Zeitschrift: Berichte des Geobotanischen Institutes der Eidg. Techn. Hochschule, Stiftung Rübel

Herausgeber: Geobotanisches Institut der Eidg. Techn. Hochschule, Stiftung Rübel

Band: 52 (1985)

Artikel: Influence of seed bank and small mammals on the floristic composition of limestone grassland (Mesobrometum) in Northern Switzerland = Einfluss von Samenvorrat und Kleinsäugern auf die floristische Zusammensetzung von Halbtrockenrasen (Mesobrometen) in d...

Autor: Ryser, Peter / Gigon, Andreas

DOI: https://doi.org/10.5169/seals-377730

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Mehr erfahren

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. En savoir plus

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. Find out more

Download PDF: 11.01.2026

ETH-Bibliothek Zürich, E-Periodica, https://www.e-periodica.ch

Ber.Geobot.Inst.ETH., Stiftung Rübel, Zürich **52** (1985), 41-52

Influence of seed bank and small mammals on the floristic composition of limestone grassland *(Mesobrometum)* in Northern Switzerland

Einfluss von Samenvorrat und Kleinsäugern auf die floristische Zusammensetzung von Halbtrockenrasen (Mesobrometen) in der Nordschweiz

by

Peter RYSER and Andreas GIGON

1. INTRODUCTION

Within the investigations of the coexistence of plant species in grassland ecosystems on the Randen hills in Northern Switzerland by the Geobotanical Institute ETH Zürich, LEUTERT (1983) studied the importance of voles (Microtus arvalis Pall.) for plant species richness. His investigations show, that the irregular use of space, selective grazing and changing of soil factors by these animals have great effects on the vegetation pattern and raise plant species densities in meadow ecosystems.

In the present work the role of the seed bank in the increase of species density by the voles is studied. Most of the meadows of the Randen hills were formerly arable land and it is also investigated if there are seeds of agricultural weeds in the soil, which can be brought to the soil surface by the voles and thus contribute to an increase in species density. Weeds can form very large and long-living seed banks (CHIPPINDALE and MILTON 1934, ROBERTS 1981) and many of the species promoted by the voles usually occur in weed communities (LEUTERT 1983). The presence of weed seeds would also be of interest for nature conservation because during

the last decades many weed species have become rare due to the intensification of agriculture (LANDOLT et al. 1982, SCHUMACHER 1980). The present paper is a revised excerpt from RYSER (1984).

ACKNOWLEDGEMENTS

We are grateful to Prof. Dr. E. LANDOLT for constructive remarks and to numerous persons in the Geobotanical Institute who helped throughout the course of the work. A partial support by the Swiss National Sciene Foundation is gratefully acknowledged.

2. STUDY SITE AND METHODS

The study area was located in Northern Switzerland, on the Randen near Schaffhausen. Two meadows were investigated: a Medicago falcatae-Mesobrometum on Gräte (National Grid reference 688230/290950), on a site which was not ploughed for at least 100 years, if ever, and a Dauco-Salvio-Mesobrometum on Emmerberg (689500/290400), on a site which was ploughed for the last time about 40 years ago.

Soil samples were collected on both sites over an area of about 2000 m^2, in September 1983 and in April 1984. They were taken with a metal corer with a diameter of 5.4 cm down to a depth of 10 cm. On the Emmerberg most of the samples could be taken only to a depth of 5 cm due the stony soil (rendzina). In September 48 cores were taken from each site, in April 68. The cores were sectioned into depth-layers of 2.5 cm and the corresponding layers of four neighbouring cores (within a distance of max. 2m) were bulked.

Further samples were collected on hills of common vole, the volume of each sample being 230 cm^3 (equal to a bulked layer of a soil sample). The number of these samples was 24 in September 1983 and 17 in April 1984.

The soil samples were placed in a glass-house in shallow dishes as a 1-1.5 cm thick layer on a 3 cm-layer of quartz sand and watered regularly with tap or deionized water. The seedlings which emerged were counted weekly and removed after identification. To encourage seed germination and to prevent the growth of mosses, the soil in the samples was stirred every 2-4 weeks. The germination in the samples was observed for 10 months; the September-samples from Oktober 1983 to August 1984 and the April-samples from May 1984 to May 1985. The latter ones were kept 2 months outdoors in winter.

For comparison with the seed bank the vegetation was mapped with the frequency method. 200 samples of 23 cm^2 were taken in late June and the presence of the species in these samples was registered. Species not found in these samples, but seen on the study area during the period of investigation, were listed separately.

The plant nomenclature follows that of HESS et al. 1976-80.

3. RESULTS

3.1. THE SEED BANK IN THE SOIL

Study site Gräte: From the soil samples taken on Gräte seedlings of 37 species emerged. The number of emerged seedlings corresponds to a seed-density of about 3000 seeds per square meter in the topmost 10 cm soil. The most numerous species were Carex flacca, Linum catharticum, Plantago lanceolata, P. media, Cerastium caespitosum, Picris hieracioides, and Trifolium dubium (Fig. 1a)

Study site Emmerberg: 46 species germinated from the soil samples taken on Emmerberg; the calculated seed density was over 5000 per m^2 in the topmost 5 cm soil. Veronica arvensis and Stellaria media were the most frequent species, other frequent species were Cerastium caespitosum, Plantago lanceolata, Poa pratensis, and Bellis perennis (Fig. 1b)

Most species had the largest part of their seeds in the topmost 2.5 cm. This depth distribution was very pronounced particularly for Picris hieracioides and Plantago lanceolata. Species with a large part of their seeds in the deeper layers were Carex flacca, Stellaria media, Hypericum perforatum, and Ranunculus bulbosus and, in a smaller amount (only 1-4 seeds found), Papaver dubium, Stachys recta, and Linaria minor.

3.2. COMPARISON BETWEEN THE SEED BANK AND THE ABOVE-GROUND VEGETATION

Large differences between the species composition of the vegetation and that of the seed bank were found (Fig. 1). There were 37 species growing on the Gräte, which were not found in the seed bank, on the Emmerberg 31 species. Conversely, some species which germinated from the soil samples were absent from the above-ground vegetation on the study site. The number of species present only in the seed bank was 6 in the soil samples of Gräte, in those of Emmerberg 8. Most of these species were however found growing in the neighbourhood.

In the seed bank of Emmerberg many weedy species were overrepresented in comparison to the above ground vegetation (Stellaria media, Veronica arvensis). On the Gräte only few weed seeds were found.

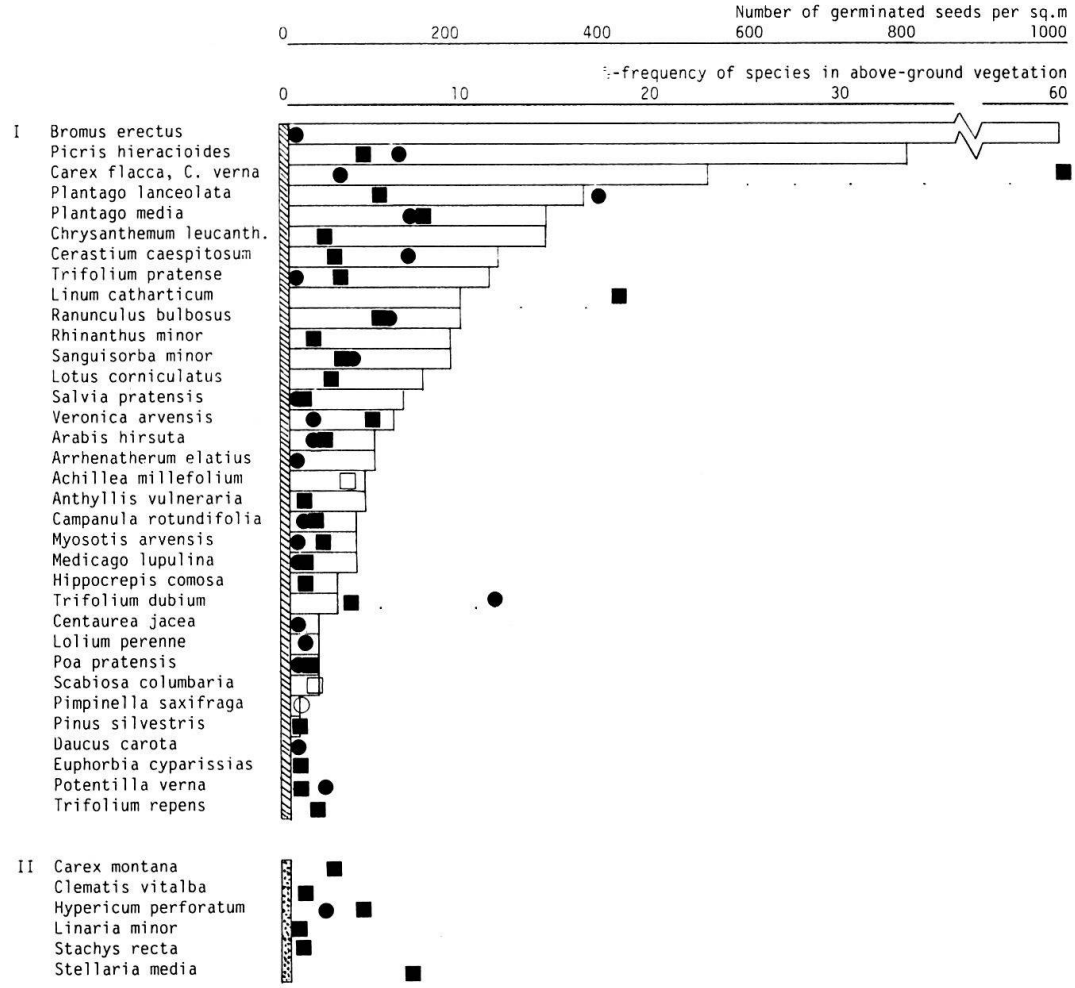
Causes for the absence of species in the seed bank are possibly a poor fructification because of unfavourable environmental conditions or a too early mowing. The seed bank also shows great seasonal and yearly fluctuations (THOMPSON and GRIME 1979, SCHENKEVELD and VERKAAR 1984), so that the results obtained depend largely on the time of sampling. This is clearly seen with most grasses, the seeds of which often germinate already in autumn. Therefore the number of germinated grass seeds was larger in the September-samples than in those of April.

Most of the species not found in the seed bank were rare in the vegetation and as discussed in chapt. 3.4, species only scantily present in

the seed bank can remain unfound with the size of the sample used. It is also possible, that the duration of the experiment was too short to enable all seeds to germinate.

3.3. SEED BANK IN THE VOLE HILLS

The seed densities in the samples of vole-hills were smaller than in the upper soil layers. This is easy to understand, because the voles mix soil from the deeper, seed-poor layers with the upper ones. Seeds of 27 species were found in vole-hill-samples of Gräte, 3 of them missing in the cored soil samples. The corresponding numbers of species in the samples of Emmerberg were 40 resp. 2 (tab. 1). Seeds of the species found exclusively in the vole-hill-samples were however scanty and so do not allow any conclusions, because their absence in the soil samples is likely to be accidental.



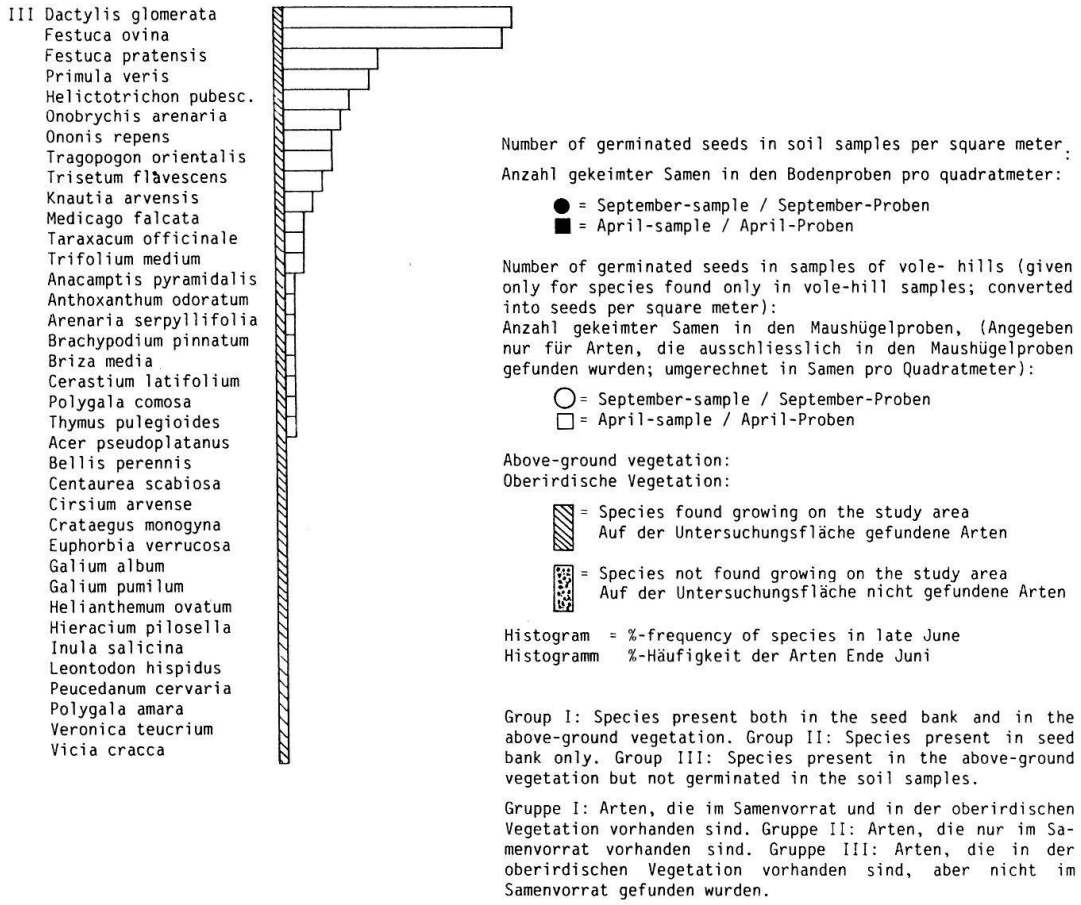


Fig. 1. Comparison between the seed bank in the soil and the %-frequency of the species in the above- ground vegetation.
Abb. 1. Vergleich zwischen Samenvorrat im Boden und %-Häufigkeit der Arten in % in der oberirdischen Vegetation.

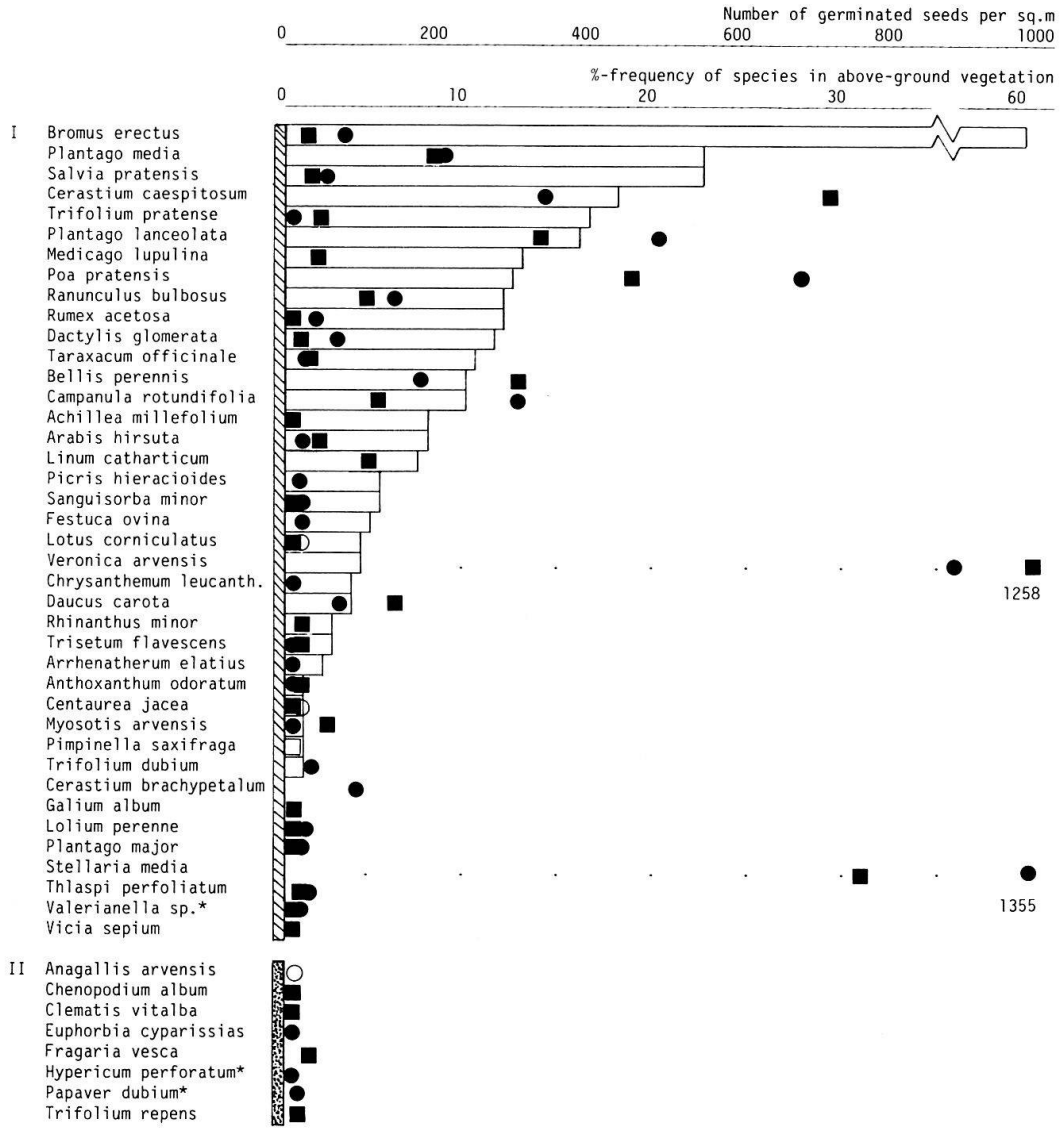
a) Study site Gräte. Seed densities for the topmost 10cm.
Untersuchungsfläche Gräte. Samendichten in den obersten 10cm.

3.4. STATISTICS OF THE INVESTIGATION OF THE SEED BANK

Because of the very heterogeneous distribution of the seeds in the soil, large samples are necessary to estimate the seed bank. For the assessment of the accuracy of the results of this study the confidence interval (t-distribution, p=0.1) was calculated for the results obtained. The spatial seed distribution was characterized by coefficient of variation (the ratio of standard deviation and the mean, ZAR 1984) and this coefficient was also used for the calculation of the theoretical sample size necessary to reach more accurate results about seed densities, with a confidence interval of ±10%.

For the whole seed bank the confidence interval was about ±25% of the mean. To reach a confidence interval of ±10% a 6 times larger sample would be necessary. The species with numerous seeds in the seed bank had a confidence interval of ±30-50%. For the species with only a few seeds found, the interval was up to 100% and more, which indicates that species with such a distribution were not necessarily found with the sample size used. To reach an accuracy with a confidence interval of ±10% for these species a sample about 100 times larger would have been necessary.

As a conclusion we can say that the study gives a satisfactory accuracy for the size of the whole seed bank and for the seed density of the abundant species, but the species with a small seed content in the soil are not completely assessed. The effort for the complete assessment of the seed bank would however be too large for practical investigations.



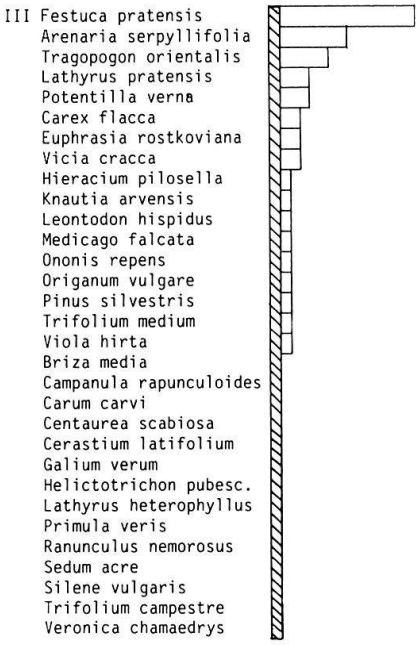


Fig. 1. Comparison between the seed bank in the soil and the %-frequency of the species in the above- ground vegetation.
Abb. 1. Vergleich zwischen Samenvorrat im Boden und %-Häufigkeit der Arten in % in der oberirdischen Vegetation.

b) Study site Emmerberg. Seed densities for the topmost 5cm, except species marked with *, seeds of which were found only in depth of 5-10cm.
Untersuchungsfläche Emmerberg. Samendichten angegeben für die obersten 5cm, ausser bei den mit * markierten Arten, von denen Samen nur in der Tiefe von 5-10cm gefunden wurden.

4. DISCUSSION

4.1. THE IMPORTANCE OF THE SOIL SEED BANK FOR SPECIES DIVERSITY OF GRASSLANDS IN CONNECTION WITH VOLE ACTIVITY

LEUTERT (1983) found, that the plant species density of non-fertilized meadows can be raised by 16% by vole activity. The species increasing in cover or appearing newly in non-fertilized meadows due to the activity of voles occur frequently at edges of woods, in weed communities or in fertilized meadows. One of the most important effects of voles promoting these species is the forming of gaps in the canopy, together with selective grazing and fertilizing effects. The gaps present an opportunity

Table 1. Number of germinated seeds from the samples of vole hills.
Tab. 1. Anzahl gekeimter Samen aus den Maushügelproben.

sample collected in	September 1983		April 1984	
sample size	24 x 230cm^3		17 x 230cm^3	
site	Gräte	Emmerberg	Gräte	Emmerberg
Anthoxanthum odoratum		37		
Arrhenatherum elatius		17		
Bromus erectus	1	58		3
Dactylis glomerata		34		1
Festuca ovina		3		
Lolium perenne	4	9		
Poa pratensis	1	85	2	13
Trisetum flavescens		4		
Carex flacca			28	
Carex montana			2	
Anagallis arvensis		1		
Achillea millefolium		5	6	
Arabis hirsuta	7	6		
Bellis perennis		7		8
Campanula rotundifolia	7	29	3	18
Cerastium caespitosum	18	98	1	31
Centaurea jacea	3	3		
Chrysanthemum leucanthem.	4	1	1	1
Daucus carota		3		
Galium album		1		1
Hippocrepis comosa			1	
Hypericum perforatum	2		3	
Linum catharticum			6	6
Lotus corniculatus		1		1
Medicago lupulina				5
Myosotis arvensis		2		1
Papaver dubium		1		
Picris hieracioides	15	2	5	
Pimpinella saxifraga	1			1
Plantago lanceolata	24	89	2	32
Plantago major		1		1
Plantago media	6	23	15	9
Ranunculus bulbosus	4	15	3	3
Rhinanthus minor			1	1
Rumex acetosa		3		2
Salvia pratensis	3	10		3
Sanguisorba minor			1	1
Scabiosa columbaria			7	
Stellaria media	2	68		24
Taraxacum officinale		2		
Trifolium dubium	2	1		
Trifolium pratense		2	1	7
Trifolium repens				1
Veronica arvensis	4	60		37
unidentified	1	12	1	1
	109	693	89	212

for species dispersed from the surrounding plant communities to establish. More important is however, that species with seeds already in the seed bank find conditions there that allow them to germinate, grow up, and set seed. Many short-lived species in permanent grasslands are mainly found growing in gaps in the canopy, made e.g. by moles, rabbits or ants (WATT 1974, GRUBB 1976, VERKAAR et al. 1983). Although these species form only a minor and temporal part of the above-ground vegetation, they can dominate the seed bank as is typical for species whose growing populations are subject to periodical local extinction (SILVERTOWN 1982). The seeds remain dormant in the soil until the site is disturbed again and then can be recruited to the growing population. This strategy is called "hop-skip-jump" strategy (KREBS 1972) and it enables a temporally limited existence of these species in the gaps in the vegetation, called "spurious cohabitation" by HARPER et al. (1961). On the grassland of Randen, Arabis hirsuta, Myosotis arvensis, Veronica arvensis, Trifolium dubium, and Cerastium brachypetalum are examples of short-lived species mainly found on vole-colonies. In the investigations by LEUTERT (1983) flowering individuals of M. arvensis were found only in these gaps. In the present study particularly V. arvensis is characterized by a very large seed bank on the study site of Emmerberg.

The voles can also influence the seed dispersal. Fruits of some species, like M. arvensis or C. brachypetalum, have adhesive structures on their surface enabling them to adhere to the fur of small mammals (MüLLER-SCHNEIDER 1983). Of special interest in the present study was however the vertical transport of the seeds by voles. Seeds conserved in the soil since the site was arable land can be brought to the surface by the voles and thus also influence the floristic composition of the meadows. This is indicated by the few seeds of Papaver dubium, which were found only in samples taken beneath 5cm depth on Emmerberg and also in vole-hill samples. Also the seeds of Stellaria media, which obviously date back to a former time of arable farming can germinate in disturbed sites and contribute to the species richness of the present vegetation. Seeds of this easily germinating species were numerous at all depths but growing individuals were found only on sites where the soil had been artficially disturbed. That S. media is missing in gaps made by voles is possibly due to the extreme climate on these sites free of vegetation.

The influence of the seeds brought on the surface by burrowing animals can also lead to greater changes of the vegetation, when growing species do not form a persistent seed bank. JALLOQ (1975) found in the soil brought to the surface by the moles on a reseeded pasture only minor amounts of seeds of sown species such as Lolium perenne and Trifolium repens, and suggests that this handicap in recolonizing the mole hills could be one mechanism leading to the displacement of these species.

4.2. CONSERVATION OF SEEDS IN THE SOIL AND THE CONSEQUENCE FOR NATURE CONSERVATION

The seed bank can also be important for nature conservation, if seeds of locally extinct species have survived in the soil. These species could be brought back into the vegetation when the management of the site is changed so that the conditions are favourable for the germination of

these seeds. Examples of such "returning" of extinct species to disturbed sites, where the conservation of seeds in the soil also plays a role, are mentioned by KRAUSE (1978). ROWELL et al. (1982) report the germination of seeds of Viola persicifolia in soil samples from a region where this species had not been found growing for over 60 years. The conservation of weed seeds in the soil, where these species have not been found growing for a long time is reported by many authors, e.g. by CHIPPINDALE and MILTON (1934), FOERSTER (1956) and SCHENKEVELD and VERKAAR (1984). In view of these arguments MOORE (1983) suggests, that in future nature conservation areas should also be established on grounds of the potential flora in the seed bank. And MAJOR and PYOTT (1966) emphasize, that the seed bank should be considered as a part of the flora.

Apart from conserving species the importance of the seed bank for the nature protection can also be in conserving genotypes. The genetic diversity of many weed species has decreased due the increased selection pressure of intensified agriculture in the last decades (LANDOLT et al. 1982) and especially in the case of annual species such as weeds the effect of the seed bank as an evolutionary filter is pronounced (TEMPLETON and LEVIN 1979).

In the present study seeds of many weedy species (Stellaria media, Papaver dubium, Anagallis arvensis, Chenopodium album) were found in the soil of Emmerberg. In the vegetation of the study site and in the neighbourhood they were found only sparsely or not at all, and their seeds were found, in contrast to most other species, mainly in deeper soil layers. This indicates that these seeds date back to times of arable farming on the site 40 years ago. Seeds of endangered species were however not found, but only two sites were investigated, and species only scantily present in the seed bank are not necessarily found with the size of sample used. Very deep samples could also not be taken. These would have been particularly interesting when assessing conservation of seeds of rare and endangered arable weeds.

SUMMARY

The influence of the seed bank in the soil on the species composition of non-fertilized limestone grasslands (Mesobrometum), especially in relation to the activity of the common vole (Microtus arvalis Pall.), was investigated in the Randen hills of Northern Switzerland. Samples of undisturbed soil and of vole-hills were taken from two meadows of different management history in September and in April and placed in a greenhouse. The seedlings were identified and recorded during 10 months.

1. There were great differences between the species composition of the vegetation and that of the seed bank.
2. On the study site of Emmerberg many weedy species were overrepresented in the seed bank compared to the above-ground vegetation. These seeds obviously date back to the time when the site was ploughed for the last time, about 40 years ago. In contrast weed seeds were sparse in the study area of Gräte, which has not been ploughed for over a 100 years.

3. The voles can raise the number of species in the meadows by bringing seeds from the deep-lying seed bank to the surface. This is however of minor importance because of the small densities of seeds in deep soil layers. Much more important for the species composition is the making of gaps in the canopy by voles, where many short-lived species can grow temporally and set seed. The seed bank of these species can be very large.

ZUSAMMENFASSUNG

Der Einfluss des Samenvorrates im Boden auf die Artenzusammensetzung von Magerrasen (Mesobrometen), insbesondere infolge der Aktivität der Feldmaus (Microtus arvalis Pall.) wurde auf dem Randen in der Nord-Schweiz untersucht. Bodenproben und Proben von Maushügeln wurden im September 1983 und im April 1984 auf 2 Wiesen, die unterschiedliche Bewirtschaftungsgeschichte aufweisen, gesammelt. Die Keimlinge wurden während 10 Monaten protokolliert.

1. Die Artenzusammensetzung der Vegetation und des Samenvorrates waren sehr verschieden.
2. Im Vergleich zur oberirdischen Vegetation waren im Samenvorrat auf der Untersuchungsfläche Emmerberg viele Ackerwildkrautarten übervertreten. Diese Samen stammen offensichtlich aus Zeiten vor 40 Jahren, als die Fläche zum letzen Mal beackert wurde. Auf der Untersuchungsfläche Gräte, die mindestens seit 100 Jahren nicht mehr gepflügt wurde, waren die Ackerwildkrautsamen hingegen selten.
3. Die Artenzahl von Wiesen kann durch die Mäuse vergrössert werden, indem sie Samen aus dem tiefliegenden Samenvorrat auf die Oberfläche bringen. Das ist jedoch von geringen Bedeutung, da die Samendichten in den tiefen Bodenschichten klein sind. Viel wichtiger für die Artenzusammensetzung ist das Schaffen von Kahlstellen, auf denen viele kurzlebige Arten vorübergehend wachsen und Samen bilden können. Der Samenvorrat dieser Arten kann sehr gross sein.

REFERENCES

CHIPPINDALE H.G. and MILTON W.E.J., 1934: On the viable seeds present in the soil beneath pastures. J.Ecol. 22, 508-531.

FOERSTER E., 1956: Ein Beitrag zur Kenntnis der Selbstverjüngung von Dauerweiden. Z.Acker- und Pfl.Bau 100, 273-301.

GRUBB P.J., 1976: A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk grassland ecosystem. Biol.Conserv. 10, 53-76.

HARPER J.L., CLATWORTHY J.N.,MCNAUGHTON I.H. and SAGAR G.H., 1961: The evolution of closely related species living in the same area. Evolution 15, 209-227.

HESS H.E., LANDOLT E. und HIRZEL R., 1976-1980: Flora der Schweiz und angrenzender Gebiete. (2. Aufl.). Birkhäuser, Basel. 3. Bde. 2690 S.

JALLOQ M.C., 1975: The invasion of molehills by weeds as a possible factor in the degeneration of reseeded pasture. I. The buried viable

seed population of molehills from four reseeded pastures in West Wales. J.Appl.Ecol. 12, 643-657.

KRAUSE W., 1978: Gezielte Bodenentblössung und Anlage frischer Wasserflächen als Mittel der Bestandserneuerung in Naturschutzgebieten. Beih.Veröff. Naturschutz Landschaftspflege Bad.-Württ. 11, 247-250.

KREBS C.J., 1972: Ecology. The experimental analysis of distribution and abundance. Harper & Row, New York. 694 S.

LANDOLT E., FUCHS H.P., HEITZ Ch. und SUTTER R., 1982: Bericht über die gefährdeten und seltenen Gefässpflanzen der Schweiz ("rote Liste"). Ber.Geobot.Inst.ETH, Stiftung Rübel, Zürich 49, 195-218.

LEUTERT A., 1983: Einfluss der Feldmaus, Microtus arvalis (Pall.), auf die floristische Zusammensetzung von Wiesen-Oekosystemen. Veröff. Geobot.Inst. ETH, Stiftung Rübel, Zürich 79. 126 S.

MAJOR J. and PYOTT W.T., 1966: Buried viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. Vegetatio 13, 253-282.

MOORE P.D., 1983: Seeds of thought for plant conservationists. Nature 303, 572.

MüLLER-SCHNEIDER P., 1983: Verbreitungsbiologie (Diasporologie) der Blütenpflanzen. 3. Aufl. Veröff.Geobot.Inst.ETH, Stiftung Rübel, Zürich 61. 226p.

ROBERTS H.A., 1981: Seed banks in soils. Adv.Appl.Biol. 6, 1-55.

ROWELL T.A., WALTERS S.M. and HARVEY H.J., 1982: The rediscovery of the Fen Violet, Viola persicifolia Schreber, at Wicken Fen, Cambridgeshire. Watsonia 14, 183-184.

RYSER P., 1984: Samenvorrat im Boden und Mikrostandorte für das Aufwachsen neuer Pflanzen in Wiesen des Randens bei Merishausen. Diplomarbeit Geobot.Inst. ETH, Stiftung Rübel, Zürich. 79 pp. (unpubl.)

SCHENKEVELD A.J. and VERKAAR H.J., 1984: The ecology of short-lived forbs in chalk grasslands: distribution of germinative seeds and its significance for seedling emergence. J.Biogeogr. 11, 251-260.

SCHUMACHER W., 1980: Schutz und Erhaltung gefährdeter Ackerwildkräuter durch Integration von landwirtschaftlicher Nutzung und Naturschutz. Natur und Landschaft 55, 447-453.

SILVERTOWN J.W., 1982: Introduction to plant population ecology. Longman London and New York. 209p.

TEMPLETON A.R. and LEVIN D.A. 1979: Evolutionary consequences of seed pools. Am.Nat. 114, 232-249.

THOMPSON K. und GRIME J.P., 1979: Seasonal variation in the seed bank of herbaceous species in ten contrasting habitats. J.Ecol. 67, 893-921.

WATT A.S.,1974 : Senescence and rejuvenation in ungrazed chalk grassland (grassland B) in Breckland: The significance of litter and moles. J.Appl.Ecol. 11, 1157-1171.

VERKAAR H.J., SCHENKEVELD A.J. and BRAND J.M., 1983: On the ecology of short lived forbs in chalk grasslands: micro-site tolerances in relation to vegetation structure. Vegetatio 52, 91-102.

ZAR J.H., 1984: Biostatistical analysis. 2nd ed. Prentice Hall, Englewood Cliffs, N.J. 718p.

Address of the authors: Peter RYSER, dipl.Natw.ETH
Prof. Dr. Andreas GIGON
Geobotanisches Institut ETH
Stiftung Rübel
Zürichbergstrasse 38
CH-8044 Zürich