

Restoration of steppic sandy grassland using deep-sand deposition, inoculation with plant material and grazing: a 10-year study

Restitution von Steppenrasen auf der Grundlage von Tiefensand- Aufschüttung, Inokulation mit pflanzlichem Material und Beweidung: eine Studie über 10 Jahre

Christian Storm¹, Carsten Eichberg², Michael Stroh³ & Angelika Schwabe^{1,*}

¹Technische Universität Darmstadt, Department of Biology, Schnittspahnstr. 10, 64287 Darmstadt,
Germany, storm@bio.tu-darmstadt.de; schwabe@bio.tu-darmstadt.de;

²Universität Trier, Regional and Environmental Sciences, Geobotany, Behringstr. 21, 54296 Trier,
Germany, eichberg@uni-trier.de;

³Landkreis Darmstadt-Dieburg, Jägertorstr. 207, 64289 Darmstadt, Germany, m.stroh@ladadi.de

*Corresponding author

Abstract

Inland sand vegetation, in our case steppic sandy grassland on base-rich soils, is highly endangered in Europe and therefore in the focus of restoration ecology. While there are studies which deal with short-term restoration success, results for an extended time are rare. We were able to analyse the success of a three-step restoration measure for 10 years.

The experiment was established on an ex-arable field in the Upper Rhine valley, Hesse, Germany. The three-step restoration approach comprised 1) abiotic restoration by deep-sand deposition, 2) inoculation with raked/mown plant material from two different donor sites with well-developed *Koelerion glaucae/Allio-Stipetum* vegetation and 3) low-intensity grazing by donkeys. The vegetation of the restoration and donor sites (also serving as reference sites to assess restoration success) was sampled on six permanent plots, respectively. Data analyses included ordination, classification and target-species ratios (TSR: relation of target species to all species).

Detrended correspondence analysis revealed a continuous succession of the restoration plots towards the corresponding reference plots: open soil decreased, ruderal species declined and target species increased. While speed of succession decreased, there was still a further improvement in the tenth year. The qualitative TSR (number of target species) reached a plateau after the sixth year with values only slightly lower than at the reference sites. The quantitative TSR (cover of target species) showed a steady improvement and even excelled one reference site. *Koelerion glaucae* species were present with constancy 17–67% since the 3rd year, with 33–100% since the 7th year. It does not completely resemble either reference site due to a mixture of propagules of both donor sites (e.g. by wind and donkeys) and input from the surroundings. Already in the first year, three Red-list species established themselves, since the 8th year 23 Red-list/near-threatened species have been present. Some ruderal species colonised the restoration site and occurred permanently.

Additionally, we studied the establishment of the highly threatened species *Bassia laniflora* after inoculation for 6–12 years on three further plots adjacent to the other ones. One of these plots was located on a former sandy field without abiotic restoration; two other plots represented typical *Koelerion glaucae* vegetation on a newer deep-sand deposition. *Bassia laniflora* established itself well on all plots.

We conclude that restoration of steppic sandy grassland, including highly threatened species, was not only permanently, but increasingly successful over a time span of 10 years. Management by grazing, however, will remain essential to suppress ruderalisation.

Keywords: abiotic restoration, *Allio-Stipetum*, *Bassia laniflora*, donkey grazing, *Koelerion glaucae*, ordination, Red-list species, seed transfer, succession, target species

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

An ongoing decline in area and connectivity of nutrient-poor, species-rich grasslands due to the loss of traditional land-use practices in many areas has led to small remnant plant populations which are threatened by genetic bottlenecks (YOUNG et al. 1996, MIDDLETON 2013). To guarantee the long-term survival of rare grassland plant species and their communities, restoration of degraded grasslands is required and the physical or functional connection of existing grasslands in a particular region has to be improved (BAKKER & BERENDSE 1999). Usually, a combination of abiotic and biotic constraints hampers the success of restoration projects (BAKKER & BERENDSE 1999, WALKER et al. 2004, HÖLZEL et al. 2012). This is especially true on ex-arable land, where soils are enriched in nutrients and impoverished in germinable seeds of target species (WALKER et al. 2004).

High nutrient levels in the soil are detrimental to the establishment of low-competitive target species of species-rich grasslands (SÜSS et al. 2004, FAGAN et al. 2008). Many studies have shown that soil conditions must be similar to target sites in order to guarantee restoration success. Techniques that have been found to successfully restore degraded topsoils are: topsoil removal (HÖLZEL & OTTE 2003, KIEHL & PFADENHAUER 2007, GILHAUS et al. 2015), soil layer inversions (EICHBERG et al. 2010, ÖDMAN et al. 2011) and coverage of nutrient-rich topsoils with nutrient-poor substrate (EICHBERG et al. 2010). In general, restoration measures changing topsoil conditions go along with disturbance lowering or deactivating plant competition and depleting seed banks of particularly non-target species. The mechanism of controlling competitive plant species by means of disturbance is essential also in the long-term maintenance of remnant or restored grasslands (MIDDLETON 2013).

Another important constraint to grassland diversity is seed limitation (PYWELL et al. 2002). In many cases the availability of habitat-specific seeds (seed rain of neighbouring plant populations, soil seed banks) as well as animal seed vectors are severely restricted and not sufficient to allow re-establishment of target species. Hence, the artificial transfer of germinable seeds is a further pre-requisite for restoration success. Various techniques of seed transfer are used in ecological restoration (for publications before 2010 see the review of KIEHL et al. 2010): 1) transfer of mown and/or raked plant material (EICHBERG et al. 2010, RYDGREN et al. 2010), 2) seeding (PRACH et al. 2012, GRMAN et al. 2015), 3) low-intensity grazing with mobile livestock herds (FREUND et al. 2014). In comparison to seeding, the transfer of mown and/or raked material has the advantage that it potentially comprises all plant species (including cryptogams) of a donor vegetation stand in natural proportions. Additionally, it potentially includes individuals of invertebrates (e.g. snails) and – particularly in raked material (high share of soil substrate) – soil organisms, such as mycorrhizal fungi (cf. MOYNAHAN et al. 2002) that influence plant fitness and community composition. There is evidence that the transfer of seed-containing plant material is superior to grazing as a method to establish optimal starting conditions of a desired vegetation development (RASRAN et al. 2007, COIFFAIT-GOMBAULT et al. 2011). However, hay transfer and grazing

in combination can lead to a higher plant species richness than the application of both treatments solely (COIFFAIT-GOMBAULT et al. 2011). In early restoration stages, a main function of seed-containing plant material is the supply of a high number of target-species seeds and a main function of grazing is the generation of microsites that promote germination and establishment, especially in ecosystems with reduced water availability (e.g. seed-bed preparation by livestock trampling, FAUST et al. 2011).

Short-term studies revealed that a three-step approach comprising abiotic restoration (reduction of soil nutrients), biotic restoration (transfer of plant material) and management (grazing) was effective in restoring grasslands (RASRAN et al. 2007, EICHBERG et al. 2010). As a follow-up management grazing turned out to be an effective tool because it reduces competition, enables seed exchanges and creates various microsites for seedling establishment (ROSENTHAL et al. 2012). On our restoration site we applied low-intensity donkey grazing. There are good experiences with this type of management in sandy grassland – even for small areas below 1 ha – resulting in the reduction of, e.g., competitive ruderal graminoids (SÜSS & SCHWABE 2007, STROH & SÜSS 2011). The combination of disturbance (mechanically or zoogenic) and seed addition turned out to be particularly effective in restoring degraded grasslands (PYWELL et al. 2002, MARTIN & WILSEY 2006, EDWARDS et al. 2007, RASRAN et al. 2007, SCHMIEDE et al. 2012).

A major goal of research in restoration ecology is the analysis of vegetation development towards target plant communities (e.g. HÖLZEL et al. 2012). Three main approaches have been realised for such analyses: chronosequence approaches (FAGAN et al. 2008, PRACH et al. 2012, ALBERT et al. 2014), single-year approaches (GILHAUS et al. 2015: 8 years after restoration) and multi-year approaches on permanent plots with various duration (PATZELT et al. 2001: 6 year, DONATH et al. 2007: 4 year, EDWARDS et al. 2007: 4 year, RYDGREN et al. 2010: 3 year, AUESTAD et al. 2016: 9 year). Longer-term studies of vegetation development on restoration sites are scarce (but see AUESTAD et al. 2016). However, these studies are important to avoid over-optimistic perspectives and overhasty decisions in habitat management (GODEFROID et al. 2011). In a meta-analysis, GODEFROID et al. (2011) found a declining trend in the survival, flowering and fruiting of re-introduced plants, suggesting that most attempts to re-establish native plant species will be unsuccessful in the long run.

In our study, we focused on grazed, species-rich open steppic sandy grassland in the Northern Upper Rhine valley, Germany. Habitats belonging to this system are characterised by a high share of threatened plant species and are listed as priority habitat types within the EU 92/43 Habitat Directive: *Koelerion glaucae* Volk 1931: priority type 6120, *Allio sphaerocephali-Stipetum capillatae* Korneck 1974: priority type 6240 (EUROPEAN COMMISSION 2007). We carried out a restoration project including deep-sand deposition (covering of ex-arable soil), inoculation with raked/mown plant material from donor sites and grazing management. The restoration site is linearly shaped and connects two existing areas: one target and one older restoration site (Fig. 1, 2). Our study aims at analysing vegetation development on the restoration corridor in relation to well-developed target/donor sites. Here, we present the results after 10 years (for results after 4 years see EICHBERG et al. 2010).

Additionally, we studied the establishment of the annual steppic species *Bassia laniflora* (*Chenopodiaceae*) after inoculation directly alongside the corridor over 6–10 years. *Bassia laniflora* is one of the rarest plant species in Germany and critically endangered (KORNECK et al. 1996, BUTTLER et al. 1997, HODVINA & CEZANNE 2008). Furthermore it is one of the few indigenous plant species in Germany with C4 metabolism (AKHANI et al. 1997, KA-



Fig. 1. Study area with the restoration site (corridor) ‘R’ with plots R1–R6. The photograph was taken on 12th August 2012, seven years after deep-sand deposition. The reference area ‘S’ with plots S1–S3 is located north of the corridor. South of the corridor a part of an old restoration area (from 1999) with plot B1 (*Bassia laniflora*-plot) is visible. The small deep-sand deposition of 2008 with the *Bassia laniflora*-plots B2 and B3 is situated northwest of the corridor. Aerial photo: ‘Hessische Verwaltung für Bodenmanagement und Geoinformation’ in cooperation with ‘Landkreis Darmstadt-Dieburg’.

Abb. 1. Untersuchungsgebiet mit der Restitutionsfläche (Korridor) „R“ mit den Plots R1–R6. Die Aufnahme entstand am 12. August 2012, sieben Jahre nach der Sanddeposition. Nördlich des Korridors liegt die Leitbildfläche „S“ mit den Plots S1–S3. Südlich des Korridors befindet sich ein Teil einer älteren Restitutionsfläche (von 1999) mit dem Plot B1 (*Bassia laniflora*-Plot). Die kleine Sandaufschüttung von 2008 mit den *Bassia laniflora*-Plots B2 und B3 liegt nordwestlich des Korridors. Luftbild: Hessische Verwaltung für Bodenmanagement und Geoinformation in Kooperation mit dem Landkreis Darmstadt-Dieburg.



Fig. 2. Restoration site (corridor) in June 2015. Aspect of *Koeleria glauca* with dry moss carpets (mainly *Tortula ruraliformis*) in the foreground; flower aspect of *Euphorbia seguieriana* in the background (Photo: A. Schwabe).

Abb. 2. Restitutionsgebiet (Korridor) im Juni 2015. Aspekt von *Koeleria glauca* mit trockenen Moos-Teppichen (vor allem *Tortula ruraliformis*) im Vordergrund; Blühaspekt von *Euphorbia seguieriana* im Hintergrund (Foto: A. Schwabe).

DEREIT & FREITAG 2011). The only occurrences in Germany (characterising the northwestern margin of the mainly continental distribution area) are in the Upper Rhine valley between Sandhausen (near Heidelberg) and Mainz/Ingelheim (HODVINA & CEZANNE 2008). At the end of the 19th century, *B. laniflora* was common in this area (DOSCH & SCRIBA 1888).

In this study, we addressed the following questions: (1) Is it possible to restore steppic sandy grassland on ex-arable land by means of a three-step approach including deep-sand deposition, inoculation with raked/mown plant material and low-intensity grazing by donkeys permanently over an extended time (10 years)? (2) Is it possible to establish populations of the rare species *Bassia laniflora*?

2. Material and methods

2.1 Sandy area in the northern Upper Rhine valley

In late glacial and early post-glacial times calcareous sands were blown out from the Rhine terraces and were eastwardly deposited, mainly between Sandhausen/Mannheim and Mainz/Darmstadt. Today steppic species are present in this area, like *Bassia laniflora*, *Koeleria glauca*, *Jurinea cyanoides* and *Poa badensis*, but also submediterranean (e.g. *Silene conica*) and subatlantic (e.g. *Corynephorus canescens*) species, forming a special combination of plant species in a biogeographically marginal situation concerning the steppic species (SÜSS et al. 2010). Relatively high annual average temperatures and (regarding temperate regions) low precipitation is typical for this area (9.7 °C and 658 mm a⁻¹; 1961–1990, Frankfurt/Main Airport, Deutscher Wetterdienst, www.dwd.de).

2.2 Restoration experiment

In 2005, we established a field experiment to study the restoration of steppic sandy grassland on an ex-arable field. The restoration site ('R') is situated near Seeheim-Jugenheim, 40 km south of Frankfurt/Main ($8^{\circ}37' E$, $49^{\circ}46' N$, 120 m a.s.l.). The aim of this restoration measure was to connect a well-developed *Koelerion glaucae/Allio-Stipetum* vegetation complex in a nature reserve and an older restoration area by a corridor (250 m x 22 m; Fig. 1).

We applied the three-step approach (EICHBERG et al. 2010, see above) including nutrient reduction, species transfer and grazing:

1. Nutrient-poor sand substrate from deep layers was deposited to a height of 1.5–3 m on the soil surface. Soil analyses showed that this abiotic restoration technique was successful in providing nutrient contents similar to sites with well-developed steppic sandy grassland (Supplement E1). The mean extractable phosphate-P content was $12.5 \pm 1.2 \text{ mg kg}^{-1}$ dry soil (mean \pm standard error), which is below a threshold of $15\text{--}20 \text{ mg kg}^{-1}$, above which the association character species *Stipa capillata* declines in our study area (SÜSS et al. 2004). The mean nitrate-N ($0.3 \pm 0.02 \text{ mg kg}^{-1}$ dry soil) and ammonium-N ($0.6 \pm 0.1 \text{ mg kg}^{-1}$ dry soil) concentrations were even lower in the deep sand than in the soils of the reference sites.
2. One week after its creation, the corridor was inoculated with raked/mown plant material from one of two donor sites: Site 'S' (Fig. 1) is the above mentioned *Koelerion glaucae/Allio-Stipetum* vegetation complex directly nearby the restoration site, whereas site 'T' ('Standortübungsplatz', $8^{\circ}36' E$, $49^{\circ}51' N$, 115 m a.s.l.) is situated some kilometres away in a former military area. Both donor sites are characterised by threatened calcareous sand vegetation (mainly *Koelerion glaucae*), partly (especially at site 'S') *Allio-Stipetum capillatae*. Site 'T' is dominated by pioneer stages with, e.g., *Corynephorus canescens*, *Phleum arenarium* and *Cetraria aculeata*.
The raked plant material (uprooted plant individuals and their fragments, litter, bryophytes, lichens, soil particles) was harvested by a windrower or by hand, depending on the size of the donor site. The phyto- and necromass fraction of the transferred raked material was about $0.02\text{--}0.04 \text{ kg dry weight m}^{-2}$ and the sand fraction was appr. $0.01\text{--}0.06 \text{ kg dry weight m}^{-2}$ (site 'S', raked by hand, range of three samples) or ca. $0.27\text{--}0.36 \text{ kg dry weight m}^{-2}$ (site 'T', raked by machine, range of three samples); see EICHBERG et al. (2010).
3. Donkey grazing with low intensity was applied for approximately three weeks each year. Shrub establishment was reduced manually, and marginal *Calamagrostis epigejos* clones were reduced manually outside the plots.

2.3 Field work

The vegetation of the restoration site 'R' and the donor sites 'S' and 'T' was sampled on permanent plots (each 25 m^2 in size) using the modified Braun-Blanquet cover-abundance scale (BARKMAN et al. 1964). The donor sites served also as reference sites to evaluate restoration success, providing data about intact target plant communities. At the restoration site 'R', six permanent plots were established and monitored yearly from 2005 to 2014. The plots R1–R3 were inoculated mainly with plant material from donor site 'T', whereas R4–R6 received predominantly material from the adjacent donor site 'S'. At both donor sites, three permanent plots were established and recorded yearly 1995–2014 ('S', with 4–6 missing years) or 2004 and 2006–2008 ('T').

2.4 Statistical analyses

For comparison of the plot types 'R', 'S' and 'T' we give mean values \pm standard errors in all cases. Ordination of the vegetation data was performed by detrended correspondence analysis. The relevé data were rank-transformed beforehand (as suggested by VAN DER MAAREL 1979 and evaluated by LEPŠ & HADINCOVÁ 1992). Calculation of cover class means and subsequent square root transformation leads to very similar results, in general (LEYER & WESCHE 2007) as well as in our case. Rare species were downweighted and axes rescaled with 26 segments. As software we used PC-ORD 6.15 (MJM Software, Gleneden Beach, OR, USA). As an after-the-fact evaluation of the ordination efficien-

cy, coefficients of determination between Sørensen distances in the ordination space and the original space were determined; these represent the explained variance of the respective ordination axis. Non-metric multidimensional scaling led essentially to the same results (not shown). Additionally, a cluster analysis of the same data set was performed with Ward's method and relative Euclidean distance measure. Mean Sørensen distances between the restoration and the corresponding reference plots (presence-absence data) were calculated for the first and last study year.

In order to evaluate restoration success we defined two target-species ratios:

$$(1) \text{ Qualitative target-species ratio (TSR}_{\text{qual}}) = \frac{\text{number of target plant species}}{\text{total number of plant species}}$$

$$(2) \text{ Quantitative target-species ratio (TSR}_{\text{quant}}) = \frac{\text{cover sum of target plant species}}{\text{cover sum of all plant species}}$$

The cover-abundance scale was transformed to cover values beforehand ($r = 0.1\%$, $+ = 0.3\%$, $1 = 1\%$, $2m = 3\%$, $2a = 9\%$, $2b = 19\%$, $3 = 38\%$, $4 = 63\%$, $5 = 88\%$). Both ratios have a range between 0 and 1. Target species are defined as species with main occurrence in one of the following phytosociological classes: *Koelerio-Corynephoretea* or *Festuco-Brometea*.

2.5 Establishment of *Bassia laniflora*

Bassia laniflora does not occur at the donor sites 'T' and 'S'. We provide data on this species from three additional plots 'B' ($\approx 25 \text{ m}^2$) located alongside the corridor (Fig. 1). Plot 'B1' is situated on a former sandy field between the corridor and another restoration site (the latter described in STROH et al. 2002, 2007) and was not covered with deep sand, but grazed by sheep and donkeys. The lack of abiotic restoration is reflected in higher phosphate-P concentrations (67 mg kg^{-1} dry soil) whereas the nitrate and ammonium concentrations as well as the pH value are within a normal range (Supplement E1). After two status quo relevés 1999 and 2003, the plot was inoculated by raked plant material of site 'U' in Darmstadt-Eberstadt (nature reserve 'Düne am Ulvenberg', $8^\circ38' \text{ E}$, $49^\circ48' \text{ N}$). This plot was monitored yearly until 2014. The plots B2 and B3 are situated on a newer deep-sand deposition (enlargement of the corridor after cutting of *Populus x canadensis* trees in September 2008), were inoculated in November 2008 by raked plant material from sites 'U' and 'S' and monitored yearly from 2009 to 2014. Raking technique, grazing and vegetation monitoring was applied as described in Sections 2.2 and 2.3.

2.6 Nomenclature and data of Red-list species

Nomenclature of vascular plant species refers to WISSKIRCHEN & HAEUPLER (1998), of bryophytes to KOPERSKI et al. (2000) and of lichens to SCHOLZ (2000).

Categorisation of Red-list species (Tables 1, 2 and Section 3.2) refer to the federal state of Hesse: BUTTLER et al. (1997) for vascular plant species and SCHÖLLER et al. (1996) for lichens. There were no bryophytes with Red-list status in our plots.

3. Results

3.1 General overview

The ordination diagram (Fig. 3) depicts the vegetation of the reference and restoration plots. Both axes together explain 85% of the floristic variability. Since the third axis does not explain further variance, we do not show it. The plots of the two reference sites 'T' and 'S' are clearly separated, but the relevés of each plot show only minor inter-annual fluctuations as indicated by the short trajectories.

The restoration plots, on the contrary, are characterised by long, relatively straight trajectories, indicating succession. The trajectories do not point exactly to either reference site but instead to midpoints in between both reference sites. The midpoints are different for R1–R3 and R4–R6, reflecting the origin of the plant material they have been inoculated with.

The distances between the relevés of the first and second year are relatively large, which means a high speed of succession in the beginning of the restoration process. In the following years, this speed slowed down, but even in the last year there was a notable further approximation towards the midpoints of the reference plots.

The mean Sørensen distances (\pm standard error) between the restoration plots R1–R3 and their reference site ‘T’ dropped from 0.83 ± 0.05 in 2005 to 0.47 ± 0.02 in 2014, and between R4–R6 and ‘S’ from 0.85 ± 0.01 to 0.50 ± 0.01 .

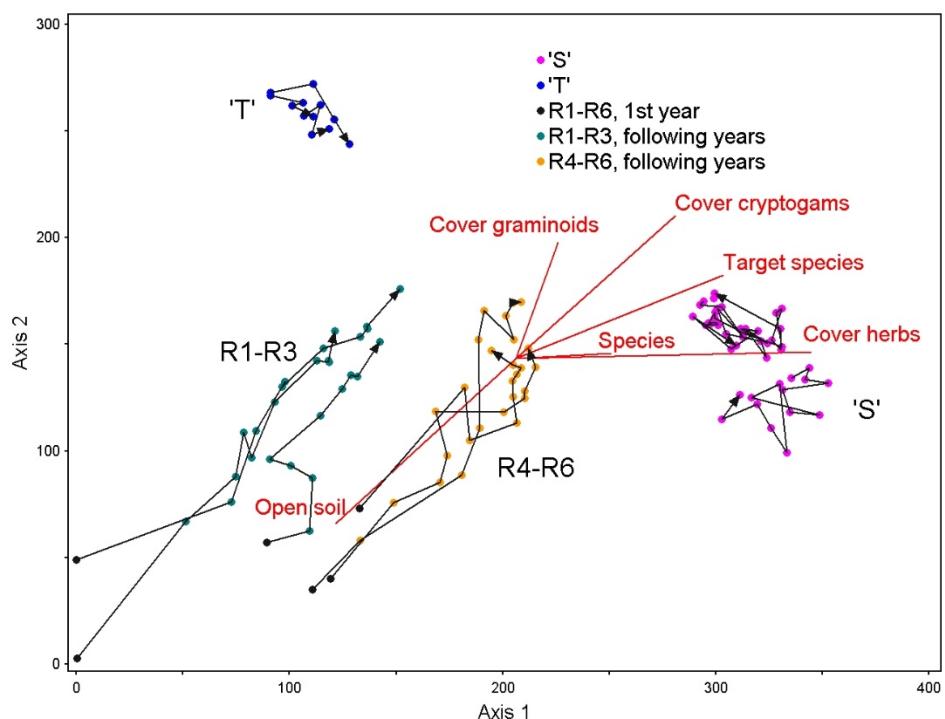


Fig. 3. Detrended correspondence analysis of the vegetation data (rank-transformed cover-abundance values). The timepoints of each restoration or reference permanent plot are connected by trajectories. Colours indicate the affiliation to five classes according to cluster analysis. The vectors of structural and diversity variables are printed in red colour (species = species number). Axes scaling: 100 = 1 SD unit. Axis 1 explains 68% and axis 2 an additional 16% of the variance in the data set.

Abb. 3. Detrended correspondence analysis der Vegetationsdaten (rangtransformierte Artmächtigkeiten). Die Aufnahmen jeder Restitutions- bzw. Referenz-Dauerfläche in den verschiedenen Jahren sind durch Trajektorien verbunden. Die Farben geben die Zugehörigkeit zu fünf Klassen gemäß der Clusteranalyse an. Die Vektoren von strukturellen bzw. Diversitätsvariablen sind rot eingetragen (species = Artenzahl). Achsenkalierung: 100 = 1 SD-Einheit. Achse 1 erklärt 68 % und Achse 2 weitere 16 % der Gesamtvarianz im Datensatz.

The vectors of structural and diversity variables in Figure 3 indicate some conspicuous differences between the plot types and changes during succession of the restoration plots. The reference plots ‘S’ exhibit the highest cover of herbs and species number of all plots, as can be gathered from the fact that the vectors of these variables point directly towards the ‘S’ plots. The reference plots ‘T’ are in turn characterised by a slightly greater cover of graminoids than the plots ‘S’. The succession trajectories run parallel to the bisecting line of axes 1 and 2 which is also the case for several of the vectors. Thus the following changes in the course of succession can be seen: increasing of the number of target species and of the cover of cryptogams and decreasing percentage of open soil, which continuously declined from $99 \pm 0.2\%$ to $39 \pm 8\%$, which is still much more than at the reference plots (‘S’: $9 \pm 2\%$, ‘T’: $10 \pm 3\%$).

The dendrogram of the vegetation classification is not shown, instead the affiliation to five classes is indicated in the ordination diagram Figure 3 by colours. The classification complements the results of the ordination. The five classes are ‘T’, ‘S’, R1–R6 in the first year, R1–R3 in the following years and R4–R6 in the following years. This underlines the special character of the restoration plots in the first year as well as the separation of the restoration plots according to different reference sites.

3.2 Summarising variables

The success of restoration can be summarised by the development of the target species ratios TSR at the restoration plots along the time axis. The mean TSR_{qual} (Fig. 4) started with a low value (\pm standard error) of 0.30 ± 0.03 and reached gradually a value of 0.65 ± 0.03 in 2014. This is a marked improvement but still lower than the mean value of the reference sites (0.74 ± 0.03). The graph also indicates a plateau after the sixth year with no clear further improvements.

The $\text{TSR}_{\text{quant}}$ values (Fig. 4) on the other hand started with an equally low value of 0.31 ± 0.02 . The increase in the following years is surprisingly congruent with TSR_{qual} , but $\text{TSR}_{\text{quant}}$ does not show saturation so far and attained 0.73 ± 0.03 after 10 years. This is exactly the benchmark set by the reference plots (0.73 ± 0.02).

The amelioration of both TSR over time could be due to an increasing number/cover of target species or a reduced number/cover of all species, so Figures 5 and 6 depict these variables for further clarification. As can be seen from Figure 5, the total species number increased from 16.3 ± 1.6 to 28.8 ± 1.7 . A plateau was reached after the fifth year. At the reference plots, a mean of 28.8 ± 1.3 (‘S’) and 21.8 ± 1.6 (‘T’) was found, which demonstrates an equal or even higher phytodiversity at the restoration plots ten years after restoration.

The mean number of target species at the restoration plots (Fig. 5) rose from 4.8 ± 0.5 in 2005 to 18.5 ± 1.0 in 2014. The increase was distinctive in the beginning and shows a flattening after some years, but still some augmentation in the last years. After ten years, the number of target species lay in between the reference sites ‘S’ (20.6 ± 1.0) and ‘T’ (15.4 ± 0.7). This increase was steeper than that of the total number of species in the first six years, which caused the amelioration of TSR_{qual} .

The mean number of Red-list species per plot also increased markedly from 0.3 ± 0.2 to 10.5 ± 0.9 , a value which equals the reference plots ‘S’ (10.5 ± 0.9) and excels ‘T’ (6.6 ± 0.5).

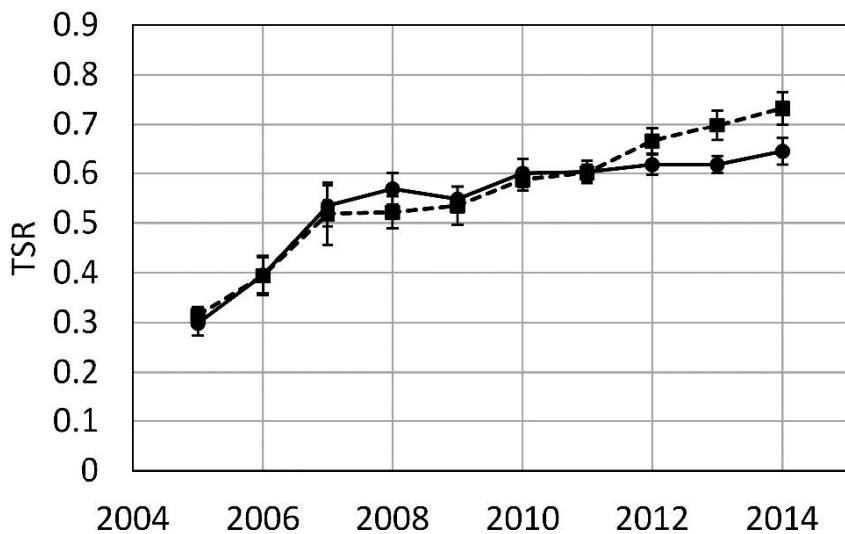


Fig. 4. Mean target species ratios of the restoration plots during the study period. Solid line: Qualitative target species ratio. Dotted line: Quantitative target species ratio. Error bars indicate standard errors of the six permanent plots.

Abb. 4. Mittlere Zielartenindizes der Restitutionsflächen über die Untersuchungszeit. Durchgezogene Linie: Qualitativer Zielartenindex. Gestrichelte Linie: Quantitativer Zielartenindex. Die Fehlerbalken geben den Standardfehler der sechs Dauerflächen an.

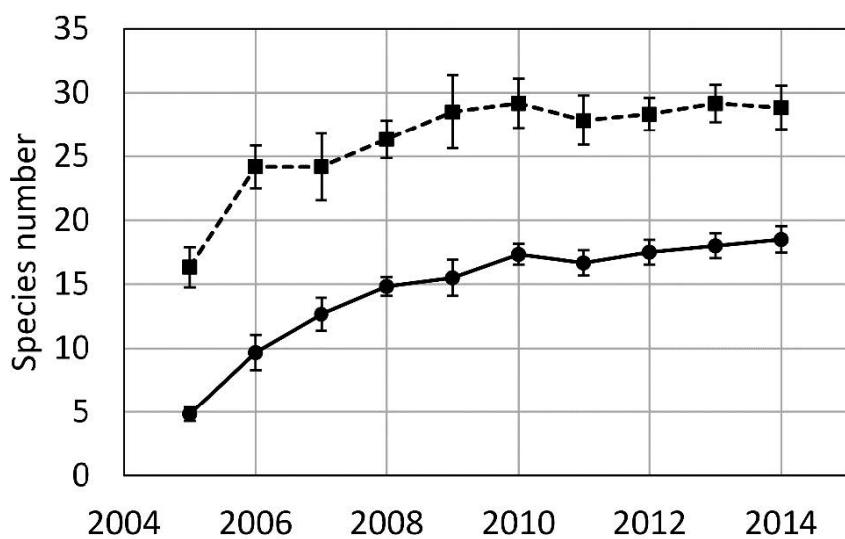


Fig. 5. Mean species numbers of the restoration plots during the study period. Solid line: Target species. Dotted line: All species. Error bars indicate standard errors of the six permanent plots.

Abb. 5. Mittlere Artenzahlen der Restitutionsflächen über die Untersuchungszeit. Durchgezogene Linie: Zielartenzahl. Gestrichelte Linie: Gesamtartenzahl. Die Fehlerbalken geben den Standardfehler der sechs Dauerflächen an.

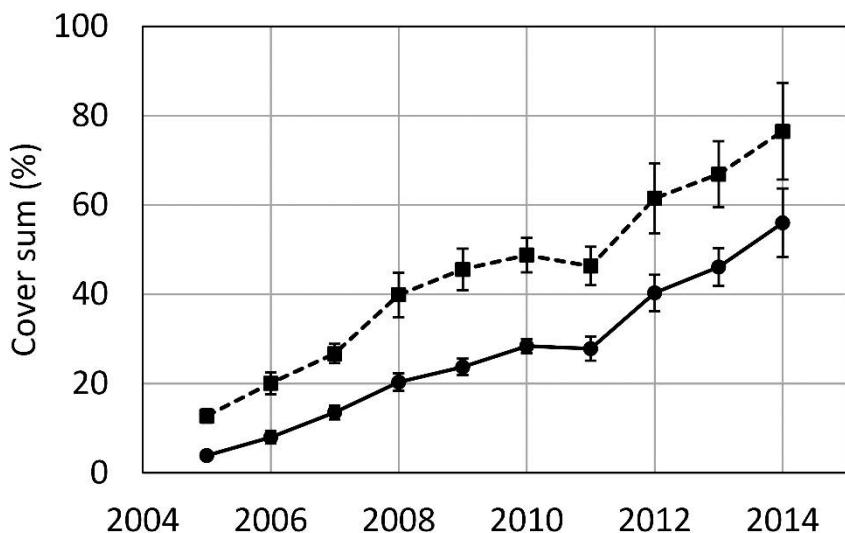


Fig. 6. Mean cover sums of the restoration plots during the study period. Solid line: Target species. Dotted line: All species. Error bars indicate standard errors of the six permanent plots.

Abb. 6. Mittlere Deckungssummen der Restitutionsflächen über die Untersuchungszeit. Durchgezogene Linie: Zielarten. Gestrichelte Linie: alle Arten. Die Fehlerbalken geben den Standardfehler der sechs Dauerflächen an.

Both, the cover sum of all species and the cover sum of target species (Fig. 6) increased steadily without saturation even after ten years. But the relative increase of target species was twice as high (on average + 128% each year) than that of all species (on average + 61% each year), which therefore caused a constant improvement of the restoration plots as measured by $\text{TSR}_{\text{quant}}$.

The mean number of ruderal species at the restoration plots dropped from 8.2 ± 1.0 in 2005 to 5.0 ± 0.7 in 2014. However, this group is still more present than on the reference plots ('S': 2.7 ± 0.6 , 'T': 1.3 ± 0.1).

3.3 Constancy table of the restoration site and comparisons with reference sites

The floristic composition of the restoration plots changed over the 10-year study period (Table 1). In the first year, three Red-list species established themselves on at least one of the plots; seven years later this number increased to 23 (among them *Alyssum montanum* subsp. *gmelinii*, *Fumana procumbens*, *Koeleria glauca*, *Poa badensis*). Nine further target species were already present in the first year at least at one plot; this number increased to 15 species after 10 years. Target species of later successional stages (e. g., *Ononis repens*, *Phleum phleoides*, *Stipa capillata*) established themselves in the second to fourth year, but only in the case of *Phleum phleoides* was there a considerable increase, up to 100% constancy. *Koelerion glaucae* species were present with constancies of 17–67% since the 3rd year and with 33–100% since the 7th year.

The number of ruderal species which occurred at least at one restoration plot was high in the first year: 19, but it decreased to 12 after ten years. A number of ruderal species appeared only in the first year: *Amaranthus blitoides*, *Amaranthus retroflexus*, *Chenopodium strictum*, *Digitaria sanguinalis*, *Eragrostis minor*, *Poa annua*, *Polygonum aviculare* agg. and *Veroni-*

Table 1. Constancy table (percentages) of the plots R1–R6 (sand corridor) for the studied ten-year period. t: target species, r: ruderal species, o: other species. B (if not in headline): bryophyte species. Koel. g.: characteristic species of the *Koelerion glaucae* alliance in the area.

Tabelle 1. Stetigkeitstabelle (Prozente) der Plots R1–R6 (corridor) für die untersuchten 10 Jahre. t: Zielarten, r: Ruderalarten o: andere Arten. B (wenn nicht in Überschrift): Moosart. Koel. g.: charakteristische Arten des *Koelerion glaucae*-Verbändes im Gebiet.

Column	1	2	3	4	5	6	7	8	9	10
Year	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
Open soil [%] average	99	97	93	89	85	86	82	63	53	39
Absolute numbers red-list/near-threatened taxa	3	13	15	19	22	22	22	23	23	23
Mean species numbers (average)	16.3	24.2	24.2	26.3	28.5	29.2	27.8	28.3	29.2	28.8
Red-list/near-threatened species: vascular plants										
t Asperula cynanchica	17	50	67	67	50	67	67	67	67	67
t Thymus serpyllum	17	17	50	50	50	50	67	67	67	67
t Alyssum montanum subsp. <i>gmelinii</i> (Koel. g.)	.	33	67	67	83	83	100	100	100	100
t Dianthus carthusianorum	.	17	17	17	17	17	17	17	17	17
t Fumana procumbens	.	17	17	33	50	50	50	50	50	50
t Medicago minima	.	67	100	100	100	100	100	100	100	83
t Phleum arenarium	.	17	33	50	67	67	67	67	67	83
t Poa badensis (Koel. g.)	.	17	33	33	33	50	50	50	50	50
t Silene conica	.	67	67	50	67	83	67	83	83	100
t Silene otites	.	17	50	83	33	50	67	67	67	67
t Euphorbia seguieriana	.	.	50	67	67	67	67	67	67	67
t Koeleria glauca (Koel. g.)	.	.	17	17	17	33	33	33	33	33
t Phleum phleoides	.	.	33	50	50	50	67	83	83	100
t Veronica verna	.	17	.	.	17	17	17	17	17	17
t Hippocrepis comosa (near threatened)	.	.	.	17	33	33	17	17	17	33
t Stipa capillata	.	.	.	17	17	17	17	17	17	17
t Koeleria macrantha	.	.	.	17	17	17	17	17	17	17
t Corynephorus canescens	17	33	33	33	33	50
t Vicia lathyroides	17	17	17	17	50	33
Red-list species: lichens										
o Cladonia furcata subsp. <i>subrangiformis</i>	67	100	100	100	100	100	100	100	100	100
t Peltigera rufescens	.	17	.	17	33	67	67	67	67	83
t Cetraria aculeata	17	17	17
Other target species										
t Artemisia campestris	67	67	67	67	83	83	100	100	100	100
t Centaurea stoebe s.l.	50	50	50	50	50	50	67	67	67	67
t Euphorbia cyparissias	17	33	17	33	33	33	17	17	17	17
t Tortula ruraliformis (B)	83	83	100	100	100	100	100	100	100	100
t Sedum acre	50	17	17	67	83	83	33	33	.	17
t Arenaria serpyllifolia agg.	.	67	83	83	100	100	100	83	83	100
t Cerastium semidecandrum	.	33	50	50	50	100	83	100	100	100

Column Year	1 2005	2 2006	3 2007	4 2008	5 2009	6 2010	7 2011	8 2012	9 2013	10 2014
t <i>Helianthemum nummularium</i> subsp. <i>obscurum</i>	.	33	50	50	50	50	50	67	67	67
t <i>Holosteum umbellatum</i>	.	50	33	50	33	33	33	50	67	67
t <i>Sedum sexangulare</i>	.	33	33	33	33	33	33	33	33	33
t <i>Rumex acetosella</i>	33	33	33	50	50	50	.	17	17	.
t <i>Erophila verna</i>	.	33	.	17	.	33	33	33	67	50
t <i>Trifolium arvense</i>	.	.	17	.	17	17	17	17	17	17
t <i>Echium vulgare</i>	50	50	17	50	17	.	17	.	.	.
t <i>Acinos arvensis</i>	.	.	17	17	17	17	17	17	.	.
t <i>Erodium cicutarium</i>	33	17	33	17	33
t <i>Petrorhagia prolifera</i>	.	.	33	17	.	50	.	.	17	.
t <i>Ononis repens</i>	17	17	17	33
t <i>Saxifraga tridactylites</i>	17	17	17
t <i>Medicago lupulina</i>	67	17
t <i>Myosotis stricta</i>	.	17
t <i>Vulpia myuros</i>	17
Ruderal species										
r <i>Carex hirta</i>	17	17	17	17	17	17	17	17	17	17
r <i>Elymus repens</i>	67	83	83	83	100	100	100	100	100	50
r <i>Oenothera biennis</i> s.l.	17	50	17	50	100	83	83	83	67	50
r <i>Rubus caesius</i>	67	67	33	33	33	17	17	17	17	17
r <i>Bromus tectorum</i>	.	50	83	100	100	100	100	100	100	100
r <i>Conyza canadensis</i>	.	83	100	83	50	33	50	50	50	17
r <i>Poa angustifolia</i>	.	17	33	33	33	33	33	33	33	33
r <i>Calamagrostis epigejos</i>	.	.	17	33	33	50	67	83	83	83
r <i>Cynodon dactylon</i>	.	.	17	17	33	33	50	50	50	50
r <i>Equisetum arvense</i>	.	.	17	17	17	17	17	17	17	17
r <i>Bromus sterilis</i>	33	67	17	33	50	33	17	.	.	.
r <i>Salsola kali</i> subsp. <i>tragus</i>	67	100	83	33	50
r <i>Verbascum densiflorum</i>	17	17	17	17	17
r <i>Veronica arvensis</i>	.	50	50	50	17
r <i>Vicia villosa</i> s.l.	17	17	17	.	.	33
r <i>Fallopia convolvulus</i>	17	33	33
r <i>Setaria viridis</i>	83	17	33	.
r <i>Apera spica-venti</i>	.	17	50	.	.	17
r <i>Vicia hirsuta</i>	17	17	17	.	.	.
r <i>Chenopodium album</i> subsp. <i>album</i>	67	67
r <i>Urtica dioica</i>	17	17
r <i>Viola tricolor</i> agg.	17	33
r <i>Bromus h. subsp. hordeaceus</i>	.	50	17
r <i>Senecio vulgaris</i>	.	17	17
r <i>Digitaria sanguinalis</i>	100
r <i>Polygonum aviculare</i>	83

Column Year	1 2005	2 2006	3 2007	4 2008	5 2009	6 2010	7 2011	8 2012	9 2013	10 2014
r Amaranthus blitoides	33
r Amaranthus retroflexus	17
r Chenopodium strictum s.l.	33
r Eragrostis minor	33
r Poa annua	17
r Veronica persica	17
r Lactuca serriola	.	33
r Galium aparine	.	17
r Senecio vernalis	.	17
Other species: herbs and grasses										
o Dactylis glomerata	.	33	17	50	50	50	33	33	33	17
o Silene v. subsp. vulgaris	.	.	17	33	33	33	33	33	33	33
o Festuca ovina agg.	.	.	17	33	33	67	67	67	67	67
o Silene latifolia subsp. alba	17	33	17	17	17
o Plantago lanceolata	17	17	17	.	.	.	17	.	.	.
o Lolium perenne	17	33	17
o Crepis capillaris	.	33	17	.	17
o Cerastium holosteoides	17	33	33
o Thymus pulegioides	17	17
o Achillea millefolium agg.	.	17	17
o Galium mollugo agg.	.	.	17	17
o Rhinanthus minor	17
o Agrostis stolonifera	.	17
o Holcus lanatus	.	17
o Vicia angustifolia	.	.	.	17
Other species: bryophytes										
o Hypnum cupressiforme var. lacunosum	67	67	67	67	67	67	67	67	67	67
o Brachythecium albicans	.	.	.	83	100	100	100	100	100	100
o other Akrokarpi	33	17	.	17	17	17
o Bryum argenteum and cf. argenteum	33	33
Woody species										
o Pinus sylvestris (herb layer)	100	100	100	83	83	33	17	.	.	.
o Pinus sylvestris (shrub layer)	33	.	.	.
o Prunus avium juv.	17	50	17	17	17	17
o Cotoneaster spec. (herb layer)	17	17	17	17
o Juglans regia juv.	.	.	.	17	17	17
o Quercus robur juv.	.	.	17

ca persica or in the second year: *Galium aparine*, *Lactuca serriola* and *Senecio vernalis*. The annual ruderal species *Salsola kali* subsp. *tragus* (with C4 metabolism), typical for open sandy sites in our study area, characterised the first five years of the vegetation development. Despite its spiny leaf apices it was heavily grazed by the donkeys.

A total of 52 target species was found at least at one reference plot in at least one year (44 at ‘S’, 24 at ‘T’; Supplement E2). The two donor sites are different with respect to their successive stage: At the reference site ‘S’, 45% of all target species were *Festuco-Brometea* species compared to only 17% at reference site ‘T’. This explains the different position of ‘T’ and ‘S’ plots in the ordination diagram (Fig. 3). Altogether 42 target species could be detected at least once at the restoration plots, 36% of which were *Festuco-Brometea* species. Thirty-five of these species occurred also on ‘T’ and/or ‘S’ (group 2 in Supplement E2), which means that 67% of the target species of the donor sites were successfully transferred to the restoration site.

A group of 11 ruderal species colonising the restoration plots might originate from the donor sites, among them clonal grasses like *Calamagrostis epigejos* and *Poa angustifolia*.

No establishment on the plots could be found until yet for the following 17 target species (group 1 in Supplement E2): *Allium sphaerocephalon*, *Alyssum alyssoides*, *Bromus erectus*, *Centaurea scabiosa*, *Cladonia convoluta*, *Cladonia rangiformis*, *Galium verum* s.l., *Helichrysum arenarium*, *Medicago falcata*, *Orobanche arenaria*, *Poa bulbosa*, *Potentilla incana*, *Sanguisorba minor*, *Scabiosa canescens*, *Tortella inclinata*. *Hieracium pilosella* occurs on the corridor, but is not represented in the plots. *Jurinea cyanoides* was present at the corridor near the permanent plots for some years, but meanwhile the species vanished. This species also established itself at one of the *Bassia* plots (B3) in the second year, but disappeared in the fifth year.

Additionally, seven target species (group 3 in Supplement E2), which were never found at the reference plots, occurred on the restoration plots and contributed to the high TSR values: *Acinos arvensis*, *Erodium cicutarium*, *Hippocratea comosa*, *Medicago lupulina*, *Rumex acetosella*, *Sedum acre* and *Vulpia myuros*. *Hippocratea comosa* is the feeding plant for the caterpillars of the threatened butterfly species *Lysandra (Polyommatus) bellargus*, which built up a large population at the restoration site and its vicinity.

Also the bulk of the ruderal species (24 species, group 3 in Supplement E2), which were found solely at the restoration plots, probably did not come from the donor sites.

3.4 Additional plots with establishment of *Bassia laniflora*

At the plot on ex-arable land without deep-sand cover (B1), *Bassia* occurred since 2004 with increasing abundance (Supplement S1). In 2014, the last study year, it reached a cover of 10% representing a high number of individuals since this species is of a gracile growth. This site was relatively rich in phosphate-P (see Section 2.5 and Supplement E1). At the two other plots with abiotic restoration, *Bassia* reached cover values up to 1% continuously over six years so far. Seedlings emerged in late spring (Fig. 7).

4. Discussion

4.1 Restoration of steppic sandy grassland

The restoration of target plant communities will be incomplete if initial habitat stage or environmental factors restrain plant recovery or if the applied restoration technique is not optimal (BULLOCK et al. 2011). Here, however, we found a relatively complete restoration of endangered steppic sandy grassland by means of a three-step approach after 10 years: A high proportion of target species of the donor sites (67%) has been successfully transferred to the



Fig. 7. *Bassia laniflora* seedlings in early May in a *Tortula ruraliformis* carpet (year 2005, permanent plot B1, see Supplement S1) (Photo: A. Schwabe).

Abb. 7. *Bassia laniflora*-Keimpflanzen im frühen Mai in einem *Tortula ruraliformis*-Teppich (Jahr 2005, Dauerfläche B1, s. Beilage S1) (Foto: A. Schwabe).

restoration site, target species cover was similar to that of the reference plots (with still increasing tendency) and floristic similarity of restoration plots and reference plots increased over time. The following aspects have probably been beneficial to this restoration success (cf. GODEFROID et al. 2011): adequate preparation of the site (installation of nutrient-poor deep sand), use of seed-containing plant material of multiple and stable (non-declining) target communities, presence of adjacent grasslands and the intensification of seed exchange between adjacent and restored areas by establishing regular donkey grazing as a management measure (record of donkey endozoochory see FREUND et al. 2015).

Nevertheless there were still some differences between restoration and donor sites after 10 years. Restoration plots did not show exactly the same plant communities as the corresponding reference plots but also developed new structures. This was probably caused by a mixture of propagules of both donor sites on the receptor site (e.g. by means of wind and donkeys) and an input from the surroundings. At the end of the study period, the whole corridor was still dominated by pioneer species (*Koelerion glaucae*), which is highly desired from the point of nature conservation. The fact that later successional species (such as *Stipa capillata*) have so far low cover values can be explained by the disturbance effect of grazing (phytomass removal, gap creation) which favours early successional stages (SÜSS & SCHWABE 2007, SCHWABE et al. 2013). However, grazing seems not to be the only cause for the observed slow vegetation development. According to our studies of spontaneous succession on non-grazed permanent plots located at donor site 'S' (SÜSS et al. 2010, see also Fig. 3), transitional stages (*Koelerion glaucae/Allio-Stipetum*) showed a very slow development over 10–12 years. Restrictions in water and nutrient availability on sandy, non-manured soils are probably further explanatory factors.

Interestingly, the number of target species stagnated since the 6th year after restoration (indicating that the seed potential of the raked material is exhausted) whereas the total cover of target species increased steadily over the whole study period. Asymptotic (TSR_{qual}) and linear (TSR_{quant}) restoration trajectories are promising developments within restoration projects (BULLOCK et al. 2011).

There was a set of species that was not transferred to the restoration site. In our view, this phenomenon has not a simple explanation but is attributable to various possible reasons: 1) establishment only outside the permanent plots (e.g. *Hieracium pilosella*, *Jurinea cyanoides*), 2) rarity at the donor site and therefore low seed content in the transferred plant material (*Poa bulbosa*, *Jurinea cyanoides* only at one reference plot with abundance 2m or +, respectively), 3) environmental conditions hampering the establishment (too harsh for the more mesophytic species: *Bromus erectus*, *Galium verum*, *Medicago falcata*, *Sanguisorba minor*).

Management by grazing will remain essential for the long-term success of sand grassland restoration in many aspects. First, grazing is essential in suppressing the growth of ruderal plant species, especially *Calamagrostis epigejos*, by reducing biomass and increasing light availability. If environmental conditions are not extremely harsh (SÜSS et al. 2004, 2010), *C. epigejos* is able to establish mono-dominant, species-poor stages in grassland successions and shades out subordinate species (SOMODI et al. 2008). A significant reduction of *C. epigejos* cover by grazing as compared to non-grazed plots has been shown previously for different plots of the wider study area (SCHWABE et al. 2004, 2013). In terms of diversity, the occurrence of ruderal species is less problematic or even enriches ecosystems. On the restoration plots, the number of ruderal species (mainly annuals) was quite high in the first year, decreased over time, and, after 10 years, was still higher than on the reference plots. Ruderal species belong inherently to grazed ecosystems because they profit from disturbance and local nutrient accumulations. A dominance of ruderal species in ephemeral initial stages on bare ground is not grazing-specific but a typical phenomenon in ecological restoration, and has been found in studies with inoculated plots (RYDGREN et al. 2010) as well as in studies dealing with spontaneous succession (PRACH et al. 2014). Additionally, ruderal species offer in many cases important pollen resources for highly endangered wild-bee species (KRAUSCH 2011, BEIL et al. 2014). Second, grazing is essential in facilitating plant regeneration. Ungulates disperse a wide range of seeds (including many target species) and create seed beds for plant establishment (ROSENTHAL et al. 2012). In North American tallgrass prairies, it has been proved that the combination of seed addition and grazing activity can facilitate seedling emergence even in initial stages of grassland restoration (MARTIN & WILSEY 2006).

A development of restored sites towards target plant communities has been reported also in the context of spontaneous grassland succession (FAGAN et al. 2008, ALBERT et al. 2014, PRACH et al. 2014, GILHAUS et al. 2015). Within a multi-site analysis including a range of soil moisture conditions in the Czech Republic, PRACH et al. (2014) found an increase in total plant species numbers and target species over time in most spontaneous successional seres. In Hungarian old-fields, cover of target species was higher in older stages of spontaneous succession (ALBERT et al. 2014). However, success of natural regeneration depends on the presence of natural sources of seeds, such as soil seed banks or adjacent target plant communities (FAGAN et al. 2008, GODEFROID et al. 2011, GILHAUS et al. 2015). On many locations, dispersal limitation hinders the development of target communities on restoration sites or leads to slow progresses (KIRMER & MAHN 2001). Even in landscapes with well-connected habitat patches, complete natural regeneration of species-rich grasslands can take

over a century (REDHEAD et al. 2014). The anemochorous seed input from adjacent vegetation can be biased by grasses dominating the seed spectrum over herbs (DIACON-BELLI et al. 2013).

4.2 Establishment of *Bassia laniflora* populations

In our study, *Bassia laniflora* established new populations, with the largest number of individuals on ex-arable land that has not been modified by deep-sand deposition (reflecting its slightly ruderal strategy). This site was relatively rich in phosphate-P (Supplement E1) and was characterised by a community type comprising only few Red-list species. The results of the plots with deep-sand addition (B2, 3) showed that a continuous establishment of *Bassia* seedlings was possible over the complete time period of 6 years. In the plots B2 and B3, *Bassia* was present as part of the *Jurineo cyanoidis-Koelerietum glaucae* Korneck 1974, a characteristic association of the base-rich sandy sites of the northern upper Rhine valley (KORNECK 1974), but very rare.

The number of sites with occurrence of *Bassia* in the Darmstadt region did not increase over the last 20 years by natural dispersal processes (the period we monitored for this area). Mostly, the seedlings germinated in direct vicinity to the parental individuals. *Bassia laniflora* is probably not able to build-up permanent soil seed banks in the study region. We did not find the species in the frame of our seed bank studies (KROLUPPER & SCHWABE 1998, EICHBERG et al. 2006); moreover, there are no reports of permanent seed banks for *B. laniflora* in other publications. High inter-annual fluctuation in the numbers of individuals has been reported for *B. laniflora* (Fig. 5 in SCHWABE et al. 2000) and germination tests in the laboratory revealed a germination rate of only 12% (SCHWABE et al. 2000).

5. Conclusions

After 10 years, we conclude that the used three-step restoration approach: 1) deposition of deep sand, 2) transfer of plant material, 3) grazing management was successful in re-establishing steppic sandy grassland. The target community complex developed under low-intensity donkey grazing, which is an effective tool to manage threatened open sand vegetation and decrease the influence of competitive ruderal species.

The spreading of raked material on raw sandy soil in combination with grazing management is suitable to establish new populations of the critically endangered, annual species *Bassia laniflora*. An abiotic habitat restoration is not mandatory in the case of this slightly ruderal species, if a sufficient disturbance regime is realized (e.g. by low-intensity grazing). Since there is evidence that *B. laniflora* is a “poor disperser”, we regard this species as strongly depending on human assistance in colonising new sites.

Erweiterte deutsche Zusammenfassung

Einleitung – Die fortwährende Verkleinerung der letzten gut ausgebildeten Flächen und die Verschlechterung ihrer Vernetzung in der mitteleuropäischen Landschaft betrifft in besonderem Maße auch Sandtrockenrasen. Die Fragmentierungen in den stark bevölkerten Gebieten führen zu kleinen Restpopulationen von Pflanzen- und Tierarten und zu Problemen der genetischen Verarmung (YOUNG et al. 1996, MIDDLETON 2013). Um das langfristige Überleben kleiner Pflanzenpopulationen und ihrer Habitate zu gewährleisten, sind Maßnahmen der Restitution dringend erforderlich (BAKKER & BERENDSE 1999). Steppenartige Sandtrockenrasen auf basenreichem Substrat, die wir im Gebiet der nördlichen-

Oberrheinebene bei Darmstadt/Darmstadt-Dieburg (Hessen) untersuchen, sind als prioritäre Habitattypen in der EU 92/43 Habitat-Direktive gelistet: *Koelerion glaucae*: Typ 6120, *Allio sphaerocephalii-Stipetum capillatae* Korneck 1974: Type 6240 (EUROPEAN COMMISSION 2007).

Das hier vorgestellte Restitutionsprojekt eines neu angelegten Korridors zwischen zwei Sandlebensräumen umfasste folgende drei Maßnahmen: 1) abiotische Restitution (Deposition von nährstoffarmem, basenreichem Tiefensand auf einem früheren Sandacker), 2) biotische Restitution (Inokulation mit Pflanzenmaterial von gut entwickelten Spenderflächen) sowie 3) Management (Eselbeweidung). Vor dem Hintergrund der Frage nach dem langfristigen Restitutionserfolg dieses 3-Stufen-Ansatzes untersuchten wir die Vegetationsentwicklung der Restitutionsfläche im Vergleich zu den Spenderflächen, die somit auch als Leitbildflächen dienen, über einen Zeitraum von 10 Jahren. Zudem prüften wir auf weiteren Dauerflächen die Populationsentwicklung der hoch gefährdeten Sand-Radmelde (*Bassia laniflora*) nach Rechguttransfer über einen Zeitraum von 6–12 Jahren.

Leitende Fragen dieser Studie waren: (1) Ist es möglich, steppenartige Sandtrockenrasen auf ehemaligem Acker längerfristig zu restituieren mit Hilfe eines 3-Stufen-Ansatzes, der Tiefensand-Deposition, biotische Restitution mit Inokulation und nachfolgendes Beweidungsmanagement umfasst? (2) Ist es möglich, Populationen der stark gefährdeten Sand-Radmelde (*Bassia laniflora*) längerfristig in Pionier-Sandrasen zu etablieren?

Material und Methoden – Die Untersuchungen fanden im hessischen Sandgebiet auf der Gemarkung von Seeheim-Jugenheim (Kreis Darmstadt-Dieburg) statt. Die basenreichen Sande wurden im Spätglazial und frühen Postglazial aus den Terrassen des Rheins ausgeweitet und immer wieder umgelagert.

Die Restitutionsfläche (R) liegt zwischen einer gut entwickelten Leitbildfläche (S) und einer Alt-Restitutionsfläche (STROH et al. 2002, 2007). Sie stellt einen nährstoffarmen Tiefensand-Korridor dar (250 m x 22 m, Höhe der Aufschüttung 1,5–3 m; Nährstoffdaten im Anhang E1), der beide Altflächen verbindet (Abb. 1, 2). Kurz nach der Sanddeposition wurde der Korridor mit gerechtem/gemähten Material von zwei gut entwickelten Spenderflächen inokuliert (Fläche S: *Koelerion glaucae-/Allio-Stipetum*-Komplex, inokuliert auf den Plots R1–R3; T: mit *Koelerion glaucae* und Pionierstadien von z. B. *Corynephorus canescens*, *Phleum arenarium*, inokuliert auf den Plots R5–R6). Eselbeweidung mit geringer Besatzdichte wurde für ca. drei Wochen jährlich als Pflegemaßnahme eingesetzt. Gehölze und randliche *Calamagrostis epigejos*-Polykormone sind punktuell manuell reduziert worden. Die Vegetation der Restitutionsfläche und der Spenderflächen wurde mit pflanzensoziologischen Aufnahmen auf Dauerflächen (je 25 m²) dokumentiert. Die Datenanalyse umfasste Ordinations- (detrended correspondence analysis, DCA) und Klassifikationsverfahren (Clusteranalyse nach Ward) sowie die Berechnung der floristischen Unähnlichkeit (Abstandsmaß nach Sørensen) und von „Target Species Ratios“ (TSR: Verhältnis von Zielarten der *Koelerio-Corynephoretea* und *Festuco-Brometea* zu allen Arten; qualitativ und unter Einbeziehung der Deckungssummen: quantitativ). Die Entwicklung der Plots wurde auch mit pflanzensoziologischen Stetigkeitstabellen dokumentiert.

Die stark gefährdete Art *Bassia laniflora* kam auf den Spenderflächen „T“ und „S“ nicht vor. Wir stellen Daten zur Etablierung dieser Art nach Rechguttransfer vor (drei Dauerflächen in Nähe zum Korridor). Eine der Flächen wurde abiotisch nicht restituier und weist eine relativ hohe Phosphatkonzentration im Boden auf (67 mg Phosphat-P kg⁻¹ Trockenboden, Anhang E1). Diese Flächen konnten 12 Jahre bzw. 6 Jahre mit pflanzensoziologischen Aufnahmen dokumentiert werden.

Ergebnisse – Die DCA (Abb. 3) zeigt eine kontinuierliche floristische Entwicklung der Restitutionsplots (R1–R6) in Richtung auf die Spenderflächen. Die mittlere floristische Unähnlichkeit nach Sørensen (± Standardfehler) zwischen den restituierten Plots R1–R3 und ihrer Spenderfläche „T“ verringerten sich von $0,83 \pm 0,05$ im Jahr 2005 auf $0,47 \pm 0,02$ im Jahr 2014, und zwischen R4–R6 und „S“ von $0,85 \pm 0,01$ auf $0,50 \pm 0,01$. Der Offenboden-Anteil auf den Restitutionsplots nahm ab, die Anzahl der Ruderalarten verminderte sich und die Anzahl an Zielarten nahm zu. Klassifikationsverfahren untermauerten die Gruppierungen der Plots in der Ordination, indem sie die Restitutionsplots entsprechend der Herkunft des Spendermaterials auf trennten. Die Entwicklung der qualitativen TSR-Werte erreichte nach dem sechsten Jahr ein Plateau mit Werten, die nur leicht von denen der Spenderflächen

abwichen. Der quantitative TSR zeigte eine stetige Erhöhung über die Zeit und übertraf noch die Werte einer Spenderfläche. *Koelerion glaucae*-Arten erreichten eine Stetigkeit von 17–67 % seit dem dritten Jahr und von 33–100 % seit dem siebten Jahr (Abb. 4a, b). Die Ziel- und sonstigen Arten stiegen in ihrer Anzahl bis ca. zum sechsten Jahr an (Abb. 5a, b); die Deckungen aller Arten und speziell der Zielarten erhöhten sich kontinuierlich über die gesamte Periode (Abb. 6a, b). Die Stetigkeitstabelle der Plots auf dem Sand-Korridor (Tab. 1) zeigt, dass sich bereits im ersten Jahr drei Rote-Liste-Arten etablierten; seit dem achten Jahr sind 23 Rote-Liste-Arten vorhanden (darunter *Alyssum montanum* subsp. *gmelinii*, *Fumana procumbens*, *Koeleria glauca*, *Poa badensis*). Neun weitere Zielarten waren bereits im ersten Jahr vorhanden (mindestens auf einem Plot); diese Zahl erhöhte sich auf 15 Arten nach 10 Jahren. Zielarten der weiter entwickelten Sukzessionsstadien (z. B. *Ononis repens*, *Phleum phleoides*, *Stipa capillata*) etablierten sich im zweiten bis zum vierten Jahr, aber nur im Falle von *Phleum phleoides* gab es eine beträchtliche Zunahme bis zu 100 % Stetigkeit.

Die Zahl der Ruderalarten, die mindestens auf einem Plot im Sand-Korridor vorkamen, war im ersten Jahr hoch (19); sie erniedrigte sich auf 12 nach 10 Jahren. Die besonders auf Sandstandorten typische Ruderalart *Salsola kali* subsp. *tragus* zeigte in den ersten fünf Jahren der Entwicklung hohe Stetigkeit; trotz der bewehrten Blätter wurde die Art stark von den Eseln gefressen und ging dann zurück.

Die floristischen Beziehungen zwischen dem Korridor und den Spenderflächen werden im Anhang E2 aufgeschlüsselt. 67 % der Zielarten der Spenderflächen zeigten einen Etablierungserfolg auf der Restitutionsfläche. Es gab einige Arten, die nicht übertragen werden konnten (u. a. *Poa bulbosa*, *Bromus erectus*, *Galium verum*, *Medicago falcata*, *Sanguisorba minor*).

Die Untersuchungen an *Bassia laniflora* zeigten, dass nach 12 Jahren auf der Fläche ohne abiotische Restitution die höchste Deckung (10 %) nachzuweisen war (Beilage S1). Auf den beiden Plots mit abiotischer Restitution erreichte *Bassia* innerhalb von sechs Jahren bis zu 1 % Deckung. Die Keimlinge entwickelten sich im Spätfrihling (Abb. 7).

Diskussion – Wir konnten mit dem 3-Stufen-Ansatz eine relativ vollständige und langfristige Restitution der gefährdeten *Koelerion glaucae/Allio-Stipetum*-Lebensraumtypen erreichen. Die folgenden Aspekte haben diesen Erfolg mit hoher Wahrscheinlichkeit ermöglicht (s. auch GODEFROID et al. 2011): eine adäquate Vorbereitung der Restitutionsfläche durch die Verwendung von nährstoffarmem Sand; Transfer von Diasporen-haltigem Pflanzenmaterial von intakten Spenderflächen durch den Menschen und Diasporen-Austauschprozesse zwischen Spender- und Restitutionsfläche durch die Weidetiere (zum Nachweis von Esel-Endozoochorie s. FREUND et al. 2015). Trotzdem gibt es nach 10 Jahren noch floristische Unterschiede zwischen der Restitutionsfläche und den Spenderflächen. Die Tatsache, dass die Arten mittlerer Sukzessionsstadien (z. B. *Stipa capillata*) bisher nur relative niedrige Stetigkeiten und Deckungen auf dem Korridor erreichen, kann durch das dynamische System der Eselbeweidung erklärt werden. Dieses erhält die frühen Stadien durch Phytomasse-Entnahme und Lückenbildung. Dies konnten wir auch in verschiedenen anderen Untersuchungen in unserem Gebiet dokumentieren (SÜSS & SCHWABE 2007, SCHWABE et al. 2013). Hinzu kommt, dass allgemein die Sukzession in diesen edaphisch extremen Lebensräumen bei niedrigen Nährstoffwerten des Substrates sehr langsam abläuft (SÜSS et al. 2010). Diese ausgeprägte Präsenz von *Koelerion glaucae*-Vegetation auf Restitutionsflächen ist aus Sicht des Naturschutzes sehr erwünscht. Bemerkenswert ist, dass die Zahl der Zielarten nach dem sechsten Jahr stagnierte und sich zeigt, dass damit offenbar das Diasporenpotential des aufgebrachten Pflanzenmaterials erschöpft ist. Die Gründe dafür, dass sich verschiedene Arten nicht etablieren konnten, sind sicherlich mehrschichtig, so z. B. die allgemeine Individuenarmut auf den Spenderflächen (z. B. *Poa bulbosa*) oder auch zu harsche Bedingungen auf dem Korridor für eher mesophytische Arten (*Bromus erectus*, *Galium verum* u. a.). Die Deckungssumme der etablierten Zielarten nahm hingegen beständig zu.

In unserer Studie konnte *Bassia laniflora* besonders große Populationen auf einem ehemaligen Acker mit relativ hohen Boden-Phosphat-Werten und Beweidungsregime aufbauen. Aber auch auf den besonders nährstoffarmen Tiefensandflächen gelang die Etablierung neuer Bestände, hier sogar in der typischen Vergesellschaftung im *Jurineo cyanoidis-Koelerietum glaucae* Korneck 1974. Allgemein ist die Anzahl der Vorkommen von *Bassia* im Untersuchungsgebiet in den letzten 20 Jahren nicht gestiegen, die Art fehlt auch in der Diasporenbank im Boden (KROLUPPER & SCHWABE 1998, EICHBERG et

al. 2006). Hohe inter-annuelle Fluktuation der Individuen (Fig. 5 in SCHWABE et al. 2000), niedrige Keimungsraten und fehlende Lückendynamik in den Beständen sind sicherlich Hauptfaktoren, auch für die starken Rückgänge in anderen Gebieten.

Schlussfolgerungen – Wir folgern, dass die Restitution von artenreichen steppenartigen Rasen auf ehemaligen Sandäckern erfolgreich war für die untersuchte Periode von 10 Jahren. Zugrunde lag ein 3-Stufen-Ansatz mit 1) Deposition von nährstoffarmem Tiefensand, 2) Transfer von Pflanzenmaterial, 3) Eselbeweidung. Das Beweidungsmanagement wird essentiell bleiben, um den langzeitigen Erfolg der Restitutionsmaßnahme zu gewährleisten. So konnte im weiteren Untersuchungsgebiet z. B. eine signifikante Reduktion der Deckung von *Calamagrostis epigejos* in beweideten im Vergleich zu unbeweideten Flächen nachgewiesen werden (SCHWABE et al. 2004, 2013).

Für die Art *Bassia laniflora* konnte festgestellt werden, dass sie als „poor disperser“ wahrscheinlich eine stetige Hilfe in Form von Inokulationen mit Rechigut benötigt, um neue Stellen besiedeln zu können. Dieses Verfahren ist sehr erfolgreich.

Acknowledgements

The sand corridor was constructed as part of a ‘Testing and Development’ project. We thank the ‘German Federal Ministry for Environment, Nature Conservation and Nuclear Safety’, the ‘German Federal Agency for Nature Conservation’ and the ‘Landkreis Darmstadt-Dieburg’ for financial and logistic support. The corridor inoculation and grazing management was carried out by R. Stürz (Ober-Ramstadt). We thank Dr. S. Dittrich and one anonymous reviewer for valuable suggestions improving the manuscript and Dr. A. Thorson (Oxford) for editing the English text.

Supplements

Supplement S1. Plots B1-B3 with the highly threatened *Bassia laniflora*.

Beilage S1. Plots B1-B3 mit der hochgradig gefährdeten *Bassia laniflora*.

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Soil data (0-10 cm) from the two study areas.

Anhang E1. Bodendaten (0-10 cm) aus zwei Untersuchungsgebieten.

Supplement E2. Species data for all plot types.

Anhang E2. Angaben zu den Pflanzenarten aller Untersuchungsflächen.

References

- AKHANI, H., TRIMBORN, P. & ZIEGLER, H. (1997): Photosynthetic pathways in *Chenopodiaceae* from Africa, Asia and Europe with their ecological, phytogeographical and taxonomical importance. – Plant Syst. Evol. 206: 187–221.
- ALBERT, A.-J., KELEMEN, A., VALKÓ O., MIGLÉCZ, T., CSECSERITS, A., RÉDEI, T., DEÁK, B., TÓTHMÉRÉSZ, B. & TÖRÖK, P. (2014): Secondary succession in sandy old-fields: a promising example of spontaneous grassland recovery. – Appl. Veg. Sci. 17: 214–224.
- AUESTAD, I., RYDGREN, K. & AUSTAD, I. (2016): Near-natural methods promote restoration of species-rich grassland vegetation – revisiting a road verge trial after 9 years. – Restor. Ecol. 24: 381–389.
- BAKKER, J.P. & BERENDSE, F. (1999): Constraints in the restoration of ecological diversity in grassland and heathland communities. – Trends Ecol. Evol. 14: 63–68.

- BARKMAN, J.J., DOING, H. & SEGAL, S. (1964): Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. – *Acta Bot. Neerl.* 13: 394–419.
- BEIL, M., KRATOCHWIL, A., STORM, C. & SCHWABE, A. (2014): Community structure and diversity of vegetation and flower-visiting wild bees (*Hymenoptera: Apoidea*) in sandy dry grassland: are there congruent characteristics? – *Phytocoenologia* 44: 175–192.
- BULLOCK, J.M., ARONSON, J., NEWTON, A.C., PYWELL, R.F. & REY-BENAYAS, J.M. (2011): Restoration of ecosystem services and biodiversity: conflicts and opportunities. – *Trends Ecol. Evol.* 26: 541–549.
- BUTTLER, K.P., CEZANNE, R., FREDE, A., GREGOR, T., HAND, R., HODVINA, S. & KUBOSCH, R. (1997): Rote Liste der Farn- und Samenpflanzen Hessens. 4. Fassung. – Wiesbaden: 187 pp.
- COIFFAIT-GOMBAULT, C., BUISSON, E. & DUTOIT, T. (2011): Hay transfer promotes establishment of Mediterranean steppe vegetation on soil disturbed by pipeline construction. – *Rest. Ecol.* 19: 214–222.
- DIACON-BELLI, J.C., EDWARDS, P.J., BUGMANN, H., SCHEIDECKER, C. & WAGNER, H.H. (2013): Quantification of plant dispersal ability within and beyond a calcareous grassland. – *J. Veg. Sci.* 24: 1010–1019.
- DONATH, T.W., BISSELS, S., HÖLZEL, N. & OTTE, A. (2007): Large scale application of diaspore transfer with plant material in restoration practice – Impact of seed and microsite limitation. – *Biol. Conserv.* 138: 224–234.
- DOSCH, L. & SCRIBA, J. (1888): Excursionsflora der Blüten- und höheren Sporenpflanzen mit besonderer Berücksichtigung des Grossherzogtums Hessens und der angrenzenden Gebiete. 3rd ed. – Verlag Emil Roth, Giessen: 616 pp.
- EDWARDS, A.R., MORTIMER, S.R., LAWSON, S.R., LAWSON, C.S., WESTBURY, D.B., HARRIS, S.J., WOODCOCK, B.A. & BROWN, V.K. (2007): Hay strewing, brush harvesting of seed and soil disturbance as tools for the enhancement of botanical diversity in grasslands. – *Biol. Conserv.* 134: 372–382.
- EICHBERG, C., STORM, C., KRATOCHWIL, A. & SCHWABE, A. (2006): A differentiating method for seed bank analysis: validation and application to successional stages of *Koelerio-Corynephoretea* inland sand vegetation. – *Phytocoenologia* 36: 161–189.
- 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.
- EUROPEAN COMMISSION (2007): Interpretation Manual of European Union Habitats. – EUR 27: 1–142.
- FAGAN, C.K., PYWELL, R.F., BULLOCK, J.M. & MARRS, R.H. (2008): Do restored calcareous grasslands on former arable fields resemble ancient targets? The effect of time, methods and environment on outcomes. – *J. Appl. Ecol.* 45: 1293–1303.
- FAUST, C., EICHBERG, C., STORM, C. & SCHWABE, A. (2011): Post-dispersal impact on seed fate by livestock trampling – a gap of knowledge. – *Basic Appl. Ecol.* 12: 215–226.
- FREUND, L., CARRILLO, J., STORM, C. & SCHWABE, A. (2015): Restoration of a newly created inland-dune complex as a model in practice: impact of substrate, minimized inoculation and grazing. – *Tuexenia* 35: 221–248.
- FREUND, L., EICHBERG, C., RETTA, I. & SCHWABE, A. (2014): Seed addition via epizoochorous dispersal in restoration: an experimental approach mimicking the colonization of bare soil patches. – *Appl. Veg. Sci.* 17: 74–85.
- GILHAUS, K., VOGT, V. & HÖLZEL, N. (2015): Restoration of sand grasslands by topsoil removal and self-greening. – *Appl. Veg. Sci.* 18: 661–673.
- GODEFROID, S., PIAZZA, C., ROSSI, G., BUORD, S., STEVENS, A.-D., AGURAIUJA, R., COWELL, C., WEEKLEY, C.W., VOGG, G., IRIONDO, J.M., JOHNSON, I., DIXON, B., GORDON, D., MAGNANON, S., VALENTIN, B., BJUREKE, K., KOOPMAN, R., VICENS, M., VIREVAIRE, M. & VANDERBORGH, T. (2011): How successful are plant species introductions? – *Biol. Conserv.* 144: 672–682.
- GRMAN, E., BASSETT, T., ZIRBEL, C.R. & BRUDVIG, L.A. (2015): Dispersal and establishment filters influence the assembly of restored prairie plant communities. – *Rest. Ecol.* 23: 892–899.
- HODVINA, S. & CEZANNE, R. (2008): Die Sand-Radmelde (*Bassia laniflora*) in Hessen. – *Bot. Naturschutz Hess.* 21: 89–113.
- HÖLZEL, N., BUISSON, E. & DUTOIT, T. (2012): Species introduction – a major topic in vegetation restoration. – *Appl. Veg. Sci.* 15: 161–165.

- HÖLZEL, N. & OTTE, A. (2003): Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material. – *Appl. Veg. Sci.* 6: 131–140.
- KADEREIT, G. & FREITAG, H. (2011): Molecular phylogeny of *Camphorosmeae* (*Camphorosmoideae*, *Chenopodiaceae*): Implications for biogeography, evolution of C4-photosynthesis and taxonomy. – *Taxon* 60: 51–78.
- KIEHL, K., KIRMER, A., DONATH T., RASRAN, L. & HÖLZEL, N (2010): Species introduction in restoration projects – Evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. – *Basic Appl. Ecol.* 11: 285–299.
- KIEHL, K. & PFADENHAUER, J. (2007): Establishment and persistence of target species in newly created calcareous grasslands on former arable fields. – *Plant Ecol.* 189: 31–48.
- 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.
- KOPERSKI, M., SAUER, M., BRAUN, W. & GRADSTEIN, S.R. (2000): Referenzliste der Moose Deutschlands. – *Schriftenr. Vegetationskd.* 34: 1–519.
- KORNECK, D., SCHNITTNER, M. & VOLLMER, I. (1996): Rote Liste der Farn- und Blütenpflanzen (Pteridophyta et Spermatophyta) Deutschlands. – *Schriftenr. Veg.kd.* 28: 21–187.
- KRAUSCH, S. (2011): E+E-Vorhaben “Ried und Sand”: Erfolge bei der Restitution von Sandlebensräumen für Wildbienen. – In: SÜSS, K., STORM, C. & SCHWABE, A. (Eds.): *Ried und Sand: Biotopverbund und Restitution durch extensive Landbewirtschaftung*. – *Naturschutz Biol. Vielfalt* 110: 215–234.
- KROLUPPER, N. & SCHWABE, A. (1998): Ökologische Untersuchungen im Darmstadt-Dieburger Sandgebiet (Südhessen): Allgemeines und Ergebnisse zum Diasporen-Reservoir und -Niederschlag. – *Bot. Naturschutz Hess.* 10: 59–89.
- LEPŠ, J. & V. HADINCOVÁ (1992): How reliable are our vegetation analyses? – *J. Veg. Sci.* 3: 119–124.
- LEYER, I. & WESCHE, K. (2007): Multivariate Statistik in der Ökologie. – Springer, Berlin: 232 pp.
- MARTIN, L.M. & WILSEY, B.J. (2006): Assessing grassland restoration success: relative roles of seed additions and native ungulate activities. – *J. Appl. Ecol.* 43: 1098–1109.
- MIDDLETON, B.A. (2013): Rediscovering vegetation management in preserves: trading experiences between cultures and continents. – *Biol. Conserv.* 158: 271–279.
- MOYNAHAN, O.S., ZABINSKI, C.A. & GANNON, J.E. (2002): Microbial community structure and carbon-utilization diversity in a mine tailings revegetation study. – *Rest. Ecol.* 10: 77–87.
- ÖDMAN, A.M., MARTENSSON, L.-M., SJÖHOLM, C. & OLSSON, P.A. (2011): Immediate responses in soil chemistry, vegetation and ground beetles to soil perturbation when implemented as a restoration measure in decalcified sandy grassland. – *Biodivers. Conserv.* 20: 3039–3058.
- PATZELT, A., WILD, U. & PFADENHAUER, J. (2001): Restoration of wet fen meadows by topsoil removal and germination biology of fen species. – *Restor. Ecol.* 9: 127–136.
- PRACH, K., JONGEPIEROVÁ, I. & ŘEHOUNKOVÁ, K. (2012): Large-scale restoration of dry grasslands on ex-arable land using a regional seed mixture: establishment of target species. – *Restor. Ecol.* 21: 33–39.
- PRACH, K., ŘEHOUNKOVÁ, K., LENCOVÁ, K., JÍROVÁ, A., KONVALINKOVÁ, P., MUDRÁK, O., ŠTUDENT, V., VANĚČEK, Z., TICHÝ, L., PETŘÍK, P., ŠMILAUER, P. & PYŠEK, P. (2014): Vegetation succession in restoration of disturbed sites in Central Europe: the direction of succession and species richness across 19 seres. – *Appl. Veg. Sci.* 17: 193–200.
- PYWELL, R.F., BULLOCK, J.M., HOPKINS, A., WALKER, K.J., SPARKS, T.H., BURKE, M.J. & PEEL, S. (2002): Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. – *J. Appl. Ecol.* 39: 294–309.
- RASRAN, L., VOGT, K. & JENSEN, K. (2007): Effects of topsoil removal, seed transfer with plant material and moderate grazing on restoration of riparian fen grasslands. – *Appl. Veg. Sci.* 10: 451–460.
- REDHEAD, J.W., SHEAIL, J., BULLOCK, J.M., FERRERUELA, A., WALKER, K.J. & PYWELL, R.F. (2014): The natural regeneration of calcareous grassland at a landscape scale: 150 years of plant community re-assembly on Salisbury Plain, UK. – *Appl. Veg. Sci.* 17: 408–418.
- ROSENTHAL, G., SCHRAUTZER, J. & EICHBERG, C. (2012): Low-intensity grazing with domestic herbivores: A tool for maintaining and restoring plant diversity in temperate Europe. – *Tuexenia* 32: 167–205.
- RYDGREN, K., NORDBAKKEN, J.-F., AUSTAD, I., AUESTAD, I. & HEEGAARD, E. (2010): Recreating semi-natural grasslands: A comparison of four methods. – *Ecol. Eng.* 36: 1672–1679.

- SCHMIEDE, R., OTTE, A. & DONATH, T.W. (2012): Enhancing plant biodiversity in species-poor grassland through plant material transfer – the impact of sward disturbance. – *Appl. Veg. Sci.* 15: 290–298.
- SCHÖLLER, H. (coll. with CEZANNE, R. & EICHLER, M.) (1996): Rote Liste der Flechten Hessens. – Hessisches Ministerium des Innern und für Landwirtschaft, Forsten und Naturschutz, Wiesbaden: 76 pp.
- SCHOLZ, P. (2000): Katalog der Flechten und flechtenbewohnenden Pilze Deutschlands. – Schriftenr. Vegetationskd. 31: 1–298.
- SCHWABE, A., STORM, C., ZEUCH, M., KLEINE-WEISCHEDE, H. & KROLUPPER, N. (2000): Sandökosysteme in Südhessen: Status quo, jüngste Veränderungen und Folgerungen für Naturschutz-Maßnahmen. – *Geobot. Kolloqu.* 15: 25–45.
- SCHWABE, A., SÜSS, K. & STORM, C. (2013): What are the long-term effects of livestock grazing in steppic sandy grassland with high conservation value? Results from a 12-year field study. – *Tuexenia* 33: 189–212.
- SCHWABE, A., ZEHM, A., EICHBERG, C., STROH, M., STORM, C. & KRATOCHWIL, A. (2004): Extensive Beweidungssysteme als Mittel zur Erhaltung und Restitution von Sand -Ökosystemen und ihre naturschutzfachliche Bedeutung. – In: FINCK, P., HÄRDITLE, W., REDECKER, B. & RIECKEN, U. (Eds.): Weidelandschaften und Wildnisgebiete. – Schriftenr. Landschaftspfl. Naturschutz 78: 39–61.
- SOMODI, I., VIRÁGH, K. & PODANI, J. (2008): The effect of expansion of the clonal grass *Calamagrostis epigejos* on the species turnover of a semi-arid grassland. – *Appl. Veg. Sci.* 11: 187–192.
- STROH, M. & SÜSS, K. (2011): Beweidungsstruktur und Herdenmanagement im E+E-Vorhaben „Ried und Sand“. – In: SÜSS, K., STORM, C. & SCHWABE, A. (Eds.): Ried und Sand: Biotopverbund und Restitution durch extensive Landbewirtschaftung. – *Naturschutz Biol. Vielfalt* 110: 69–86.
- STROH, M., STORM, C. & SCHWABE, A. (2007): Untersuchungen zur Restitution von Sandtrockenrasen: das Seeheim-Jugenheim-Experiment in Südhessen (1999 bis 2005). – *Tuexenia* 27: 287–306.
- STROH, M., STORM, C., ZEHM, A. & SCHWABE, A. (2002): Restorative grazing as a tool for directed succession with diaspore inoculation: the model of sand ecosystems. – *Phytocoenologia* 32: 595–625.
- SÜSS, K. & SCHWABE, A. (2007): Sheep versus donkey grazing or mixed treatment: results from a 4-year field experiment in *Armerio-Festucetum trachyphyllae* sand vegetation. – *Phytocoenologia* 37: 135–160.
- SÜSS, K., STORM, C. & SCHWABE, A. (2010): Sukzessionslinien in basenreicher offener Sandvegetation des Binnenlandes: Ergebnisse aus Untersuchungen von Dauerbeobachtungsflächen. – *Tuexenia* 30: 289–318.
- SÜSS, K., STORM, C., ZEHM, A. & SCHWABE, A. (2004): Succession in inland sand ecosystems: which factors determine the occurrence of the tall grass species *Calamagrostis epigejos* (L.) Roth and *Stipa capillata* L.? – *Plant Biol.* 6: 465–476.
- VAN DER MAAREL, E. (1979): Transformation of cover-abundance values in phytosociology and its effects on community similarity. – *Vegetatio* 39: 97–114.
- 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.* 119: 1–8.
- WISSLKIRCHEN, R. & HAEUPLER, H. (1998): Standardliste der Farn- und Blütenpflanzen Deutschlands. – Ulmer, Stuttgart: 765 pp.
- YOUNG, A., BOYLE, T. & BROWN, T. (1996): The population genetic consequences of habitat fragmentation for plants. – *Trends Ecol. Evol.*: 413–418.

Table 2. Plots B1-B3 with the highly threatened *Bassia laniflora*. B1: former field without abiotic restoration, B2-3: deep-sand accumulation. t: target species, r: ruderal species, o: other species. B: Bryophyte species, L: Lichen species. 120 a.s.l.; 8°37' E, 49°46' N.

Table 2. Plots B1-B3 mit der hochgradig gefährdeten *Bassia laniflora*. B1: ehemaliger Acker ohne abiotische Restitution. B2-3: Tiefensand-Akkumulation. t: Zielarten, r: Ruderalarten, o: andere Arten. B: Moosarten, L: Flechtenarten. 120 m ü.M.; 8°37' E, 49°46' N.

Supplement E1. Soil data (0-10 cm) from the two study areas (unpublished data, C. Schwebel and C. Storm). pH values were measured in 0.01 mol l⁻¹ calcium chloride after centrifugation. To assess plant-available nitrate and ammonium calcium chloride extracts (0.0125 mol l⁻¹) were made (50 g soil + 200 ml; shaking for 60 min.; Anon. 1991). Phosphate was measured in calcium acetate/calcium lactate extracts (CAL) (10 g soil + 200 ml, shaking for 90 min.; Anon. 1991). N and P analyses were carried out photometrically by means of a Skalar Segmented Flow Analysator. All concentration data refer to oven-dry soil (70 °C). Mean values of samples of June and September 2005 were calculated. SE: standard error.

Anhang E1. Bodendaten (0-10 cm) aus zwei Untersuchungsgebieten (unveröffentlichte Daten, C. Schwebel und C. Storm). Die pH-Werte wurden in 0,01 mol l⁻¹ Calciumchlorid nach Zentrifugation gemessen. Um pflanzenverfügbares Nitrat und Ammonium zu ermitteln, wurden Calciumchlorid-Extrakte hergestellt (50 g Boden + 200 ml, 60 min. Schütteln; Anon. 1991). Phosphat wurde in Calciumacetat/Calciumlaktat-Extrakten (CAL) gemessen (10 g Boden + 200 ml, 90 min. Schütteln, Anon. 1991). Die N- und P-Bestimmungen wurden photometrisch am Skalar Segmented Flow Analysator durchgeführt. Alle Angaben zu Gehalten beziehen sich auf den Trockenboden (70 °C). Es wurden die Mittelwerte von Proben vom Juni und September 2005 berechnet. SE = Standardfehler.

	pH		NO ₃ ⁻ -N (mg/kg)		NH ₄ ⁺ -N (mg/kg)		PO ₄ ³⁻ -P (mg/kg)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Reference plots S (n = 3)	7,4	0,0	1,6	0,1	0,8	0,1	7,7	2,0
Restoration plots R (n = 6)	7,6	0,0	0,3	0,0	0,6	0,1	12,5	1,2
<i>Bassia</i> plot B1 (n = 1)	7,5		1,0		0,9		67,3	

Reference:

Anon. (1991): (Verband der landwirtschaftlichen Untersuchungs- und Forschungsanstalten). Methodenbuch, Vol. 1, Die Untersuchung von Böden. 4th ed. – VDLUFA-Verlag, Darmstadt: 1570 pp.

Supplement E2. Species data for all plot types ('T': donor site for R1–3, 'S': donor site for R4–6). Absolute constancies for the whole investigation period are given (if one species occurred at least one year in one plot it was assigned constancy 1). The sample size is three in each group. Column 1: indication of target, ruderal and other species, Column 2: indication of *Koelerio-Corynephoretea* and *Festuco-Brometea* species, Columns 3–6: indication of donor sites 'T', 'S' and plot numbers of restoration site. (**) species regularly or (*) episodically present on site 'R', but not on sampled plots.

Anhang E2. Angaben zu den Pflanzenarten aller Untersuchungsflächen („T“ Spenderfläche für R1–3, „S“ Spenderfläche für R4–6). Angegeben sind die absoluten Stetigkeiten über die gesamte Untersuchungszeit (wenn eine Art in einem Plot in wenigstens einem Jahr vorkam, wurde dies als Stetigkeit 1 gezählt). Der Stichprobenumfang beträgt drei in jeder Gruppe. Spalte 1: Angabe von Zielart (t), Ruderalart (r) oder sonstiger Art (o). Spalte 2: Angabe der *Koelerio-Corynephoretea*- und *Festuco-Brometea*-Arten. Spalten 3–6: Angabe der Spenderflächen 'T' und 'S' sowie der Probeflächennummern der Restitutionsflächen. (**) Art kam regelmäßig bzw. (*) gelegentlich auf der Restitutionsfläche vor, aber nicht in den Probeflächen.

Column	1	2	3	4	5	6
			T	S	R1-R3	R4-R6
1. Reference plots only						
Helichrysum arenarium	t	KC	3	2	.	.
Alyssum alyssoides	t	KC	1	1	.	.
Hieracium pilosella (**)	t	KC	1	1	.	.
Bromus erectus	t	FB	.	3	.	.
Allium sphaerocephalon	t	FB	.	3	.	.
Galium verum agg.	t	FB	.	3	.	.
Cladonia rangiformis	t	.	3	.	.	.
Cladonia convoluta	t	.	3	.	.	.
Sanguisorba minor	t	FB	.	2	.	.
Poa bulbosa	t	KC	1	.	.	.
Jurinea cyanoides (*)	t	KC	.	1	.	.
Medicago falcata	t	FB	.	1	.	.
Potentilla incana	t	FB	.	1	.	.
Orobanche arenaria	t	FB	.	1	.	.
Scabiosa canescens	t	FB	.	1	.	.
Centaurea scabiosa	t	FB	.	1	.	.
Tortella inclinata	t	.	1	.	.	.
Cerastium arvense	r	.	3	.	.	.
Arabidopsis thaliana	r	.	1	.	.	.
Daucus carota	r	.	1	.	.	.
Papaver sp.	r	.	1	.	.	.
Spergula arvensis	r	.	1	.	.	.
Cladonia pyxidata agg.	o	.	2	.	.	.
Asparagus officinalis	o	.	1	1	.	.
Rhacomitrium canescens s.l.	o	.	3	.	.	.
Campanula rapunculus	o	.	2	.	.	.
Helictotrichon pubescens	o	.	2	.	.	.
Hypericum perforatum	o	.	2	.	.	.
Viola rupestris	o	.	2	.	.	.
Robinia pseudoacacia juv.	o	.	1	.	.	.
Cladonia spec.	o	.	1	.	.	.
Verbascum lychnitis	o	.	1	.	.	.
Brachypodium pinnatum	o	.	1	.	.	.
Ceratodon purpureus	o	.	1	.	.	.
Securigera varia	o	.	1	.	.	.
Potentilla verna agg.	o	.	1	.	.	.
			T	S	R1-R3	R4-R6
2. Reference and restoration plots						
Arenaria serpyllifolia agg.	t	KC	3	3	3	3
Cerastium semidecandrum	t	KC	3	3	3	3
Artemisia campestris	t	FB	2	3	3	3
Medicago minima	t	KC	3	2	3	3
Tortula ruraliformis	t	.	3	2	3	3
Centaurea stoebe s.l.	t	FB	3	1	3	1
Erophila verna	t	KC	2	1	2	2
Holosteum umbellatum	t	KC	3	2	1	3
Koeleria glauca	t	KC	3	2	2	.
Petrorhagia prolifera	t	KC	1	3	3	.
Saxifraga tridactylites	t	KC	3	3	1	.
Veronica verna	t	KC	3	1	.	2
Myosotis stricta	t	KC	3	3	.	1
Corynephorus canescens	t	.	3	.	2	1
Silene conica	t	.	3	.	3	3
Echium vulgare	t	.	3	.	3	1
Phleum arenarium	t	KC	3	.	3	2
Silene otites	t	FB	.	3	3	3
Alyssum montanum subsp. gmelinii	t	KC	.	3	3	3
Phleum phleoides	t	FB	.	3	2	3
Euphorbia cyparissias	t	FB	.	3	1	1
Asperula cynanchica	t	FB	.	3	1	3
Euphorbia seguieriana	t	FB	.	3	1	3
Helianthemum nummularium subsp. obscurum	t	FB	.	3	1	3
Thymus serpyllum	t	KC	.	3	2	2
Vicia lathyroides	t	KC	.	2	1	2
Ononis repens subsp. repens	t	FB	2	.	2	.
Cetraria aculeata	t	.	3	.	1	.
Koeleria macrantha	t	FB	2	.	1	.
Poa badensis	t	KC	.	3	.	3
Fumana procumbens	t	FB	.	3	.	3
Sedum sexangulare	t	KC	.	2	.	2
Stipa capillata	t	FB	.	3	.	1
Dianthus carthusianorum	t	FB	.	3	.	1
Trifolium arvense	t	KC	.	1	.	1
Bromus tectorum	r	.	3	2	3	3
Oenothera biennis agg.	r	.	2	2	3	3
Salsola kali subsp. tragus	r	.	1	3	3	3
Bromus h. subsp. hordeaceus	r	.	1	.	3	1
Senecio vernalis	r	.	1	2	.	1
Calamagrostis epigejos	r	.	3	2	3	3
Bromus sterilis	r	.	1	1	2	3
Poa angustifolia	r	.	1	1	1	1
Silene latifolia subsp. alba	r	.	1	1	1	1
Vicia villosa	r	.	1	1	1	1
Vicia hirsuta	r	.	1	.	.	1
Brachythecium albicans	o	.	3	1	3	3
Cladonia furcata	o	.	3	1	3	3
Hypnum lacunosum	o	.	2	3	1	3
Peltigera rufescens	o	.	2	2	2	3
Pinus sylvestris	o	.	2	2	3	3
Festuca ovina agg.	o	.	3	1	3	3
Crepis capillaris	o	.	2	1	2	.
Vicia angustifolia	o	.	3	.	1	.
Quercus robur juv.	o	.	1	.	1	.
			T	S	R1-R3	R4-R6
3. Restoration plots only						
Sedum acre	t	KC	.	.	3	3
Medicago lupulina	t	FB	.	.	3	1
Erodium cicutarium	t	KC	.	.	1	1
Rumex acetosella	t	KC	.	.	3	.
Hippocratea comosa	t	FB	.	.	2	.
Vulpia myuros	t	KC	.	.	1	.
Acinos arvensis	t	KC	.	.	.	1
Chenopodium album subsp. album	r	.	.	.	3	3
Conyza canadensis	r	.	.	.	3	3
Digitaria sanguinalis	r	.	.	.	3	3
Elymus repens	r	.	.	.	3	3
Polygonum aviculare agg.	r	.	.	.	3	2
Setaria viridis	r	.	.	.	3	2
Apera spica-venti	r	.	.	.	2	2
Fallopia convolvulus	r	.	.	.	1	3
Rubus caesius	r	.	.	.	2	2
Cynodon dactylon	r	.	.	.	2	1
Chenopodium strictum s.l.	r	.	.	.	1	1
Senecio vulgaris	r	.	.	.	1	1
Eragrostis minor	r	.	.	.	2	.
Viola tricolor s.l.	r	.	.	.	2	.
Carex hirta	r	.	.	.	1	.
Equisetum arvense	r	.	.	.	1	.
Amaranthus blitoides	r	2
Lactuca serriola	r	2
Veronica arvensis	r	3
Amaranthus retroflexus	r	1
Galium aparine	r	1
Urtica dioica	r	1
Verbascum densiflorum	r	1
Veronica persica	r	1
Prunus avium juv.	o	.	.	.	2	3
Dactylis glomerata	o	.	.	.	2	1
Lolium perenne	o	.	.	.	1	1
Plantago lanceolata	o	.	.	.	1	.
Achillea millefolium agg.	o	.	.	.	1	.
Agrostis stolonifera	o	.	.	.	1	.
Holcus lanatus	o	.	.	.	1	.
Juglans regia juv.	o	.	.	.	1	.
Rhinanthus minor	o	.	.	.	1	.
Thymus pulegioides	o	.	.	.	1	.
Bryum cf. argenteum	o	2
Ceratium holosteoides	o	2
Silene vulgaris subsp. vulgaris	o	2
Cotoneaster spec.	o	1
Galium mollugo agg.	o	1
Poa annua	o	1