OTTE, V., SCHIEFELBEIN, U., SCHOLZ, P., SCHULTZ, M., STORDEUR, R., FEUERER, T., HEINRICH, D. & JOHN, V. (2010): Checklist of lichens and lichenicolous fungi in Germany. Version #1: 01 December 2010. – URL: <http://www.gwdg.de/~mhauck>.

Michael Jeschke
 FB VI / Geobotany
 University of Trier
 Behringstr. 21
 54296 Trier, GERMANY
 jeschke@uni-trier.de

Co-ordinating editor: Thomas Becker
 Manuscript received: 02.11.2009; accepted: 24.03.2012