Die ökologische Bedeutung von Samenbanken, Keimung und Etablierung für die Renaturierung von Auenwiesen
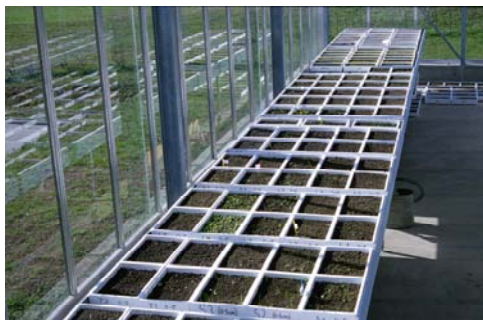
Ecological significance of seed banks, germination and establishment for the restoration of flood-meadows

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Inhalt

Kapitel 1

Einleitung

Durch agrarische Nutzung entstandene Grünlandgesellschaften sind in der temperaten Zone Europas aufgrund ihres pflanzlichen Artenreichtums von herausragender Bedeutung für die Erhaltung regionalspezifischer Biodiversität. Grundvoraussetzungen für die oft bemerkenswert hohe Artendichte sind eine nur mäßige Produktivität und eine regelmäßige Störung durch Mahd oder Beweidung, wodurch ein Konkurrenzausschluss unterbunden und die Koexistenz zahlreicher Pflanzenarten auf kleinstem Raum ermöglicht wird (Huston 1994, Grime 2001). Sowohl eine Erhöhung der Produktivität mittels Düngung als auch eine Aufgabe oder Intensivierung der Störungsfrequenz durch Mahd oder Beweidung führen rasch zu einer Verringerung des Artenreichtums, der zunächst vor allem stenöke, zumeist besonders kleinwüchsige und konkurrenzschwache Arten betrifft (Lepš 1999, Olde Venterink et al. 2001). Während der vergangenen 50 Jahre sind in Mittel- und Westeuropa sowohl durch die Aufgabe landwirtschaftlicher Grenzstandorte, als auch durch Melioration und nachfolgende ackerbauliche Nutzung massive Grünlandverluste zu verzeichnen. Auf den verbliebenen Flächen haben landwirtschaftliche Intensivierungsmaßnahmen, wie mineralische Düngung, Gülleapplikation, Entwässerung, Vielschnittnutzung, sowie die Einsaat von Hochleistungsgräsern oft zu einer massiven Artenverarmung geführt (Korneck et al. 1998). Überproportional stark betroffen ist von diesen quantitativen und qualitativen Verlusten vor allem das Grünland der leicht meliorierbaren und ackerbaulich gut nutzbaren Tieflagen, wo ehemals häufige oder gar landschaftsprägende artenreiche Grünlandgesellschaften heute oft nur noch als kleinflächige Fragmente innerhalb von Schutzgebieten existieren (z. B. Böger 1991).

In besonderem Maße gilt dies auch für die überflutungsgeprägten Stromtalwiesen des Verbandes *Cnidion* (Balátová-Tuláčková 1969), deren Kernareal im kontinentalen Osteuropa liegt. Ökologisch kennzeichnend für diese Auengrünlandgesellschaften ist der extrem unausgeglichene Wasserhaushalt ihrer Standorte. Während die mit der Schneeschmelze einsetzenden Hochwasser im Frühjahr und Frühsommer oft zu wochenlangen Überschwemmungen führen, kommt es im trocken-heißen Sommer häufig zu einer scharfen Austrocknung der Böden, welche die Vegetation bei fehlendem Grundwasseranschluss unter Trockenstress setzt. Verstärkt wird dieser betont wechselfeuchte Standortcharakter oft durch

sehr feinkörnige, oft tonreiche Böden, die in Feuchtphasen zur Luftarmut und Vernässung neigen, während hochsommerliche Trockenphasen eine tiefgründige Verhärtung und Schrumpfrissbildung bewirken (Dister 1980, Hölzel 1999). Der variable Wasserhaushalt der Standorte findet seinen deutlichen Niederschlag in der floristischen Struktur der *Cnidion*-Wiesen und führt zu einem charakteristischen Nebeneinander von nässetoleranten Sumpf- und Flutrasenarten, Wechselfeuchtezeigern, mesophytischen Grünlandarten und sogar ausgeprägt trockenheitstoleranten Arten aus Steppenrasen und thermophilen Saumgesellschaften (Böger 1991, Burkart 1998, Šeffer & Stanová 1999, Leyer 2002). Im semiariden Klima der osteuropäischen Steppenzone wird das Artenspektrum zusätzlich bereichert durch salztolerante Pflanzen (Balátová-Tuláčková 1969).

Allen besonders charakteristischen Arten der *Cnidion*-Wiesen ist gemein, dass sie sowohl eine phasenweise Überschwemmung als auch eine starke Austrocknung der Standorte zu überstehen vermögen. Entsprechend der niveauabhängigen Überflutungshäufigkeit treten etageal differenziert mehr ausgesprochene Sumpf- und Flutrasenarten oder aber mesophytische Grünlandarten und Trockenheitszeiger stärker in den Vordergrund, ohne dass aber eine der genannten Artengruppen zur alleinigen Dominanz gelangen würde (Dister 1980, Burkart 1998, Hölzel 1999, Šeffer & Stanová 1999, Leyer 2002). Stark ausgeprägt sind auch überflutungs- oder witterungsbedingte saisonale Fluktuationen der Abundanz und Dominanz der beteiligten Arten (Balátová-Tuláčková 1979), welche die jährlich häufig stark wechselnden Umweltbedingungen widerspiegeln und den *Cnidion*-Auenwiesen einen im Vergleich zu anderen Grünlandgesellschaften ausgesprochen dynamischen, bisweilen fast ruderal anmutenden Charakter verleihen.

In Deutschland sind ökologische Bedingungen, die denen der osteuropäischen Tieflandflüsse ähneln, ausschließlich im Einzugsbereich der trocken-warmen, klimatisch bereits deutlich subkontinental getönten großen Stromtäler der Oder, der Elbe, des nördlichen Oberrheins, des mittleren Mains und der niederbayerischen Donau zu finden. Entsprechend der daraus resultierenden Arealmuster werden *Cnidion*-Gesellschaften in Mitteleuropa häufig als Stromtalwiesen und die sie charakterisierenden Pflanzensippen als Stromtalarten bezeichnet (Korsch 1999, Burkart 2001). Viele charakteristische Arten des *Cnidion* stoßen bereits am Rhein an die Westgrenze ihrer Verbreitung (Hultén & Fries 1986).

Aufgrund ihrer sehr engen Areal- und Habitatbindung und des ungünstigen Erhaltungszustands ihrer Lebensräume müssen viele bezeichnende Stromtalwiesenarten inzwischen mitteleuropaweit als stark gefährdet eingestuft werden (Schnittler & Günther 1998).

Infolge der massiven quantitativen und qualitativen Verluste ist die Neuschaffung und Wiederherstellung von artenreichem Grünland vor allem in den agrarisch besonders intensiv genutzten Regionen Mittel- und Westeuropas spätestens seit den 70er Jahren zunehmend in den Mittelpunkt von Naturschutzmaßnahmen gerückt (Bakker 1989, Muller et al. 1998, Bakker & Berendse 1999). Anfangs standen dabei die Wiederherstellung adäquater Standorts- und Nutzungsverhältnisse im Vordergrund der Bemühungen. Bei ersterem ging es vor allem darum, überschüssige Nährstoffe zu entziehen und damit die Produktivität des Standorts auf das Niveau der Zielgemeinschaft zurückzuführen (Gough & Marrs 1990, Oomes et al. 1996, Snow et al. 1997, Tallowin et al. 1998). Eine Reduktion der Nutzungsintensität oder bei Brache eine Wiederaufnahme der Nutzung konnte vor allem durch Ausgleichszahlungen und vertragliche Vereinbarungen mit Landwirten über Agrar-Umweltprogramme erzielt werden.

Zahlreiche Untersuchungen zeigen, dass entsprechende Renaturierungsmaßnahmen oft nur von bescheidenem Erfolg gekrönt waren. Selbst nach erfolgreicher Aushagerung und Installierung einer adäquaten Nutzung stellten sich die angestrebten Artengemeinschaften meist nicht oder nur in völlig unzureichendem Maße ein (Bakker 1989, Berendse et al. 1992, Hutchings & Booth 1996, Pegtel et al. 1996). Zielarten konnten sich selbst nach Jahrzehnten in der Regel nur dann etablieren, wenn sie bereits im Bestand oder dessen unmittelbarer Nähe vorhanden waren. Zu analogen Resultaten kommen Aussaatexperimente, welche belegen, dass der Artenreichtum in Grünlandbeständen in hohem Maße durch die Verfügbarkeit von Samen beeinflusst wird (Tilman 1997, Stampfli & Zeiter 1999, Turnbull et al. 2000, Pywell et al. 2002, Smith et al. 2002).

Durch die Vielzahl gleichlautender Befunde rückten die früher kaum beachteten populationsbiologischen Aspekte der generativen Vermehrung, Ausbreitung und Etablierung zunehmend in den Mittelpunkt des Interesses von Renaturierungsökologen. Fehlende Persistenz der Samenbank, geringes (Fern-) Ausbreitungsvermögen und der Mangel an Regenerationsnischen („safe sites" sensu Harper 1977) in geschlossenen Grasnarben werden spätestens seit Mitte der 90er Jahre intensiv als zusätzlich limitierende Faktoren bei der Wiederherstellung und Neuschaffung von artenreichen Grünlandgesellschaften diskutiert und analysiert (Bakker et al. 1996, Hutchings & Booth 1996ab, Křenová & Lepš 1996, Kotorová & Lepš 1999, Stampfli & Zeiter 1999).

Zur Reetablierung von seltenen Pflanzengemeinschaften der Stromtalwiesen wurden ab Mitte der 80er Jahre in den Auen am hessischen Oberrhein großflächige Renaturierungsmaßnahmen eingeleitet. Von einer direkten Wiederanbindung vormals ausgedeichter Ackerflächen an das

Überflutungsregime des Rheins versprach man sich hierbei eine rasche Wiederherstellung der Zielartengemeinschaften (Dister et al. 1992). Dies sollte u. a. durch den Eintrag von Diasporen bei Hochwasserereignissen gewährleistet werden, der im Falle von Auenökosystemen oft als besonders effektiv und relevant angesehen wird (Malanson 1993, Bonn & Poschlod 1998, Goodson et al. 2001). Eigene Untersuchungen zum Renaturierungserfolg belegen, dass die hochgesteckten Erwartungen bislang kaum erfüllt wurden (Hölzel et al. 2002, Donath et al. 2003, Bissels et al. accepted). Ähnlich wie bei vielen anderen Renaturierungsprojekten konnte über Nährstoffentzüge durch regelmäßige Mahd zwar eine erfolgreiche Absenkung der Produktivität auf das Niveau der Zielgemeinschaften erreicht werden, doch blieb die gewünschte Etablierung typischer Arten der Stromtalwiesen bislang weitgehend aus. Stattdessen werden die Flächen auch nach 20 Jahren Laufzeit der Maßnahmen nach wie vor von wenigen, trivialen Grünland- und Ruderalarten dominiert und unterscheiden sich immer noch grundlegend von artenreichen Altbeständen. Selbst bei günstiger Umfeldsituation mit großen und vitalen Vorkommen von Zielarten in direktem Kontakt zu den Renaturierungsflächen schreitet eine Artenanreicherung nur sehr schleppend und zögerlich voran (Donath et al. 2003). Dies betrifft nicht nur seltene Zielarten, sondern auch viele wenig anspruchsvolle, im Naturraum noch allgemein häufige Grünlandkräuter wie etwa *Sanguisorba officinalis, Rumex acetosa* und *Centaurea jacea*. Trotz vergleichbarer Erfahrungen in anderen Renaturierungsprojekten in Flussauen (z. B. Bischoff 2002) bleiben mögliche Ursachen hierfür und deren relative Bedeutung wie Kurzlebigkeit der Samenbank, geringes Samenaufkommen, Ineffektivität von (fluviatilen) Ausbreitungsprozessen, Mangel an Regenerationsnischen oder extreme Sensibilität in der Keimungs- und Etablierungsphase in Ermangelung einschlägiger Untersuchungen bei vielen der relevanten Arten zunächst im Dunkeln.

Die in den nachfolgenden Kapiteln dargestellten Untersuchungen sollen zum kausalen Verständnis des geringen Erfolgs bisheriger Wiederherstellungsmaßnahmen beitragen, sowie darauf aufbauend Wege für eine Neuorientierung in der Renaturierungspraxis aufzeigen.
Die sich aus der Evaluierung der bisherigen Renaturierungspraxis (Donath et al. 2003, Bissels et al. accepted) ergebende Haupthypothese der Arbeit besagt, dass der unbefriedigende Maßnahmenerfolg in erster Linie auf eine Samenlimitierung infolge der geringen Ausbreitungskapazität und Samenbankpersistenz der Zielarten zurückzuführen ist. Als weitere limitierende Einflussgrößen werden nachteilige Keimungsansprüche (z. B. Schütz 2000b) und

der Mangel an Regenerationsnischen (z. B. Eriksson & Ehrlén 1992, Zobel 2000) in die Betrachtung mit einbezogen.

In Kapitel 2 erfolgt auf der Basis eines umfangreichen Satzes selbst erhobener Samenbank- und Vegetationsdaten eine Einschätzung der Langlebigkeit der Bodendiasporenbanken in Auenwiesen. Informationen zur Persistenz von Samen sind von Praxisrelevanz, da sie es ermöglichen zu beurteilen, welche Arten potenziell in der Lage sind, einen Beitrag zur Artenanreicherung durch Rekrutierung aus der Samenbank zu leisten (Bakker et al 1996). Für die charakteristischen Arten der hier untersuchten Auenwiesen fehlten entsprechende Daten bislang fast vollständig. Zugleich wird eine neue und verbesserte Methode zur Abschätzung der Tendenz einer Art langlebige Bodendiasporenbanken aufzubauen vorgestellt.

Fluviatiler Transport entlang von Fließgewässerkorridoren gilt gemeinhin als besonders effektiver Prozess der Diasporenausbreitung (z. B. Bonn & Poschlod 1998). Damit verknüpft sind erhebliche Renaturierungserwartungen bei der Wiederherstellung auentypischer Überflutungsverhältnisse (Dister et al. 1992). Bislang liegen aber kaum empirische Befunde vor, welche belegen könnten, ob diese Erwartungen im Falle hydrologisch stark regulierter mitteleuropäischer Tieflandströme tatsächlich realistisch und gerechtfertigt sind. Zur Abschätzung der Bedeutung des fluviatilen Eintrags werden in Kapitel 3 Bodendiasporenbanken in drei hydrologisch definierten Auenkompartimenten untersucht, die sich hinsichtlich der Eintragsbedingungen für Diasporen bei Überflutungen grundsätzlich voneinander unterscheiden. Für die Rezentaue wird als Zeichen regelmäßigen fluviatilen Eintrags ein besonders hoher Anteil allochthoner Arten in der Diasporenbank angenommen, während ein entsprechender Einfluss in der selten überfluteten Hybridaue abgeschwächt und in der von hohen Winterdeichen geschützten Altaue nicht feststellbar sein sollte.

In Kapitel 4 werden Veränderungen in Bodendiasporenbanken von Auenwiesen nach zwei Perioden mit stark unterschiedlichem Überflutungsgeschehen analysiert. Ziel dieser Studie ist es, Erkenntnisse über die Einflüsse von langanhaltenden Hochwasserereignissen auf die Dynamik der Diasporenbank von Auenwiesen zu gewinnen. Hierzu liegen bisher kaum empirische Befunde vor.

In Kapitel 5 wird mit Hilfe von Labor- und Freilandexperimenten das Keimungsverhalten von insgesamt 42 charakteristischen Pflanzenarten der Stromtalwiesen eingehend analysiert. Ziel

dieser Untersuchungen ist es zu eruieren, ob die untersuchten Arten keimungsökologische Charakteristika aufweisen, die als spezifische Anpassung an die besonderen Habitatbedingungen von Stromtalwiesen verstanden werden können. Darüber hinaus sollte geklärt werden, ob gegebenenfalls keimungsökologische Ursachen für die auffällige Habitat- und Arealbegrenzung in Mitteleuropa sowie für das Scheitern einer Etablierung in Renaturierungsvorhaben geltend gemacht werden können (z. B. Schütz 2000b).

Kapitel 6 dokumentiert die Ergebnisse eines Renaturierungsexperiments, in dem erprobt wird, ob durch die Übertragung von diasporenhaltigem Mahdgut aus artenreichen Altbeständen eine rasche und möglichst vollständige Wiederherstellung der Zielartengemeinschaft erreicht werden kann. Dieses Experiment dient auch der Überprüfung der Haupthypothese dieser Arbeit, dass der geringe Etablierungserfolg von Zielarten bei bisherigen Renaturierungsmaßnahmen in erster Linie auf eine Samen- und Ausbreitungslimitierung zurückzuführen ist. Zur Schaffung besonders günstiger Keimungs- und Etablierungsbedingungen wurde auf der Maßnahmenfläche zugleich ein Oberbodenabtrag vorgenommen. Kapitel 6 analysiert eingehend die Effekte dieser Maßnahmen auf Bodennährstoffhaushalt, Diasporenbank und pflanzliche Sukzession.

Auch dem in Kapitel 7 dargestellten Ansaatexperiment liegt die Hypothese einer Samenlimitierung von Zielarten der Stromtalwiesen zugrunde. Darüber hinaus soll überprüft werden, ob auf ehemaligen Ackerflächen ohne Oberbodenabtrag und damit erhöhter Produktivität und verschärftem Konkurrenzdruck gleichzeitig auch eine Regenerationsnischenlimitierung besteht. Hierzu wurden Samen von sechs charakteristischen Arten der Stromtalwiesen in einem faktoriellen Etablierungsexperiment mit verschiedenen Behandlungsvarianten (Schaffung künstlicher Bestandeslücken, Hinzufügung von Streuauflagen) ausgesät und deren Entwicklung über drei Jahre beobachtet. Die Anlage dieses Experiments erfolgte sowohl in einer jungen Ackerbrache als auch in einem artenarmen Grünlandbestand, beides charakteristische Ausgangssituationen der Grünlandrenaturierung in der Untersuchungsregion.

In Kapitel 8 werden die wesentlichen Ergebnisse der Kapitel 2 bis 7 zusammengefasst und abschließend in ihrer Bedeutung für die Renaturierungspraxis diskutiert.

Kapitel 2

Assessing soil seed bank persistence in flood-meadows: which are the easiest and most reliable traits?

Norbert Hölzel & Annette Otte

Abstract

To assess seed bank persistence of target species in endangered flood-meadows (alliances *Cnidion & Molinion*), we investigated the established vegetation and the soil seed bank of 46 plots for three and two years, respectively. As representative traits of seed persistence we calculated various continuous indices that refer to the frequency and abundance of a particular species in above-ground vegetation and in different soil depths. Furthermore, we tested the significance and soundness of easily observed traits such as maximum seed density per plot and seed attributes (mass, size and shape) as predictors of soil seed bank features.In linear regression the indices, which referred to the distribution of species in above-ground vegetation and soil seed bank in our data (seed accumulation index, SAI) showed the best agreement ($R^2 = 0.64$) with the 'seed longevity index' that was derived from the database by Thompson et al. (1997) for a set of 115 species. The second best predictor ($R^2 = 0.39$) of the seed longevity index was maximum seed density per plot in the lower soil layer (5-10 cm), whereas depth distribution indices and seed attributes showed weaker albeit significant relatedness. The dynamic character of flood-meadows was reflected by a high proportion of species with a strong tendency to accumulate seeds in the soil relative to their importance in above-ground vegetation. Most of these species follow a ruderal strategy, exploiting gaps after flood disturbances, while the dominants of flood-meadows tended to have short-lived seed banks. Compared to other grassland types, a relatively high proportion of rare and endangered target species can be expected to form long-term persistent seed banks. However, only under marginal conditions that facilitate seed survival in the soil (e.g. fallow) are these persistent seed banks likely to contribute to restoration.

Based on the results of our study, we conclude that easily observed traits of persistence such as seed weight, size and shape do not meet the accuracy needed in scientific and practical applications. Thus, there is a crucial demand for further seed bank studies in poorly investigated habitats and rare species.

Keywords: *Cnidion, Molinion,* Depth distribution, Restoration, Seed accumulation index, Seed longevity index, Seed shape, Seed size, Seed weight,

Nomenclature: Wisskirchen & Haeupler (1998).

Introduction

There is in an increasing demand for reliable autecological information on seed banks not only for scientific work in plant biology and ecology but also as a decision tool in habitat and landscape management. This applies in particular to restoration projects, which have become a major topic on the agenda of nature conservation and biodiversity preservation during the past two decades. The lack of substantial seed sources due to limited dispersal of target species has been increasingly identified as the main constraint on restoration, even under favourable site and management conditions (Bakker & Berendse 1999). In this context, soil seed banks are considered to play an important role in restoring former species diversity (Bakker et al. 1996). Seeds of target species are expected to have survived beneath plant communities that have been destroyed or degraded at some time in the past. At the same time, it has been shown that the risk of local extinction increases in species with short-lived seed banks, particularly in fragmented landscapes (Stöcklin & Fischer 1999). Due to the heterogeneity of approaches and the shortcomings in the available data, Thompson et al. (1997) suggested a rather coarse classification of seed bank types that emphasises seed longevity:

- transient: persistent for < 1yr.;
- short-term persistent: 1-5 yrs.;
- long-term persistent: > 5 yrs.

Only the latter can be expected to play a significant role in the restoration of species-richness. Thus, the determination of seed longevity is a key question to assess if and how far soil seed banks may contribute to the regeneration of a specific plant community (e.g. McDonald et al.

1996, Bekker et al. 1997) as well as for the assessment of the local extinction risk (Stöcklin & Fischer 1999). Presently, there is a strong bias in seed bank studies towards common species of arable land and pastures, whereas there are large information deficits for the rare and threatened species that are most relevant in restoration (Bakker et al. 1996, Thompson et al. 1998). This also applies to flood-meadows of the alliance *Cnidion*, which belong to the most endangered wet grassland communities in Europe. Due to their high biodiversity value and their unfavourable conservation status, *Cnidion* meadows are presently the target of large-scale restoration efforts in several parts of their Central European range (Šeffer & Stanová. 1999, Bischoff 2002, Hölzel et al. 2002). However, until recently (Hölzel & Otte 2001), no information was available on seed longevity in their very specific and highly threatened flora (Schnittler & Günther 1999). Judging from the experience in other dynamic amphibious habitats (e.g. van der Valk & Davis 1978, Schneider & Sharitz 1986, Bekker et al. 1999, Jutila 2001), one can expect that recruitment from the persistent seed bank may also play an essential role in the restoration of flood-meadows.

Methods to measure seed persistence in the soil are presently anything but comprehensive and straightforward, and to date satisfactory methodical standards have not been established (Thompson et al. 1997). The following approaches are most commonly used to assess seed persistence in the soil: (i) burial experiments (e.g. Jensen 2001), (ii) distribution of a certain species in established vegetation and various soil depths (Thompson et al. 1997), (iii) seed attributes such as mass, size and shape (Thompson et al. 1993, Bekker et al. 1998).

Burial experiments require a run-time of least five years. Additionally, they are fraught with misinterpretations due to their artificial nature (Bakker et al 1996, Thompson et al. 1997). Thus, in the present study, seed longevity in flood-meadows was investigated by a refined and extended combination of the latter two approaches. Based on a fairly large and consistent dataset we examined, which traits of seed banks and seeds are the most reliable and straightforward to assess seed longevity in a threatened habitat type.

Material and Methods

Study sites

The studied flood-meadows are situated in the Holocene flood-plain of the northern Upper Rhine between the tributaries Neckar to the south and Main to the north (core area: 49°51′ N / 8°23′ E, 83-91 m a.s.l.). In this region flood-meadows occupy finely grained, calcareous alluvial soils that are irregularly inundated by high water levels of the River Rhine. In conjunction with the comparatively warm and dry climate (10.3 °C mean annual temperature and 580 mm annual precipitation), the irregularity of flooding results in a high seasonal and inter-annual variation in ecological conditions. The 46 flood-meadows that were analysed represent a broad variety of vegetation types in terms of flooding regime, soil nutrient status and management and cover almost the entire spectrum of possible target species. Grassland communities in flood-meadows are ordered along an elevational gradient, which reflects differences in average flooding frequency and duration. They range from mown *Magnocaricion* stands at the lowest elevations, over *Cnidion* stands at intermediate levels to alluvial *Arrhenatherion* communities that cover the rarely inundated highest positions in the flood-plain (Dister 1980, Hölzel 1999). Besides these main ecological types, two further important subtypes can be distinguished: 8 plots originate from former arable fields and poplar plantations that were restored into grassland about 10 to 15 years ago, while 6 plots comprise strictly oligotrophic alluvial *Molinion* communities that are confined to particularly nutrient-poor sites where the loamy topsoil was removed in the past.

Above-ground vegetation sampling

Species composition of vascular plants in above-ground vegetation was sampled each year from 1998 to 2000 on 46 permanent plots of 200 m². Species abundance was visually estimated on a modified Braun-Blanquet-scale (van der Maarel 1979). Sampling of vegetation usually took place in June. In 1999, when the above-ground vegetation of many plots at low elevations was destroyed by heavy flooding in May/June, sampling took place in August after resprouting of the meadows.

Seed bank sampling

Sampling of soil seed banks was carried out in September 1997 and repeated in September 1999 to cover two years with contrasting flooding conditions. Whereas the season before the first sampling in 1997 was unusually dry, the period before the second sampling in 1999 was characterised by a series of high and und long lasting flooding events in winter, spring and early summer. Differences between the two years of sampling will be reported elsewhere (Hölzel & Otte submitted).

Within each of the 46 permanent plots, 20 cores of 3 cm diameter and 10 cm depth were taken at random locations after thoroughly removing living and dead plant material from the soil surface. Thus, the data represent the soil seed bank in the strict sense without the superficial diaspore litter deposited during the sampling year (Urbanska 1992). The soil cores were then divided into 0 - 5 cm and 5 - 10 cm sections. The soil samples represent 141 cm² of the soil surface and 1410 cm³ of the soil volume in each plot and were thus well above the minimum requirements given by Oomes & Ham (1983) for studies of seeds in grassland.

We analysed seed banks by the seedling emergence method (Roberts 1981), which was continued for 36 months. For further detailed information see Hölzel & Otte (2001).

Seed persistence traits

To achieve formalized seed persistence criteria, we defined various traits that were applied in a modified way in previous studies (Thompson et al. 1997, Bekker et al. 1998). Basically, these traits refer to the relationship between the occurrence of a species in above-ground vegetation and in the soil as well as to the vertical distribution of seeds within the soil profile. To define seed bank types from this kind of data, Thompson et al. (1997) used a simple dichotomous key that only gives a rough and strictly categorical estimation of seed longevity, which must be seen as a concession to the highly inconsistent and heterogeneous information compiled in their database. In the present study, we developed several indices of seed persistence that make it possible to allocate species along continuous gradients. Since the application of such indices always depends on extensive seed bank and vegetation study with a large set of samples, we also tried to assess the reliability of easier traits. Thus, besides maximum seed densities per plot at different soil depths, we also included seed morphological attributes such as mass, size and shape in the analysis. These parameters are thought to be

predictors of depth distribution and seed-longevity (Thompson et al. 1993, Bekker et al. 1998, Thompson et al. 1998; but see Leishman & Westoby 1998, Moles et al. 2000).

Seed accumulation index (SAI)

Two indices were created to express the relationship between the presence of a certain species in above-ground vegetation and in the soil seed bank in a continuous way we created two indices. The first index relates the plot frequency of a certain species in above-ground vegetation (AV_f) with its frequency in the soil seed bank (SB_f):

$$AV/SB_{freq} \text{ index} = (SB_f / (SB_f + AV_f)) * 100.$$

The second index relates cumulative cover of a certain species over all plots (AV_q) to the total number of seeds recorded in the seed bank over all plots in both years of sampling (SB_q):

$$AV/SB_{quant} \text{ index} = (SB_q / (SB_q + AV_q)) * 100.$$

Since there was considerable flood-induced inter-annual variation in species dominance, cover in a certain plot was calculated as an average of three years with contrasting flooding conditions namely: 1998 = very dry, 1999 = very wet, 2000 = medium. Both indices range between 0 (only present in above-ground vegetation and therefore strictly transient) and 100 (only present in the soil seed bank and therefore strictly persistent).

To integrate frequency as well as quantitative aspects of species occurrence in above-ground vegetation and seed bank, we merged the two indices into a single one by the addition of both values and division by two. We call this complex index 'seed accumulation index' (SAI), since it expresses the tendency in a certain species to accumulate seeds in the soil, rather than the potential seed longevity.

Depth distribution indices

A high proportion of deeply buried seeds is usually regarded as a strong indicator of persistent seed banks (Thompson et al. 1997, Bekker et al. 1998). To describe depth distribution of seeds in the soil we used indices similar to those described above. The first one describes plot frequencies of a certain species in the lower layer of 5-10 cm (LL_f) in relation to those in the upper layer of 0-5 cm (UL_f):

DD_{freq} index = $(LL_f / (LL_f + UL_f)) * 100$

The second depth distribution index refers to the relationship between the total number of seeds in a certain species over all plots in both years of sampling in the lower (LL_q) and in the upper layer (UL_q), respectively:

DD_{quant} index = $(LL_q / (LL_q + UL_q)) * 100$

Both indices also range from 0 (only present in upper layer) to 100 (only present in the lower layer).

Maximum seed densities

Additionally, we chose maximum seed density in a certain species per plot during a single sampling occasion in the lower layer of 5-10 cm (LL_{max}), and in the entire profile depth of 0-10 cm (T_{max}) as an indicator of persistence. We expected these traits to be particularly useful in assessing the potential for seed accumulation in the soil within a particular species.

Seed attributes

Physical seed attributes such as mass (*M*), size (*S*) and shape (*SH*) are thought to be major determinants for depth distribution of seeds in the soil and therefore also play a significant role in estimating seed longevity (Thompson et al. 1993, Bekker et al. 1998, Moles et al. 2000). Light, small and rotund-shaped seeds are expected to penetrate the soil more readily, facilitating the creation of long-term persistent seed banks due to dark dormancy and escape from predation (Grime et al. 1981, Thompson 1987).

Seed mass was measured as an average of at least 1000 seeds, average length and breadth was calculated as the median of 20 grains. Additional data on common species were derived from Grime et al. (1988), Korsma (1930) and Jensen (unpubl.). Based on the assumption that the maximum surface area of seeds determines the probability of burial, we defined size as the product of length and breadth. In contrast to Thompson et al. (1993), Bekker et al. (1998) and Moles et al. (2000), who used a three dimensional approach, shape was defined by us as the ratio of length and breadth. Given the same volume, spherical to lens-shaped seeds are considered to be more easily buried than slim elongated seeds.

Data analysis

Trees and shrubs, and herbaceous species with less than three occurrences either in above-ground vegetation or in the seed bank, were omitted from the dataset. For 27 species, no data on seed attributes were available, which left 152 species for the final analysis. The values of LL_{max} and T_{max} and those of mass (M), size (S) and shape (SH) were log-transformed prior to analysis.

To evaluate the reliability of the SAI and its two components as a measure of persistence, we used the 'seed longevity index' of Bekker et al. (1998) for a set of 115 species:

Longevity index (L) = ((SP + LP) / (T + SP + LP))

where (SP + LP) is the total number of short-term and long-term persistent records, and (T + SP + LP) the total number of transient plus short-term plus long-term persistent records in the database of Thompson et al. (1997).

The underlying correlation structure of seed longevity traits was explored in a principal component analysis (PCA). Simple and multiple linear regression models were used to check the predictive power of seed longevity traits. In multiple regressions we applied the more robust stepwise backward selection (Zar 1999). All statistical analyses were carried out with STATISTICA 6.0.

Results

Variation structure of traits

The principal-component analysis (PCA) revealed the correlation structure of the longevity traits calculated from our data set. The first three axes of the PCA ordination explained 56%, 18% and 11%, respectively, of the variation in the dataset (Table 1).

There was a very close negative correlation between the first axis and the traits AV/SB_{freq}, AV/SB_{quant}, log T_{max} and log LL_{max} and to a lower degree DD_{freq} and DD_{quant} indicating a significant interdepencence between all these traits directly calculated from our data. In contrast, log seed mass (M) and log seed size (S) loaded strongest on axis two and log seed

shape (*SH*) on axis three. Thus, the variation structure of these seed attributes differed from those of the other traits.

Table 1. Explained variance and correlation structure of seed longevity traits in PCA ordination (first three axes). High correlations are given in bold.

n = 152	Axis 1	Axis 2	Axis 3
Explained variance (%)	59.12	15.46	10.63
AV/SB$_{freq}$ index	**-0.88**	0.01	0.12
AV/SB$_{quant}$ index	**-0.90**	-0.01	0.18
DD$_{freq}$ index	**-0.81**	-0.36	-0.32
DD$_{quant}$ index	**-0.72**	-0.40	-0.36
LOG (T$_{max}$)	**-0.88**	-0.09	0.10
LOG (LL$_{max}$)	**-0.92**	-0.16	-0.08
LOG (*M*)	0.63	**-0.72**	0.11
LOG (*S*)	0.63	**-0.70**	-0.02
LOG (*SH*)	0.37	0.24	**-0.80**

Performance of seed persistence traits

Simple linear regression analysis for a set of 115 species between the seed-longevity-index of Bekker et al. (1998) as dependent variable and the various traits of persistence as predictor variable resulted in each case in a highly significant correlation (Table 2).

The indices that relate frequency (AV/SB$_{freq}$) and abundance (AV/SB$_{quant}$) of a certain species in the above-ground vegetation and in the seed bank exhibited the best correlation with a high proportion of explained variance (R^2 of 0.60 and 0.58, respectively). An even higher correlation ($R^2 = 0.64$) was achieved with the seed accumulation index (SAI) (Fig. 1), which combines both indices.

Seed densities per single plot in the lower layer (log LL$_{max}$) and the entire sampled profile (log T$_{max}$) gave the second best correlation with the seed longevity index (R^2 of 0.39 and 0.34, respectively). In contrast, the predictive power of the depth distribution indices DD$_{freq}$ and DD$_{quant}$ was considerably lower ($R^2 = 0.21$ and 0.20, respectively). An identical proportion of variance was explained by the seed attributes log mass (*M*) and log size (*S*), while log shape (*SH*) showed the poorest ($R^2 = 0.09$) correlation. In multiple linear regression with stepwise backward selection including the easily observed traits 'maximum plot density' and 'seed

Table 2. Simple linear regression models with the 'seed longevity index' (Bekker et al. 1998) as dependent variable and various traits of seed persistence calculated from the flood-meadow dataset as predictor variables.

n = 115	Longevity index (L)	Significance
SAI	$L = 0.0077 \times SAI + 0.0797$	$R^2 = 0.64^{***}$
AV/SB_{freq}	$L = 0.009 \times AV/SB_{freq} + 0.112$	$R^2 = 0.60^{***}$
AV/SB_{quant}	$L = 0.0059 \times AV/SB_{quant} + 0.0952$	$R^2 = 0.58^{***}$
DD_{freq}	$L = 0.0057 \times DD_{freq} + 0.2468$	$R^2 = 0.21^{***}$
DD_{quant}	$L = 0.056 \times DD_{quant} + 0.2785$	$R^2 = 0.20^{***}$
Log (T_{max})	$L = 0.0849 \times \log(T_{max}) + 0.2984$	$R^2 = 0.34^{***}$
Log (LL_{max})	$L = 0.0927 \times \log(LL_{max}) + 0.3905$	$R^2 = 0.39^{***}$
Log (M)	$L = -0.0903 \times \log(M) + 0.3555$	$R^2 = 0.22^{***}$
Log (S)	$L = -0.1204 \times \log(S) + 0.4939$	$R^2 = 0.21^{***}$
Log (SH)	$L = -0.2302 \times \log(SH) + 0.5363$	$R^2 = 0.09^{***}$

attributes', only maximum density in the lower layer (log LL_{max}) and log mass (M) were added to the model, which resulted in an $R^2 = 0.44$. Thus, the addition of log (M) to the model led to an increase in explained variance of only 5 %.
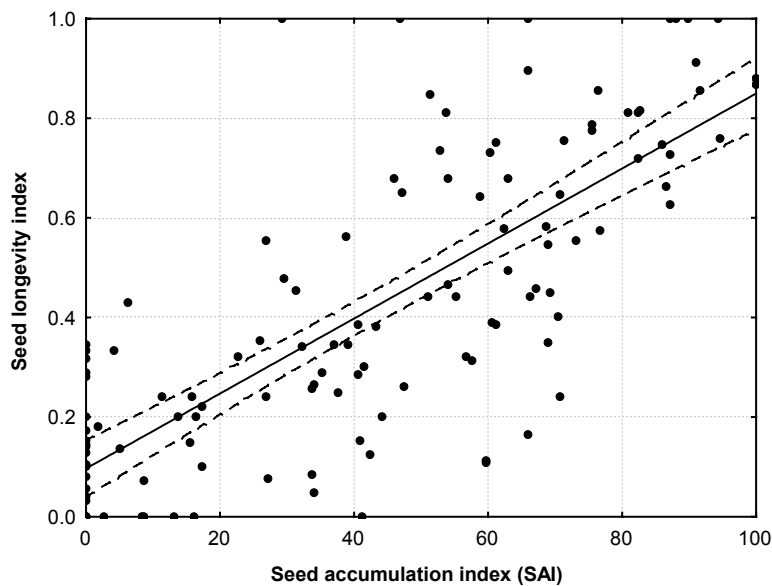
Fig. 1. Correlation between the seed longevity index of Bekker et al. (1998) and the seed accumulation index (SAI) for a set of 115 species. Regression line and 95 % confidence intervals are shown.

Influence of seed traits on seed accumulation and depth distribution

As already indicated by the PCA ordination (Table 1) there was a strong intercorrelation between the seed attributes mass and size. Consequently, in multiple regression with stepwise backward selection (n = 152) only log mass (*M*)and log shape (*SH*) were added to the model (Table 3). Explained variance was highest for the SAI (R^2 = 0.38) and maximum densities at both measured soil depths (R^2 = 0.27). In contrast, there was a much lower but still significant correlation between log mass (*M*) and the two depth distribution indices (R^2 of 0.10 and 0.06, respectively).

Table 3. Multiple linear regression models with stepwise backward selection of various traits of seed accumulation and depth distribution as dependent variable and seed mass (*M*), size (*S*) and shape (*SH*) as predictor variables.

n = 152	Seed attributes (*M*), (*S*), (*SH*)	Significance
SAI	= -9.59 x log (*M*) – 26.0 x log (*SH*) + 50.78	R^2 = 0.38***
DD_{freq}	= -4.95 x log (*M*) + 24.1	R^2 = 0.10***
DD_{quant}	= -3.78 x log (*M*) + 19.03	R^2 = 0.06**
Log (T_{max})	= -0.58 x log (*M*) – 1.60 x log (*SH*) + 1.77	R^2 = 0.27***
Log (LL_{max})	= -0.57 x log (*M*) – 1.28 x log (*SH*) + 0.52	R^2 = 0.27***

Species patterns of seed accumulation in flood-meadows

Due to its high correlation with the seed longevity index we used the seed accumulation index (SAI) to assess seed persistence in the studied flood-meadows. The application of the SAI to our data set resulted in a continuous and very differentiated ranking of species (Appendix 1). Species with high index values were predominantly therophytes or perennials that follow a ruderal life strategy. With few exceptions, such as *Potentilla reptans, Ranunulus repens, Lysimachia vulgaris, Poa trivialis* and *Agrostis stolonoifera* species with high scores were scarce or completely absent in above-ground vegetation. In contrast, most of the dominant grasses and forbs of flood meadows, such as *Alopecurus pratensis, Elymus repens, Festuca arundinacea, Carex disticha, Lathyrus pratensis and Vicia cracca* had very low index values. Among the target species of flood-meadows only a limited proportion of about 40 % reached high index values of more than 50.

Discussion

In our study the tendency of a certain species to accumulate seeds in the soil relative to cover in the established vegetation, expressed by the SAI, was revealed to be the best predictor of seed persistence among all tested traits. The very good agreement ($R^2 = 0.64$) with the 'seed longevity index' of Bekker et al. (1998) is at first surprising, since theoretically considerable flaws can be expected. Potentially, the SAI may be strongly influenced by seasonal seed production causing misinterpretations in seed longevity. However, due to the exclusion of superficial diaspore litter during sampling this effect was obviously largely eliminated. This becomes particularly evident in certain abundant species with massive seed production but short-lived seeds, such as *Alopecurus pratensis*, *Arrhenatherum elatoris* and others, which were entirely absent from the soil seed bank samples. Nevertheless, there is still a problem with differences in seed production among species with persistent seeds, and this may cause misinterpretations. However, due to the combination of a frequency index with a quantitative index within the SAI, this problem seems to be at least partially diluted.

With the application of the SAI to our data set it was possible to express the tendency in a certain species to accumulate seeds in the soil in a continuous and very differentiated way. In comparison to the strictly categorical dichotomous classification key of Thompson et al. (1997), this must be regarded as a considerable improvement in allocating species along a gradient of seed persistence. As with the seed longevity index the soundness of the SAI will increase with the number of records of a certain species within the data set. The SAI may be applied to other data sets if the relevant vegetation and seed bank data are available. As indicated by the performance of the AV/SB$_{freq}$, even pure presence-absence data may be sufficient to obtain reasonable results.

Depth distribution, highly ranked by other authors (e.g. Thompson et al. 1997), was revealed to be a significant but comparably weak predictor of seed persistence in the soil ($R^2 = 0.21$). The correlations in the present study were in line with those obtained by Bekker et al. (1998). Judging from our results, we believe that the vertical distribution of seeds in the soil (in our example DD$_{quant}$) as a trait of persistence may cause serious flaws and contradictions. Even in species with large long-term persistent seed banks we usually found a steep decrease in seed densities from the upper to the lower layer (Appendix 1). In contrast, higher concentrations in the lower layer are largely confined to particular situations: Typically they occur at sites where singular disturbances or changes in management (e.g. conversion of arable land into grassland, afforestation) have led to a drastic decline or complete disappearance of formerly

common species in above above-ground vegetation (e.g. arable weeds). This means that in most other cases depth gradients will lead to an underestimation of persistence. In other words, equal or higher concentrations in the lower layer are surely a good indicator of persistence but not necessarily vice versa.

Maximum seed concentrations per plot in the lower layer gave a considerably higher correlation with the seed-longevity index ($R^2 = 0.39$), which was also true for the entire measured soil profile ($R^2 = 0.34$). Potentially, maximum seed densities including the upper part of the soil profile (in our case 0-10 cm) may yield flawed estimations of longevity due to the regular input of short-term persistent seeds (e.g. Thompson & Grime 1979). As already mentioned this effect was largely reduced by the exclusion of superficial diaspore litter during sampling. In contrast, lower soil layers (in our case 5-10 cm) are usually insignificantly affected by seasonal seed rain (e.g. Poschlod & Jackel 1993), indicating that the burial of seeds is a time-consuming process (Thompson et al. 1997). Thus, the likelihood that short-term persistent seeds will reach deeper soil layers in high quantities is low. A more serious problem is related to differences in seed production among species with long-term persistent seed bank. Species with small seeds and therefore usually heavy seed production (e.g. genera *Veronica* and *Juncus*) are more likely to reach high concentrations in the lower layer than those with relatively large seeds and/or low and irregular seed production (e.g. genus *Carex*). This may easily lead to an underestimation of seed longevity in the latter. Principally, the same problem as in depth distribution can occur: High seed concentrations in the lower layer are a good trait of seed longevity but not necessarily vice versa. Particularly in studies with poor documentation of established vegetation, high maximum seed densities in the lower layer may give a relatively sound assessment of long-term persistence. They are also particularly relevant for restoration practices, since the likelihood that buried seeds will be exhumed e.g. by earthworm, rodent or mole activity, increases with density.

In accordance with Thompson et al. (1993), Bekker et al. (1998), Hodkinson et al. (1998) and Funes et al. (1999), we found a significant negative correlation between the seed attributes mass and shape and the seed longevity index. The predictive power of seed attributes was even higher when the seed accumulation index (SAI) and maximum densities per plot were used as the dependent variable. In line with Bekker et al. (1998) seed attributes were revealed to be relatively poor predictors of depth distribution, which reflects the general problems of depth gradients as a seed persistence trait, as discussed above. Although we used a two-dimensional approach to describe seed shape, our correlations were even better than those obtained by Bekker et al. (1998). Generally, seed shape proved to be a less significant

predictor of seed accumulation and persistence than seed mass, as found by other authors (e.g. Moles et al. 2000).

In principal, our results confirm that there is a trend in small and even shaped seeds to be incorporated into the soil more easily. However, we question the practical usefulness of this relationship, since the overall variation between seed attributes and persistence is still far too large to give a sufficient accurate assessment for a particular species (Fig. 2). Species with a seed mass below around 0.14 mg almost generally exhibit a strong tendency to accumulate seeds in the soil whereas seeds with a mass above 2.7 mg are mostly completely absent from the soil seed bank (Fig. 2). Between these thresholds, however, all kinds of variations may occur.
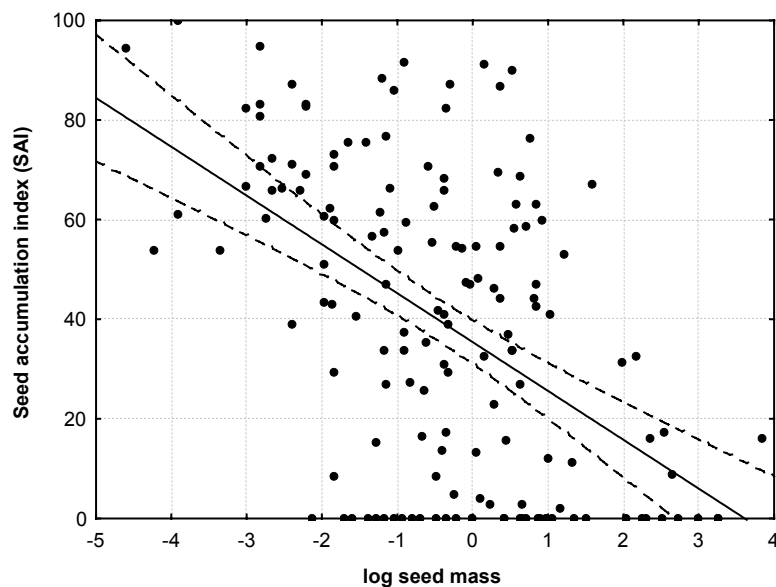
Fig. 2. Correlation between the seed accumulation index (SAI) and log seed mass for a set of 152 species. Regression line and 95 % confidence intervals are shown.

Significance of seed bank persistence in flood-meadows

In flood-meadows of the type studied, seasonal and inter-annual variations in flooding height and frequency cause distinct vegetation dynamics along elevational gradients. According to the results of the SAI (Appendix 1), this particular disturbance regime is reflected by a relatively high number of species with large persistent seed banks compared to other, more stable grassland types (Grime 2001). Typically, these species play a subordinate role in established vegetation. Their existence is strongly facilitated by regular disturbances of the turf in the course of flooding events and following draw-down that weaken dominant grasses and create gaps with low competition (Hölzel unpubl. data). Besides annuals such as

Centaurium pulchellum and *Veronica peregrina,* short-growing carpet-forming ruderals such as *Glechoma hederacea, Poa trivialis, Potentilla reptans* and *Veronica serpyllifolia* are most common and characteristic among the species with persistent seed banks in flood-meadows. In contrast, the highly competitive dominants of flood-meadows tend to have transient or short-lived seed banks (Appendix 1).

Our findings are in accordance with theory (Thompson & Grime 1979, Thompson et al. 1998, Grime 2001) that predicts a close relation between the degree of disturbance in a habitat and the tendency in species to form long-term persistent seed banks.

In comparison with other threatened grassland types such as dry chalk grasslands (Poschlod & Jackel 1993, Hutchings & Booth 1996a, Bakker et al. 1996, Stöcklin & Fischer 1999) a considerable proportion of the particularly specific target species of flood-meadows, such as *Allium angulosum, Arabis nemorensis, Cardamine parviflora, Carex tomentosa, Cerastium dubium, Pseudolysimachion longifolium, Thalictrum flavum, Viola elatior, V. persicifolia* and *V. pumila* was revealed to accumulate persistent seed banks (Appendix 1). Most of these species are relatively weak competitors and tend to exploit gaps created by flood-induced disturbances. However, as many as about 60 % of the target species showed no or only a minor tendency to accumulate seeds in the soil, among them a high proportion of *Apiaceae* (*Cnidium dubium, Peucedanum officinale, Selinum carvifolia, Silaum silaus*) and *Asteraceae* (*Cirsium tuberosum, Inula britannica, I. salicina, Senecio paludosus, Serratula tinctoria*). Generally, seed accumulation and persistence was much lower in character species of *Molinion* meadows (e.g. *Gentiana pneumonanthe, Succisa pratensis*), which usually exist under more stable conditions, than in those of *Cnidion* meadows, which are subject to regular flood disturbance. A relatively high proportion of the target species in the studied flood-meadows can be expected to emerge from the persistent soil seed bank in the course of restoration measures. Indeed, we often observed a sudden re-appearance of target species such as *Arabis nemorensis, Cerastium dubium, Viola elatior* and *V. persicifolia* at locations where these species have been absent from established vegetation for years and decades, after clear-cutting of shrubbery and poplar plantations or after reintroduction of mowing to fallows and reeds (Hölzel et al. 2002). However, such positive examples seem to be largely restricted to situations that benefit the preservation of persistent seeds in the soil (Milberg 1995, Bekker et al. 1997, Falińska 1999). In contrast, arable cultivation usually leads to a rapid depletion in the persistent seed banks of the former plant communities (e.g. McDonald 1993, Hutchings & Booth 1996a, Bischoff 2002, Donath et al. in print). Under such circumstances, the

contribution of buried viable seeds to the restoration of former species richness will often be of low significance (e.g. McDonald et al. 1996, Smith et al. 2002, Vécrin et al. 2002).

Conclusions

Although strongly advocated by Thompson et al. (1998), seed attributes such as mass, size and shape generally showed the same relatively poor performance in predicting seed bank characteristics as in the study by Bekker et al. (1998). We believe that such 'easy' traits (cf. Weiher et al. 1999) are not likely to meet the increasing requirements for solid autecological information from those concerned with plant functional theory, modelling, or management and conservation issues. As in the case of data on seed longevity purely derived from artificial burial experiments (e.g. Bakker et al. 1996, Thompson et al. 1997), too many crude flaws and contradictions occur (e.g. Leishman & Westoby 1998, Moles et al. 2000). Doubtless, seed attributes cannot substitute further empirical seed bank studies in poorly investigated vegetation types and rare species.

Despite the very good agreement that was found between the seed longevity index and seed accumulation index it must be kept in mind that neither indices can be expected to be perfectly correlated with the actual or potential seed longevity. Attempts at an 'exact' determination of longevity were often revealed to be frustratingly specific, due to the dominance of marginal conditions and the fuzzy nature of seed persistence in the soil (e.g. Bekker et al. 1997, 1998). In contrast, indices based on broad empirical evidence may give an average assessment for the tendency in a particular species to accumulate seeds in the soil, which is often much more relevant for scientific and practical applications.

Appendix 1. Seed accumulation index (SAI), absolute frequency (n = 46) and abundance in above-ground vegetation (AV) and soil seed bank (SB) at two depths, and maximum seed densities per plot at two depths for 187 species recorded in the study. Abundance in AV is given as cumulative cover and in the SB as total number of seeds over all plots. Target species of flood-meadows are printed in bold.

| Species | SAI | Frequency | | Abundance | | Maximum |
| | | AV | SB | AV | SB | Seeds / m² |
			0-5 / 5-10		0-5 / 5-10	0-10 / 5-10
Cyperus fuscus	100	0	1 / 3	0	5 / 5	560 / 210
Erucastrum gallicum	100	0	2 / 3	0	2 / 7	420 / 350
Juncus articulatus	100	0	9 / 11	0	73 / 65	2590 / 1400
Sagina procumbens	100	0	4 / 2	0	4 / 3	140 / 140
Arenaria serpyllifolia	95	2	13 / 8	<1	49 / 20	1680 / 840
Centaurium pulchellum	94	1	7 / 6	<1	33 / 40	3290 / 1750
Anagallis arvensis	92	1	1 / 5	<1	43 / 23	3290 / 770
Chenopodium album	91	4	14 / 14	1	91 / 91	3010 / 1750
Chenopodium hybridum	90	1	2 / 3	<1	5 / 52	2940 / 2730
Chenopodium polyspermum	88	7	17 / 14	3	412 / 479	10290 / 7140
Solanum nigrum	87	1	3 / 3	<1	17 / 20	1120 / 770
Veronica catenata	87	2	4 / 4	<1	20 / 11	770 / 280
Erophila verna agg.	87	1	3 / 2	<1	20 / 4	1260 / 210
Chenopodium rubrum	87	1	3 / 1	<1	8 / 2	350 / 140
Polygonum aviculare	87	1	0 / 3	<1	0 / 5	210 / 210
Stellaria media	86	2	5 / 2	<1	9 / 5	280 / 140
Veronica peregrina	83	4	7 / 5	3	818 / 235	13440 / 3780
Cerastium dubium	83	2	4 / 4	3	886 / 230	31780 / 5950
Capsella bursa-pastoris	83	7	11 / 10	1	55 / 41	2030 / 910
Veronica serpyllifolia	82	12	22 / 18	2	197 / 98	2450 / 1400
Lamium purpureum	82	2	3 / 3	1	25 / 13	1470 / 630
Arabis nemorensis	81	6	10 / 8	6	570 / 89	6230 / 1260
Sonchus asper	77	10	11 / 4	1	21 / 6	560 / 210
Juncus alpinus	77	5	3 / 2	1	15 / 7	2100 / 280
Persicaria maculosa	76	4	5 / 3	1	6 / 13	770 / 700
Plantago major intermedia	75	11	15 / 11	17	104 / 33	1680 / 420
Urtica dioica	75	5	7 / 2	2	10 / 8	490 / 490
Silene flos-cuculi	73	22	20 / 15	22	455 / 79	6020 / 700
Cardamine parviflora	72	4	3 / 4	6	65 / 28	1820 / 770
Poa trivialis	71	31	28 / 20	36	378 / 125	4550 / 1120
Lythrum salicaria	71	25	19 / 13	10	87 / 52	3570 / 630
Cerastium holosteoides	71	26	26 / 18	16	82 / 27	1190 / 280
Trifolium repens	71	9	7 / 4	2	15 / 8	420 / 210
Ajuga reptans	69	9	7 / 6	13	228 / 31	4340 / 490
Veronica arvensis	69	19	15 / 8	12	104 / 19	840 / 700

Appendix 1 continued

Carex panicea	69	8	6 / 4	17	32 / 13	2590 / 560
Trifolium hybridum	69	6	4 / 4	11	283 / 78	8470 / 1960
Viola persicifolia	68	4	4 / 1	5	5 / 1	770 / 70
Galeopsis tetrahit	67	3	0 / 2	1	0 / 11	700 / 700
Pseudolysimachion longifolium	67	14	9 / 6	20	246 / 56	7000 / 1610
Rorippa sylvestris	66	8	5 / 3	8	60 / 64	3150 / 1820
Leucanthemum vulgare agg.	66	24	18 / 12	16	65 / 20	700 / 210
Hypericum perforatum	66	9	6 / 3	3	15 / 5	420 / 140
Glechoma hederacea	66	21	17 / 14	15	50 / 31	1120 / 350
Rorippa palustris	66	4	2 / 2	1	19 / 36	2100 / 1540
Viola elatior	63	3	2 / 2	11	57 / 11	2660 / 490
Ranunculus repens	63	29	21 / 21	103	286 / 101	3640 / 980
Cardamine pratensis agg.	63	3	2 / 0	0	2 / 0	70 / 0
Linum catharticum	62	9	6 / 2	9	30 / 4	490 / 210
Myosotis arvensis	61	9	6 / 4	11	34 / 6	980 / 210
Agrostis stolonifera	61	22	15 / 7	47	95 / 38	1610 / 560
Mentha acquatica	61	3	1 / 1	1	10 / 2	490 / 140
Epilobium tetragonum	60	13	4 / 3	2	6 / 3	210 / 70
Achillea millefolium	60	28	19 / 7	35	84 / 38	1820 / 1540
Carex hirta	60	10	4 / 3	10	93 / 7	2030 / 280
Barbarea stricta	60	7	3 / 1	2	14 / 2	490 / 140
Medicago lupulina	59	11	7 / 3	4	8 / 3	140 / 70
Valerianella locusta	59	12	8 / 1	9	29 / 1	770 / 70
Allium angulosum	58	15	8 / 4	15	63 / 5	1400 / 70
Potentilla reptans	58	37	25 / 21	194	339 / 186	7980 / 2660
Lysimachia vulgaris	57	23	10 / 12	77	102 / 63	4620 / 840
Potentilla erecta	55	5	1 / 0	2	1 / 0	420 / 0
Carex tomentosa	55	16	6 / 6	10	19 / 8	420 / 140
Thalictrum flavum	55	18	6 / 1	17	45 / 4	1540 / 280
Rorippa amphibia	54	3	0 / 1	1	0 / 3	210 / 210
Daucus carota	54	16	7 / 5	13	23 / 6	490 / 140
Carex flacca	54	7	1 / 0	4	2 / 0	1330 / 0
Juncus compressus	54	4	0 / 1	0	0 / 3	210 / 210
Juncus inflexus	54	3	1 / 0	0	2 / 0	140 / 0
Carex spicata	53	21	8 / 6	15	27 / 14	700 / 350
Mercurialis annua	53	4	0 / 1	0	0 / 2	140 / 140
Conyza canadensis	51	8	2 / 0	1	4 / 0	140 / 0
Mentha arvensis	51	9	2 / 3	3	3 / 4	140 / 70
Vicia angustifolia	50	23	13 / 3	34	47 / 3	560 / 70
Viola pumila	48	21	8 / 5	24	39 / 7	630 / 140
Galium palustre	48	13	4 / 2	20	15 / 4	980 / 140
Trifolium dubium	47	14	6 / 2	13	21 / 2	350 / 70
Eleocharis palustris agg.	47	7	2 / 2	2	2 / 2	140 / 70
Euphorbia esula	47	22	3 / 4	12	18 / 19	1120 / 770
Ranunculus polyanthemos agg.	47	19	6 / 3	10	19 / 4	420 / 140
Rumex crispus	46	29	12 / 2	15	19 / 3	350 / 140
Carex riparia	44	3	1 / 0	1	1 / 0	70 / 0
Cirsium tuberosum	44	3	2 / 0	3	3 / 0	140 / 0
Linaria vulgaris	43	4	1 / 0	1	2 / 0	140 / 0
Poa palustris	43	12	5 / 2	11	9 / 5	350 / 280
Centaurea jacea	42	25	10 / 5	30	28 / 10	980 / 350
Taraxacum officinale agg.	42	32	21 / 15	128	58 / 29	1120 / 350
Galium boreale	41	3	1 / 0	1	1 / 0	70 / 0
Viola hirta	41	10	4 / 3	8	5 / 4	140 / 70
Poa angustifolia	41	39	27 / 21	309	141 / 46	980 / 350
Trifolium campestre	40	16	4 / 1	22	33 / 2	1190 / 140

Appendix 1 continued

Prunella vulgaris	39	18	7 / 1	11	10 / 1	140 / 70
Bellis perennis	39	9	2 / 2	7	7 / 3	490 / 140
Potentilla anserina	37	11	2 / 2	15	14 / 3	630 / 140
Scutellaria galericulata	37	4	0 / 0	2	0 / 0	140 / 0
Plantago lanceolata	37	26	10 / 1	31	25 / 1	490 / 70
Rumex acetosa/thyrsiflorus	35	24	13 / 3	88	42 / 3	560 / 70
Genista tintoria	35	4	2 / 0	32	10 / 0	210 / 0
Deschampsia cespitosa	34	16	6 / 3	28	12 / 3	350 / 70
Galium wirtgenii	34	36	11 / 5	55	35 / 9	560 / 350
Stachys palustris	34	15	3 / 1	13	5 / 1	210 / 70
Lotus corniculatus	34	26	3 / 1	13	12 / 1	490 / 70
Iris sibirica	33	5	2 / 0	9	5 / 0	210 / 0
Cirsium arvense	32	36	10 / 4	50	17 / 9	280 / 210
Vicia irsuta	31	3	1 / 0	2	1 / 0	70 / 0
Scutellaria hastifolia	31	11	1 / 2	15	6 / 4	280 / 140
Carex acuta	30	7	5 / 1	71	14 / 1	350 / 70
Erigeron annuus	29	8	2 / 0	3	2 / 0	70 / 0
Carex praecox	29	17	3 / 3	18	9 / 3	280 / 70
Galium album	27	26	5 / 0	18	9 / 0	140 / 0
Solidago canadensis	27	6	0 / 1	2	0 / 1	70 / 70
Ranunculus acris	27	17	2 / 1	6	3 / 1	140 / 70
Holcus lanatus	27	6	2 / 0	5	2 / 0	70 / 0
Veronica teucrium	26	3	1 / 0	3	1 / 0	70 / 0
Molinia caerulea agg.	26	5	1 / 1	91	4 / 5	350 / 350
Trifolium pratense	23	22	3 / 2	16	4 / 2	140 / 70
Lathyrus pratensis	17	36	5 / 1	58	14 / 1	280 / 70
Carex disticha	17	21	4 / 1	103	18 / 1	560 / 70
Dactylis glomerata	16	32	3 / 3	38	4 / 5	280 / 210
Iris pseudacorus	16	14	1 / 0	8	1 / 0	70 / 0
Euphorbia palustris	16	8	1 / 0	4	1 / 0	70 / 0
Succisa pratensis	16	8	1 / 0	23	1 / 0	140 / 0
Myosotis scorpioides agg.	15	5	1 / 0	6	1 / 0	70 / 0
Phalaris arundinacea	14	22	3 / 2	95	5 / 4	140 / 140
Selinum carvifolia	13	4	1 / 0	15	1 / 0	70 / 0
Symphytum officinale	12	30	2 / 2	42	2 / 2	140 / 70
Galium aparine aparine	11	20	1 / 2	25	1 / 3	140 / 70
Vicia cracca	9	41	4 / 0	65	6 / 0	140 / 0
Inula salicina	9	19	2 / 1	106	2 / 1	140 / 70
Valeriana pratensis	8	21	2 / 0	45	4 / 0	210 / 0
Calamagrostis epigejos	6	23	0 / 0	55	0 / 0	350 / 0
Festuca rubra agg.	5	13	1 / 0	36	1 / 0	70 / 0
Carex acutiformis	4	20	1 / 0	55	2 / 0	140 / 0
Serratula tinctoria	3	22	0 / 0	81	0 / 0	70 / 0
Sanguisorba officinalis	3	28	0 / 1	52	0 / 1	70 / 70
Festuca arundinacea	2	31	1 / 0	168	1 / 0	70 / 0
Alopecurus pratensis	0	39	0 / 0	473	0 / 0	0 / 0
Elymus repens	0	36	0 / 0	727	0 / 0	0 / 0
Arrhenatherum elatius	0	34	0 / 0	123	0 / 0	0 / 0
Equisetum arvense	0	29	0 / 0	18	0 / 0	0 / 0
Asparagus officinalis	0	24	0 / 0	7	0 / 0	0 / 0
Festuca pratensis	0	23	0 / 0	43	0 / 0	0 / 0
Silaum silaus	0	23	0 / 0	11	0 / 0	0 / 0
Lysimachia nummularia	0	22	0 / 0	21	0 / 0	0 / 0
Rubus caesius	0	20	0 / 0	51	0 / 0	0 / 0
Convolvulus arvensis	0	18	0 / 0	12	0 / 0	0 / 0
Persicaria amphibia	0	17	0 / 0	18	0 / 0	0 / 0

Appendix 1 continued

Bromus hordeaceus	0	14	0 / 0	13	0 / 0	0 / 0
Peucedanum officinale	0	14	0 / 0	48	0 / 0	0 / 0
Phragmites australis	0	14	0 / 0	17	0 / 0	0 / 0
Agrimonia eupatoria	0	13	0 / 0	4	0 / 0	0 / 0
Lactuca serriola	0	12	0 / 0	2	0 / 0	0 / 0
Trisetum flavescens	0	12	0 / 0	21	0 / 0	0 / 0
Cirsium vulgare	0	10	0 / 0	11	0 / 0	0 / 0
Arctium lappa	0	9	0 / 0	3	0 / 0	0 / 0
Filipendula ulmaria	0	9	0 / 0	2	0 / 0	0 / 0
Pastinaca sativa	0	8	0 / 0	1	0 / 0	0 / 0
Senecio erucifolius	0	8	0 / 0	4	0 / 0	0 / 0
Fragaria vesca	0	7	0 / 0	24	0 / 0	0 / 0
Calystegia sepium	0	6	0 / 0	1	0 / 0	0 / 0
Crepis biennis	0	6	0 / 0	1	0 / 0	0 / 0
Tragopogon pratensis	0	6	0 / 0	1	0 / 0	0 / 0
Vincetoxicum hirundinaria	0	6	0 / 0	5	0 / 0	0 / 0
Achillea ptarmica	0	5	0 / 0	4	0 / 0	0 / 0
Bromus inermis	0	5	0 / 0	10	0 / 0	0 / 0
Cnidium dubium	0	5	0 / 0	7	0 / 0	0 / 0
Lathyrus tuberosus	0	5	0 / 0	3	0 / 0	0 / 0
Phleum pratense	0	5	0 / 0	2	0 / 0	0 / 0
Allium vineale	0	4	0 / 0	1	0 / 0	0 / 0
Carex elata	0	4	0 / 0	8	0 / 0	0 / 0
Carex vesicaria	0	4	0 / 0	6	0 / 0	0 / 0
Colchicum autumnale	0	4	0 / 0	1	0 / 0	0 / 0
Gentiana pneumonanthe	0	4	0 / 0	2	0 / 0	0 / 0
Lathyrus palustris	0	4	0 / 0	3	0 / 0	0 / 0
Lemna minor	0	4	0 / 0	4	0 / 0	0 / 0
Senecio paludosus	0	4	0 / 0	2	0 / 0	0 / 0
Vicia sepium	0	4	0 / 0	2	0 / 0	0 / 0
Butomus umbellatus	0	3	0 / 0	1	0 / 0	0 / 0
Caltha palustris	0	3	0 / 0	1	0 / 0	0 / 0
Dipsacus fullonum	0	3	0 / 0	8	0 / 0	0 / 0
Echinochloa crus-galli	0	3	0 / 0	0	0 / 0	0 / 0
Equisetum palustre	0	3	0 / 0	1	0 / 0	0 / 0
Helicotrichon pubescens	0	3	0 / 0	2	0 / 0	0 / 0
Lycopus europaeus	0	3	0 / 0	1	0 / 0	0 / 0
Plantago media	0	3	0 / 0	2	0 / 0	0 / 0

Kapitel 3

The impact of flooding-regime on the soil seed bank of flood-meadows

Norbert Hölzel & Annette Otte

Abstract

We assessed the significance of flooding for the floristic composition of seed banks in flood-meadows of the northern valley of the Upper Rhine. We compared three hydrological compartments of the alluvial plain, consisting of the regularly flooded land between the river and low summer dykes (functional flood-plain), the occasionally flooded land between summer dykes and high winter dykes (hybrid flood-plain) and the land behind the winter dykes, which is now only submerged by ascending groundwater (fossil flood-plain). Due to their different flooding regime, the three compartments should differ with respect to the prevailing conditions of diaspore input.

The seed density of soil samples increased with the duration of flooding in the three compartments, while species richness and the proportion of species not occurring in the vegetation was constant. The increase in seed density can be largely attributed to an increase of disturbance indicators, which are present in the above-ground vegetation and capable of forming a long-term persistent seed bank.

No effects of flooding on the composition of seed banks in the three flood-plain compartments were found. The differences in seed bank composition can be largely explained by corresponding differences in above-ground vegetation and former and present-day meadow management. Seeds of species absent from above-ground vegetation can be attributed to the local species pool present in the immediate vicinity of the study plots. We discuss consequences of the results for the restoration of species-rich flood-plain meadows.

Keywords: Flood-plain; Seed dispersal; Restoration; River Rhine.

Nomenclature: Wisskirchen & Haeupler (1998).

Introduction

In large river valleys influenced by subcontinental climatic conditions the meadows subjected to regular flooding contain a large number of highly specialized, characteristic plant species (alliance *Cnidion* sensu Balatova-Tulackova 1969). Due to changes in hydrology and management they have become extremely rare and are considered endangered plant communities (Korneck et al 1996). Larger Central European remnants of these flood-meadows are found in the catchments of the rivers Elbe and Oder (Burkart 1998, Korsch 1999) and in the plains along the northern Upper Rhine (Dister 1980, Böger 1991, Hölzel 1999). Restoration of flood-plains aiming at the re-establishment of species-rich meadows has been pursued for some 20 years. The reconnection of dyked areas to the flooding regime of the river Rhine is thought to be a prerequiste for the fast restoration of species-rich meadows, partly because diaspores are expected to be transported and deposited in the course of flooding events (Dister et al. 1992).

Flooding is widely regarded as a significant vector of dispersal in flood-plain ecosystems (Sauer 1988, Malanson 1993, Bonn & Poschlod 1998). However, to date there have been few empirical studies on this subject. Almost all previous work was carried out on flood-plain forests (Schneider & Sharitz 1988, Schwabe 1991, Hughes & Cass 1997) or grasslands (Skoglund 1990, Finlayson et al. 1990, Nilsson et al. 1991) in relatively natural flood-plains. In contrast, the anthropogeneous flood-meadows along large rivers with strongly altered hydrological regimes have only rarely been the object of such investigation (McDonald 1993, McDonald et al. 1996, Kleinschmidt & Rosenthal 1995). The sparsity and divergence of findings severely hampers the assessment of the role, which alluvial diaspore transport plays in flood-plain ecosystems in general and in the restoration of flood-meadows in particular (Bakker et al. 1996, Poschlod 1996).

As direct measurement of the quality and quantity of diaspore deposition is fraught with methodological problems due to the irregular nature of flooding events (cf. Skoglund 1990), we tried to assess its significance by analysing the composition of soil seed banks. We made use of the fact, that the persistent part of the seed bank forms an archive reflecting cumulative effects of previous inputs of diaspores over many years (Baker 1989).

Due to the construction of dykes the holocene flood-plain of the river Rhine is now separated into three hydrological compartments, which differ with respect to the conditions of diaspore deposition during flooding events.

a) The <u>functional flood-plain</u> consisting of the land between the river and summer dykes is directly flooded by water loaded with fine sediment during high water of the Rhine. This relatively natural flooding regime theoretically allows a regular and free input of diaspores.

b) The <u>hybrid flood-plain</u> which is between summer and winter dykes is only reached by extreme high water, that spills over the summer dykes (from 4 meter above mean water level at the water-gauge at Worms upward) or in the event of breaking dykes. At high river levels that do not overtop the summer dykes ground depressions in this compartment may be submersed by ascending groundwater. An input of diaspores from river water may occur at a frequency of ca. three years according to the long-term mean for the period 1977-1996.

c) The <u>fossil flood-plain</u> on the landward side of the winter dykes is only submerged in low depressions by the ascent of clear, sediment-free groundwater accompanying high water levels of the Rhine. Deposition of diaspores by river water is precluded.

In this study we compare the seed banks of the three hydrological compartments of the holocene flood-plain and tested the hypothesis that there would be a larger allochthonous influence on the soil seed bank in the functional flood-plain and a smaller influence in the hybrid flood-plain. This hypothesis implies that seed banks in the functional flood-plain should have larger numbers of seeds and a significantly higher proportion of species absent from the existing above-ground vegetation, which are supposed to be induced during floods from the upstream part of the catchment (Hughes & Cass 1997). These effects are expected to be most marked at the lowest levels of the functional flood-plain, which are subject to most frequent flooding. We therefore first investigated gradients of flooding frequency within the three flood-plain compartments.

The questions addressed in this paper are:

1. Can significant quantitative and qualitative differences in the seed bank of flood-meadows be measured along a gradient of flooding frequency?

2. Are different flooding regimes in the hydrological compartments of the Rhine flood-plain reflected in the respective seed banks?

3. Do properties of the seed banks support the assumption that diaspore input via flooding contributes to the restoration of species-rich flood-meadows?

Methods

Study sites

The sampling plots are situated in the Hessian portion of the holocene flood-plain along the northern Upper Rhine between the tributaries Neckar to the south and Main to the north. The meadows of the studied type occupy fine-grained calcareous alluvial soils, which are irregularly flooded during high water levels of the Rhine. In conjunction with the warm and rather dry climate of the region (580 mm annual precipitation, 10.3 °C mean annual temperature at the meteorological station of Worms; Müller-Westermeier 1990) this results in high variability of soil water potential. While winter, spring and early summer often bring floods, summers may be markedly dry. These conditions are similar to those prevailing along the large rivers of the eastern European lowlands, which is reflected in the occurrence of specialist plants of subcontinental distribution such as *Allium angulosum, Cnidium dubium, Scutellaria hastifolia* and *Viola pumila*, which are close to the northwestern limits of their areas (Hultén & Fries 1986).

Flood-meadows are differentiated along an elevational gradient of decreasing flooding frequency (Dister 1980, Hölzel 1999). The highest levels of the flood-plain, which are submerged for less than eight days per year in the long-term mean, are occupied by alluvial *Arrhenatherion*-communities. *Allium angulosum-Alopecurus pratensis*-floodmeadows (*Cnidion*) occur at intermediate elevation subject to 8 - 26 days of flooding per year. The lowest level with 26 - 82 days of flooding per year is covered by *Rumex crispus-Poa palustris*-floodmeadows (*Magnocaricion*) typically dominated by reed and swamp species (Dister 1980). In principle this sequence is also valid in the hybrid and fossil compartments of the flood-plain, although their hydrology is complicated by the dynamics of pressure water and flooding frequency, which can not be estimated directly from the level of the river Rhine (Böger 1991).

Sampling

The sampling of above-ground vegetation and seed banks was carried out on permanent quadrats spread out over the whole study area. Sixteen plots were situated in the functional, 12 in the hybrid and eight in the fossil flood-plain. The majority of stands (12) in the functional compartment are *Allium angulosum-Alopecurus pratensis*-floodmeadows, while

lower-elevation reedswamps (*Magnocaricion*) and higher elevation meadows (*Arrhenatherion*) are represented by two plots each. Half of the 12 plots in the hybrid flood-plain are *Cnidion*-meadows, half are alluvial *Arrhenatherion*-meadows; four of the latter originated from arable fields 15 years ago. The plots in the fossil compartment are in low-lying depressions regularly submerged by groundwater and are classified as *Cnidion*-meadows.

The plots in the functional and hybrid compartment are situated within a distance of 500 to 2,500 m from the recent main channel of the river Rhine. Most of the plots in the functional compartment are found along ancient, silted up river channels, which are directly connected to the main channel during high water levels.

While meadows in the fossil flood-plain are mown late in the year (August/September) and irregularly, the stands of the hybrid and functional compartments are regularly mown once or twice with a first cut in June. With the exception of two plots in the hybrid flood-plain the plots receive no fertiliser.

Above-ground vegetation

Above-ground vascular species composition was sampled on 200 m² permanent plots containing two subplots of 25 m² nested within two subplots of 100 m². Species abundance was visually estimated on a modified Braun-Blanquet-scale with cover degree 2 subdivided into 2m, 2a and 2b (van der Maarel 1979). For data analysis we pooled the samples of the very dry year 1998 with those of 1999, when flooding was unusually intense, so that we were able to survey species composition in two years with substantially different ecological conditions. Re-sampling in the wet year 1999 added a considerable number of species to the list.

Seed bank

Sampling of seed banks was carried out in September 1997 using a soil corer of three cm in diameter. Within each 200 m² plot 20 cores of 10 cm depth were taken at random locations after thoroughly removing living and dead plant material from the soil surface. The soil cores were then divided into 0 - 5 cm and 5 - 10 cm sections. Thus the data represent the soil seed bank in the strict sense without the superficial diaspore litter deposited in the sampling year (Urbanska 1992). The soil samples represent 141 cm² of the soil surface and 1410 cm³ of the

soil volume in each plot and were thus well above the minimum requirements for studies of seeds in grassland given by Oomes & Ham (1983).

We analysed seed banks by the seedling emergence method (Roberts 1981). After removing vegetative plant material the soil samples were transferred in a two to three cm thick layer to 18 x 28 cm styrofoam basins and exposed in free air conditions. The basins were protected against diaspore input and heating by covering with flat, white gauze lids. Control basins filled with sterile soil were placed between the samples. In summer the basins were watered regularly. Germinated seedlings were identified and removed once every few weeks. Unidentifiable specimens were transferred to pots and grown until they could be named. When germination declined, the samples were dried for two weeks in a greenhouse, the soil material was crumbled, mixed, watered and again exposed in free air. The seed bank study was continued for 36 months. After 24 months only very few seedlings (less than 1%) and no additional species were recorded.

Data analysis

We classified the longevity of seeds according to the three categories proposed by Thompson et al. (1997) and by using the extensive database contained in their book:
 - transient: persistent for < 1yr.;
 - short-term persistent: 1-5 yrs.;
 - long-term persistent: > 5 yrs.

Regarding established vegetation and soil seed bank at two depths like Thompson et al. (1997), we classified species not mentioned in their database.
As allochthonous we define species in the seed bank, which were never recorded in the above-ground vegetation of the plots during two years of sampling.
For plots in the functional flood-plain we calculated the mean annual duration of flooding for the period 1977-1996 by using data from the gauge of the river Rhine at Worms and topography. Additionlly unweighted mean Ellenberg indicator values for moisture were calculated for above-ground vegetation plots on the basis of the list given by Ellenberg et al. (1991). In the functional flood-plain the mean Ellenberg values for moisture showed a high correlation with the directly measured values of mean flooding duration derived from the gauge (Spearman's ρ = 0.87, *P* = 0.000052). Thus we used the mean Ellenberg values to

describe the flooding situation in the hybrid and fossil compartment, where the mean annual duration of flooding cannot be derived directly from the Rhine water level.

We correlated environmental variables and properties of the seed bank using non-parametric Spearman's ρ. For normally distributed data with homogeneous variances/covariances (Sen & Puri test) we compared means using the parametric Tukey Honest-Significance test (HSD) for unequal sample sizes. For non-normal data, first a Kruskal-Wallis-Anova was performed; second pairwise differences between categories were checked by multiple non-parametric Mann-Whitney U-tests using Bonferroni-corrected significance levels.

All calculations were performed on log-transformed species data matrices (cluster analysis, CCA, ANOVA). Species with less than four occurrences and two samples from the functional flood-plain with extreme high values in diaspore densities were eliminated in these analyses. Except for the ordinations all calculations were carried out using STATISTICA 5.1 for Windows 97 (Statsoft Inc. 1998).

We classified seed banks using the Ward clustering algorithm (Jongman et al. 1995) with the squared Euclidean distance as a measure of dissimilarity. To identify possible factors controlling seed bank composition we used ordinations carried out by CANOCO 4 software (ter Braak & Smilauer 1998). We first performed a detrended correspondence analysis (DCA, with detrending by segments) of the above-ground vegetation species matrix resulting in four ordination axes representing 40.5 % of the total variance in species data. The first axis had a length of 2.235 standard deviation units, which indicates the appropriateness of a unimodal response model. The sample scores of the four DCA-axes were subsequently used as constraining ("environmental") variables in canonical correspondence analyses of the seed bank matrix. We also selected the following additional constraining variables: Mean Ellenberg indicator value for moisture (Ellenberg et al. 1991) and dummy variables for time of mowing (early, late) and previous use as arable field. The different diaspore input conditions of the three flood-plain compartments were described as an ordinal variable in a ranking order from fossil (0), through hybrid (1) to functional (2). In the ordination diagramm this ordinal variable was treated like a quantitative variable (Jongman et al. 1995). We did explicitly not use soil chemical variables such as organic matter content, C/N-ratio, CAL-soluble P and K in the topsoil, as these have been previously shown to have little direct influence on seed bank composition (Bekker et al. 1997). To test the choice of unimodal species responses we performed a detrended CCA (DCCA, detrending by segments), which gave a gradient length of 2.831 for axis 1. In order to isolate the effect of flood-plain

compartment on seed banks we performed a decomposition of variance by running a series of partial CCAs as proposed by ter Braak & Smilauer (1998, p. 258).

Results

Influence of flooding on seed banks

Table 1 illustrates the differences in seed bank species along a gradient of increasing flooding in a sample of seven plots in the functional flood-plain. The composition of seed bank changed considerably with increasing flooding duration which was also the case in above-ground vegetation. The total number of seeds increased, while total species richness was not affected.

Rumex crispus-Poa palustris-flood-meadows that would be subject to frequent and very long inundation periods had seed densities of more than 50,000 seeds / m², more than 80 % of which were contributed by a few therophyte species such as *Cerastium dubium* and *Veronica peregrina*. Likewise in *Allium angulosum-Alopecurus pratensis*-flood-meadows a small number of perennial species like *Veronica serpyllifolia*, *Potentilla reptans* and *Poa trivialis* contributed the majority of seeds.

The seed density at soil depth 5 - 10 cm was significantly positively correlated to the duration of flooding (Table 2), whereas at soil depth 0 - 5 cm a trend was visible, but not significant. The correlation between mean indicator value for moisture and seed density was also significant, which did not change when the 36 sampling plots from all flood-plain compartments were included. In contrast, there was no significant relationship between seed bank species richness or the number of allochthonous seeds and the duration of flooding or the moisture value.

Table 1. Composition of the seed banks in meadows of the functional flood-plain along an elevation gradient (3 m) of increasing duration of flooding. The first five samples are ordered along a transect (horizontal distance 100 m, vertical distance 2 m), the last two samples, representing rare flood-meadows with extremely long flooding duration, are added from an other site. Figures are no. of seeds/sample (140 cm² * 10 cm). Seed numbers: in bold = species present in above-ground vegetation and seed bank; underlined = species absent from the above-ground vegetation samples both in 1998 and 1999, but present within less than 100 m around the sampling plots; in italics = species absent from the above-ground vegetation samples both in 1998 and 1999 and not found within 100 m around the sampling plot.

	Arrhenatherion			*Cnidion*		*Magnocaricion*	
Days of flooding/year	1	6	10	20	25	82	82
Indicator value for moisture	4.5	4.7	4.9	5.4	5.8	7.5	7.5
Total no. of seeds	38	58	105	98	124	756	823
No. of seeds/m²	2260	4060	7350	6860	8680	52920	57610
No. of speciesl	15	13	19	13	13	17	12
Galium album	1						
Viola hirta	2						
Vicia angustifolia	2						
Linum catharticum	2						
Ajuga reptans	3						
Ranunculus polyanthemophyllos	4						
Arenaria serpyllifolia	6						
Trifolium pratense		1					
Carex praecox		3					
Achillea millefolium		1	1				
Allium scorodoprasum		14	32				
Plantago lanceolata	1	2	3				
Rumex acetosa/thyrsiflorus	3	4	5				
Poa angustifolia	7	10	4	1	5		
Veronica arvensis	3	4	2	9	3		
Taraxacum officinale agg.	1	1			3		
Cerastium holosteoides		4	1	3	2		
Veronica serpyllifolia		10	24	35	17		
Leucanthemum ircutianum		3		1			
Trifolium dubium				3			
Galium wirtgenii			6	6			
Carex spicata			1	2	1		
Glechoma hederacea			2		4		
Potentilla reptans			2	18	12		
Poa trivialis			4	14	18	6	
Ranunculus repens		1	4	2	30	52	28
Silene flos-cuculi			1	3	27	22	19
Cerastium dubium						401	454
Veronica peregrina						190	147
Trifolium hybridum						41	100
Cardamine parviflora						16	22
Plantago major intermedia						8	24
Veronica catenata						3	11
Galium palustre						2	11
Carex acuta						4	3
Rorippa sylvestris						3	
Rorippa amphibia						3	
Poa palustris						2	
Rumex crispus						1	
Lythrum salicaria						1	
Myosotis scorpioides agg.							1
Trifolium repens							1
Species not typical of meadows							
Sonchus asper	1						
Chenopodium polyspermum	1		2				
Cirsium arvense			1				
Urtica dioica			1	1			
Artemisia vulgaris			4				
Lapsana communis					1		
Ranunculus ficaria					1		
Galeopsis tetrahit						1	
Indet.	1		5				2

Table 2. Relationships between mean duration of flooding (mF) calculated from data of the Worms gauge, mean Ellenberg indicator value for moisture (mM) and seed bank variables (Spearman rank correlation); alloch. = only species absent from above-ground vegetation; otherwise total numbers of species and seeds are given including allochthonous species.
* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

		Variable pair	Spearman ρ	*P-level*
Functional flood-plain	n = 16	mF / n Seeds 0-5	**0.50**	0,0505.
		mF / n Seeds 5-10	**0.70**	**
		mF / n Spec. 0-10	-0.21	n. s.
		mF / n Spec. allocht.	-0.10	n. s.
		mF / n Seeds allocht.	0.01	n. s.
		mM / n Seeds 0-5	**0.56**	*
		mM / n Seeds 5-10	**0.80**	***
Total flood-plain	n = 36	mM / n Seeds 0-5	**0.54**	***
		mM / n Seeds 5-10	**0.64**	***
		mM / n Spec. 0-10	0.18	n. s.
		mM / n Spec. allocht.	-0.13	n. s.
		mM / n Seeds allocht.	-0.00	n. s.

Comparison of seed banks by hydrological flood-plain compartments

The seed banks in the fossil flood-plain contained significantly more seeds at depth 0 - 5 cm and had a higher species richness than the functional and hybrid compartments (Table 3). It also had significantly higher total numbers of seeds (0 - 10 cm) than the functional flood-plain. Other differences were not significant.

The cluster dendrogram (Figure 1) shows clear differences in seed bank classification for the three flood-plain compartments at a residual sum of squares of 50 %. Only two seed banks situated on particularly low ground in the hybrid flood-plain were classified along with the samples from the functional compartment, while, conversely one *Arrhenatherum*-meadow at higher level in the functional compartment was grouped with the hybrid flood-plain samples. The dendrogram indicates a higher degree of similarity between the seed banks of the functional and the hybrid compartments, while the samples from the fossil flood-plain are more removed from the remainder.

Table 3. Mean number and standard error of seed bank variables in the three flood-plain compartments; A = functional flood-plain n = 14 (*16), B = hybrid flood-plain n = 12, C = fossil flood-plain n = 8; different letters indicate significant differences ($P < 0.05$) according to Tukey HSD Post hoc-Test for unequal n; n Seeds = mean number of all seed, n Spec. = mean number of species; allocht. = species absent from above-ground vegetation.

	A	**B**	**C**	**P-level**
n Seeds/m² 0-5	4795 +-526[a]	5221 +-991[a]	9109 +-1274[b]	**
n Seeds/m² 5-10	1870 +-233	3372+-725	2957 +-454	n. s.
n Seeds/m² 0-10	6665 +-680[a]	8593 +-1526[ab]	12066 +-1520[b]	*
n Spec. 0-10*	16.6+-1.1[a]	16.3 +- 0.9[a]	22.4 +-1.7[b]	*
n Spec. allocht. 0-10*	3.3 +- 0.5	5.7 +-1.1	4.1 +-0.4	n. s.
n Seeds allocht./m² 0-10	1106 +-196	2744 +-1267	1477 +-630	n. s.
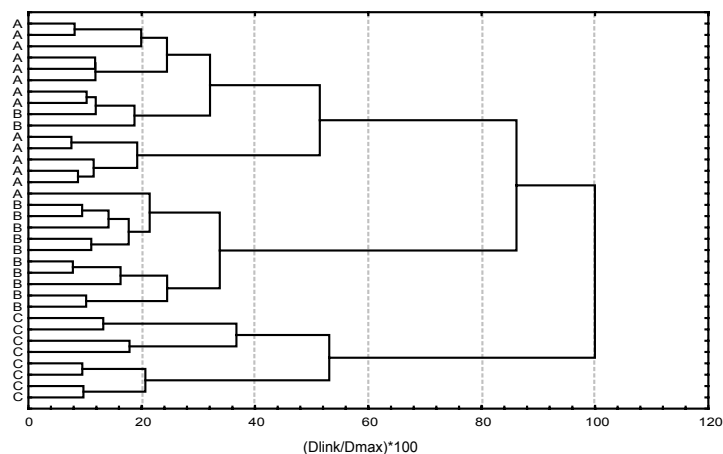
Fig. 1. Cluster dendrogram of 34 seed bank samples from flood-meadows calculated by the Ward algorithm with squared Euclidean distance; A = functional flood-plain, B = hybrid flood-plain, C = fossil flood-plain.

In the ordination diagram of the CCA with all constraining variables included (Figure 2) a gradient from functional and hybrid to fossil flood-plain samples is visible along the first axis. Two out of four above-ground vegetation DCA-axes loaded strongly on axis 1, as did the indicator value for moisture and late mowing. Axis 2 ordered stands mainly with regard to their position in the functional or in the hybrid flood-plain. One above-ground vegetation DCA-axis and previous use as arable field loaded relatively strongly on axis 2 as well. The constraining variables explained 46.3 % of the total variance in the composition of the seed banks (Table 4).
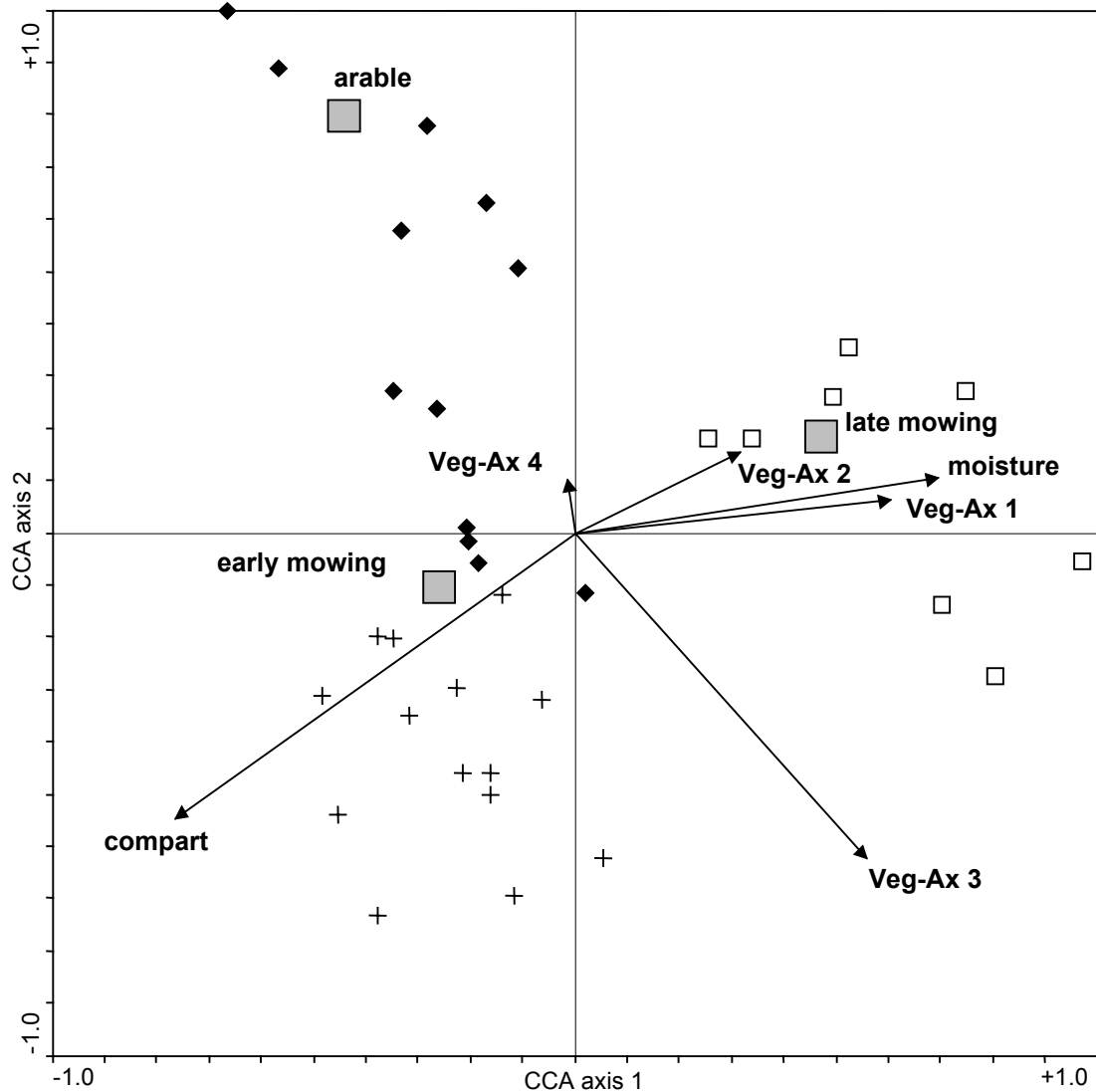
Fig. 2. CCA-diagram in biplot scaling showing the position of seed bank samples in relation to environmental variables. Vegetation axes as explaining variables are derived from a DCA of above-ground vegetation at the sample sites. Nominal and ordinal environmental variables are given as arrows; categorical variables are given as grey squares by their centroid. Origin of samples: crosses = functional flood-plain; diamonds = hybrid flood-plain, squares = fossil flood-plain.

Taken as the only constraining variable in CCA the flood-plain compartments explained 11.8 % of the total inertia (Table 4). However, if all remaining environmental variables were defined as covariables in partial CCA, explained variance dropped to as little as 3.2 % and was no longer significant. In contrast after adjustment for the compartment membership the other environmental variables together still explained 34.6 % of variance, with existing above-ground vegetation and management as the most important once.

Table 4. Results of various CCA analyses isolating the effect of flood-plain compartment and other environmental variables on the soil seed bank. Expl var. = Explanatory variables; Covar. = Covariables; Eigenv. = Sum of all canonical eigenvalues – measure for explanatory power of the explanatory variables (total inertia = 2.744); % = percentage of explained variance; F = F-ratio statistics for the test on the trace; P = corresponding probability value obtained by the Monte-Carlo-permutation test (199 permutations). Explanatory variables: C = flood-plain compartment; V = existing above-ground vegetation, M = recent and former management, F = mean Ellenberg value for moisture.

Expl. var.	Covar.	Eigenv.	%	F	P
M, F, C, V	-	1.27	46.3	2.70	0.005
C	-	0.32	11.8	4.26	0.005
C	M, F, V	0.09	3.2	1.48	0.055
M, F, V	C	0.95	34.6	2.30	0.005
V	C	0.68	24.7	2.73	0.005
M	C	0.36	13.2	2.63	0.005
F	C	0.22	8.1	3.12	0.005

Comparison of species composition

Of all 140 species found in the soil seed banks 17 exhibited a pattern that depended significantly on flood-plain position (Appendix 1). The differences were most marked between the functional and the hybrid on the one hand and the fossil flood-plain on the other. Most of the species, which were missing or extremely infrequent in the functional and hybrid compartments, were also absent from the above-ground vegetation of these compartments (*Arabis nemorensis*, *Pseudolysimachion longifolium*). Functional and hybrid flood-plain differed mostly by the occurrence of arable weeds such as *Chenopodium album*, *Capsella bursa-pastoris* and *Stellaria media* in their soil seed banks.

Among the allochthonous species *Veronica serpyllifolia* was characteristic of functional flood-plain seed banks, while *Juncus articulatus* in particular and, less markedly, *Centaurium pulchellum* were preferably found in the fossil compartment. All other statistically significant differences between compartments corresponded to differences in the above-ground vegetation.

Discussion

Influence of flooding duration on the seed banks

Although the studied flood-meadows were subject to marked changes in water availability, which included extended periods of drought, there was a clear increase in seed density in the soil with increasing duration of flooding. The fact that this relationship was particularly strong at a depth of 5 - 10 cm may be interpreted as a result of the lower susceptibility of this portion of the seed bank to seasonal variations in climate and flooding. The fraction of the lower soil depth thus best represents a mean state of the systems. Increases of seed density with soil moisture have been found in numerous studies of mesotrophic to eutrophic wet meadows (e. g. Chippendale & Milton 1934, Champness & Morris 1948, Thompson & Grime 1979), where the increase in seed density was mainly due to various species of *Juncus*. As shown by Bekker et al. (1998) the survival of seeds of *Juncus* and some other species typical of wet meadows seems to be favoured by anoxic conditions prevailing under constant high ground-water levels.

In flood-meadows with a variable moisture regime as in this study, the genus *Juncus* is hardly represented (cf. McDonald et al. 1996). The increase in seed density was mainly contributed by turf gaps colonising indicators of disturbance such as *Ranunculus repens, Potentilla reptans, Poa trivialis* and *Veronica serpyllifolia*, which increased with flooding frequency also in above-ground stands . At the lowest, frequently flooded levels of the flood-plain the seed bank of flood-meadows was dominated by high densities of seeds of ruderal therophytes such as *Cerastium dubium, Cardamine parviflora* and *Veronica peregrina*, which reflected a higher frequency of disturbance and unstable ecological conditions (Grime et al. 1988).

Higher seed densities associated with frequent flooding in flood-meadows seem not be a result of conditions that are more favourable to seed persistence, such as frequent water saturation and poorly areated soil (Baskin & Baskin 1989, Bekker et al. 1998), but of a change in predominant plant strategy types. This is reflected by the more frequent occurrence of species capable of forming large and long-lived seed banks, which must be considered an adaptation to high interannual variation of ecological conditions (Leck 1989, Poschlod 1996). It is remarkable, that as much as 50 % of the specialized large river macrophyte species (*Viola pumila, Arabis nemorensis, Pseudolysimachion longifolium, Cerastium dubium, Cardamine parviflora* among others) form persistent seed banks. A comparable situation has been

reported by Finlayson et al. (1990) from northern Australian flood-plains, by van der Valk (1981) for temporary lakes in North American prairies and by Bekker et al. (1999) for dune slacks on the Dutch North Sea coast.

The seed numbers that we measured in *Cnidion*-flood-meadows of intermediate elevation and flooding frequency are within the range reported by McDonald et al. (1996) from ecologically similar grasslands on the river Thames in southern England. However, they are markedly lower than those under Central European wet meadows in minerotrophic fens and mineral swamps (Fischer 1987, Schopp-Guth 1997), which is mainly due to the low abundance of *Juncus* seeds.

Alluvial influences on the seed bank

The differences in seed bank composition as reflected in cluster analysis (Figure 1) can, according to CCA results (Figure 2), be largely explained by analoguous gradients in the above-ground vegetation and present use of the study meadows. The study provided no indication for the expected strong allochthonous influences on seed banks in the functional flood-plain. The higher seed density in the fossil flood-plain may be due to the more extensive management with late mowing that this compartment receives, which is likely to enhance the deposition of seeds.

The seed bank species that were not present in the vegetation stands were almost exclusively present in the local species pool of the immediate surroundings of our plots and would probably establish successfully after long periods of inundation. Thus, we observed a sudden development of *Veronica serpyllifolia* and *Chenopodium polyspermum* after major floods in 1999, both species, which had previously been found in the seed bank only. This illustrates, that in flood-plains a single vegetation survey is insufficient for identifying the allochthonous status of species, that may establish large populations from the seed bank only after major disturbances of the turf by flooding instead of being deposited by floodwater. The conjecture, that allochthonous seeds are imported from nearby sources, is supported by the strong occurrence of arable weeds in the hybrid flood-plain. These weeds are not restricted to former fields but appear also in plots, which have never been subject to agricultural use, but are situated in the vicinity of present-day or former arable fields. This finding may be explained by a residual enrichment of seeds derived from adjacent fields in low elevation depressions during the retreat of high waters. In the functional flood-plain, where arable fields are non-existent we never found such high densities of weed seeds.

Other authors have obtained similar results indicating the significance of flooding for short-distance dispersal of seeds (Schneider & Sharitz 1988, Skoglund 1990, Schwabe 1991, Kleinschmidt & Rosenthal 1995). Yet in all these studies there were also seeds attributable to long-distance transport by floods. In contrast to most other studies Hughes & Cass (1997) found very high proportions of allochthonous seeds in river margin forest in Vermont/USA: of 73 species occurring in the soil seed bank and fresh alluvial sediment only 25 were also present in above-ground vegetation. However, these authors did not discuss the possibility of nearby occurrence of some of these species.

In our investigations seeds strongly suggesting remote transport were rare exceptions. One reason for this surprising result could be that most of the above mentioned studies were carried out in close proximity to riverbeds with more natural morphology and hydrology. Such flood-plains may have substantially more potential seed sources to be dispersed with flooding than is the case along the largely confined Upper Rhine, which has lost most of its natural flood-plains.

A second reason could be the considerable distance of our study plots from the river. Skoglund (1990) and Schwabe (1991), for example, found seeds indicative of long-range transport mainly in drift or sediment deposited close to the riverbank. The flood-meadows in our study, on the other hand, are hardly reached by substantial loads of mineral and organic sediment even by exceptional floods because of their remoteness from the river and the resulting low speed of water movement (Dister 1980). It is in these areas with low sediment loads and relatively low nutrient availability where most present-day and potential sites for species-rich flood-meadows are situated.

Conclusions for restoration management

Our comparative study of seed banks in meadows along the Rhine yielded no indication of significant remote input of seeds in the functional flood-plain. Weedy and ruderal species widespread in the Rhine catchment, such as *Chenopodium album*, *Capsella bursa-pastoris* or *Stellaria media*, were surprisingly entirely absent from seed banks of the functional flood-plain.

Considering the absence of these common species capable of forming persistent seed banks, the probability of much rarer species to arrive by remote transport in floods must be considered as nearly non-existing. If we further consider that the majority of upstream remnants of species-rich flood-meadows containing the target species of conservation is

restricted to dyked fossil compartments of the plain (Thomas 1990), long-distance input is largely impossible under the given conditions. However, along with the results of Kleinschmidt & Rosenthal (1995), our study also stresses the significance of inundation for short-distance dispersal of seeds. This possibility requires viable populations of the target species in the vicinity of restoration areas.

In summary we conclude that limited dispersal, which has been identified as one of the main obstacles to restoring rare species in grasslands (Bakker et al. 1996), is unlikely to be overcome by the restoration of more natural flooding regimes under the present-day conditions prevailing along most Central European rivers. As in many other cases, the successful restoration of flood-meadow target species crucially depends on supplementary measures like the transfer of seeds with plant litter from source populations (cf. Patzelt 1998).

Appendix 1: Frequency (percentage of samples per compartment in which the species occurred) in above-ground vegetation (V) and in the seed bank (D). Absolute no. of seeds at 0 - 5 (a) and 5 - 10 cm (b) soil depth. Flood-plain compartments: A = functional flood-plain, B = hybrid flood-plain, C = fossil flood-plain. Type of seed bank (SB-type) according to Thompson et. al. (1997) and own results: LP = long-term persistent, SP = short-term persistent, T = transient. Pairwise Mann-Whitney U-Tests using Bonferroni corrected significance levels; species with less than 4 occurrences not tested, *P*-levels see Table 2.

		A n = 16			B n = 12			C n = 8			M.-W U-test		
SB-type	Species	V	D	*a b*	V	D	*a b*	V	D	*a b*	AB	AC	BC
LP	*Potentilla reptans*	81	75	*177 / 10*	92	67	*27 / 2*	75	75	*28 / 1*	-	-	-
LP	*Cerastium holosteoides*	56	56	*22 / 6*	67	67	*27 / 7*	75	63	*17 / 6*	-	-	-
LP	*Ranunculus repens*	69	94	*135 / 63*	25	8	*- / 1*	75	75	*79 / 14*	***	-	**
LP	*Taraxacum officinale* agg.	88	75	*18 / 11*	92	58	*25 / 13*	50	13	*4 / -*	-	-	-
LP	*Poa trivialis*	69	50	*114 / 26*	75	75	*132 / 41*	25	38	*18 / 10*	-	-	-
LP	*Chenopodium polyspermum*	-	44	*8 / 0*	-	67	*228 / 24*	-	25	*1 / 2*	-	-	-
LP	*Veronica serpyllifolia*	-	81	*87 / 65*	25	17	*5 / 1*	-	25	*5 / -*	**	*	-
LP	*Glechoma hederacea*	38	50	*8 / 9*	58	42	*23 / 9*	25	50	*6 / 7*	-	-	-
LP	*Achillea millefolium*	63	31	*8 / -*	67	67	*47 / 33*	100	50	*6 / 1*	-	-	-
LP	*Silene flos-cuculi*	44	50	*58 / 20*	25	-	*- / -*	100	88	*45 / 16*	*	-	***
LP	*Leucanthemum ircutianum*	31	31	*7 / 1*	67	25	*8 / -*	88	88	*24 / 7*	-	**	*
LP	*Rumex acetosa/thyrsiflorus*	88	50	*27 / -*	50	42	*6 / 1*	38	13	*1 / -*	-	-	-
SP/LP?	*Veronica arvensis*	50	44	*26 / -*	75	50	*22 / 1*	25	13	*2 / -*	-	-	-
LP	*Arenaria serpyllifolia*	-	31	*15 / 2*	-	50	*7 / 3*	-	25	*6 / -*	-	-	-
LP	*Poa angustifolia*	88	38	*30 / 5*	100	25	*6 / 3*	100	50	*- / 6*	-	-	-
LP	*Sonchus asper*	6	13	*2 / 1*	-	58	*14 / 4*	-	38	*2 / 1*	-	-	-
LP	*Lythrum salicaria*	-	6	*1 / -*	-	33	*16 / 4*	-	88	*16 / 12*	-	***	-
LP	*Cirsium arvense*	38	13	*2 / 1*	100	42	*8 / 3*	100	38	*5 / 2*	-	-	-
LP	*Chenopodium album* agg.	-	-	*- / -*	-	58	*12 / 16*	-	38	*2 / 1*	**	-	-
LP	*Capsella bursa-pastoris*	-	-	*- / -*	25	67	*38 / 24*	-	25	*4 / -*	***	-	-
LP	*Rumex crispus*	50	31	*4 / 2*	25	17	*2 / -*	38	38	*3 / -*	-	-	-
LP	*Plantago lanceolata*	63	44	*17 / 1*	67	17	*2 / -*	25	-	*- / -*	-	-	-
SP/LP?	*Galium wirtgenii*	88	44	*26 / 7*	75	-	*- / -*	88	25	*3 / 1*	-	-	-
LP	*Daucus carota*	6	6	*1 / -*	83	58	*16 / 5*	25	13	*3 / -*	**	-	-
SP/LP	*Carex spicata*	56	38	*6 / 2*	42	8	*- / 1*	38	25	*8 / 4*	-	-	-
LP	*Plantago major intermedia*	13	19	*26 / 7*	8	33	*9 / 1*	-	13	*4 / -*	-	-	-
LP	*Centaurea jacea*	56	25	*5 / 2*	50	17	*2 / 3*	50	25	*11 / 4*	-	-	-
LP	*Vicia angustifolia*	44	13	*4 / -*	75	33	*10 / 1*	25	25	*2 / -*	-	-	-
LP	*Juncus articulatus*	-	6	*- / 1*	-	8	*1 / 1*	-	100	*41 / 45*	-	***	***
LP	*Viola pumila*	38	25	*10 / 1*	33	8	*2 / 1*	63	25	*9 / 1*	-	-	-
LP	*Arabis nemorensis*	-	-	*- / -*	-	8	*8 / -*	75	75	*235 / 40*	-	***	**
LP	*Urtica dioica*	13	25	*3 / 6*	-	8	*4 / 1*	25	13	*1 / -*	-	-	-
LP	*Stellaria media*	-	-	*- / -*	8	50	*8 / 3*	-	-	*- / -*	**	-	-
SP/LP?	*Pseudolysimachion longifolium*	25	13	*12 / -*	-	-	*- / -*	63	50	*145 / 36*	-	*	-
SP	*Allium angulosum*	6	19	*5 / -*	-	8	*3 / -*	13	13	*5 / -*	-	-	-
LP	*Trifolium repens*	19	13	*1 / 1*	33	-	*- / -*	-	38	*8 / -*	-	-	-
LP	*Medicago lupulina*	31	13	*1 / 1*	25	17	*1 / 1*	13	13	*1 / -*	-	-	-
LP	*Centaurium pulchellum*	-	6	*1 / 2*	-	-	*- / -*	-	50	*23 / 30*	-	*	*
LP	*Myosotis arvensis*	-	-	*- / -*	33	8	*- / 1*	63	50	*22 / 5*	-	**	-
LP	*Trifolium pratense*	50	25	*4 / 1*	67	-	*- / -*	38	-	*- / -*	-	-	-
SP	*Allium scorodoprasum*	75	25	*58 / -*	8	-	*- / -*	38	-	*- / -*	-	-	-
SP	*Valerianella locusta*	13	13	*12 / -*	50	17	*3 / -*	25	-	*- / -*	-	-	-
SP/LP?	*Galium mollugo* agg.	25	6	*1 / -*	75	17	*2 / -*	100	13	*1 / -*	-	-	-
SP/LP?	*Epilobium tetragonum*	-	13	*1 / 1*	42	17	*4 / -*	25	-	*- / -*	-	-	-
LP	*Viola hirta*	31	13	*2 / 1*	8	-	*- / -*	38	25	*2 / 2*	-	-	-
LP	*Poa palustris*	6	6	*2 / -*	17	8	*1 / 1*	38	25	*4 / 4*	-	-	-
LP	*Phalaris arundinacea*	19	-	*- / -*	25	8	*1 / -*	50	38	*2 / 2*	-	*	-
LP	*Agrostis stolonifera* agg.	-	-	*- / -*	-	-	*- / -*	13	50	*26 / 14*	-	*	**
LP	*Ajuga reptans*	-	6	*2 / 1*	8	-	*- / -*	38	38	*102 / 9*	-	-	-
SP/LP?	*Carex disticha*	38	6	*3 / -*	-	-	*- / -*	88	38	*10 / -*	-	-	-
LP	*Veronica peregrina*	13	19	*278 / 60*	-	-	*- / -*	-	-	*- / -*	-	-	-
SP/LP?	*Carex acuta*	13	19	*10 / -*	-	-	*- / -*	-	-	*- / -*	-	-	-
LP	*Ranunculus ficaria*	13	19	*4 / 2*	-	-	*- / -*	-	-	*- / -*	-	-	-
SP/LP?	*Barbarea vulgaris*	19	19	*9 / -*	-	-	*- / -*	-	-	*- / -*	-	-	-
LP	*Rorippa sylvestris*	-	13	*5 / 9*	-	8	*1 / 2*	-	-	*- / -*	-	-	-
LP	*Veronica catenata*	-	13	*10 / 4*	-	8	*5 / 1*	-	-	*- / -*	-	-	-
LP	*Hypericum perforatum*	-	6	*- / 1*	17	17	*3 / -*	38	-	*- / -*	-	-	-
SP/LP?	*Ranunculus polyanthemophyllos*	25	6	*3 / 1*	50	17	*2 / 2*	63	-	*- / -*	-	-	-
SP/LP?	*Carex praecox*	-	6	*3 / -*	42	17	*2 / 1*	25	-	*- / -*	-	-	-
LP	*Anagallis arvensis*	-	6	*- / 1*	-	17	*40 / 4*	-	-	*- / -*	-	-	-
LP	*Chenopodium hybridum*	-	-	*- / -*	-	25	*5 / 41*	-	-	*- / -*	-	-	-
LP	*Persicaria maculosa*	-	-	*- / -*	-	25	*4 / 10*	-	-	*- / -*	-	-	-
LP	*Solanum nigrum*	-	-	*- / -*	-	25	*17 / 18*	-	-	*- / -*	-	-	-
SP/LP?	*Carex hirta*	31	13	*50 / 3*	-	-	*- / -*	38	13	*1 / -*	-	-	-
LP	*Lotus corniculatus*	63	6	*1 / -*	50	-	*- / -*	38	25	*3 / 1*	-	-	-
SP/LP?	*Thalictrum flavum*	31	-	*- / -*	25	8	*1 / -*	38	25	*18 / -*	-	-	-
LP	*Carex acutiformis*	-	-	*- / -*	-	8	*- / 1*	63	25	*2 / 1*	-	-	-
LP	*Mentha arvensis*	-	-	*- / -*	-	-	*- / -*	-	38	*1 / 3*	-	*	-
SP/LP?	*Potentilla anserina*	19	13	*7 / -*	-	-	*- / -*	63	-	*- / -*	-	-	-

Appendix 1 continued

LP	*Prunella vulgaris*	31	13	2 / -	-	-	- / -	38	-	- / -	-	-	-
LP	*Bellis perennis*	31	13	7 / 3	-	-	- / -	50	-	- / -	-	-	-
SP/LP?	*Carex tomentosa*	19	13	3 / 2	-	-	- / -	50	-	- / -	-	-	-
SP/LP?	*Leontodon autumnalis*	13	13	14 / 3	-	-	- / -	-	-	- / -	-	-	-
LP	*Cerastium dubium*	13	13	690 / 165	-	-	- / -	-	-	- / -	-	-	-
LP	*Cardamine parviflora*	13	13	35 / 3	-	-	- / -	-	-	- / -	-	-	-
LP	*Galium palustre*	13	13	13 / -	-	-	- / -	-	-	- / -	-	-	-
LP	*Trifolium hybridum*	13	13	129 / 12	8	-	- / -	-	-	- / -	-	-	-
LP	*Galeopsis tetrahit*	-	13	- / 11	8	-	- / -	-	-	- / -	-	-	-
SP/LP?	*Leontodon hispidus*	-	6	2 / -	-	8	3 / -	-	-	- / -	-	-	-
LP	*Euphorbia esula*	31	6	3 / 11	58	8	1 / -	50	-	- / -	-	-	-
LP	*Carex panicea*	-	6	- / 1	-	-	- / -	25	13	- / 2	-	-	-
SP	*Lathyrus pratensis*	81	6	1 / -	75	-	- / -	100	13	1 / -	-	-	-
SP/LP?	*Symphytum officinalis*	44	6	1 / -	50	-	- / -	75	13	1 / 1	-	-	-
LP	*Hypochoeris radicata*	-	-	- / -	-	8	1 / -	-	13	2 / -	-	-	-
SP/LP?	*Ranunculus acris*	50	-	- / -	17	17	2 / 1	38	-	- / -	-	-	-
SP/LP?	*Trifolium campestre*	31	-	- / -	58	17	7 / 2	13	-	- / -	-	-	-
LP	*Erucastrum gallicum*	-	-	- / -	-	17	2 / 6	-	-	- / -	-	-	-
LP	*Chaenorhinum minus*	-	-	- / -	-	17	2 / 1	-	-	- / -	-	-	-
LP	*Lamium purpureum*	-	-	- / -	17	17	23 / 11	-	-	- / -	-	-	-
SP/LP?	*Stachys palustris*	-	-	- / -	-	-	- / -	25	25	4 / -	-	-	-
SP/LP?	*Lysimachia vulgaris*	31	-	- / -	17	-	- / -	100	25	4 / -	-	-	-
LP	*Linum catharticum*	6	6	2 / -	8	-	- / -	25	13	3 / -	-	-	-
LP	*Cardamine pratensis*	6	-	- / -	-	-	- / -	13	25	2 / -	-	-	-
SP/LP?	*Geranium dissectum*	-	-	- / -	-	-	- / -	13	25	3 / 1	-	-	-
T/SP?	*Cirsium tuberosum*	-	-	- / -	-	-	- / -	25	25	3 / -	-	-	-
SP/LP?	*Inula salicina*	19	-	- / -	8	-	- / -	75	25	2 / 1	-	-	-
SP/LP?	*Deschampsia cespitosa*	31	6	2 / 1	-	-	- / -	63	-	- / -	-	-	-
LP	*Rorippa amphibia*	6	6	- / 3	-	-	- / -	-	-	- / -	-	-	-
SP/LP?	*Myosotis scorpioides*	13	6	1 / -	-	-	- / -	-	-	- / -	-	-	-
LP	*Artemisia vulgaris*	-	6	4 / -	-	-	- / -	-	-	- / -	-	-	-
LP	*Trifolium dubium*	31	6	3 / -	33	-	- / -	13	-	- / -	-	-	-
LP	*Lapsana communis*	-	6	- / 1	8	-	- / -	-	-	- / -	-	-	-
LP	*Erigeron annuus*	-	6	1 / -	33	-	- / -	-	-	- / -	-	-	-
LP	*Chenopodium rubrum*	-	6	1 / -	-	-	- / -	-	-	- / -	-	-	-
T/SP?	*Valeriana pratensis*	69	6	1 / -	8	-	- / -	75	-	- / -	-	-	-
LP	*Poa annua*	-	-	- / -	-	8	- / 1	-	-	- / -	-	-	-
SP/LP?	*Linaria vulgaris*	-	-	- / -	8	8	2 / -	38	-	- / -	-	-	-
LP	*Scrophularia nodosa*	-	-	- / -	-	8	- / 1	-	-	- / -	-	-	-
LP	*Polygonum aviculare*	-	-	- / -	-	8	- / 3	-	-	- / -	-	-	-
LP	*Mercurialis annua*	-	-	- / -	8	8	- / 2	-	-	- / -	-	-	-
LP	*Veronica hederifolia*	-	-	- / -	-	8	1 / -	-	-	- / -	-	-	-
LP	*Reseda lutea*	-	-	- / -	-	8	1 / -	-	-	- / -	-	-	-
LP	*Cyperus fuscus*	-	-	- / -	-	8	5 / 3	-	-	- / -	-	-	-
LP	*Papaver rhoeas*	-	-	- / -	8	8	9 / 4	-	-	- / -	-	-	-
SP/LP?	*Conyza canadensis*	6	-	- / -	17	8	2 / -	-	-	- / -	-	-	-
LP	*Fallopia convolvulus*	-	-	- / -	-	8	3 / -	13	-	- / -	-	-	-
LP	*Kickxia elatine*	-	-	- / -	8	8	3 / 7	-	-	- / -	-	-	-
LP	*Veronica persica*	-	-	- / -	-	8	2 / -	-	-	- / -	-	-	-
LP	*Thlaspi arvense*	-	-	- / -	-	8	2 / -	-	-	- / -	-	-	-
LP	*Matricaria recutita*	-	-	- / -	-	8	- / 1	-	-	- / -	-	-	-
LP	*Persicaria lapathifolia*	-	-	- / -	-	8	1 / -	-	-	- / -	-	-	-
LP	*Alliaria petiolata*	-	-	- / -	17	8	1 / 1	-	-	- / -	-	-	-
LP	*Galium aparine*	13	-	- / -	42	8	1 / 1	25	-	- / -	-	-	-
LP	*Sagina procumbens*	-	-	- / -	-	-	- / -	-	13	- / 2	-	-	-
T/SP?	*Sanguisorba officinalis*	44	-	- / -	50	-	- / -	100	13	- / 1	-	-	-
SP	*Iris spuria*	-	-	- / -	-	-	- / -	25	13	1 / -	-	-	-
SP	*Veronica teucrium*	-	-	- / -	-	-	- / -	38	13	1 / -	-	-	-
SP/LP?	*Lepidium campestre*	-	-	- / -	-	-	- / -	25	13	2 / -	-	-	-
LP	*Erophila verna*	-	-	- / -	-	-	- / -	-	13	2 / -	-	-	-
LP	*Mentha aquatica*	-	-	- / -	-	-	- / -	-	13	5 / 2	-	-	-
SP/LP?	*Lotus tenuis*	-	-	- / -	-	-	- / -	13	13	1 / -	-	-	-
LP	*Holcus lanatus*	6	-	- / -	-	-	- / -	38	13	1 / -	-	-	-
LP	*Amaranthus hybridus* agg.	-	-	- / -	-	-	- / -	-	13	- / 1	-	-	-
SP	*Trifolium medium*	-	-	- / -	-	-	- / -	25	13	1 / -	-	-	-
LP	*Solidago canadensis*	-	-	- / -	8	-	- / -	-	13	- / 1	-	-	-
SP	*Iris pseudacorus*	13	-	- / -	17	-	- / -	50	13	1 / -	-	-	-
LP	*Gnaphalium uliginosum*	-	-	- / -	-	-	- / -	-	13	1 / -	-	-	-
SP	*Eleocharis palustris* agg.	-	-	- / -	-	-	- / -	13	13	1 / -	-	-	-
SP	*Festuca arundinacea*	38	6	1 / -	67	-	- / -	88	-	- / -	-	-	-
LP	*Amaranthus retroflexus*	-	6	1 / -	-	-	- / -	-	-	- / -	-	-	-

Kapitel 4

Inter-annual variation in the soil seed bank of flood-meadows over two years with different flooding patterns

Norbert Hölzel & Annette Otte

Abstract

Persistent soil seed banks are presumed to play a significant role in bridging and exploiting the effects of major flood disturbances in riparian systems. However, presently there is little empirical data on the correlation between flooding and seed bank dynamics. The objective of this study was to assess the impact of inter-annual flooding variation on soil seed bank dynamics in flood-meadows. We analysed seed bank composition at 46 plots along the northern Upper Rhine River, Germany, after two periods with contrasting flooding conditions (1996-1997: low and rare flooding; 1998-1999 high and very frequent flooding).

Between both sampling occasions the total number of seedlings emerging from the seed bank decreased by 50 % and average species-richness per sample by 30 %, irrespective of the sampling depth. Similar decline occurred in mesophytes and wetland species as well as over different functional groups, with the exception of legumes. Considerable compositional changes in the seed bank were also indicated by shifts in DCA ordination and by the comparison of similarity matrices from both years with the Mantel test. The Mantel test also confirmed that compositional changes were more pronounced in the seed bank than in above-ground vegetation. There was poor correlation between the decline in total seed densities and species in the soil seed bank and environmental variables such as flooding duration and ecological groupings such as flood-plain compartment and seed bank community types. Further distinct patterns of decline and persistence were evident only at the species level. While 21 species displayed a significant decline, only two species increased. Annual arable

weeds and perennial ruderals with high temperature or nutrient requirements to break dark dormancy were amongst the most significantly declining species. In contrast, there was no decline in typical winter annuals and certain perennials that preferably germinate in autumn and fall into dormancy at the beginning of the warm period. Generally, differences in germination requirements and dormancy cycles of species gave the best explanation for the patterns of decline and persistence after intense flooding.

Given these findings, the heavy depletion of the persistent soil seed bank we observed is most likely attributed to a post-flood germination flush due to very favourable recruitment conditions prevailing during the draw-down period after early summer flooding in 1999.

The results of our study suggest that persistent soil seed banks are of outstanding importance to bridge and exploit the highly variable hydrological conditions that are typical of flood-meadows. Thus, they play a significant role in maintaining the floristic diversity of this habitat type over time and space.

Introduction

Flooding dynamics are of major importance in structuring vegetation and plant diversity along riparian systems. While such flood induced dynamics in above-ground vegetation have been studied previously (e.g. Balátová-Tuláčková 1979, Vervuren et al. 2003), little is known about the effects of floods on the size and composition of soil seed banks and their potential role in regeneration after such major disturbances. As emphasized in a recent review by Goodson et al. (2001), there are generally enormous research gaps relating to interactions between fluvial processes and riparian seed banks. Regeneration from the persistent soil seed bank was found to be an important and even dominant process in succession after draw down and rewetting in temporary wetlands (e.g. van der Valk & Davis 1978, van der Valk 1981, Casanova & Brock 2000) as well as in disturbance driven tidal freshwater and salt marshes (e.g. Parker & Leck 1985, Baldwin et al. 1996, Bekker et al. 1999, Jutila 2001). Thus, we presumed that soil seed banks might play a comparable role in riparian grasslands, which are also subject to irregular und unpredictable flood disturbances.

In a previous study (Hölzel & Otte 2001) we analysed the impact of fluvial input on the composition of soil seed banks in flood-meadows by the comparison of different hydrological flood-plain compartments that differ with respect to their connectivity to the river system. The

focus of the present paper will be on the inter-annual variation in soil seed banks of flood-meadows over two years with contrasting flooding conditions prior to sampling.

Effects of inundation on soil seed banks are usually examined in factorial experiments that simulate flooding by the submergence of soil samples under artificial laboratory conditions. Most of these studies revealed a clear inhibition in germination of many semi-terrestrial and terrestrial species by constant inundation, while only the emergence of certain aquatic species was significantly facilitated (van der Valk & Davis 1978, Gerritsen & Greening 1989, Finlayson et al. 1990, Seabloom et al. 1998, Abernethy & Willby 1999, Boedeltje et al. 2002, Nicol et al. 2003). In contrast, Jutila (2001) found a strong and general increase in germination from the soil seed banks in Baltic coastal grasslands when 7 weeks of inundation were followed by a period of draw-down. Comparable phenomena were observed by Schneider & Sharitz (1986) in draw-down parts of a riverine swamp forest after spring floods. Such conditions are quite similar to those prevailing in flood-meadows, whose soil seed bank proved to be rich in species and individuals (Hölzel & Otte 2001). Thus, we suspected that temporary flooding may act as a germination cue (Leck 1989) that enhances recruitment from the persistent soil seed bank. To assess the effects of inter-annual variations in flooding we compared the composition of above-ground vegetation and soil seed banks at field study plots in two years with extremely contrasting flooding conditions. Field studies of year-to-year variation in wetland seed banks are still extremely scarce. The few analyses that were conducted to date, e.g. by Bonis et al. (1995); Leck & Simpson (1995), revealed a predominant impact of contrasting hydrological conditions between years on short term variation in the soil seed banks. The same was expected for the flood-meadows in the present study, although due to our observational approach other agents besides flooding cannot be completely ruled out.

The main questions addressed in this article are:

- how did soil seed banks change in size and composition between the two periods with contrasting flooding conditions,

- did the relationship between soil seed bank and established above-ground vegetation change,

- are there differences in the soil seed bank response among individual species or functional species groups,

- are such different responses related to ecological gradients such as flooding height and diaspore input conditions?

Material and methods

Study sites

The studied flood-meadows are situated in the Holocene flood-plain of the northern Upper Rhine, Germany, between the tributaries Neckar to the south and Main to the north (core area: 49°51′ N / 8°23′ E, 83-91 m a.s.l.). The irregularity of floods in conjunction with the rather dry and warm climate in the region results in a high seasonal and inter-annual variability in soil water potential. Three hydrological compartments can be distinguished within the Holocene flood-plain: The <u>functional flood-plain</u> is still subject to direct and unhampered flooding during high water levels of the River Rhine, whereas the <u>hybrid flood-plain</u> is directly inundated only during extremely high floods that spill over low summer dykes. The <u>fossil flood-plain</u>, protected by high winter dykes, is only subject to indirect flooding by ascending groundwater (for further details see Hölzel & Otte 2001).

In the functional and hybrid compartments, flooding heights reach a maximum of 3 to 4 meters over terrain and may lead to an almost complete die-back of above-ground biomass in the meadows when floods occur in summer during the main vegetation period (e.g. Vervuren et al. 2003). In contrast, flooding by ascending groundwater in the fossil compartment reaches a maximum height of barely more than 50 cm, which is tolerated by many flood-resistant plants and leads only partly to a die-back in above-ground vegetation. Out of the 46 analysed flood-meadows 18 are situated in the functional, 12 in the hybrid and 16 in the fossil flood-plain compartment. Grassland types in the flood-plain are typically ordered along an elevational gradient that reflects zones of different average flooding frequency (Dister 1980, Burkart 1998, Hölzel 1999, Leyer 2002). The highest parts of the flood-plain that are on average flooded for less than 8 days per year are occupied by mesophytic alluvial meadows (alliance *Arrhenatherion*). At intermediate elevations that are submerged on average for 8 to 26 days per year these are replaced by alluvial wet meadows (alliance *Cnidion*). Grasslands at the lowest elevations, with an average flooding of 26 to 81 days, comprise damp tall sedge meadows (*Magnocaricion*). The majority of sampled stands are situated at the intermediate flooding level of *Cnidion*-communities (34), while *Magnocaricion* and *Arrhenatherion* types are only represented with six stands, respectively. Within these hydrological main types two further important categories may be distinguished that differ considerably from the others in terms of use history and trophic conditions: 8 plots originate from former arable land that was restored into grassland some 15 years ago, whereas 6 plots in the fossil flood-plain comprise

strictly oligotrophic *Molinion* communities that are confined to particularly nutrient poor sites where the loamy topsoil was removed in the past. The plots in the functional and hybrid compartments are mown once a year in June or July, while in the fossil flood-plain compartment mowing usually takes place in September. During the relevant period of observation there were no significant changes in the type and intensity of management in the studied meadows.

Flooding conditions before seed bank sampling

In the two hydrological years before the first sampling in September 1997 only three minor flooding events with water levels above four meters at the nearby gauge of Worms (average mean water level 2.2 m) occurred (Fig. 1), none of them lasting for more than three or four days. Compared with the long-term mean this was an unusually dry period (Table 1).
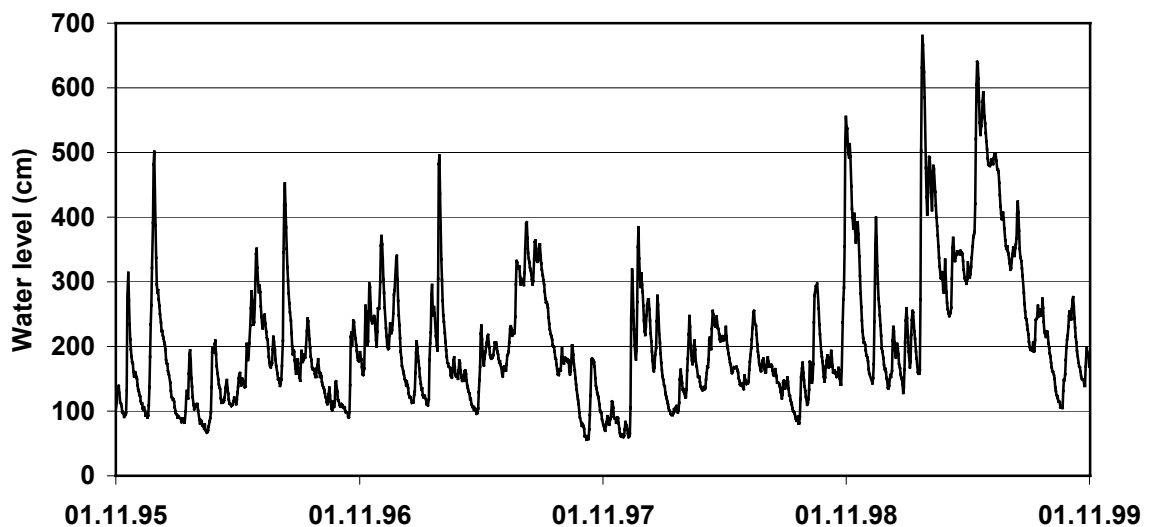
Fig. 1. Water levels of the River Rhine at the gauge station of Worms in the two hydrological years before seed bank sampling in September 1997 and 1999. Corresponding grassland communities: 3 to 4m = *Magnocaricion*; 4 to 5m = *Cnidion*; > 5m *Arrhenatherion*.

Due to low height and short duration of flooding the hybrid and fossil compartments were not inundated at all and even in the functional compartment, the total number of days with water levels above 4 and 5 m reached only 17 and 6 %, respectively, compared with the long term average (Table 1).

Table 1. Duration of high water levels (in days) of the River Rhine at the gauge station of Worms: A: two hydrological years (01.11.95-30.10.97) before the first sampling; B: two hydrological years (01.11.97-30.10.99) before the second sampling; C: 20 year mean (1981-2000) for two hydrological years. Corresponding grassland communities: 3 to 4m = *Magnocaricion*; 4 to 5m = *Cnidion*; > 5m *Arrhenatherion*. In column A and B two figures are given: days above water level in the first column / percentage of C.

| | | Time period | |
Gauge height	A	B	C
> 3 m	73 / 45	177 / 108	164
> 4 m	9 / 17	81 / 156	52
> 5 m	1 / 6	31 / 194	16
> 6 m	0	8 / 267	3

This situation changed completely in the season before the second sampling took place in September 1999. Whereas the hydrological year 1998 was also extremely dry, in 1999 a series of three very high and long lasting floods occurred (Figure 1) in early November (2 weeks), late February/early March (3 weeks) and May/June (6 weeks). The latter was an exceptionally long-lasting early summer flood that was topped during the past 20 years only by a summer flood in 1987, which lasted almost nine weeks. Compared with the two years before the first sampling the duration of flooding at the gauge level above 4 and 5 m increased by a factor of nine and 30, respectively (Table 1). Deviation in flooding duration from the long-term average increased considerably with flooding height and reached almost double values at the level above 5 m. This means that the hydrological conditions at the higher levels of the flood-plain differed more strongly from average than in the lower ones.

Sampling

Above-ground vascular plant species composition was sampled each year from 1998 to 2000 on 46 permanent plots (200 m²) containing two subplots of 100 m². Species abundance was visually estimated on a modified Braun-Blanquet-scale (van der Maarel 1979). Sampling of vegetation usually took place in June. In 1999, when the vegetation in most of the plots in the functional and fossil compartments was destroyed by heavy flooding in May/June, sampling was conducted in August after resprouting of the meadows.

Sampling of seed banks was carried out in September 1997 and 1999 using a 3 cm diameter soil corer. Within each 200 m² plot 20 cores of 10 cm depth were taken at random locations

after thoroughly removing living and dead plant material from the soil surface. The soil cores were then divided into 0 - 5 cm and 5 - 10 cm sections.

We analysed seed banks by the seedling emergence method (Roberts 1981). After removing vegetative plant material, the soil samples were transferred in a 2-3 cm thick layer to 18 x 28 cm styrofoam basins and exposed for 36 months in free air conditions. Germinated seedlings were identified and removed once every few weeks (for further details see Hölzel & Otte 2001). Nomenclature of vascular plant species follows Wisskirchen & Haeupler (1998).

Data analysis

We used the non-parametric Wilcoxon signed rank test for paired samples to test for significant differences between years in seed bank characteristics such as number of seedlings and species, as well as in the proportion of different functional groups. Functional groups such as annuals, perennial ruderals, grasses, meadow forbs and legumes were formed according to data given by Ellenberg et al. (1992) and Grime et al. (1988). A single species could be attributed to one or more groups, e.g. *Trifolium dubium* was included in annuals as well as in legumes. According to the Ellenberg moisture value species were categorised as mesophytes (moisture value < 6) or wetland species (moisture value > 6).

To explore shifts in seed bank community structure we used the DCA ordination, a method of indirect gradient analysis (Jongman et al. 1995). DCA assumes a unimodal distribution of species along gradients. Running a DCA with detrending by 26 segments revealed a gradient length of 5.23 SD units and thus the appropriateness of the DCA. The DCA ordination was performed on square root transformed data matrices to reduce the unduly influence of high seedling numbers on ordination results (van der Maarel 1979). For the same reason, species with less than two occurrences were omitted from the dataset. The DCA ordination graphs were used for a visual determination of main seed bank community types.

We chose the Mantel test to compare the community structure in seed bank and above-ground vegetation matrices before and after disturbance by floods in 1999. The Mantel test evaluates a null hypothesis of no relationship between two distance matrices without any reduction of the underlying species space (Legendre & Legendre 1998). The measure of strength of relationship is expressed by the standardized Mantel test statistic (*r*) that ranges from 1 (high) to -1 (low). The significance of the correlation was tested using Monte Carlo statistics with 1000 randomised runs (McCune & Mefford 1999). The Mantel test was performed on presence absence matrices using the Sørensen (Bray-Curtis) distance measure.

To describe the changes in the seed bank between the two years of observation, we calculated for each sample pair the Sørensen (Bray-Curtis) distance measure and the % change in total number of seeds and species-richness as well as the % change of certain functional species groups.

For the comparison of these properties by categories such as flood-plain compartment and seed bank community type we used the non-parametric Kruskal-Wallis ANOVA. To evaluate the relationship between the above-mentioned measures of change in the seed bank and flooding duration, we used the non-parametric Spearman rank correlation coefficient. Flooding duration for each plot was calculated from gauge data, field observations and topography.

For DCA ordination and the Mantel test we used the software package PC-ORD 4.0 (McCune & Mefford 1999). All other statistics were performed with STATISTICA 6.0.

Results

A total of 11583 seedlings of 174 species emerged from the seed bank samples. 117 species were recorded in both years, whereas 42 and 15 species were found only in 1997 and 1999, respectively. There was a 50 % decline in total number of seedlings between 1997 and 1999 irrespective of the sampling depth (Table 2). The mean number of species decreased by about 30 % at both sampling depths. With the exception of legumes, a significant decline could be observed across all functional groups. The decline in annuals and perennial ruderals was about 10 % higher than in perennial grasses and meadow herbs. Seed numbers in typical wetland species declined in the same order of magnitude as those in mesophytes.

Response of individual species and species groups

As many as 21 individual species displayed a significant decrease between 1997 and 1999, while only 2 species increased (Table 3). There was also a considerable decline in many other species. These changes were, however, not statistically significant, often due to low frequencies within the dataset. Besides some annual arable weeds, such as *Chenopodium polyspermum, Sonchus asper* and *Capsella bursa-pastoris,* the majority of significantly declining species comprised carpet-forming perennial ruderals such as *Potentilla reptans,*

Table 2. Comparison of seed bank properties of 46 samples from flood-meadows in 1997 and 1999. Significant decline (-) or increase (+) according to the non-parametric Wilcoxon test for paired sample: --- = $p < 0.001$, n.s. = not significant.

	Year		Change	Wilcoxon-
	97	99	%	test
N$^{\underline{o}}$ seeds 0 – 5cm (total)	5282	2687	-49	---
N$^{\underline{o}}$ seeds 5 - 10cm (total)	2036	1050	-48	---
N$^{\underline{o}}$ seeds 0 - 10cm (total)	7749	3834	-51	---
N$^{\underline{o}}$ of species 0 - 5 cm	16.3	11.6	-29	---
N$^{\underline{o}}$ of species 5 - 10 cm	10	7	-30	---
N$^{\underline{o}}$ of species 0 - 10 cm	18.7	13.5	-28	---
N$^{\underline{o}}$ of annuals	68.8	32.1	-53	---
N$^{\underline{o}}$ of perennial ruderals	45.7	19.5	-57	---
N$^{\underline{o}}$ of grasses	21.7	12	-45	---
N$^{\underline{o}}$ of perennial meadow herbs	41.3	23.5	-43	---
N$^{\underline{o}}$ of legumes	6.5	4.2	-35	n.s.
N$^{\underline{o}}$ of wetland species	94.5	48.3	-51	---
N$^{\underline{o}}$ of mesophytes	25.8	12.9	-50	---

Ranunculus repens, Poa trivialis, Taraxacum officinalis, Veronica serpyllifolia and *Glechoma hederacea*, as well as some ruderal tall herbs such as *Lythrum salicaria* and *Cirsium arvense*. Mesophilious grassland species that are usually confined to the drier parts of flood-meadows, such as *Achillea millefolium*, *Rumex acetosa*, *Galium verum*, *Daucus carota*, *Plantago lanceolata* and *Centaurea jacea* also displayed a significant decline. In contrast, there was no significant or only minor decline in many herbaceous species typical of flood-meadows and other wet grasslands such as *Silene flos-cuculi, Lysimachia vulgaris, Rumex crispus, Arabis nemorensis, Pseudolysimachion longifolium, Allium angulosum* and *Viola pumila*. Contrary to the general trend in therophytes, typical winter annuals such as *Veronica arvensis, V. peregrina, Arenaria serpyllifolia, Vicia angustifolia and Trifolium dubium* did not show any decrease.

Table 3. Comparison of species occurrence in the seed bank of 46 plots in flood-meadows in 1997 and 1999. M = Ellenberg moisture value (1 = very dry to 9 = damp); LF = life form: T = Therophyte, G = Geophyte, H = Hemicryptophyte, Ch = Chamaephyte; LH = life histoy: P = Perennial, A = Annual (w = winter, s = summer), M = Moncarp; CSR = Established strategy (all data derived from Ellenberg et al. 1992 and Grime et al. 1988). Significant decline (-) or increase (+) according to non-parametric Wilcoxon test for paired sample: -/+ = *p* < 0.05, --/++ = *p* < 0.01, ---/+++ = *p* < 0.001. Rare species, with less than three occurrences in one year not shown.

Species	M	LF	LH	C-S-R	Frequency 97	Frequency 99	Total number 97	Total number 99	Change n	Change %	Wilcoxon test
Potentilla reptans	6	H	P	CR/CSR	27	20	392	133	-259	-66	---
Ranunculus repens	7	H	P	CR	25	16	310	77	-233	-75	---
Cerastium holosteoides	5	Ch/T	P/A	R/CSR	24	15	88	21	-67	-76	--
Poa trivialis	7	H	P	CR/CSR	22	25	363	140	-223	-61	--
Chenopodium polyspermum	6	T	As	-	22	7	675	217	-458	-68	---
Veronica serpyllifolia	6	H	P	R/CSR	21	17	180	115	-65	-36	-
Taraxacum officinale agg.	5	H	P	R/CSR	21	8	72	15	-57	-79	--
Silene flos-cuculi	7	H	P	CSR	18	16	286	248	-38	-13	n.s.
Lythrum salicaria	8	H	P	CR/CSR	18	15	184	50	-134	-73	---
Glechoma hederacea	6	H	P	CSR	18	13	63	18	-45	-71	---
Achillea millefolium	4	H/Ch	P	CR/CSR	18	9	96	26	-70	-73	-
Leucanthemum vulgare	4	H	P	CR/CSR	16	13	51	34	-17	-33	n.s.
Poa angustifolia	4	H	P	CSR	15	28	52	135	83	160	++
Veronica arvensis	4	T	Aw	SR	14	14	52	71	19	37	n.s.
Plantago intermedia	7	H	P	R/CSR	14	13	66	72	6	9	n.s.
Rumes acetosa	X	H	P	CSR	14	6	35	10	-25	-71	-
Cirsium arvense	X	G	P	C	14	3	25	4	-21	-84	---
Sonchus asper	6	T	Aws	R/CR	14	2	25	2	-23	-92	---
Arenaria serpyllifolia	4	T	Aws	SR	13	8	33	36	3	9	n.s.
Chenopodium album	4	T	As	R/CR	12	13	114	68	-46	-40	n.s.
Juncus articulatus	9	H	P	CSR	12	8	93	45	-48	-52	--
Capsella bursa-pastoris	5	T	Asw	R	12	6	71	25	-46	-65	-
Lysimachia vulgaris	8	H	P	C/SC	11	14	114	61	-53	-46	n.s.
Agrostis stolonifera agg.	X	H	P	CR	10	15	112	49	-63	-56	n.s.
Vicia angustifolia		T	Aw	R/CSR	10	13	19	31	12	63	n.s.
Rumex crispus	7	H	P	R/CR	10	6	11	11	0	0	n.s.
Galium verum agg.	4	H	P	SC/CSR	10	3	38	6	-32	-84	-
Arabis nemorensis	7	H	P	S/SR	9	9	369	290	-79	-21	n.s.
Carex spicata	4	H	P	-	9	5	25	16	-9	-36	n.s.
Plantago lanceolata	X	H	P	CSR	9	5	20	6	-14	-70	-
Daucus carota	4	H	M	SR/CSR	9	4	25	4	-21	-84	-
Carex panicea	8	H	P	S	8	6	89	34	-55	-62	n.s.
Pseudolysimachion longifol.	8	H	P	-	8	6	227	75	-152	-67	n.s.
Centaurea jacea	5	H	P	S/CSR	8	5	28	10	-18	-64	-
Viola pumila	7	H	P	-	7	8	24	22	-2	-8	n.s.
Allium angulosum	8	H	P	-	7	6	37	31	-6	-16	n.s.
Trifolium repens	5	Ch/H	P	CR/CSR	7	4	13	10	-3	-23	n.s.
Urtica dioica	6	H	P	C	7	1	17	1	-16	-94	-
Ajuga reptans	6	H	P	CSR	6	7	141	118	-23	-16	n.s.
Centaurium pulchellum	X	T	As	SR	6	6	59	14	-45	-76	n.s.
Linum catharticum	X	T	B/A	SR	6	6	12	26	14	117	n.s.
Medicago lupulina	4	T	A/P	R/SR	6	4	6	5	-1	-17	n.s.
Stellaria media	X	T	Aws	R	6	3	11	3	-8	-73	n.s.
Veronica peregrina	8	T	Aws	R	5	7	553	500	-53	-10	n.s.
Thalictrum flavum	8	H	P	-	5	5	44	28	-16	-36	n.s.
Hypericum perforatum	4	H	P	CR/CSR	5	4	10	10	0	0	n.s.
Juncus alpinus	9	H	P	-	5	4	70	20	-50	-71	n.s.
Myosotis arvensis	5	T	Aw	R/SR	5	4	28	12	-16	-57	n.s.
Ranunculus polyanthemos agg.	4	H	P	-	5	4	16	7	-9	-56	n.s.
Rorippa sylvatica	8	G/H	P	-	5	4	65	59	-6	-9	n.s.
Galium album	5	H	P	-	5	3	5	5	0	0	n.s.
Epilobium tetragonum	8	T	Aws	-	5	2	7	2	-5	-71	n.s.
Carex gracilis	9	H	P	-	5	1	14	1	-13	-93	-
Carex tomentosa	7	H	P	-	4	6	10	14	4	40	n.s.
Valerianella locusta	5	T	Aw	SR	4	5	15	15	0	0	n.s.
Allium scorodoprasum	7	H	P	-	4	4	58	12	-46	-79	n.s.
Cerastium dubium	7	T	Aw	-	4	4	894	222	-672	-75	n.s.
Trifolium hybridum	6	H	P	CSR	4	4	238	123	-115	-48	n.s.
Veronica catenata	9	T	A	-	4	4	21	10	-11	-52	n.s.
Viola persicifolia	8	H	P	-	4	4	25	6	-19	-76	n.s.
Euphorbia esula	4	H	P	-	4	3	18	19	1	6	n.s.
Galium palustre agg.	9	H	P	CR/CSR	4	3	34	6	-28	-82	n.s.
Phalaris arundinacea	9	H	P	C	4	3	5	4	-1	-20	n.s.
Carex disticha	9	H	P	-	4	2	15	3	-12	-80	n.s.
Lotus corniculatus	4	H	P	S/CSR	4	2	10	4	-6	-60	n.s.

Table 3 continued

|										
Poa palustris	9	H	P	-	4	2	12	2	-10	-83	n.s.
Persicaria maculata	5	T	As	R	4	2	16	3	-13	-81	n.s.
Stachys palustris	7	G	P	CR	4	2	8	2	-6	-75	n.s.
Trifolium pratense	X	H	P	CSR	4	1	5	1	-4	-80	n.s.
Viola hirta	3	H	P	S	4	1	7	2	-5	-71	n.s.
Symphytum officinale agg.	8	H/G	P	C/CR	4	0	6	0	-6	-100	n.s.
Lathyrus pratensis	6	H	P	CSR	3	5	5	10	5	100	n.s.
Trifolium dubium	5	T	Aws	R/SR	3	5	7	12	5	71	n.s.
Carex hirta	6	H	P	C/CSR	3	4	57	43	-14	-25	n.s.
Anagallis arvensis	5	T	Asw	R/SR	3	3	49	17	-32	-65	n.s.
Cardamine parviflora	7	T	Asw	-	3	3	45	48	3	7	n.s.
Carex praecox	3	H	P	-	3	3	6	6	0	0	n.s.
Sagina procumbens	5	H/T	P/A	R/CSR	3	3	4	3	-1	-25	n.s.
Chenopodium hybridum	5	T	As	-	3	2	47	10	-37	-79	n.s.
Genista tintoria	6	Ch	P	-	3	2	8	4	-4	-50	n.s.
Mentha arvensis	8	G/H	P	C/R	3	2	4	3	-1	-25	n.s.
Solanum nigrum	5	T	As	-	3	2	35	2	-33	-94	n.s.
Deschampsia cespitosa	7	H	P	SC/CSR	2	7	3	12	9	300	n.s
Prunella vulgaris	5	H	P	CSR	2	7	2	9	7	350	+
Trifolium campestre	4	T	Aw	SR	2	4	9	26	17	189	n.s
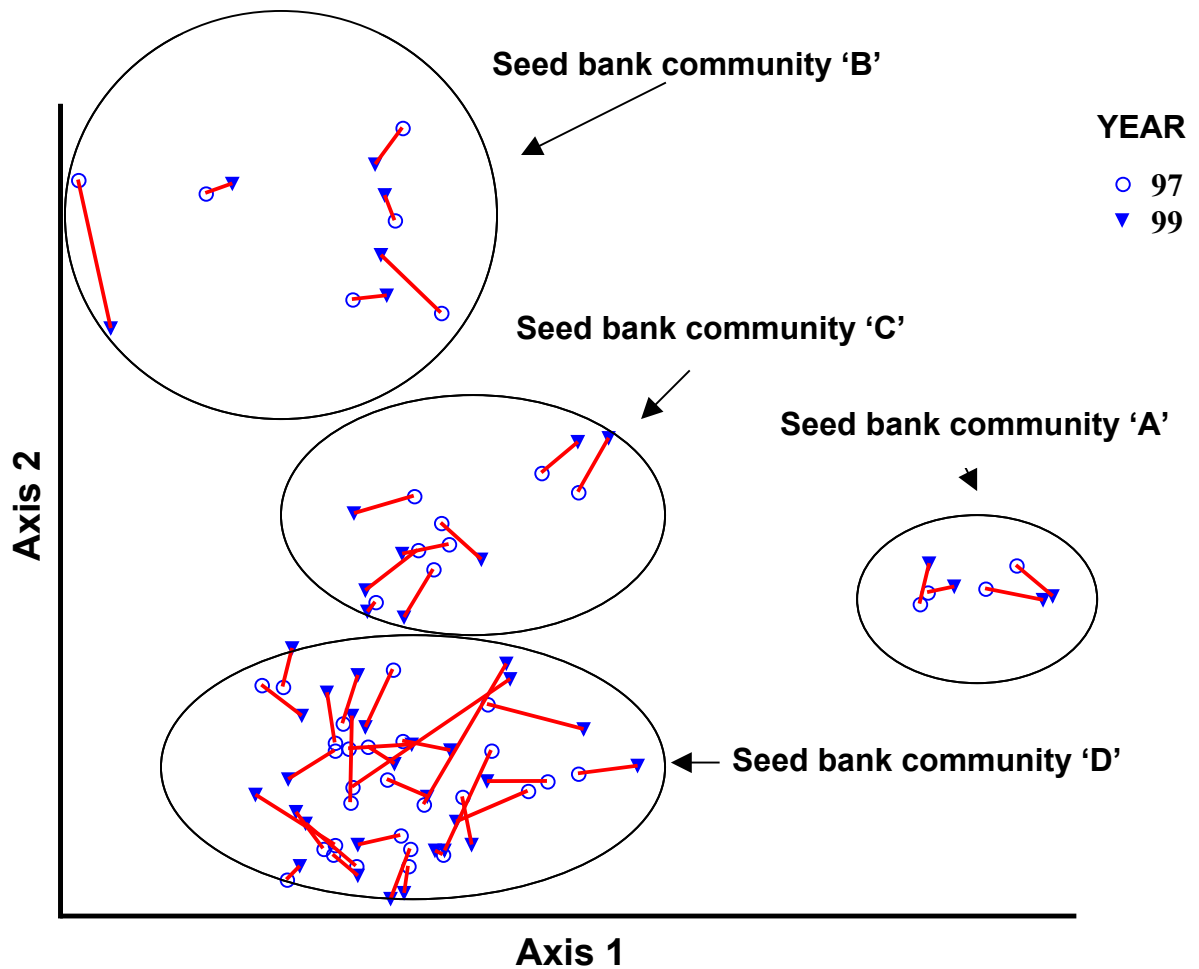
Fig. 2a. DCA-ordination (Axis 1 and 2) of soil seed bank samples from 46 flood-meadows; vectors connect samples from the same plot in two different years (1997 and 1999). Distinct soil seed bank community types that mostly reflect differences in above-ground vegetation are indicated by numbers: A = *Magnocaricion* meadows, B = *Molinion* meadows, C = *Cnidion* meadows (late mowing), D = *Cnidion + Arrhenatherion* meadows (early mowing).

Shifts in species composition

The considerable quantitative and qualitative changes in seed bank composition between the two years of observation were also indicated in the DCA graph as a shift of samples in ordination space (Figure 2a and 2b). By the combination of different ordination axes, five main seed bank community types could be distinguished that reflect analogous differences in above ground vegetation and site history. Within and among these seed bank community types shifts were rather erratic and equivocal and there was no clear general trend.
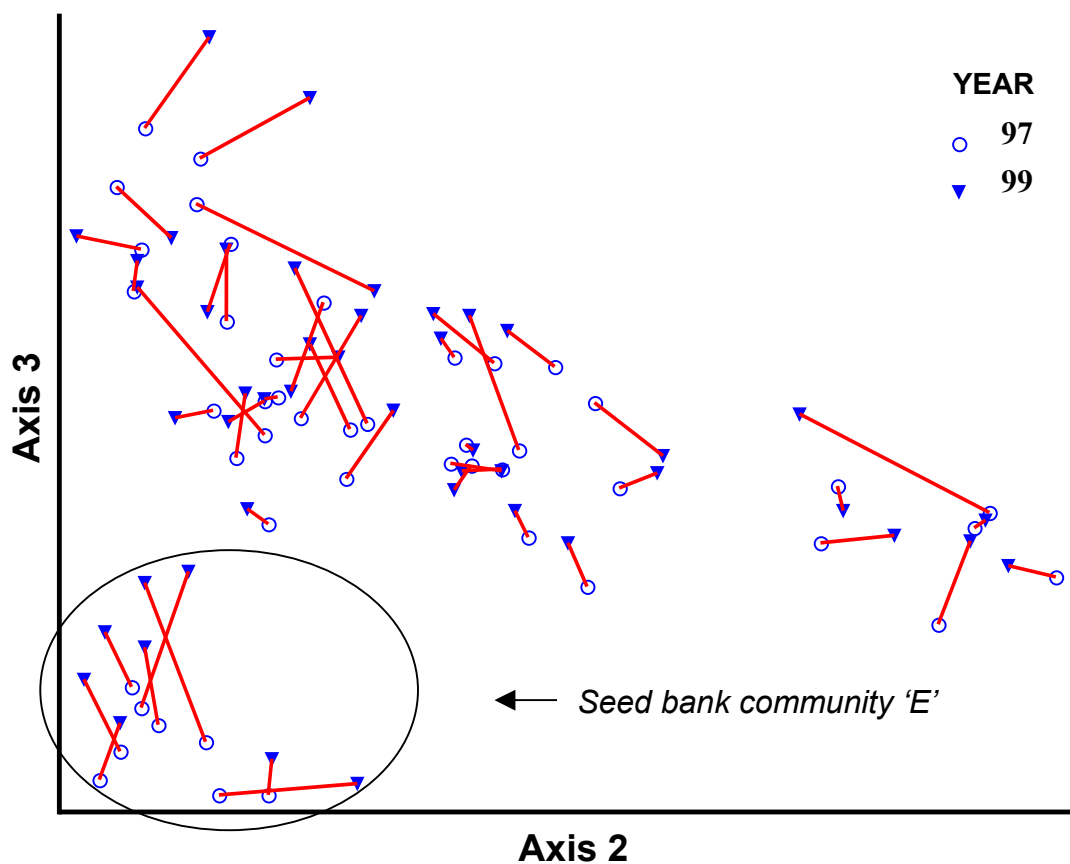
Fig. 2b. Like Figure 2a, but Axis 2 and 3. Seed bank community types: 'E' = former arable fields (out of group D in Figure 2a).

Similarity of above-ground vegetation and seed bank

According to the results of the Mantel test (Table 4) the positive relationship in similarity structure between soil seed bank and above-ground vegetation in the following season decreased considerably after major flooding in 1999. The correlation in similarity structure of seed banks before and after flooding was much lower than those in above-ground vegetation, indicating that species composition of seed banks was more strongly affected by flooding than above-ground vegetation.

Table 4. Evaluation of relationships of seed bank (SB) and above-ground vegetation (AV) distance matrices (n = 41) from different years by Mantel test. r = Standardized Mantel statistics; *p* = significance of correlation tested by Monte Carlo permutation test with 1000 random runs.

Compared matrices	r	*p*
SB 97 / AV 98	0.781	0.0010
SB 99 / AV 00	0.621	0.0010
SB 97 / SB 99	0.644	0.0010
AV 98 / AV 00	0.858	0.0010

Seed bank response in relation to environmental gradients and categories

A comparison of traits indicating changes in seed bank properties such as Sørensen similarity measure, the % decline in seed density, species-richness and certain functional species groups by flood-plain compartment and major seed bank community types revealed no statistically significant differences among categories (results not shown). Equally, there were no or only minor overall correlations between flooding duration before the second sampling and the % decline of species-richness and seed density in the seed bank (Table 5). Among the functional groups, only grasses showed a significantly higher overall decline with increasing flooding duration, which was also true for the functional and the fossil flood-plain compartment. In the hybrid flood-plain, the % change in species number in the seed bank was positively correlated with flood duration, which means that there was a higher decline in species at the dryer plots in this compartment. Only in the fossil flood-plain compartment did ruderals show a higher % decline with increasing flooding duration.

Table 5. Spearman rank correlation between flooding duration in the hydrological year 1999 (F) and % change in species number, number of all seeds and of different functional groups in the seed bank of 46 flood-meadow plots. Number of samples per flood-plain compartment are indicated in brackets. Significant correlations are given in bold: $* = p < 0.05$, $** = p < 0.01$, $*** = p < 0.001$.

	Flood-plain compartment			
	All	Functional (18)	Hybrid (12)	Fossil (16)
F / % species	0.04	-0.09	**0.62***	-0.14
F / % all seeds	-0.16	-0.06	-0.07	-0.46
F / % grasses	**-0.59***	**-0.63**	-0.34	**-0.60***
F / % ruderals	-0.19	-0.27	0.11	**-0.57***
F/ % annuals	-0.02	0.02	-0.00	-0.06
F / % herbs	-0.04	-0.18	0.24	-0.28

Discussion

Seed bank depletion by flooding?

The major finding of our study was a heavy and highly significant decline of total seed density and species-richness in the seed banks of the studied flood-meadows within a period of only two years, which took place almost uniformly over different functional groups, vegetation types and hydrological flood-plain compartments. Legumes (Fabaceae) were the only functional group that was not significantly affected by the general decline. This is obviously a result of physical dormancy due to a water-impermeable, hard-shelled testa in seeds of this family, which almost generally require scarification to trigger germination (Grime et al. 1981).

The observed short-term seed bank depletion is most probably an effect of the environmental variable flooding intensity, which differed most significantly between both sampling occasions. However, due to our observational approach, other factors besides flooding cannot be completely ruled out, which requires a cautious interpretation of the results obtained.

Firstly, the observed phenomena could be a sampling effect due to small-scaled spatial variability in seed densities within our study plots, or to differences in the timing and method of sampling and seed bank analysis. The latter is very unlikely, since we used absolutely identical sampling times and methods and the determination of seedlings was carried out by the same person and with the same intensity. Equally, small-scaled heterogeneity in seed

densities is unlikely to result in a general and highly significant trend of decline over all samples.

Another important factor that has to be considered are inter-annual differences in seed production by the established vegetation, due to changing management or weather conditions that may potentially strongly influence seed bank size and composition (e.g. Thompson & Grime 1979). However, due to the removal of superficial diaspore litter during sampling the effects of short-term seasonal differences in seed production were largely reduced. This is evident from the very low representation of dominant species with high seed production but short-lived seeds during both sampling occasions. Inter-annual differences in seed production will at first influence the upper soil layer, whereas lower soil layers are usually not significantly affected (e.g. Poschlod & Jackel 1993) due to the fact that the burial of seeds is a time-consuming process (Thompson et al. 1997). In our study, however, we found an almost identical decline in total seed density and species-richness, irrespective of the sampling depth, which is hard to explain by inter-annual differences in seed rain. These findings are further supported by the comparison of different flood-plain compartments. Whereas the first growth in the functional and hybrid flood-plain compartments was completely destroyed by high and long-lasting flooding in early summer 1999, the established vegetation of the fossil flood-plain was well preserved due to lower absolute flooding height, meaning that in many species seed production could occur largely unhampered. The same was true for the higher levels in the functional and hybrid flood-plains, which were flooded only briefly. Given a predominant influence of seed production on the observed depletion of the soil seed bank there should be a divergent response between the different hydrological flood-plain compartments and along flooding gradients. However, such patterns could definitely not be found in the analysed seed banks.

A possible explanation for the heavy seed bank depletion we observed could be that the seeds of many species died in the course of long-lasting inundation. Although seeds of certain species, e.g. *Rumex acetosa* (Voesenek & Blom 1992), may be killed by prolonged flooding, seed generally have a great tolerance towards submergence, even among strictly terrestrial species (Skoglund & Hytteborn 1990, Baskin & Baskin 2001). In our study this was confirmed by the fact that many species which usually avoid moist habitats (Table 3) did not display any decline at all in the seed bank after flooding.

More likely the observed heavy depletion of the soil seed bank may be attributed to a 'post-flood germination flush' (Jutila 2001), as has been described in other flood-plain habitats (Schneider & Sharitz 1986, Voesnek & Bloom 1992). Floods and the subsequent successive

draw-down may facilitate recruitment from the seed bank by prolonged favourable moisture supply and the creation of open gaps due to the complete or at least partial die back of above-ground vegetation (e.g. Leck 1989). Equally, temporary anoxic conditions and increased nitrogen levels may act as a germination cue to break dormancy in certain species (Baskin & Baskin 2001).

Response of individual species in the seed bank

The hypothesis of a post-flood germination flush that led to a temporary depletion in the seed bank of the studied flood-meadows is strongly supported by the patterns of decline and persistence in individual species, in particular with respect to their germination characteristics. Remarkably, among the most seriously declining species there was a high proportion of nutrient-demanding competitive ruderals such as *Ranunculus repens* and *Poa trivialis.* Typically, plants that follow this strategy exploit turf gaps after disturbances, not only by excessive lateral clonal spread, but also by recruitment from the seed bank (Grime 2001). Among the declining ruderals, there were many species with high germination temperature requirements (> 20 °C), e.g. *Potentilla reptans* (Ziron 2000), *Chenopodium polyspermum* (Otte 1996) and *Lythrum salicaria* (Grime et al. 1981, Patzelt 1998). Flooding in early summer, when such temperature requirements are met, seems to be particularly favourable for these species, since germination from the seed bank in flood-meadows is usually hampered by drought and shading through high and densely developed canopy structures at this time of the year.

Another aspect that must be considered is the input and increased availability of nutrients due to sedimentation as well as intensified mineralisation and decomposition of dead below- and above-ground biomass in the course of flooding events. High nitrate contents proved to be particularly relevant as a cue to trigger germination in darkness in nutrient-demanding annual ruderal species (Bouwmeester & Karssen 1989). Ziron (2000) and Knödler (2001) found a strongly significant increase in germination rates of *Capsella bursa-pastoris* and *Potentilla reptans* in experimental variants with nutrient addition; in *Ranunculus repens* and to a lower degree in *Poa trivialis* germination in darkness was even completely dependent on the addition of nutrients. Comparable results were obtained in *Plantago lanceolata* by Pons (1989), who interpreted the breaking of dark dormancy by elevated nitrate concentrations in the soil as a gap detection mechanism after disturbances in above-ground vegetation.

In contrast to many nutrient demanding ruderals with high temperature requirements, there was no significant decline in typical winter annuals such as *Veronica arvensis*, *Arenaria serpyllifolia*, *Vicia angustifolia*, *Trifolium dubium* and *Trifolium campestre*. These species preferably germinate at the beginning of the cool season in autumn, and partly in early spring (Baskin & Baskin 1983a, Grime et al 1988). In *Veronica peregrina*, a typical plant of temporary flooded habitats, Baskin & Baskin (1983b) showed that due to conditional seasonal dormancy the ability to germinate at high temperatures above 20 °C is lost in May and June. In line with this germination behaviour, there was no decline of this species in our study. Comparable conditional dormancy cycles have also been described in perennial species typical of wet meadows, such as *Silene flos-cuculi*, which although abundant in the seed bank did not show any decline after flooding. Exhumed seeds of this species geminated in light all year round but exhibited a cyclic pattern of germination in darkness, with a peak occurring in spring (Milberg 1994). Such dark-dormancy cycles were also found in different *Carex* species of temperate wetlands (Baskin et al. 1996, Schütz 1997).

Summarizing, we can conclude that individual germination characteristics of species, such as temperature requirements, seasonal dormancy cycles and sensitivity to nutrition, gave the best explanation for the patterns of decline and persistence in the soil seed bank after flooding. Significant effects of different temperature regimes in combination with flooding treatments on recruitment from the soil seed bank of temporary wetlands were also described by Seabloom et al. (1998). Judging from the patterns of decline and persistence of certain species in conjunction with their germination requirements and dormancy cycles we suppose that the unusually long lasting early summer flooding had the greatest impact on the observed temporary seed bank depletion, while winter floods, mostly due to low temperatures, should be of lower significance. In seed addition and plant litter transfer experiments in the same year and region, we also observed a strong facilitation in seedling recruitment after early summer flooding in comparison with non-flooded plots (Hölzel & Otte 2003).

Environmental gradients and seed bank depletion

Long lasting early summer flooding is a rather irregular and unpredictable event in the studied flood-meadows, especially at medium and higher elevation, that re-occurs on average one to two times per decade. As indicated by the Mantel test, its effects on the compositional structure of soil seed banks were even more profound than in above-ground vegetation. In above-ground vegetation, such flooding events typically lead to a significant decline in certain

flood-intolerant mesophytic species, such as *Arrhenatherum elatius* (Vervuren et al. 2003) and to an increase in abundance and dominance of species that favour damp to wet site conditions (Balátová-Tuláčková 1979, Hölzel unpubl.). In the soil seed bank, both groups may be affected irrespective of their moisture preferences (Table 2). The patterns of decline we observed between sampling plots were hard to relate to environmental gradients and groupings such as flooding duration, flood-plain compartment and seed bank community type. In contrast to other studies that found such relationships and patterns in more or less dynamic wetland ecosystems (van der Valk & Davis 1978, Keddy & Ellis 1985, Gerritsen & Greening 1989, Casanova & Brock 2000, Middleton 2000, Nicol et al. 2003), the analysed flood-meadows are predominantly terrestrial ecosystems in which flooding occurs as a more or less regular but rather short-term and unpredictable disturbance. Aquatic plants that may respond to flooding duration and height are almost completely absent from the studied seed banks. Thus, not flooding itself, but rather the period of successive draw down that provides particularly favourable moisture conditions for germination should be of major significance for the observed seed bank processes (e.g. Nicol et al. 2003). The duration of this period may be influenced by micro-topography, weather conditions and stability of certain water levels but not necessarily by the absolute duration and height of the flooding. This means that favourable germination conditions may occur in a relatively irregular manner, irrespective of elevational gradients. There were also considerable differences in structural features among plots during the relevant period of draw-down in June 1999. These differences, ranging from bare open soil to more or less closed and thick carpets of dead plants, algae (e.g. *Characea),* and drift material, without or in combination with sparse above-ground vegetation, also occurred in a rather erratic manner. Due to their impact on light conditions and soil temperatures they must be seen as another potential source of unpredictable variation, influencing recruitment from the seed bank (e.g. Seabloom et al. 1998). Poor correlations between environmental variables and seedling densities during draw-down were also described by Welling et al. (1988).

Our results clearly suggest that species-specific facilitation of recruitment from the soil bank, as well as persistence in the course of flooding events, have a significant impact on structuring and maintaining the floristic diversity in flood-meadows. In accordance with other studies from dynamic amphibious habitats (e.g. Abernethy & Willby 1999, Brock & Rogers 1998, Bonis et al. 1995), the major ecological function of persistent soil seed banks in flood-meadows appears to be the exploitation and bridging of the effects of highly variable hydrological conditions.

Kapitel 5

Ecological significance of seed germination characteristics in flood-meadow species

Norbert Hölzel & Annette Otte

Summary

In climate chamber and outdoor experiments we analysed germination traits of 42 vascular plant species typical of flood-meadows of the alliance *Cnidion*. In Central Europe such flood-meadows and their highly endangered character species are confined to large lowland river corridors with a dry and warm climate. Due to the prevailing ecological conditions, particularly the extremely high variability in soil moisture potential, it was hypothesised that flood-meadow species exhibit specific strategies in terms of germination phenology, temperature requirements and primary dormancy to avoid constraints on seedling recruitment imposed by flooding, drought and competition from established vegetation. Furthermore, we expected that germination characteristics could be a key for the causal understanding of range size, confinement to large river corridors, recent rarification processes, seed bank persistence and establishment success in restoration projects.

PCA ordination of germination traits reflected a continuous gradient of increasing primary dormancy levels ranging from species with a high capacity for fast and almost complete germination over a wide range of temperatures to those with high and narrow temperature requirements and/or a delayed and asynchronous emergence. Many of the studied species germinated only at relatively high temperature in the year of shedding, but the primary conditional dormancy disappeared in most cases after a period of cold wet stratification. Chilling and high temperature requirements were revealed to be the most common strategies for avoidance of harmful autumn and winter germination. The majority of the studied species tends to exploit particularly favourable regeneration niches in early spring. Surprisingly, many species with large long-term persistent soil seed banks exhibited relatively low dormancy

levels in light; this was correlated with small seed size and a consequent higher probability of burial. We found no relationship between germination characteristics and river corridor confinement or Central European range size. However, there was a significant trend in endangered species towards higher temperature requirements and delayed, asynchronous germination. This is presumably disadvantageous under the environmental conditions of subcontinental flood-meadows.

Key words: Dormancy, germination temperature requirements, grassland restoration, principal component analysis, seed bank, stratification

Introduction

The temporal and spatial limitation of the "regeneration niche" (Grubb 1977) has been increasingly identified as one of the most critical constraints in the life-cycle of plant populations, and is a factor that may severely reduce diversity in plant communities (e. g. Stampfli & Zeiter 1999). Recruitment from seeds is often strongly hampered or even condemned to failure through competition by established vegetation (Rusch & Fernández-Palacios 1995, Kotorová & Lepš 1999) as well as unfavourable environmental conditions such as frost and drought (Silvertown & Dickie 1980, Ryser 1993). Consequently, successful germination and seedling establishment in a given species will often depend on its ability to avoid or minimize such constraints. Numerous previous studies have shown that seeds of many species boast the aptitude to identify suitable conditions for seedling recruitment (Grime 2001). Narrow temperature requirements, dormancy cycles induced or broken by temperature fluctuations, warm or cold stratification, as well as other environmental factors, such as fire or nitrate concentrations, are all mechanisms that regulate the onset of germination and help in detection of favourable micro-sites with low competition (Thompson et al. 1977, Grime et al. 1981, Baskin & Baskin 2001). Such dormancy breaking mechanisms were revealed to be of particular importance in species typical of temperate wet grasslands (e.g. Milberg 1994, Schütz 1997, Knödler 2001, Jensen 2001).

Germination characteristics may play an equally important role in the formation of persistent soil seed banks. Seeds exhibiting conditional or strict dormancy (Baskin & Baskin 2001) are more likely to be buried and to establish large persistent reservoirs in the soil (Thompson et al. 1993, Grime 2001). Seed regeneration strategies are now considered as a key for the causal

understanding of the decline, persistence or spread of species in changing landscapes (e. g. Schütz 2000b).

Information on germination characteristics is also particularly relevant for habitat restoration, in which species-enrichment largely depends on re-establishment by artificially introduced or naturally dispersed seeds (e. g. Bakker & Berendse 1999, Patzelt et al. 2001). By the creation of suitable regeneration niches at the right time of the year, management schemes may positively influence germination and the subsequent fate of seedlings (Olff et al. 1994, Kotorová & Lepš 1999, Schütz 2000b). If seeds of target species are introduced artificially, information on germination phenology, dormancy, response to storage and pre-treatments are essential to increase the likelihood of seeding success (Keller & Kollmann 1999, Budelsky & Galatowitsch 1999). However, knowledge on germination characteristics is still extremely scarce particularly in rare and endangered species targeted for conservation and there are a great variety of possible response types (e.g. Baskin & Baskin 2001). This also applies to declining and endangered species-rich flood-meadows of the alliance *Cnidion* that include a large number of rare plant species of Central European conservation concern (Schnittler & Günther 1999, Hölzel et al. 2002). In their Central European distribution these alluvial grasslands are strictly confined to large river corridors with dry and warm subcontinental climatic conditions (Korsch 1999, Burkart 2001). This distribution pattern is reflected by the occurrence of many highly specialised eastern species that are uncommon in Central Europe and close to the western limit of their range, such as *Allium angulosum, Cnidium dubium, Scutellaria hastifolia* and *Viola pumila* (Hultén & Fries 1988). Ecologically these flood-meadows are characterized by an extremely high variability in soil water potential (Burkart 1998, Leyer 2002). Whereas winter, spring and early summer may often bring floods summers are markedly dry and rapidly hardening clay soils are common (DISTER 1980, Hölzel 1999). Thus, successful seedling recruitment may be hampered by flooding as well as by drought (Hölzel & Otte 2003) and there is only a relatively narrow time window with favourable germination conditions.

In the present study, we investigated if there is a specific response in germination characteristics of the typical flora of flood-meadows to these particular ecological conditions. Furthermore, we attempted to assess whether germination characteristics can provide an explanation for the strict confinement of many character species to large river corridors with subcontinental climatic conditions. According to their Central European distribution pattern, it is postulated that characteristic flood-meadow species tend to have high temperature requirements for germination.

The study was carried out in the framework of a large-scale restoration project aimed at the re-establishment of species-rich flood-meadows on ex-arable land by the transfer of diaspores with plant material from remnant stands (Hölzel & Harnisch 2002, Hölzel & Otte 2003). It is often claimed (e.g. Patzelt 1998, Schütz 2000b) that declining, rare and endangered species tend to have detrimental germination requirements. Thus, we expected that germination traits could be a key to detect the underlying mechanisms of successful or failing re-establishment of target species as well as for the optimisation of restoration measures.

Material and Methods

Study species

Seeds of 42 species were collected in bulk from autochthonous populations in flood-meadows along the northern Upper Rhine River, Germany, between the tributaries Neckar to the south and Main to the north. Seed sampling took place between May and October depending on the time of ripening and included at least 50 different plant individuals. The species studied comprise typical constituents of subcontinental flood-meadows, representing a broad variety of families, life forms and strategy types (Table 1). Besides character species, which are more or less confined to large lowland river corridors such as *Allium angulosum, Arabis nemorensis, Cnidium dubium, Iris spuria, Scutellaria hastifolia* and *Viola pumila* (Burkart 2001) we also studied more common and widespread components like *Festuca arundinacea, Potentilla reptans, Rumex thysiflorus, Symphytum officinale* and *Veronica serpyllifolia*. The study covers almost the entire spectrum of regionally rare and endangered target species of flood-meadows (Korneck et al. 1996). Plant nomenclature follows Wisskirchen & Haeupler (1998).

Table 1. Traits of the studied species according to the following authors: Life form (Ellenberg et al. 1992), seed mass (Hölzel & Otte accepted a), river corridor area (Korsch 1999 and Burkart 2001), German Red List status (Korneck et al. 1996). Letters in bold indicate abbreviations for species names used in following tables and figures. Confinement to river corridors: ++ strong, + weak, - none. Red List status: 1 = critically endangered, 2 = endangered, 3 = vulnerable, - = not threatened.

Species	Family	Life form	Seed mass (mg)	River corridor	Red List
Allium **angu**losum	Liliaceae	G	1.74	++	3
Alopecurus **prat**enisis	Poaceae	H	0.71	-	-
Althaea **offic**inalis	Malvaceae	H	3.41	+	3
Arabis **nemo**rensis	Brassicaceae	H	0.06	++	2
Barbarea **striata**	Brassicaceae	H	0.41	++	-
Cardamine **parv**iflora	Brassicaceae	T	0.07	++	3
Carex **prae**cox	Cyperaceae	H	0.16	+	3
Carex **spic**ata	Cyperaceae	H	3.34	-	-
Carex **tome**ntosa	Cyperaceae	H	1.44	-	3
Cerastium **dubiu**m	Caryophyllaceae	T	0.11	++	3
Cirsium **tube**rosum	Asteraceae	H	2.27	-	3
Cnidium **dubiu**m	Apiaceae	H	0.39	++	2
Elymus **repe**ns	Poaceae	H	4.50	-	-
Euphorbia **palu**stris	Euphorbiaceae	H	10.47	++	3
Festuca **arun**dinacea	Poaceae	H	3.16	-	-
Galium **bore**ale	Rubiaceae	H	0.68	-	-
Galium **wirt**genii	Rubiaceae	H	0.40	+	-
Inula **brit**annica	Asteraceae	H	0.09	++	-
Inula **salic**ina	Asteraceae	H	0.16	-	-
Iris spuria	Liliaceae	G	14.62	++	2
Lathyrus **palu**stris	Fabaceae	H	12.85	+	3
Lythrum **salic**aria	Lythraceae	H	0.06	-	-
Peucedanum **offic**inale	Apiaceae	H	12.32	+	3
Poa angustifolia	Poaceae	H	0.21	-	-
Potentilla **rept**ans	Rosaceae	H	0.31	-	-
Pseudolysimachion **long**ifolium	Scrophulariaceae	H	0.05	++	3
Pulicaria **dys**enterica	Asteraceae	H	0.04	-	-
Rumex **thyr**siflorus	Polygonaceae	H	0.54	+	-
Sanguisorba **offic**inalis	Rosaceae	H	1.95	-	-
Scutellaria **hast**ifolia	Lamiaceae	H	0.68	++	2
Selinum **carv**ifolia	Apiaeae	H	1.06	-	
Senecio **palu**dosus	Asteraceae	H	0.62	++	3
Serratula **tintoria**	Asteraceae	H	1.26	-	3
Silaum **sila**us	Apiaceae	H	2.43	-	
Symphytum **offic**inale	Boraginaceae	H	3.65	-	-
Thalictrum **flav**um	Ranunculaceae	H	0.80	++	-
Valeriana **prat**ensis	Valerianaceae	H	0.62	++	-
Veronica **pere**grina	Scrophulariaceae	T	0.06	+	-
Veronica **serp**yllifolia	Scrophulariaceae	H	0.05	-	-
Viola **elat**ior	Violaceae	H	1.80	++	2
Viola **pers**icifolia	Violaceae	H	0.68	++	2
Viola **pumi**la	Violaceae	H	1.08	++	2

Experiment 1

After field collection seeds of the 40 species used in this experiment were stored dry in darkness at room temperature (ca. 20 °C) until further use during the following winter season. The germination experiments were performed by spreading 50 seeds of each species on a double layer of filter paper in sterile Petri dishes. In case of very large seeds only 25 seeds per dish were used. Five dishes per treatment were incubated in climate chambers at constant temperatures of 3, 7, 10, 15, 20, 25, 30, and 35 °C and in a further chamber with diurnally fluctuating temperatures 5/15 °C (8/16 hours). The latter temperature regime was also applied to seeds that received cold wet stratification at 3 °C for 8 weeks prior the incubation, which should mimic early spring germination conditions. The light regime in the climate chambers simulated long day conditions with 16 hours of light and 8 hours of darkness. The dishes were regularly watered with distilled water to optimise moisture conditions. The experiment lasted 6 weeks. Germinated seeds were counted and removed once every week. Germination was defined as the emergence of the radicule.

Experiment 2

Results obtained in climate chambers are often strongly divergent from those set up in outdoor germination experiments, and certain species may even completely fail to germinate under laboratory treatments (e. g. Grime et al. 1981, Patzelt 1998). Thus, we combined both approaches in order to investigate germination phenology under more natural conditions.
A total of 800 seeds of each species were sown in February into two Styrofoam basins (18 cm x 28 cm) filled with sterile garden soil and exposed at an experimental field near Giessen, Germany. During dry periods the basins were watered daily. Emerging seedlings were counted and removed at least every two weeks. The outdoor study was continued for 24 months.

Experiment 3

To investigate primary dormancy levels (Baskin & Baskin 2001) and the timing of germination under near natural conditions, seeds from a subset of 20 species were collected at the time of shedding in the field and exposed about 2 weeks later under outdoor conditions.

The mode of exposure and counting was principally the same as in experiment 2. In contrast to natural field conditions the 800 sown seeds were watered regularly during dry periods.

Characterisation of germination

For each laboratory and outdoor treatment, the percentage of seeds that had germinated after the end of the observation period was determined. To correlate temporal patterns of outdoor germination with thermal conditions we used meteorological data from the nearby (ca. 500 m) climate research station Linden. Starting on the last day with a daily average temperature below 1 °C we calculated the number of days with daily averages above 5 °C as well as total temperature sums of daily averages until the onset and the first pronounced peak in outdoor germination, respectively. Both temperature traits revealed to be highly correlated ($r^2 = 0.98$), thus we used only the number of days with averages above 5 °C for further numerical analyses.

To describe germination characteristics for each species the following values were calculated:

LOPT, the optimal temperature for germination, was calculated as weighted average of germination rates over all constant temperatures in the climate chamber experiment, according to the mode described by OLFF et al. (1994): [$(3P_3 + 7P_7 + 10P_{10} + 15P_{15} + 20P_{20} + 25P_{25} + 30P_{30} + 35P_{35}) / (P_3 + P_7 + P_{10} + P_{15} + P_{20} + P_{25} + P_{30} + P_{35})$)] in which P_3 was percentage germination at 3 °C, P_7 percentage germination at 7 °C, and so on.

LMAX, the maximum germination rate, was defined as the highest percentage of germination in one of the climate chamber treatments after six weeks.

GFAS was the maximum germination rate at constant temperature after 7 days in the climate chamber.

TFAS was the temperature at which *GFAS* was reached.

LOW was the lowest constant temperature with at least 5 % germination.

HIGH was the highest constant temperature with at least 5 % germination.

AMP was the range in degrees Kelvin between *HIGH* and *LOW*.

ALT was the difference in germination rate at fluctuating temperatures of 5/15 °C in comparison to the constant temperature of 15 °C

STRAT, the effect of cold wet stratification, was the difference in germination rate in comparison with *ALT*.

FMAX was the maximum germination rate under outdoor conditions.

ONSET was the date of outdoor germination begin in days with daily averages above 5 °C counted from the last day with a daily average below 1 °C .

FOPT was the date of the first germination peak under outdoor conditions (measured as for *ONSET*).

PEAK1 was the maximum germination during one single count as a percentage of total final outdoor germination.

PEAK4 was the maximum germination during the four following weeks, measured as for *PEAK1*.

SPAN was the period in days between the first and last count, in which at least 5 % of total final outdoor germination occurred.

Data analysis

The correlation structure of germination traits was investigated by principal component analysis (PCA) on a data matrix with z-transformed standardised variable values (Legendre & Legendre 1998). The traits *LOPT, TFAS, HIGH and LOW* were not included in the analysis because their calculation requires germination under constant temperatures in the climate chamber, which did not occur in a number of species. As PCA does not accept missing values, the inclusion of these traits would have lowered the number of analysed species. Correlations between single germination traits and PCA-axis scores, on the one hand, and species attributes such as seed mass (Hölzel & Otte accepted a), seed longevity, threat status, range size and type on the other hand were examined by non-parametric Spearman rank correlation coefficients. As a measure of seed longevity we applied the seed accumulation index (SAI) given in Hölzel & Otte (accepted a) for 36 of the studied species. To describe range size on a Central European scale we used grid frequency data from the German flora mapping project provided by the electronic resource Floraweb (BfN 2003). Threat status was assessed by a simple ordinal scale ranging from 0 (unthreatened) to 2 (strongly threatened) based on the list of Korneck et al. (1996). In the same way river corridor confinement was allocated from the specifications of Korsch (1999) and Burkart (2001). Differences between groups were tested using a non-parametric Mann-Whitney U-test. All calculations were carried out with STATISTICA 6.0.

Results

Patterns of single germination traits

Under laboratory conditions only a limited proportion of the studied species (Group A, Table 2) germinated with high rates over a wide range of constant temperatures (*AMP*) or showed a clear preference for low germination temperatures (*OPT, LOW*). In contrast, many species reached maximum germination rates only at relatively high constant temperatures (*OPT*) above 20 °C (Group B, Table 2). However, in all of these species except *Althaea officinalis* and *Barbarea stricta* germination rates increased considerably after 8 weeks of cold wet stratification (*STRAT*) and following low fluctuating temperatures (5/15 °C), most strikingly in *Lythrum salicaria* and *Sanguisorba officinalis*. Positive effects of fluctuating temperatures (*ALT*) alone without stratification were less pronounced and restricted to a few species such as *Cardamine parviflora* and *Cirsium tuberosum*. In some other species they even caused a decline in germination rate. In Apiaceae and some other species (Group C, Table 2) germination under laboratory conditions was confined to the stratification treatment (*STRAT*).

A surprisingly high number of species (Group D, Table 2) almost completely failed to germinate under all laboratory treatments, showing maximum germination rates below 5 %. Under outdoor conditions in all of these species (except *Cnidium dubium*) the germination rates (*FMAX*) increased considerably and were usually well above 20 %.

In the outdoor treatment about half of the species had an initial pronounced germination peak (*FOPT*) after around 20 days with daily averages above 5 °C, which is equal to a temperature sum of ca. 200 °C. Most species with a highly positive response to the cold wet stratification treatment under laboratory conditions (*STRAT*) were found within this group. *Galium boreale, Cnidium dubium, Sanguisorba officinalis, Selinum carvifolia* and all *Viola* species showed slightly higher temperature requirements (*FOPT*) with peak germination about two weeks later (around 30 days with averages >5 °C, temperature sum > 300 °C).

However, there were also some species with explicitly deviating behaviour indicating significantly lower or higher temperature requirements. In *Cerastium dubium* and *Cardamine parviflora* outdoor germination started considerably earlier (< 10 days with averages > 5 °C, temperature sum < 100 ° C). In contrast, *Althaea officinalis*, all *Carex* species*, Inula britannica*, *I. salicina, Potentilla reptans, Scutellaria hastifolia* and *Thalictrum flavum* showed a much higher temperature requirement with a first germination peak occurring only

Table 2. Germination traits (for abbreviations see chapter 2. 5) of 42 flood-meadow species (for abbreviations see Table 1): (s) = as temperature sum, (d) = in days, n.m. = not measured.

	Species	OPT	LMAX	TFAS	GFAS	AMP	LOW	HIGH	ALT	STRAT	FMAX	ONSET(s)	ONSET (d)	FOPT(s)	FOPT (d)	PEAK1	PEAK4	SPAN
A	Cera dubi	10.6	100	15	75	17	3	20	3	0	78	81	8	81	8	96	100	0
	Alop prat	11.2	16	25	2	8	7	15	10	-6	36	142	15	142	15	55	99	28
	Card parv	13.8	98	10	65	27	3	30	46	-1	96	81	8	81	8	75	98	14
	Gali wirt	14.4	82	15	28	27	7	30	-2	-40	88	81	9	137	15	41	91	18
	Vero serp	15.1	100	20	92	22	3	25	0	-1	93	200	17	200	17	78	99	16
	Rume thyr	15.3	95	10	90	27	3	30	2	-16	81	107	9	187	17	31	66	28
	Fest arun	16.3	97	20	88	27	3	30	-2	-20	95	142	15	181	19	70	98	14
	Vero pere	18.3	98	20	73	18	7	25	-21	60	59	181	19	194	19	28	95	38
	Valer prat	18.8	69	25	53	27	3	30	14	-16	64	197	21	197	21	46	95	21
B	Gali bore	20.1	38	20	1	20	10	30	-19	21	71	197	21	313	35	47	78	48
	Pseu long	21.9	91	25	46	28	7	35	17	32	65	197	21	197	21	35	61	48
	Arab nemo	22.6	84	30	82	20	10	30	12	32	87	197	21	197	21	93	99	48
	Care spic	22.9	28	-	0	5	20	25	-2	16	84	329	35	533	56	39	88	28
	Cirs tube	23.0	66	25	51	23	7	30	35	14	46	157	16	197	21	34	81	32
	Sang offi	25.4	93	30	36	20	15	35	3	74	63	194	21	286	32	34	84	28
	Alli angu	25.8	30	25	16	10	20	30	4	22	94	157	16	197	21	50	94	18
	Serr tinc	26.5	36	35	3	20	15	35	-2	28	35	197	21	197	21	77	97	18
	Lyth sali	26.6	100	25	93	15	20	35	10	88	54	234	21	234	21	34	86	35
	Puli dys	28.3	52	30	8	5	25	30	2	33	48	181	19	181	19	53	90	38
	Inul brit	28.8	58	25	47	15	20	35	12	25	66	252	28	269	30	39	88	35
	Inul sali	29.1	75	35	73	15	20	35	0	0	17	316	34	501	49	33	74	22
	Barb stri	29.9	99	30	98	10	25	35	0	0	75	200	17	200	17	93	100	9
	Alth offi	30.5	15	30	10	10	25	35	0	0	39	828	80	828	80	31	62	90
	Thal flav	27.6	15	-	0	0	30	30	0	14	70	414	39	520	47	13	48	111
C	Cnid dubi	-	12	-	0	0	-	-	2	11	8	197	21	313	35	37	51	84
	Sila sila	-	42	-	0	0	-	-	5	37	25	197	21	197	21	84	97	18
	Peuc offi	-	38	-	0	0	-	-	0	38	48	157	16	197	21	65	95	18
	Euph palu	-	23	-	0	0	-	-	0	22	76	157	16	181	19	16	39	149
	Symp offi	-	31	-	0	0	-	-	5	26	38	181	19	181	19	25	61	45
	Sene palu	-	21	-	0	0	-	-	0	21	74	200	17	234	21	45	71	44
D	Viol pers	-	5	-	0	0	-	-	0	0	18	337	36	337	36	46	63	388
	Viol elat	-	2	-	0	0	-	-	0	2	59	295	33	342	37	21	59	77
	Viol pumi	-	2	-	0	0	-	-	0	2	66	295	33	342	37	25	92	35
	Care prae	-	0	-	0	0	-	-	0	0	24	280	28	466	49	38	82	42
	Care tome	-	0	-	0	0	-	-	0	0	54	490	56	828	80	29	38	381
	Iris spuria	-	1	-	0	0	-	-	1	-2	76	157	16	2156	164	48	84	35
	Pote rept	-	6	-	0	0	-	-	0	6	68	280	28	466	49	28	75	42
	Scut hast	-	0	-	0	0	-	-	0	0	62	466	49	882	80	19	53	88
	Elym repe	-	3	-	0	0	-	-	2	0	67	181	19	181	19	51	91	24
	Poa angu	-	2	-	0	0	-	-	2	-1	32	181	19	235	24	21	86	45
	Lath palu	n.m	n.m	n.m	n.m	n.m	n.m	n.m	n.m	n.m	35	101	11	235	24	28	30	724
	Seli carv	n.m	n.m	n.m	n.m	n.m	n.m	n.m	n.m	n.m	55	295	33	383	43	56	92	33

after 50 days with averages >5 °C and a temperature sum >500 °C. In both response groups these results largely coincided with the germination temperature requirements found in the laboratory experiment.

In 60 % of the studied species more than 80 % of the final outdoor germination took place within 4 weeks. In some, such as *Arabis nemorensis, Cerastium dubium, Serratula tinctoria Silaum silaus* and *Veronica serpyllifolia* such rates were even reached during a single count. This particularly synchronous germination behaviour is contrasted, by other species that emerged over a long period with low but constant rates. This was most obvious in *Carex tomentosa, Euphorbia palustris, Scutellaria hastifolia,* and *Thalictrum flavum*.

*Multivariate analysis of germination traits*

The principal-component analysis (PCA) revealed the correlation structure of the germination traits (Table 3, Fig. 1). The first factor axis, which explained the bulk of the variance (40.99 %), reflected a continuous gradient from species with high, rapid and strongly synchronised germination over a wide range of temperatures (left side of Fig. 2)

Table 3. Correlation between factor axes of PCA ordination and germination traits. High correlations are given in bold (for abbreviations of germination traits see chapter 2. 5).

	FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4
Eigenvalue	4.51	1.34	1.19	0.96
Variance (%)	40.99	12.16	10.81	8.71
LMAX	**-0.89**	-0.26	0.26	-0.15
GFAS	**-0.81**	-0.38	0.14	-0.16
AMP	**-0.76**	**-0.50**	0.06	-0.05
PEAK1	**-0.64**	0,26	-0.25	0.04
PEAK4	**-0.73**	**0.47**	-0.22	-0.06
ALT	-0.35	-0.24	0.05	**-0.78**
STRAT	-0.08	0,29	**0.81**	-0.25
FMAX	**-0.51**	-0.28	-0.42	-0.29
ONSET	**0.65**	-0.36	0.08	-0.18
FOPT	**0.59**	-0.20	-0.34	-0.30
SPAN	**0.62**	**-0.43**	0.14	0.12
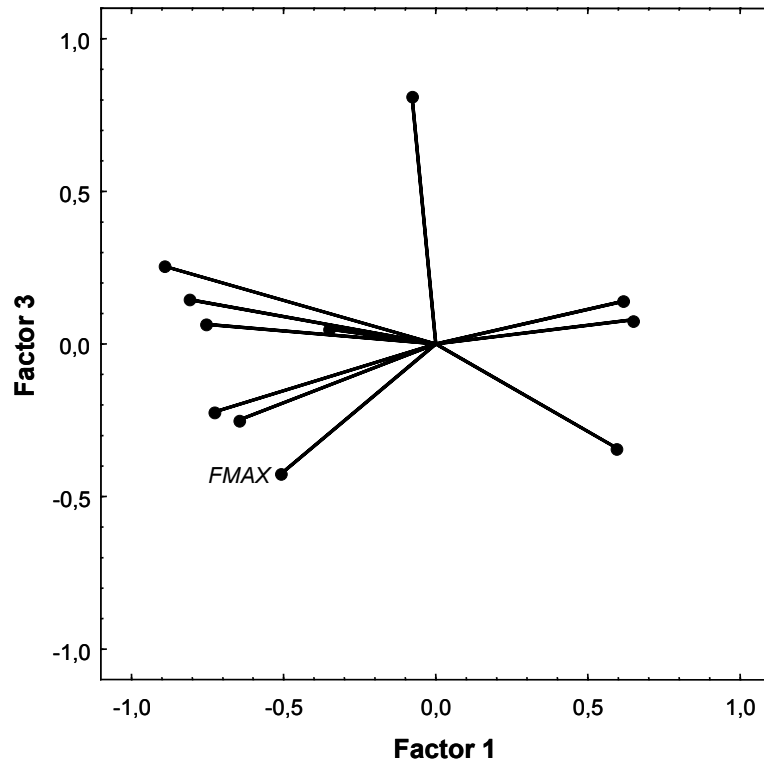
Fig. 1. Biplot displaying correlation structure of germination traits along factor axis 1 and 3 in PCA-ordination (for abbreviations of germination traits see chapter 2. 5).
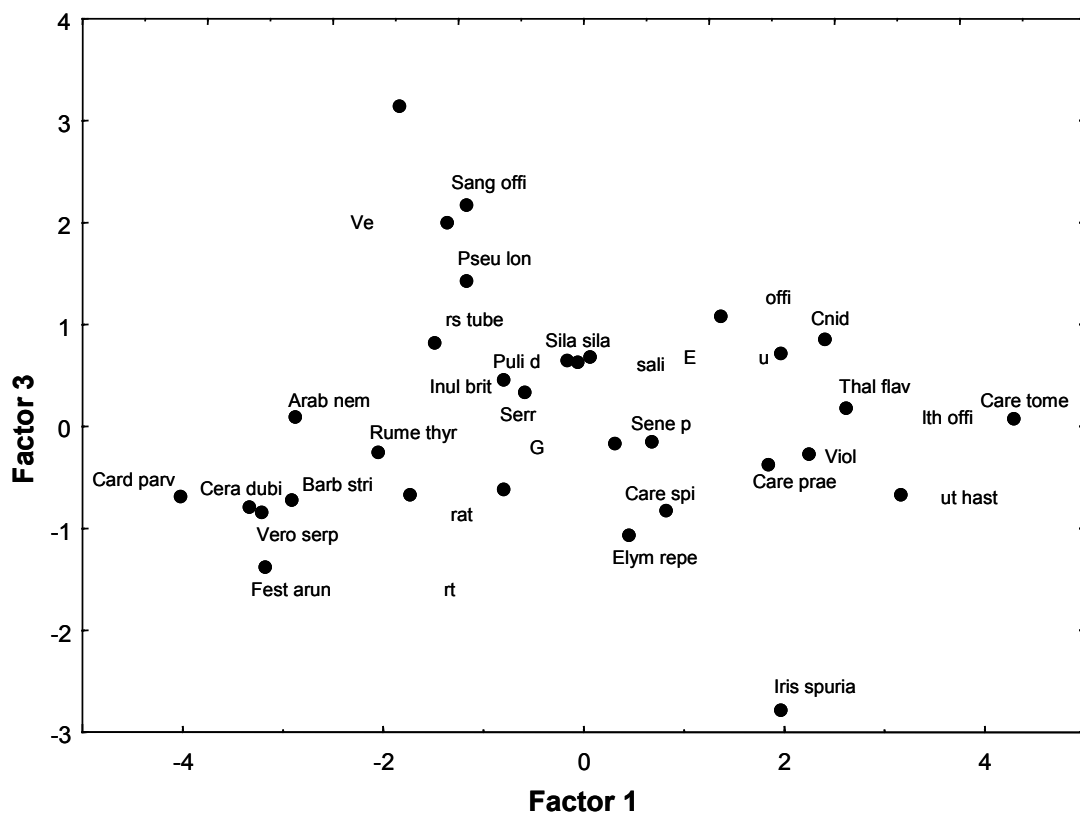
Fig. 2. Distribution of species in PCA ordination space along factor axes 1 and 3 (for abbreviations of species names see Table 1).

to those with high temperature requirements and a delayed germination over a relatively long period (right side of Fig. 2). Factor axis 2 largely coincided with the variation of *AMP, SPAN* on the one hand and *PEAK4.*on the other hand. Factor axes 3 and 4 predominantly represented the variance in *STRAT* and *ALT,* respectively (Table 3, Fig.1 and 2).

Timing of germination after natural seed shedding

In experiment 3, in which the timing of germination after natural seed release was investigated the following major response types appeared (Fig. 3):

I) Potential for complete germination within the season of shedding: Among the species used in this experiment only the therophytes *Cardamine parviflora* and *Cerastium dubium* belong to this response type. Seeds of these species reached 100 % of the final germination rate within two months after shedding in late May. Whereas germination started directly after sowing in *Cardamine parviflora* the onset of germination in *Cerastium dubium* was about 4 weeks later.

II) Potential for partial germination directly after shedding in late summer with a second peak in March/April of the following year: All species belonging to this response group germinated to a certain degree directly after shedding. However, germination stopped abruptly by the end of September at the latest, when daily averages were usually still well above 10 °C. Spring germination, in contrast, started at the earliest in late February, with a significant peak in March at temperatures considerably lower than those in early autumn when germination stopped. Only in *Inula salicina* did germination start as late as April, indicating significantly higher temperature requirements.

III) No germination in the year of shedding, but almost complete and rapid germination in March/April of the following year: Most species of this group comprise Apiaceae with relatively late seed release (September), but species with a much earlier shedding are also represented, such as *Galium boreale*. Early spring germination occurred very abruptly and was highly synchronised. Only *Cnidium dubium* showed a slightly extended germination period towards summer.

IV) Delayed, slow germination over an extended period, starting in the first summer after shedding: In most species of this response type significant germination started no earlier than late April or May and continued over the whole summer season. In *Carex tomentosa* peak germination occurred only in the second, and in *Lathyrus palustris* even in the third and fourth year (data not shown) after shedding.
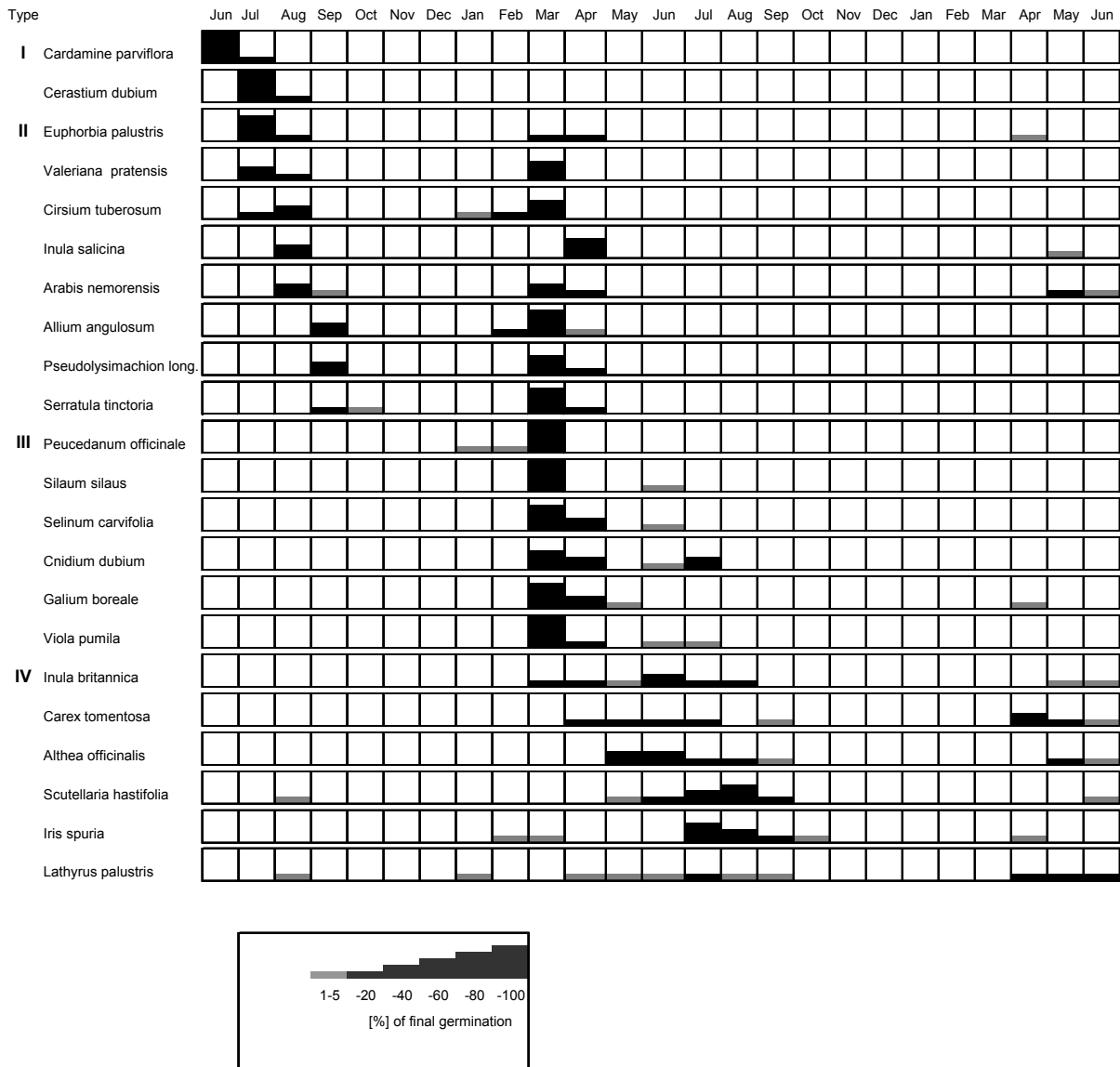
Fig. 3. Timing in germination of freshly shed seeds under outdoor conditions.

Correlation between germination characteristics and other species traits

According to Spearman rank correlation species with small seed mass tended to germinate faster (*GFAS*) ($r = -0.51$, $p < 0.001$) and had a higher temperature amplitude (*AMP*) ($r = -0.38$, $p < 0.05$) and maximum germination rate (*LMAX*) ($r = -0.44$, $p < 0.01$) under laboratory conditions. No further correlations between seed weight and germination characteristics were found.

Surprisingly, the tendency in species to build up long-term persistent soil seed banks was positively correlated with fast germination under laboratory conditions (*GFAS*) (r = 0.40 *p* = 0.02) and a high outdoor germination rate (*FMAX*) (r = 0.35 *p* = 0.04).

Spearman rank correlation also revealed a significant but relatively weak correlation (r = 0.36 *p* = 0.02) between the first factor axis in PCA ordination and Red List status. A similar relationship was found between Red List status and single germination traits such as *LMAX* (r = -0.43 p = 0.006), *GFAS* (r = -0.32 *p* = 0.04), *FOPT* (0.43 *p* = 0.03) and *SPAN* (r = 0.37 *p* = 0.02), indicating a trend towards higher dormancy levels, increased temperature requirements and asynchronous germination in endangered species. In contrast, there was no relationship at all between germination traits and river corridor confinement or Central European range size. Identical results (not shown) were obtained in group comparisons by the Mann-Whitney U-test .

Discussion

Germination strategies in flood-meadows

In flood-meadows of the studied type the survival of insufficiently developed seedlings will often be severely hampered by frost damage and prolonged flooding during the winter season (e. g. Voesenek & Blom 1992). Equally, open patches with poor competition are more likely to occur in spring after the retreat of flood water, which often creates gaps in established vegetation. Consequently, it makes ecological sense that many of the flood-meadow species studied exhibited various levels of conditional or even strict dormancy in the year of shedding, while there were fewer species that germinated spontaneously at high rates over a wide temperature range including lower temperatures.

The existing diversity of germination response types in flood-meadow species was clearly visible in PCA-ordination, which reflected a continuous gradient of increasing dormancy levels along the first factor axis (Fig. 1) with *Cardamine parvifolia* (non dormant) and *Carex tomentosa* (highly dormant) as the most extreme points of the spectrum (Fig. 2). An almost identical main gradient in germination traits was found by Olff et al. (1994) in the flora of Dutch wet meadows.

A high capacity for spontaneous germination directly after shedding is typical of many dominant Poaceae in temperate grasslands (Thompson & Grime 1979), which could be

confirmed in our study for *Festuca arundinacea*. The relatively low total germination rates compared to other studies (GRIME et al. 1981) achieved in some dominant grasses of flood-meadows, such as *Alopecurus pratensis, Elymus repens* and *Poa angustifolia*, are probably partly due to heavy mildew infestation within the climate chamber treatments and/or low quality of the seeds used.

According to Grime (2001) two major strategies can be distinguished that enable seeds to delay germination until the following spring and summer season: i) high temperature requirements for germination, which are usually not fulfilled during the autumn season, ii) a requirement for chilling to break dormancy. In accordance with Washitani & Masuda (1990), who studied germination characteristics in a moist tall grassland community in Japan, both strategy types could be found. However, our study clearly established that some species may combine both principal strategies for the avoidance of harmful late autumn and winter germination. Within the year of shedding many of the studied species such as *Allium angulosum, Arabis nemorensis, Cirsium tuberosum, Pseudolysimachion longifolium* and others showed relatively high temperature requirements to reach significant germination rates, but came out of primary conditional dormancy (Baskin & Baskin 2001) after a period of cold wet stratification. This phenomenon could be observed in the climate chamber treatments as well as under outdoor conditions. Ecologically this means that germination will stop well before the onset of the cool season while the same species are able to exploit gaps at relatively low temperatures in early spring.

Under natural habitat conditions in flood-meadows dormancy after shedding will often also be enforced by environmental constraints such as drought or shading through established vegetation. Additionally, in some species with high temperature requirements such as *Arabis nemorensis*, *Inula britannica* and *Sanguisorba officinalis* autumn germination is simply avoided by a strongly delayed seed release.

Besides conditional dormancy enforced by high temperature requirements prior to chilling, hardening of seed shells due to dry and warm weather conditions (or dry storage prior to laboratory experiments) may also be responsible for poor germination in the year of shedding (e. g. Otte 1996, Jensen 2001). This applies in particular to species that lack a response to the stratification treatment in the climate chamber but have high early spring germination rates such as *Barbarea stricta*, *Viola elatior* and *V. pumila* or those with strongly increased outdoor germination rates such as *Allium angulosum, Euphorbia palustris* and *Galium boreale.* All these species exhibit relatively hard and compact seed shells that obviously require softening in the course of prolonged outdoor stratification. In particular, *Euphorbia palustris* showed a

high initial germination rate only in seeds sown directly after shedding. When seeds were dry stored and sown in winter germination extended over a much longer period. This phenomenon may be referred to as secondary induced physical dormancy (Baskin & Baskin 2001).

As in other studies (Grime et al. 1981, Patzelt 1998) Apiaceae proved to exhibit a strict chilling requirement due to morphophysiological dormancy caused by an underdeveloped embryo (Stokes 1952, Baskin & Baskin 2001), which necessarily delays germination until the spring season.

In accordance with Milberg & Andersson (1998) we found that differences in conditional dormancy were largely compensated by cold stratification under outdoor conditions resulting in a highly synchronised germination peak in March and early April. However, there was also a group of species in which high temperature requirements did not disappear after chilling. *Althaea officinalis, Potentilla reptans Thalictrum flavum and Scutellaria hastifolia* and the *Carex*-species obviously require an obligatory extended period of warm moist incubation under outdoor conditions to come out of dormancy. This confers with results reported by other authors (Baskin & Baskin 2001, Patzelt 1998 and Schütz 1997, 2000 a, Ziron 2002). In most of these species, high temperature requirements go hand in hand with a strongly delayed and asynchronous germination over the whole summer period. Conspicuously, species with the most delayed and asynchronous germination have relatively large and compact seeds with features of physical dormancy such as water-impermeable testa (*Lathyrus palustris*) or particularly thick and hard seed coats (*Carex tomentosa, Iris spuria*). After the breaking of physical dormancy, at least *Lathyrus palustris* and *Iris spuria* exhibited no particular temperature requirements for germination, as has been found in other studies for species of the same genera (Baskin & Baskin 2001, Grime et al. 1981).

Asynchronous germination can be seen as a strategy to minimise the risk of total failure of seed regeneration due to regularly occurring disruptive environmental constraints such as drought, which is particularly relevant in species with a delayed germination during summer. Equally, this strategy seems to be a benefit in amphibious habitats with strongly fluctuating moisture conditions. Consequently, in our study high temperature requirements and/or delayed and asynchronous germination were most common in perennial species with a clear preference for the dampest parts of flood-meadows such as *Euphorbia palustris, Lathyrus palustris, Scutellaria hastifolia, Thalictrum flavum* and *Viola persicifolia*. According to Grime et al (1981) and Baskin & Baskin (2001) high temperature requirements and dormancy levels are a common feature in temperate wetland species.

Germination characteristics and seed bank persistence

In previous studies (Hölzel & Otte 2001, Hölzel & Otte accepted a) species, such as *Arabis nemorensis, Cardamine parviflora, Cerastium dubium, Lythrum salicaria, Pseudolysimachium longifolium, Potentilla reptans, Veronica peregrina, V. serpyllifolia* were revealed to build up large long-term persistent seed banks. Surprisingly, with the exception of *Potentilla reptans*, all these species exhibited relatively low dormancy levels and a high potential for fast germination in light. Thus, the formation of a long-term persistent soil seed bank is obviously completely due to dark dormancy. Typically, all these species have very small seeds, which according to Grime (2001) almost generally show an obligatory light requirement for germination. There seems to be an interesting link between the higher probability of burial in small seeds (Thompson et al. 1993, Bekker et al. 1998) and their capacity for fast and almost complete germination in light. Species with regeneration strategies involving a large persistent soil seed bank typically exploit gaps in established vegetation caused by stochastic, largely unpredictable disturbances (Thompson & Grime 1979, Grime 2001). Thus, the ability of spontaneous and rapid germination after exposure to light is an essential prerequisite for the successful exploitation of such temporary gaps. This strategy is of particular importance in ephemeral annuals of flood-meadows like *Cardamine parviflora, Cerastium dubium* and *Veronica peregrina*. However, even among these annuals significant differences could be found in the main period of germination. *Cerastium dubium* exhibited a delayed germination directly after shedding obviously due to a requirement for warm stratification to come out of dormancy at high temperatures, which is typical of facultative winter annuals (e. g. Baskin & Baskin 1983a). In seed bank experiments (Hölzel & Otte 2001) this species showed a pronounced germination peak in late summer and early autumn. Equally, mass occurrence of *Cerastium dubium* in the field coincides with years of low winter flooding intensity (Hölzel 1999). In contrast, *Veronica peregrina* is preferably a summer annual due to its strong response to cold wet stratification, which was also found by Baskin & Baskin (1983b).

Some species exhibiting particularly high dormancy levels such as *Carex tomentosa* and *Viola persicifolia* were also found to create long-term persistent soil seed banks (Hölzel & Otte accepted a). However, their densities were usually much lower than in small seeded species, which may be caused by a lower probability of burial as well as a higher potential for germination in darkness (Grime 2001). Our results suggest that only in relatively large seeded

species are dormancy levels established in germination experiments a good predictor for the capacity of a certain species to build up persistent seed banks.

Germination characteristics and rarification

We did not find any single germination trait or a multivariate response type that corresponded with the confinement of species to large river corridors. There appears to be nothing really particular in the germination behaviour of river corridor plants that could explain their conspicuous habitat and range restriction in Central Europe. A comparable set with similar variability in germination traits has been found in other temperate wet grassland communities (Washitani & Masuda 1990, Olff et al. 1994, Patzelt 1998, Jensen 2001).

Equally, there were no significant differences in germination characteristics between species with small or large Central European range. Comparable results were obtained by Thompson et al. (1999) who found no relationship between germination traits and range size of vascular plants in the British flora. Although there was a significant albeit weak trend for higher dormancy levels in endangered species, we found little evidence for the assumption made by Schütz (2000 b) that germination traits may play a prominent role in the causal understanding of rarity and decline. Regeneration characteristics are obviously outweighed by other species traits such as habitat specialism and the respective life strategy in the established phase, which have proved to be much better predictors of rarification processes in the Western and Central European flora (Korneck et al 1998, Thompson et al. 1999, Grime 2001).

Conclusions for restoration management

In species with high temperature requirements causing delayed and asynchronous summer germination, recruitment in flood-meadows will often fail due to drought and competition through established vegetation. The frequent failure of regeneration by seeds does not usually diminish the viability of existing populations, since most of the relevant species are long lived and exhibit extensive clonal growth. In contrast, this could become a serious problem in habitat restoration, in which species re-establishment crucially depends on regeneration by introduced seeds (e. g. Patzelt 1998). In a plant material transfer experiment aimed at recreation of a species-rich flood-meadow (Hölzel & Otte 2003), we found poor establishment success after four years in a number of species with delayed and asynchronous germination behaviour, such as *Lathyrus palustris, Scutellaria hastifolia, Thalictrum flavum* and almost all

Carex species. Especially in *Carex* species the very specific and narrow germination requirements are obviously a major constraint and may explain their notoriously low colonisation capacity (Grime et al. 1988, Budelsky & Galatowitsch 1999, Schütz 2000a). In most species with high germination temperature requirements, successful regeneration by seeds is probably confined to certain years with particularly favourable moisture conditions and low competition by established vegetation, as may occur in the course of prolonged early summer flooding and following draw-down (Jutila 2001, Hölzel & Otte 2003, Hölzel & Otte accepted b).

As demonstrated in this study the majority of flood-meadow species are able to exploit the particular favourable recruitment conditions (constant moisture supply, open vegetation structure) prevailing in early spring (March/early April). Management schemes that support the creation of open vegetation structures and patches of bare soil at this time of the year - such as mowing and removal of plant litter, aftermath pasture or scarring of the sward - may actively enhance regeneration by seeds (e. g. Kotorová & Lepš 1999).

Kapitel 6

Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material

Norbert Hölzel & Annette Otte

Abstract

In previous studies, limited dispersal was revealed to be the main obstacle to restoration of species-rich flood-meadows along the northern Upper Rhine in Germany. To overcome dispersal limitation we transferred freshly mown plant material from species-rich source stands to a restoration site on a former arable field (1.3 ha). Before plant material application, topsoil was removed to accelerate nutrient impoverishment and create favourable conditions for seedling recruitment.

Topsoil removal led to a drastic reduction in organic matter and essential mineral nutrients to the level of target communities (P) or even below (N, K). At a removal depth of 30 cm, content of the soil seed bank comprised exclusively of annual arable weeds, ruderals and some common grassland species, declined by 60 to 80 %, while at a removal depth of 50 cm the seed bank was almost completely eliminated. With few exceptions, all species recorded in plant material were found established at the restoration site. However, the overall correlation between seed content in plant material and establishment success was not very high.

Vegetation development at the restoration site was characterised by a rapid decline in arable weeds and ruderals, while resident grassland species and species transferred with plant material showed a steep increase from the third year onwards. After four years as many as 102 species were established that could be exclusively accounted to plant material transfer, among them many rare and highly endangered plants. Establishment of species from plant material was most successful in regularly flooded plots, due to the suppression of competitors as well as the creation of favourable moisture conditions for seedling emergence.

Diaspore transfer with plant material proved to be an extremely successful method in restoring species-rich grasslands. However, high quality of plant material and suitable site

conditions with low competition in early stages of succession seem to be essential prerequisites.

Keywords: *Cnidion*, Dispersal limitation, Grassland biodiversity, *Molinion*, Nature conservation, Path analysis, Seedling recruitment, Seed bank.

Nomenclature: Wisskirchen & Haeupler 1998

Introduction

In Central Europe, flood meadows of the *Cnidion* alliance are strictly confined to large lowland river corridors with subcontinental climatic conditions such as the valleys of the rivers Rhine, Elbe and Danube (Burkart 2001). Due to flood control, drainage, intensified use and conversion into arable land such habitats have become extremely rare and a considerable part of the characteristic flora such as *Arabis nemorensis, Cnidium dubium, Iris spuria* and *Viola pumila* has been categorised as species of Central European conservation concern (Schnittler & Günther 1999). Remnant populations of these highly endangered species are still found along the northern Upper Rhine, where they exist in mesotrophic *Cnidion* as well as in oligotrophic alluvial *Molinion* communities (Böger 1991, Hölzel 1999). In this region, large-scale restoration efforts aimed at the recreation of species-rich flood meadows at sites of former arable fields have been pursued for more than 15 years (Hölzel et al. 2002). A recent evaluation of these restoration measures revealed very poor success in re-establishing rare and endangered target species and communities, even at sites with successful lowering of soil nutrient status and productivity by regular mowing and haymaking without fertilizer application (Donath et al. 2003). These findings are in accordance with earlier studies on grassland restoration that identified the lack of viable seeds in the soil seed bank and limited dispersal of target species as the main constraints to restoration of species-rich grasslands (Bakker 1989, Berendse et al. 1992, Hutchings & Booth 1996a, Bakker et al. 1996, Pegtel et al. 1996, Muller et al. 1998, Bakker & Berendse 1999). All these studies revealed that low productivity is essential but that restoration success cannot be guaranteed in the absence of substantial seed resources. Analogous results were obtained in seed addition experiments that confirmed recruitment limitation as an important factor governing species-richness in

grasslands (Tilman 1997, Stampfli & Zeiter 1999, Turnbull et al. 2000, Pywell et al. 2002, Smith et al. 2002).

In previous years diaspore transfer with plant material has been increasingly tested as a supplementary technique in restoration ecology to overcome dispersal limitation of target species. Such measures showed considerable, but not always compelling success (McDonald 1993, Molder 1995, Biewer 1997, Tränkle 1997, Patzelt 1998, Pfadenhauer & Miller 2000, Kirmer & Mahn 2001). In fact, plant material or hay transfer is an old and traditional method that was widely used by farmers until the middle of the 20th century to create and improve grasslands (Bonn & Poschlod 1998). The fact that this agricultural practice ceased in modern times is often regarded as one main reason for dispersal limitation of species in agricultural habitats (Bakker et al. 1996).

In comparison with direct sowing of seeds, the application of diaspore transfer with plant material in habitat restoration has striking advantages: (i) potentially the entire species-pool of a plant community may be covered by material transfer, including rare species of which sowing material is often not available; (ii) the genetic variability of locally adapted ecotypes and races is preserved and maintained (e.g. Molder 1995, Pegtel 1998); (iii) on bare substrates with extreme micro-climatical conditions plant material may provide "safe sites" for seedling recruitment (Patzelt 1998, Tränkle 1997); (iv) compared to the relatively laborious and expensive collection, propagation and sowing of seeds (e.g. Stevenson et al. 2001), diaspore transfer with plant material is a cheap method that is applicable to large areas and different types of habitats. Despite these benefits, however, large-scale practical applications in restoration projects (e.g. Pfadenhauer & Miller 2000) are still scarce. Most of the previous work was conducted as small-scale studies that often comprised only a few dozens of m² (Molder 1995, Kirmer & Mahn 2001). For many habitat types and species groups – such as the rare subcontinental flood-meadows – experience regarding the effectiveness of plant material transfer is still completely lacking.

Factors that may hamper the success in plant material transfer experiments are: (i) low quality of plant material in terms of species composition and seed densities, (ii) unfavourable site conditions (soil nutrient status, moisture regime) at the target area, (iii) poor conditions for seedling recruitment due to dense canopy structure of established vegetation, (iv) adverse weather conditions (drought, frost) during the germination period causing high seedling mortality. Generally, the relative importance and interaction of these potentially hampering factors are strongly context dependent so that it is difficult to define common rules und guidelines without broad-scale field evidence (Bosshard 1999).

Recently, topsoil removal has been revealed as a very effective measure to speed up the impoverishment of nutrient-enriched sites, by concurrently forming bare substrate with poor competition (Aerts et al. 1995, Jansen & Roelofs 1996, van Diggelen et al. 1997, Patzelt et al. 2001, Tallowin & Smith 2001, Verhagen et al. 2001). Thus, we used this technique in combination with plant material transfer to create favourable site conditions for seedling recruitment. Additional positive effects we expected were: (i) increase of flooding frequency due to surface lowering, (ii) depletion of the soil seed bank and the established vegetation, (iii) reactivation of deeply buried viable seeds of target species.

Due to the high heterogeneity in seed content and species composition of plant material it is practically impossible to perform well defined factorial experiments with true replicates in randomised order (e.g. Molder 1995, Bosshard 1999). The main object of our study, however, was not to test a mechanistic hypothesis of universal validity, but rather to evaluate the efficiency of material transfer as a method for restoration practice in a concrete example. Thus we chose an observational approach that allowed us to conduct our study on a large scale and under a realistic practical scenario.

To assess the influence of plant material transfer on succession we separately analysed the two major compartments of the species pool, i.e. plant material and soil seed bank, and observed the vegetation development with different treatment variants over four years. Furthermore, we investigated the effects of topsoil removal on soil nutrient status by comparing of the original arable field with removal plots and source stands.

Materials and methods

Study site

The study site comprises a former arable field (1.3 ha) situated in the fossil dyke-protected compartment of the holocene flood-plain of the northern Upper Rhine about 30 km southwest of Frankfurt, Germany (49°51′ N / 8°23′ E, 85 m a.s.l.). The hydrological site conditions are characterised by strong fluctuations of the ground water table, averaging almost two meters per year (Böger 1991) depending on the water level of the nearby (about 300 m) main channel of the River Rhine. Due to the extremely high clay content the soil shows some unfavourable physical features such as poor aeration in wet periods, low storage capacity of plant available water and hardening in summer. During the observation period major flooding events that

lasted for several weeks occurred in March and May/June 1999 and in March/April 2001, whereas dry periods were observed every summer from early May onwards.

a) Topsoil removal depth: black   50 cm   grey   30 cm

50 m

160 m

b) Plant material treatments:

Black: Cnidion   Grey: Molinion   White: Zero plots

c) Flooding height: Black: > 20 cm   Dark grey: 10-20 cm

Light grey: < 10 cm   White: unflooded
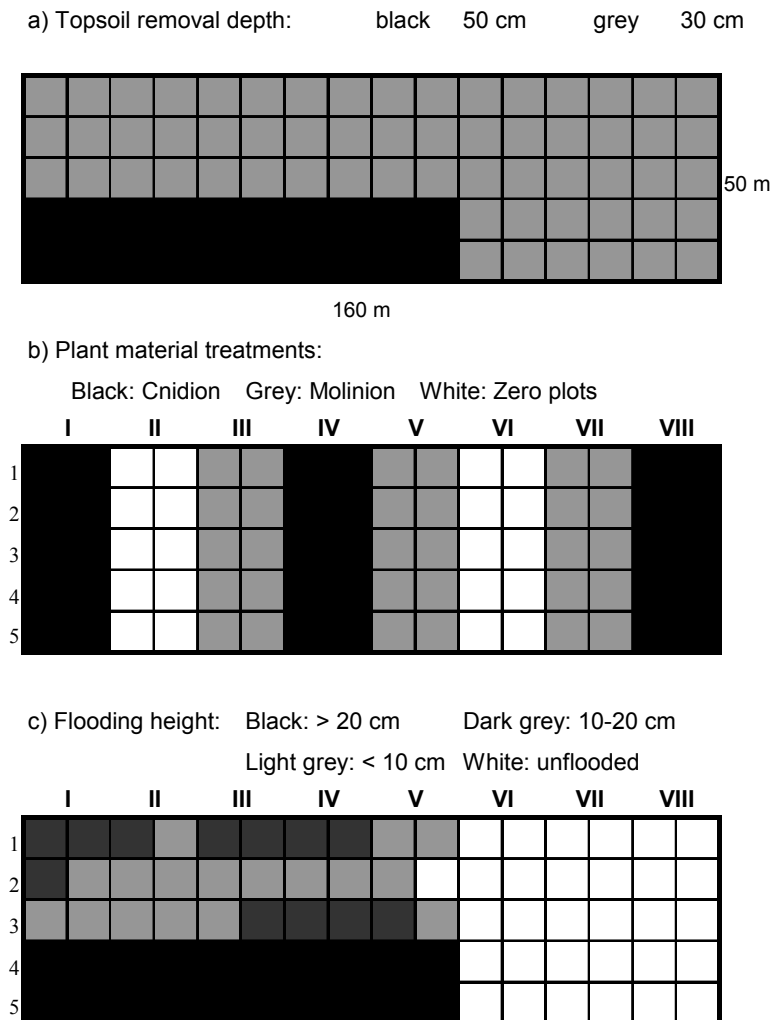
Fig. 1: Study site and treatments.

Restoration measures

For more than 20 years the study site was intensively used as an arable field until it fell fallow for nature conservation purposes in 1994. In late August 1997, the nutrient-rich topsoil was removed from almost the entire field (about 1.3 ha) down to a depth of 30 and 50 cm (Fig. 1).

After topsoil removal the area was subdivided into 8 parallel transect strips, each comprising 20 m by 50 m.

In early September 1997 four strips, and in 1998 two strips were covered with freshly mown plant material from nearby remnants of species-rich flood-meadows, while two strips remained without treatment. Plant material was harvested with conventional hay making machinery and spread manually at the restoration site in a loose 5 to 10 cm thick layer.

September was chosen as the date of transfer, because at this time the majority of target species had ripe seeds while most of the dominant grasses (e.g. *Alopecurus pratensis*) had already released their seeds (Hölzel unpubl. data). Two different types of material were used in the experiment:

(I) Alluvial *Molinion* meadows are exclusively found at regularly flooded extremely nutrient-poor sandy sites where the loam cover was removed in the past. They are floristically characterised by a strictly oligotrophic species composition with *Molinia caerulea* agg., *Carex panicea*, *Serratula tinctoria*, *Inula salicina* and *Succisa pratensis* predominating. Due to the extreme site conditions they are rather species-poor with on average of less than 30 species/100 m². Some target species such as *Gentiana pneumonanthe, Dactylorhiza incarnata* and *Iris sibirica* are restricted to this vegetation type.

(II) In contrast, *Cnidion* meadows occupy more fertile loamy and clay-rich sites, which are also regularly flooded. They are characterised by a higher proportion of nutrient demanding meadow species such as *Alopecurus pratensis, Elymus repens* and *Potentilla reptans*. However, they share many target species with the *Molinion* meadows such as *Arabis nemorensis, Pseudolysimachion longifolium, Serratula tinctoria* and *Inula salicina*. In general, they are more species-rich with on average 40 to 60 species/100 m². *Cnidion* material from a very particular salt-influenced site that contained the rare *Iris spuria* and some other salt-tolerant species such as *Lotus tenuis* and *Tetragonolobus maritimus* was only brought to strip I.

The whole restoration site was mown annually in September with a flail mower to prevent the emergence of woody plants. Due to very low productivity there was as yet no need to remove biomass.

Vegetation sampling

Each of the eight 20 m x 50 m treatment strips was subdivided into ten 10 m x 10 m quadrats (80 quadrats in total, Fig. 1). From 1998 onwards, vascular plants were recorded annually for

the entire 10 m x 10 m quadrat. Species cover and abundance values were estimated visually using a modified Braun-Blanquet scale with cover value 2 subdivided into 2m, 2a and 2b. Vegetation of the source stands was recorded in the same way every year with six quadrats in *Molinion* and *Cnidion* meadows.

Soil properties

To investigate the effects of topsoil removal, soil properties such as total nitrogen and organic carbon content, CAL soluble phosphorus and potassium were measured in four plots with 30 cm, 50 cm and without topsoil removal, respectively. In each plot, five soil cores were taken at random locations at a depth of 0-10 cm using a 3 cm in diameter soil corer, and subsequently pooled together for the analysis. The same method was applied to the 12 quadrats in the source stands to obtain a reference of the soil nutrient status in the target communities. Flooding frequency per plot was calculated using data from a neighbouring groundwater gauge, field observations and topography.

Seed bank sampling

To determine the influence of topsoil removal on the soil seed bank and the potential role of buried seeds in succession, we studied soil seed bank composition in four plots with 30 cm, two plots with 50 cm and two plots without topsoil removal. In each plot, 20 cores of 10 cm depth were taken in September 1997 at random locations with a 3 cm in diameter soil corer. The seed bank samples represent 141 cm² of the soil surface and 1410 cm³ of the soil volume at each plot.

Plant material sampling

To analyse the quantity and quality of transferred diaspores, at four treatment strips two samples of plant material were taken from the soil surface at the restoration site in February 1998 and 1999, five months after material application. Each sample comprised six quadrats of 31.6 cm by 31.6 cm that were taken at random locations and pooled together. Superficial plant material and 2 cm of the topsoil that was expected to contain discharged seeds were sampled and analysed separately. During sampling in February, we did not find any seedlings under

the plant material layer, which was in accordance with additional germination experiments (Hölzel unpubl. data).

Analysis of seed contents

Seed bank composition in the soil and in the plant material was analysed using the seedling emergence method (Roberts 1981). Soil samples were directly filled in a 2 to 3 cm thick layer in 18 cm x 28 cm styrofoam basins and exposed under free air conditions to enhance natural stratification. Plant material was mixed with sterile soil and exposed in the same way. The basins were protected against diaspore input and heating by covering them with flat, white gauze lids. In summer the basins were watered regularly. Control basins filled with sterile soil were used as spacers. Germinated seedlings were identified and removed every few weeks. Unidentifiable specimens were transferred to pots and grown until they could be determined. When germination declined the samples were dried in a greenhouse, crumbled, mixed, watered and exposed again in free air. The analysis of diaspore contents in soil and in plant material material lasted 36 months.

Data analysis

Plant species occurring at the restoration site were grouped in the following categories: 1) <u>Annual arable weeds:</u> Present in soil seed bank and/or established vegetation over the entire restoration site (including zero plots) and/or its direct periphery in the first season with sharp decline in the second season; absent from source stands. 2) <u>Perennial or at least biennial ruderals:</u> Like 1) but still highly frequent in the second year of observation; absent from source stands with few exceptions (e.g. *Cirsium arvense*). 3) <u>Resident grassland species:</u> Like 2) but typical of established grasslands in the region. Although most of these species such as *Festuca arundinacea, Poa trivialis, Achillea millefolium* and *Plantago lanceolata* also occurred in source stands and thus may be part of the plant material fraction, they were exclusively accounted to this group. 4) <u>Plant material species:</u> Present in source stands, exclusively found at plant material treatments and completely absent from zero plots in the first two seasons, absent from soil seed bank and the direct periphery of the restoration site.
Linear regression was used to assess the relationship between seed contents of species in plant material and their establishment success as well as to test the causal influence of flooding and groups of competitors on establishment success of plant material species. To separate the

direct and indirect causal covariation of flooding on establishment success we used the method of path analysis (Legendre & Legendre 1998, p. 546-551), which was performed on standardised variable values.

Means of soil nutrient variables were compared using the parametric Tukey Honest-Significance test (HSD) for unequal sample sizes. Regressions and ANOVA were performed on log-transformed data matrices using the software package STATISTICA 6.0.

Results

Effects of topsoil removal on soil nutrient status

Topsoil removal had strong effects on the soil nutrient status at the restoration site (Fig. 2).
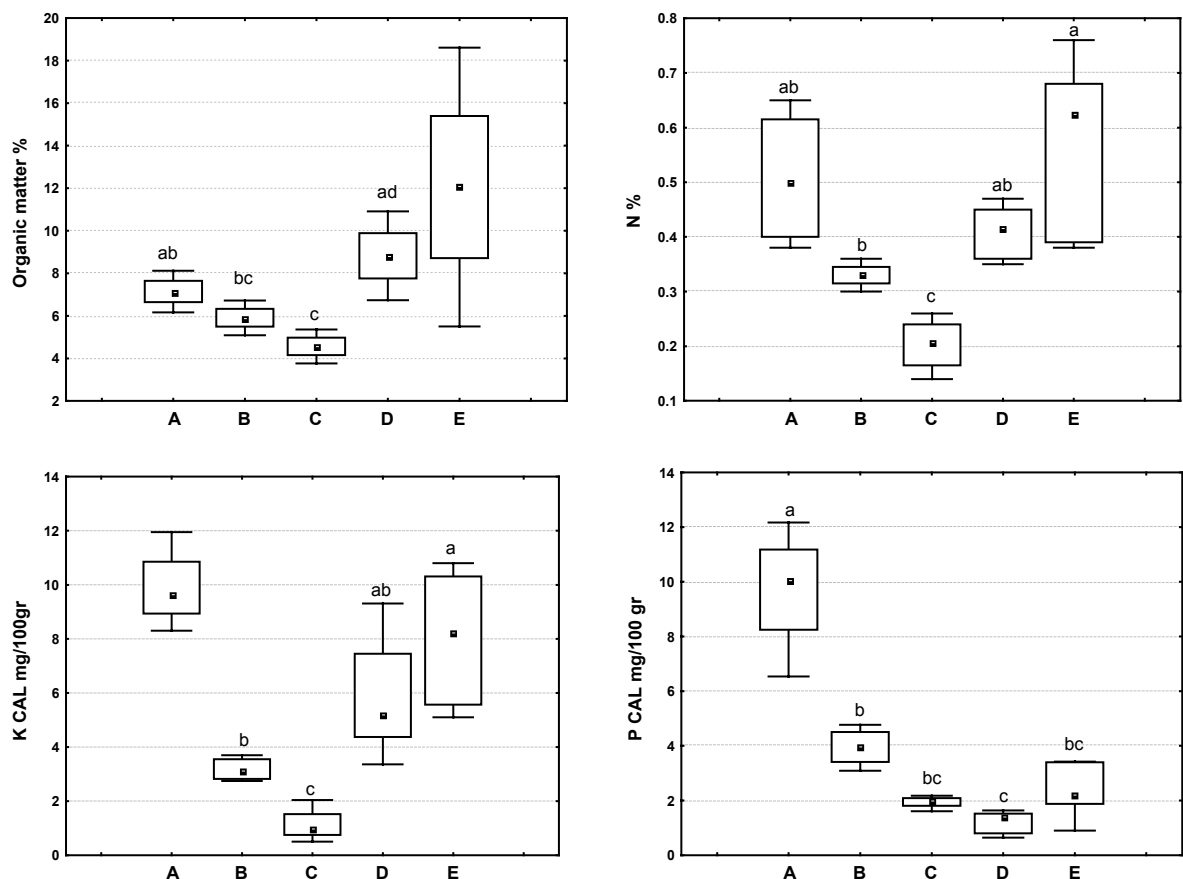
Fig. 2. Effects of topsoil removal on soil nutrient status (organic matter, total N, CAL-soluble K and P): A = Arable field without topsoil removal (n= 4); B = 30 cm removal depth (n = 4) C = 50 cm removal depth (n = 4); D = Molinion source stands (n = 6); E = Cnidion source stands (n = 6). Significant differences according to the Tukey test are indicated by different letters.

In case of plant-available P there was a sharp decline to the level of species-rich old stands of *Cnidion* meadows or even *Molinion* meadows (50 cm removal depth). Plant-available K, total N and organic matter ranged even below the values that were found in the source communities. All effects were most pronounced at a removal depth of 50 cm.

Effects of topsoil removal on soil seed bank

The size of the soil seed bank, which reached up to 12,000 seeds/m² in the young arable field fallow, declined dramatically by topsoil removal (Fig. 3). At a removal depth of 30 cm only 20 to 40 % of the former values were found, while at a removal depth of 50 cm the soil seed bank was almost completely eliminated. Seed bank composition was dominated by typical annual arable weeds such as *Chenopodium polyspermum, C. album, Erucastrum gallicum, Sonchus asper* and *Stellaria media*. However, we also found a considerable number of seeds of some common perennial meadow species such as *Poa trivialis, Achillea millefolium, Galium album* and *Medicago lupulina*. These may play an essential role even in advanced successional stages of meadow communities. No seeds of rare and endangered target species of flood-meadows were recorded.
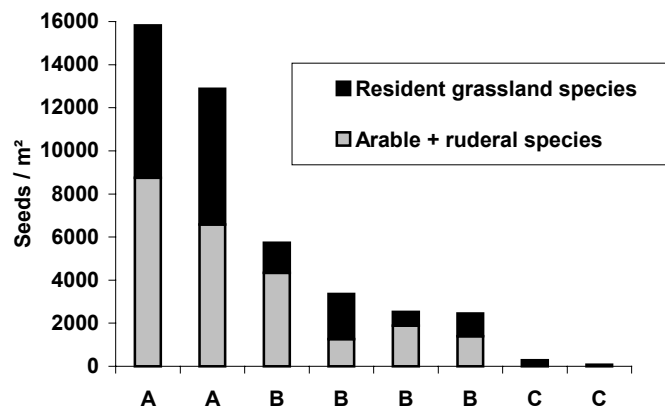
Fig. 3. Effect of topsoil removal on the size of the soil seed bank at the restoration site. Samples originating from: A = Arable field without topsoil removal; B = 30 cm removal depth; C = 50 cm removal depth.

Seed contents in plant material

A total of 19,394 individuals out of 66 species that could exclusively be accounted to transfer (species group 4) were found in the analysis of sampled plant material (Appendix 1). In

general the results displayed a considerable variation and patchiness in species distribution and seed densities between and even within material of the same origin. Total densities of plant material species usually ranged between 551 and 2125 seeds/m². In one case we found an exceptionally high density of 24,019 individuals/m² to which a single species, *Pseudolysimachion longifolium*, contributed more than 80 %. Species numbers in *Cnidion* samples ranged from 22 to 28 species/m², while they were lower in samples from *Molinion* stands with only 15 to 17 species/m². Maximum densities of more than 100 individuals/m² were reached by only nine species, among them some rare and endangered target species such as *Pseudolysimachion longifolium, Arabis nemorensis* and *Inula salicina*. In contrast, the majority (38 species) had maximum densities of only ten or less individuals/m². Compared to their dominant role in the source stands, grasses and sedges (except *Agrostis stolonifera*) were strongly underrepresented in plant material. This phenomenon was also reflected in vegetation development.

Vegetation development

In the first year of observation, the vegetation at the restoration site was still dominated by ruderals and annual arable weeds that emerged from soil seed bank and shoots remaining after topsoil removal (Fig. 4). From the second year onwards, annual arable weeds disappeared almost completely from the established vegetation, while the decline in ruderal species was more continuous over the years. In contrast, a steep increase in total cover of plant material species and resident grassland species could be observed in the third year. While total number und frequency of resident grassland species remained almost constant, there was a sharp increase in species originating from plant material. After four years a total of 102 species that could be exclusively accounted to plant material transfer was found at the restoration site (Fig. 4, Appendix 2). Among these were 31 species that are mentioned in the national German and regional Hessian Red Data Book. Species derived from plant material comprised 64 % of all species found in established vegetation in 2001 and 49 % of all species that were observed during the entire observation period.

Transfer rates for single strips ranged from 64 % to 72 % for the wet strips and from 53 % to 56 % for the dry strips (Table 1). In total 82 % of the entire species pool at the source sites was transferred after four years.
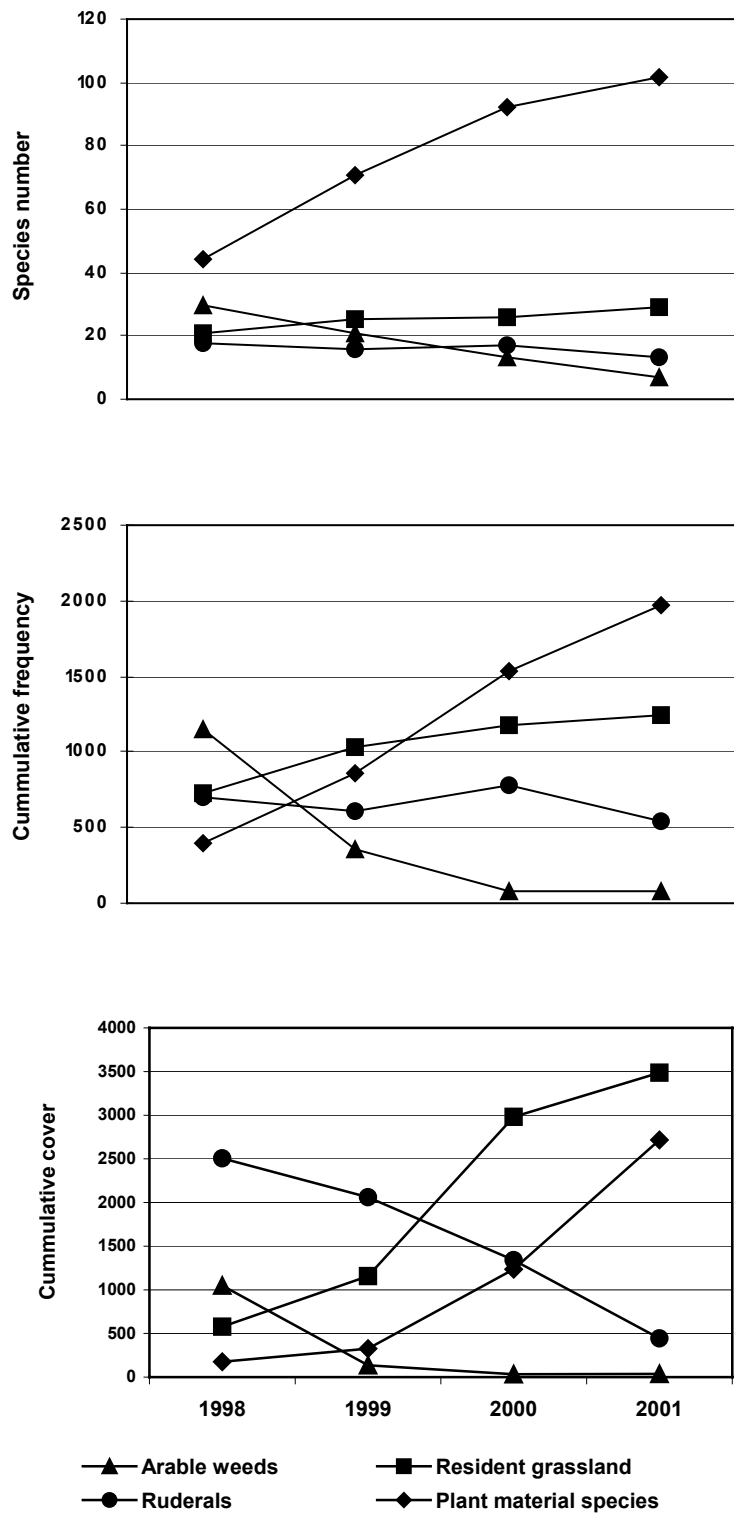
Fig. 4. Development in species number, cumulative frequency and cover of different species groups at the entire restoration site between 1998 and 2001. All plots (n = 80) are pooled together.

Table 1. Transfer rates and efficiency of plant material analysis in the different treatments. In strip V and VII seed contents in plant material were not measured (n.m.).

Strip	I	III	IV	V	VII	VIII
N$^{\circ}$ of species at source sites	97	74	84	81	75	77
N$^{\circ}$ of established species	70	48	54	54	42	41
Transfer rate in %	72	65	64	67	56	53
N$^{\circ}$ of species recorded in plant material	38	21	24	n.m.	n.m.	28
% of transferred species recorded in plant material	54	44	44	n.m.	n.m.	62

Simple linear regression between species recorded in plant material (all analysed samples pooled together) as the independent variable and established vegetation in the fourth year of observation (only strips with material sampling) as the dependent variable resulted in a considerable proportion of explained variance ($r^2 = 0.32$, $P < 0.001$). Of the species recorded in plant material, only *Carex praecox, C. tomentosa* and *C. otrubae* did not establish to date. With few exceptions, such as the legumes *Genista tinctoria*, *Ononis spinosa* and *Lotus tenuis,* species not recorded in the plant material analysis (Appendix 1) were also scarce and infrequent in established vegetation (Appendix 2). Generally, the invasion of species fromplant material treatments to neighbouring zero treatments occurred much faster in case of the wet, regularly flooded plots (Fig. 5, Appendix 2).
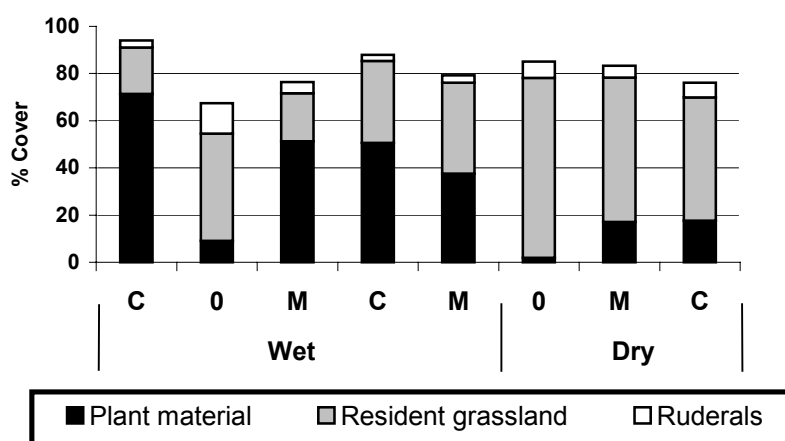
Fig. 5. Cumulative cover of different species groups along the treatment strips four years after plant material application. C = *Cnidion* material; M = *Molinion* material; 0 = Zero treatments. Wet = regularly flooded strips; Dry = never flooded strips.

Simple linear regressions of all plots with material application (n = 60) revealed a strongly negative correlation between the cover of resident grassland species and the cover of species that emerged from plant material (Fig. 6). On the other hand there was a positive correlation between the cover of plant material species and flooding height, and a negative correlation between flooding height and the cover of resident grassland species. Although decomposition of direct and indirect causal influence of flooding on establishment success by path analysis (Fig. 6) suggested a relatively high proportion of indirect causal covariation via competitors, there nevertheless remained a considerable proportion of direct covariation.

$$R^2 = 0.52$$

$$r = -0.72$$

A → B

$$r = -0.79$$
$$p = -0.57$$

$$r = 0.72$$
$$p = 0.31$$

C

$$R^2 = 0.65$$
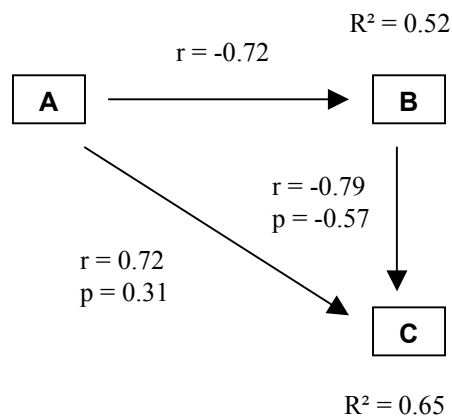
Fig. 6. Decomposition of direct and indirect causal influence of flooding on establishment success of plant material species: A = flooding height, B = cover of resident grassland species in 2001, C = cover of plant material species in 2001. r = covariation in simple linear regression, p = parameter estimate in multiple regression, R^2 = explained variance; all values significant at the level $p < 0.01$.

Discussion

Effects of plant material transfer

In the present study diaspore transfer with plant material proved to be a very effective method to overcome dispersal limitation of rare and endangered target species in habitat restoration practice. Our results are in accordance with seed addition experiments (e.g. Burke & Grime 1996, Tilman 1997, Pywell et al. 2002) that found species diversity in plant communities to be strongly governed by recruitment limitation, most commonly in early successional stages (Turnbull et al. 2000). The transfer rate was particularly high compared to other plant material transfer experiments (Tränkle 1997, Patzelt 1998, Pfadenhauer & Miller 2000). Total seed densities/m² in plant material ranged considerably below those recommended in practice for the recreation of species-rich grassland (Smith et al. 1997, Bosshard 1999, Pywell et al.

2002). Surprisingly, even species with maximum densities of less than 10 seeds/m² in plant material, which is two orders of magnitude lower than the rates normally used in seed addition experiments (Turnbull et al. 2000), established successfully. Seed content in plant material alone proved to be a rather weak predictor for establishment success and may be strongly outweighed by colonisation ability in certain species (e.g. Patzelt 1998). Low densities of grasses and sedges in plant material were also reported from other transfer experiments (Patzelt 1998, Pfadenhauer & Miller 2000), which is obviously mostly due to late mowing (Biewer 1997). Principally, this bias towards herbaceous species should not be seen as a disadvantage, since the establishment of target species is usually facilitated by the low abundance of strongly competitive grasses (e.g. Lepš 1999) and a delayed development of a closed sward (e.g. Bosshard 1999).

In accordance with other transfer experiments (e.g. Patzelt 1998, Pfadenhauer & Miller 2000), species with preferably vegetative means of spread and poor regeneration by seeds, such as the Genus *Carex* (Grime et al 1998, Schütz 2000a), were predominant among those failing to establish from plant material until now.

Effects of topsoil removal

The compelling success that was achieved must be seen in conjunction with topsoil removal that created the most favourable conditions for seedling recruitment. However, even in the present study, establishment success of species from plant material was revealed to be strongly correlated with the degree of competition by established vegetation (Fig. 6). In many experimental studies (e.g. Tilman 1993, Rusch & Fernandez-Palacios 1995, Křenová & Lepš 1996, Kotorová & Lepš 1999) micro-site limitation and competition by established plants proved to be the main constraints governing germination, growth and survival of seedlings. Due to the partial depletion of the soil seed bank and the established vegetation by topsoil removal the temporal and spatial dimension of the 'regeneration niche' (Grubb 1977) as a 'window in time' (Gross & Werner 1982) was considerably enlarged.

Besides the creation of open substrate with low competition, topsoil removal was absolutely essential for the reduction of plant-available P to the level of the target communities. This was of particular relevance for the successful establishment of `stress-tolerators´ (Grime 2001) that strictly depend on nutrient-poor site conditions, such as *Gentiana pneumonanthe* and *Succisa pratensis*, which are typical of *Molinion* meadows. Our findings are in accordance with many other studies that identified P as the major nutrient that may potentially hamper the re-

establishment of low productive species-rich grassland communities (Egloff 1983, Gough & Marrs 1990, Oomes et al. 1996, Snow et al. 1997, Tallowin et al. 1998, Olde Venterink et al. 2001).

The rapid decline of ruderals – in comparison with other old field successions (e.g. Schmidt 1993) - was obviously also an effect of the massive reduction in soil nutrient status, since the ruderal strategy is supposed to play an important role only under relatively fertile site conditions (Grime 2001). However, the negative impact of ruderals on establishment success was less significant than expected, as was also found by other authors (Bosshard 1999, Pfadenhauer & Miller 2000). In contrast, resident mesophilious grassland species were revealed to be the most prominent group that may seriously hamper recruitment from plant material, although their vitality was considerably reduced by lowering the soil nutrient content.

Increased flooding frequency due to surface lowering had an unexpectedly large influence on the establishment success of plant material species, not only by the weakening of competitors. Under the given climatic (dry and warm) and edaphic (heavy, rapidly hardening clay soils) situation, seedling recruitment seems to be strongly facilitated by floods in late spring and early summer that provide favourable moisture conditions. In summer 1999, we found mass germination and rapid seedling development on muddy surfaces created by slowly retreating flooding water. Our findings are supported by many other studies that identified drought as a main source of germination failure (Baskin & Baskin 2001) and high seedling mortality (Cavers & Harper 1967, Silvertown & Dickie 1980, Ryser 1993). One might argue that mostly additional species preferring wet site conditions were favoured by flooding und thus caused a bias towards higher establishment rates. However, we observed a general facilitation in establishment of plant material species by flooding, even in mesophilious grassland species such as *Leucanthemum vulgare* and *Centaurea jacea*. The much faster invasion of plant material species to regularly flooded zero plots underpins the significant role of flooding events for dispersal over moderate distances (Hölzel & Otte 2001).

Regional Hessian State Agency for Nature Conservation (Obere Naturschutzbehörde, RP Darmstadt) and the Federal German Agency for Nature Conservation (BfN).

Appendix 1. Species composition and seed densities (seeds/m²) in plant material samples from different treatment strips. F = frequency in samples (n = 8); Total = total number of seedlings recorded in the samples; Max = Maximum seed density per m².

Strip	I		III		IV		VIII				
Sample	a	b	a	b	a	b	a	b			
Number of plant material species	22	28	17	15	26	22	25	22			
Total number of species	41	48	31	38	51	46	54	51			
Plant material seeds n / m²	24019	993	551	1143	2125	1378	1508	607			
Plant material seeds g / m²	3.83	0.84	0.11	0.15	1.10	0.27	1.31	0.27			
Other seeds n / m²	372	213	192	262	723	1187	1303	2340			
% of other seeds / m²	2	18	26	19	25	46	46	79			
Total seeds / m²	24390	1206	743	1404	2848	2565	2812	2947	F	Total	Max
Pseudolysimachion longifolium	19899	27	18	202	1335	343	300	10	8	13280	19899
Arabis nemorensis	32	82	2	23	52	828	857	205	8	1248	857
Agrostis stolonifera agg.	72	20	253	202	50	38	12	187	8	500	253
Inula salicina	7	95	118	670	27		3	15	7	561	670
Galium wirtgenii	17	85		13	42	5	10	13	7	111	85
Poa angustifolia		7		2	35	38	52	73	6	124	73
Serratula tinctoria	3	13	33	8	7	3			6	41	33
Rumex crispus	20				102	17	42	5	5	111	102
Centaurea jacea		43			10	25	38	5	5	73	43
Potentilla reptans	15	33			17	27		5	5	58	33
Lathyrus pratensis	3				52	3	7	5	5	42	52
Carex spicata		15			8	7	12	22	5	38	22
Achillea ptarmica	1131				258	5	45		4	864	1131
Festuca rubra					17	13	2	12	4	26	17
Leucanthemum vulgare					20	3	7	3	4	20	20
Festuca arundinacea	3				2	3		10	4	11	10
Sanguisorba officinalis	5				2		3	2	4	7	5
Prunella vulgaris		2	2	2				2	4	4	2
Daucus carota	2412	383	2						3	1678	2412
Poa palustris					7	2	8		3	10	8
Succisa pratensis		2	12	3					3	10	12
Trifolium repens	3				3	7			3	8	7
Alopecurus pratensis					3	3	3		3	6	3
Allium angulosum	7	2	2						3	6	7
Ajuga reptans						2	3	2	3	4	3
Deschampsia cespitosa			2				2	2	3	3	2
Linaria vulgaris		108		2					2	66	108
Calamagrostis epigeios		8	55						2	38	55
Ranunculus repens					25	2			2	16	25
Scutellaria galericulata			13	3					2	10	13
Holcus lanatus					10		5		2	9	10
Molinia caerulea agg.			7	8					2	9	8
Hypericum perforatum					12	2			2	8	12
Carex praecox							10	3	2	8	10
Silene flos-cuculi	2						10		2	7	10
Silaum silaus		10						2	2	7	10
Senecio erucifolius	2	8							2	6	8
Carex tomentosa		3						2	2	3	3
Viola persicifolia			2	2					2	2	2
Selinum carvifolia	370								1	222	370
Peucedanum officinale						73			1	44	73
Lysimachia vulgaris			25						1	15	25
Securigera varia					23				1	14	23
Primula veris								23	1	14	23
Cnidium dubium		13							1	8	13
Iris spuria		12							1	7	12
Pastinaca sativa	10								1	6	10
Agrimonia eupatoria					7				1	4	7
Inula britannica		7							1	4	7
Linum catharticum		5							1	3	5
Stachys palustris			5						1	3	5
Phalaris arundinacea	3								1	2	3
Lepidium campestre		3							1	2	3
Silene alba					2				1	1	2
Lotus corniculatus						2			1	1	2
Symphytum officinale							2		1	1	2
Vicia cracca							2		1	1	2
Valeriana pratensis							2		1	1	2
Trifolium pratense	2								1	1	2
Thalictrum flavum	2								1	1	2
Bellis perennis		2							1	1	2
Lythrum salicaria		2							1	1	2
Veronica teucrium		2							1	1	2
Juncus inflexus			2						1	1	2

Appendix 2. Establishment success (cover in m²) of species from plant material after four years at the different treatment strips. F = plot frequency (n = 80). Species with less than three occurrences are not shown. Red list species (Korneck et al. 1996) and additional target species are given in bold.

Strip	I	II	III	IV	V	VI	VII	VIII		
Plant material origin	Cnidion	Zero	Molinion	Cnidion	Molinion	Zero	Molinion	Cnidion		
Number of species from plant material	71	46	60	58	62	25	43	43		
									F	Total cover
Agrostis stolonifera agg.	80	19.1	270	199	198.4	0.1	14.1	3.2	61	783.9
Inula salicina	11.3	3.6	32	17	10.1		10.1	1.4	58	85.5
Pseudolysimachion longifolium	55.1	3.4	9.2	65.1	8.1		3.1	5.2	56	149.2
Arabis nemorensis	11.2	2.5	2.8	11.2	11.1	0.2	7.2	0.3	56	46.5
Galium wirtgenii	35	0.3	4.3	9.1	5.1	0.1	10	12	55	75.9
Lathyrus pratensis	47	0.3	1.2	64	2.1	1	40.1	123	47	278.7
Centaurea jacea	16	1.4	1.7	11	0.2	0.1	0.4	4.5	47	35.3
Sanguisorba officinalis	4.5	0.1	0.6	8.1	1.5		0.6	5.5	47	20.9
Leucanthemum vulgare	17	21	10.1	7.1	46	1		1.2	42	103.4
Prunella vulgaris	33	1	11.1	2.1	2.2	0.1	3.4	0.5	38	53.4
Valeriana pratensis	7.2	0.3	0.2	5.4	0.1		0.4	3.7	38	17.3
Senecio erucifolius	7.2	0.4	0.4	0.2	1.4	0.2	5.4	0.4	38	15.6
Genista tintoria	2	0.3	48.2	3.1	5.5		1.6		36	60.7
Lotus corniculatus	17.1	2.1	4.1	5	2.4	0.1	20.3	1	33	52.1
Achillea ptarmica	35	4.1	3.6	11.1	2.1			0.3	32	56.2
Succisa pratensis	3.2	0.1	32.4		3.7	0.1	0.3	0.1	31	39.9
Carex spicata	32.2	2.2	0.3	3.5	1.3			0.2	31	39.7
Rumex crispus	6.2	1.1	0.6	9.1	0.3	0.1		0.2	31	17.6
Daucus carota	7.2	1.2	0.2	0.1	0.4	0.4	2.2	1.3	30	13
Bromus racemosus	3	3	2	2.2	6.1	1.2	0.2	3.5	27	21.2
Pastinaca sativa	0.3				0.7	1.1	6.1	10.1	27	18.3
Ranunculus repens	70	2.1	3.3	17	3.1	0.1			25	95.6
Vicia cracca	1.3	0.1	1.5	0.2	1.1		1.3	1.3	23	6.8
Securigera varia	3.2		1	1.2	1.1	4	21.1	27	22	58.6
Serratula tinctoria	11.2		4.4	5.1	2.3				22	23
Hypericum perforatum	2.3	1	0.2	0.1	2.1	1.3	2.2	0.2	22	9.4
Potentilla reptans	9.1		2.4	10	0.1				21	21.6
Phalaris arundinacea	0.4	1.1	2.4	1.5	2.1				21	7.5
Calamagrostis epigejos	0.1	5.1	23.1	1.2	11.1				20	40.6
Peucedanum officinale	0.1		0.3	0.1	0.2		2.3	6.2	20	9.2
Lythrum salicaria	0.2	0.4	4.1	0.4	2.3				20	7.4
Symphytum officinale	1.3		0.2	2.5	1.2		0.3	0.1	20	5.6
Bromus inermis	10		0.1	2	5.1		6.1		19	23.3
Selinum carvifolia	1.1		0.1	3.2	0.4		5.1	2.1	19	12
Deschampsia cespitosa	0.5	0.2	1.6	0.1	0.4				19	2.8
Melampyrum cristatum					4	5.1	65	0.2	18	74.3
Poa palustris	7	1.1	1	10	2				18	21.1
Agrimonia eupatoria	6.2	0.1	0.1	0.2	0.2	0.1		1.3	18	8.2
Festuca rubra	4		0.1	1.2	0.2			5.3	17	10.8
Stachys palustris	0.1	0.2	4.1	0.2	5.1	0.1			17	9.8
Vincetoxicum hirundinaria				2	0.3		5.2	4.1	16	11.6
Inula britannica	22.2	4.1	3						15	29.3
Silene flos-cuculi	4	0.1	0	5.1	0.2			0.2	15	9.6
Scutellaria galericulata		1	6.2	1.2	7				14	15.4
Primula veris							3.2	12	13	15.2
Potentilla erecta		0.1	0.7	0.1	0.3		0.1		13	1.3
Silaum silaus	0.7				0.1		0.1	0.4	13	1.3
Trifolium hybridum	3.1	1.1	0.2	1.1		0.1		0.1	12	5.7
Lysimachia vulgaris	0.3		0.4	0.4	0.1				12	1.2
Thalictrum flavum	0.1		0.6	0.3	0.2				12	1.2
Gentiana pneumonanthe		0.1	0.5		0.1		1.3		11	2
Ranunculus acris	1.2	0.2	0.1	0.2		0.1	0.1		10	1.9
Linum catharticum	1		2		5		5		9	13
Mentha arvensis	1.1		3.2		4				9	8.3
Trifolium pratense	1.3	0.1	2			0.1	0.1		9	3.6
Lotus tenuis	21	1	0.1			0.1			8	22.2
Ononis spinosa	80	0.1							7	80.1
Veronica scutellata		0.1	4.1	0.1	2				7	6.3
Vicia sepium				2.2				2.1	7	4.3
Ajuga reptans			0.1	0.1				4.1	7	4.3
Melilotus alba	3.2				0.1		0.1		7	3.4
Holcus lanatus		0.1		1.1	0.1		0.1	1.1	7	2.5
Iris sibirica			0.2		1.4				7	1.6
Juncus alpinus	0.1	4.1	2.1						6	6.3
Iris spuria	6.1	0.1							6	6.2
Clinopodium vulgare					0.1		1	2.2	6	3.3
Trifolium repens	4.1					2			5	6.1
Galium palustre agg.			1.2		1.1				5	2.3
Cirsium tuberosum				0.3				0.2	5	0.5
Pulicaria dysenterica	1.1	0.1			0.1				4	1.3
Filipendula ulmaria	0.2			0.2					4	0.4
Veronica chamaedrys								3	3	3
Betonica officinalis			0.1				2		3	2.1
Lepidium campestre	0.2	0.1							3	0.3
Ranunculus polyanthemophyllos.					0.1		0.1	0.1	3	0.3
Juncus compressus	0.2				0.1				3	0.3
Molinia caerulea agg.			0.3						3	0.3

Kapitel 7

Ecology of seedling recruitment in flood-meadow species – the relative importance of facilitation and inhibition

Norbert Hölzel

Manuskript fertiggestellt

Summary

1 In this study the relative importance of facilitation and inhibition by the surrounding vegetation matrix on seedling recruitment was studied in a seed addition experiment at two neighbouring field sites with similar physical conditions but contrasting vegetation structure (young arable field fallow versus species-poor grassland sward). Moreover, it was investigated whether the failure of establishment of rare flood-meadow species in habitat restoration is primarily due to seed- or microsite-limitation.

2 Seeds of six typical flood-meadow species were sown in four treatments combining the factors gap creation and litter addition, respectively. Seedling recruitment was monitored for 3 years.

3 Five of the six species established successfully at both sites largely irrespective of treatments, indicating a predominant seed limitation. Only in the small-seeded *Arabis nemorensis*, which was revealed to be strictly gap dependent at the meadow site, could an obvious microsite limitation be shown.

4 In all tested species gap creation in the oldfield did not lead to an increase in recruitment, indicating that there was no significant negative effect of the established vegetation. Even within the meadow site, which had a three fold higher biomass production, in five out of six species there was no positive response towards gaps. This was most likely due to disturbance by early mowing that released seedlings from competition for light through the established vegetation. In the particularly large-seeded *Iris spuria*, exhibits a delayed germination during midsummer, the response to litter addition was actually positive. Protective and interferential effects of established vegetation and litter were found to a similar degree, whereas the majority of the tested species reacted neutrally. Only for the extremes of the seed size

spectrum did the results meet predictions made by plant ecological theory. Generally, species identity was revealed to be the major factor influencing variance in recruitment.

5 The findings of this study do not support the assumption that facilitation and inhibition should always shift uniformly along a gradient of decreasing environmental harshness and increasing productivity. Conceptual models that describe the interplay of facilitation and interference as a highly dynamic equilibrium, driven by variable abiotic and biotic marginal conditions, appear to be more appropriate.

Keywords: Biomass gradient, competition, gap regeneration, litter, old field, seed addition.

Introduction

Besides the availability of substantial seed sources (Tilman 1997, Bakker & Berendse 1999, Turnbull et al. 2000, Pywell et al. 2002) the lack of suitable microsites for seedling recruitment is increasingly identified as one of the major constraints governing species diversity in temperate semi-natural grasslands (Burke & Grime 1996, Stampfli & Zeiter 1999, Kotorová & Lepš 1999, Zobel et al. 2000, Isselstein et al. 2002).

Recruitment from seeds is a particularly vulnerable stage in the life cycle of plant species and the requirements for 'regeneration niches' (Grubb 1977) may differ considerably from those of established plants. In comparison with adults, emerging seedlings are usually much more sensitive towards both, harsh abiotic conditions and competition by neighbouring plants (Grime 2001). Under environmentally benign conditions the interferential effects of established vegetation via competition for light, water and nutrients are usually predominant and increase with productivity (e.g. Foster & Gross 1998, Lepš 1999). In contrast, facilitating effects of established vegetation on seedling recruitment are most often found in unproductive habitats with harsh physical conditions particularly in terms of temperature and moisture supply (Bertness & Callaway 1994, Bertness & Hacker 1994, Callaway & Walker 1997, Tielborger & Kadmon 2000, Martinez 2003).

In temperate semi-natural grasslands the decline in species-richness is often caused by the failure of recruitment from seeds due to enlarged productivity and/or litter accumulation in the course of agricultural intensification or abandonment (e.g. Tilman 1993, Rusch & Fernandez-Palacios 1995, Foster & Gross 1998, Lepš 1999). Even in mesic, moderately productive grasslands, gaps created by disturbances of the turf are usually regarded as a prerequisite for

successful regeneration by seeds (Bullock et al. 1995, Edwards & Crawley 1999). However, the importance of gap regeneration may differ considerably among species (e.g. Fenner 1978, Kotorová & Lepš 1999, Zobel et al. 2000). Gap dependence is most evident in small seeded species, which usually exhibit a high light requirement for germination and a particularly low competitive ability in the seedling stage (Jakobsson & Eriksson 2000, Grime 2001). Equally, in many rare and declining grassland species a crucial dependence on gaps as regeneration niches could be confirmed (e.g. Křenová & Lepš 1996, Lennartson & Ostermeijer 2001). Contrary, litter accumulation due to cessation of biomass removal by management was often identified as the main factor for complete failure of regeneration by seeds and declining species-richness in semi-natural grasslands (e.g. Foster & Gross 1998, Špačková et al. 1998, Jensen & Meyer 2001). Again, this seems to apply in particular to relatively small-seeded species whereas those with larger seeds often show a neutral (e.g. Kotorová & Lepš 1999) or even a positive response (e.g. Gross 1984) to litter cover for various reasons (e.g. protection against desiccation and predation). Generally, gaps can be seen as a localised temporal release from competition (Grime 2001, Suding 2001, Jutila & Grace 2002), whereas litter layers usually enforce interference by established vegetation (Foster & Gross 1998, Grace 2001).

Recent studies (Suding & Goldberg 1999, Tielborger & Kadmon 2000) question the hypothesis by Bertness & Callaway (1994) that interferential effects of established vegetation and litter on recruitment should increase uniformly along a gradient of productivity and declining environmental harshness. In detail there seems to be a fine and more complicated balance between facilitation and inhibition depending on species identity and the impact of variable environmental conditions (Holmgren et al. 1997). In the same plant species or community considerable differences in facilitating or inhibiting effects on seedling recruitment may occur between sites and years with varying abiotic stress (De Jong & Klinkhammer 1988, Fowler 1988, Ryser 1993, Greenlee & Callaway 1996, Kadmon & Tielborger 2000).

The divergence of findings due to the vital role of species individuality and marginal conditions makes it difficult to predict the response of species in a particular habitat type without empirical evidence. Seed addition experiments including manipulative variants with gap creation and litter removal or addition are particularly helpful to assess the relative importance of seed limitation and/or the lack of suitable regeneration niches for the failure of recruitment in a particular community (e.g. Hutchings & Booth 1996b, Tilman 1997, Zobel et al 2000, Coulson et al. 2001). Despite their usefulness in theory testing (Eriksson & Ehrlén

1992), such experiments are still surprisingly rare, particularly those that follow the fate of emerging seedlings for more than one season (Turnbull et al. 2000).

Here, this approach was used to identify the reasons for recruitment failure in flood-meadows that have been subject of large-scale restoration measures along the northern Upper Rhine, Germany, during the past 20 years. Despite successful lowering of soil nutrient status and productivity these efforts were unsuccessful in re-establishing target species of nature conservation (Hölzel et al 2002, Donath et al. 2003, Bissels et al. accepted). Ecologically these flood-meadows are characterised by a high variability in soil water potential that may change between complete submergence and severe drought within a few weeks. This special type of environmental stress makes it particularly difficult to predict facilitative or inhibitive effects of established vegetation on seedling recruitment. Due to the relatively high productivity a positive effect of gap creation and a negative litter addition effect was expected. To test for consistent effects of gaps and litter treatments on recruitment the seed addition experiment was conducted at two neighbouring sites with identical physical conditions but contrasting vegetation in terms of productivity and functional characteristics i.e. a sparse arable weed community dominated by mostly short-lived ruderal herbs, and a neighbouring species-poor permanent grassland sward. The tendency towards competitive exclusion in the more highly productive fully closed grassland sward was presumed to be at least partly compensated through disturbance by mowing at the first peak of standing crop (Huston 1994, Grace 2001). With focus on the recruitment phase the following questions were posed:

- Is target species-enrichment in the studied flood-meadows limited by seed or microsite availability?
- Are there consistent effects of gaps and litter between different species and under contrasting vegetation cover?
- How do the findings concur with plant ecological theory, with emphasis on the interplay of facilitation and inhibition along productivity gradients?

Material and Methods

Study site

The study area is situated in the dyke-protected fossil compartment of the Holocene flood-plain of the northern Upper Rhine about 30 km southwest of Frankfurt am Main, Germany. The site is located in the depression of a large silt-filled meander that is irregularly inundated by ascending groundwater during high water levels of the River Rhine. Soil conditions are characterized by carbon-rich, heavy clays (Vertisols) with unfavourable physical features, such as poor aeration and rapid hardening. In conjunction with the relatively dry and warm climate of the region this results in a high variability in soil water potential: While winter and spring often bring floods, summers are markedly dry providing adverse conditions for seedling recruitment. During the period of observation several long-lasting inundations occurred: An exceptionally long flooding event took place directly after sowing from the 15. March 15 till the May 24, 2001, causing a considerable delay in the onset of germination. Extended periods of flooding also occurred in spring 2002 and winter 2002/2003.

The study site comprises two adjacent allotments with identical physical conditions but contrasting vegetation cover: One allotment was under intensive arable use until it was abandoned for flood-meadow restoration in autumn 2000. The last crop prior to abandonment was *Phacelia tanacetifolia,* which was cut with a flail mower in October 2000. No further tillage was undertaken before the seed addition experiment began in early spring 2001.

In the first year after abandonment the vegetation of the arable field fallow was dominated by a sparse cover of annual arable weeds preferring wet site conditions, such as *Persicaria lapathifolia, Juncus bufonius, Sonchus asper, Atriplex hastata* and *Veronica catenata.* In the second year these annuals were largely replaced by perennial ruderals such as *Plantago intermedia, Cirsium arvense, Poa trivialis, Polygonum amphibium, Juncus articulatus* and *Equisetum palustre,* which were still dominant in the third year. After the start of the experiment the vegetation of the arable field fallow was mown once each year in late September using a flail mower without biomass removal (typical treatment of fallows in the region).

The second allotment comprises a species-poor grassland sward, which was created in 1997 on a former arable field by sowing a commercial seed mixture. The sward is dominated by competitive meadow grasses such as *Alopecurus pratensis, Phleum pratense, Poa trivialis, Elymus repens* and the weedy tall herb *Cirsium arvense.* After the onset of the experiment the

meadow grassland was cut and biomass removed each year at the end of June (traditional hay cutting date in this region) and mown a second time using a flail mower without biomass removal in late September.

Principally, the two vegetation types represent an early and a advanced successional stage in oldfield development towards grassland, which is reflected by the predominant plant functional types, i.e. relatively short-lived ruderal herbs versus perennial grasses. The latter are supposed to impose higher degree of competition on emerging seedlings (e.g. Lepš 1999).

Study species

The studied species are characteristic components of flood-meadows with no or only limited potential for clonal spread. This means that they crucially depend on regeneration by seeds to colonise spatially isolated new sites. Except *Galium wirtgenii* (common) and *Allium angulosum* (moderately rare) all study species are very rare and strongly threatened on a Central European scale (Schnittler & Günther 1998). Seed dispersal and vulnerability in recruitment by seeds is suspected to be a main reason for their general rarity, area restriction and the low capacity to colonise new sites (Donath et al. 2003). Equally, they differ considerably in seed mass (Table 1), which is considered to be a major determinant in seedling recruitment (Jakobsson & Eriksson 2000, Grime 2001, Moles & Westoby 2002) particularly in terms of sensitivity towards competition by established vegetation (e. g. Kotorová & Lepš 1999).

Table 1. Seed mass and germination rate under optimal outdoor conditions of the studied species.

Species	Seed mass [mg]	Germination rate [%]
Allium angulosum	1.74	94
Arabis nemorensis	0.06	87
Cndium dubium	0.39	8
Galium wirtgenii	0.40	88
Iris spuria	14.62	76
Viola pumila	1.08	66

The seeds for the experiment were collected in bulk in 2000 from natural populations in the wider study region, and stored dry in darkness at room temperature until further use. The

potential for germination was tested with two replicates of 400 seeds from each species. Seeds were sown into sterile garden soil under outdoor conditions at the same time as the field experiment started. Seeds were watered regularly during dry periods and germination was followed for two years with seedlings counted and removed once every week.

Experimental design

To test for the effect of gaps and litter on seedling establishment under contrasting vegetation cover a manipulative experiment with identical design was set up in the young arable field fallow and in the neighbouring grassland sward. Six species were sown in 31.6 x 31.6 cm plots (1.000 cm²) arranged in four randomised complete blocks. In each block, the following treatments were used:

1) gap without litter

2) gap with litter

3) control (no gap, no litter)

4) control with litter

In the gap treatments the sod was stripped and all above-ground vegetation removed prior to sowing. In the litter treatments the plots were covered with a ca. 2 cm thick layer of material from a hay-bale directly after sowing.

On March 9, 2001, 100 seeds of one of the six species (one species per plot) were sown in the central 20 x 20 cm part of each of the four treatments per block (24 plots per block). None of the study species occurred at the experimental site and with the exception of *Galium wirtgenii* even not in the wider surroundings, making unsown control plots irrelevant.

Seedling establishment was monitored for 3 years with 5 counts during the main germination period in 2001 (early June to late September), three counts in 2002 (late May to mid September) and one count in late May 2003.

During the midsummer counts in 2001 and 2002 total plant cover for each plot was estimated visually with an accuracy of 5 % and dominant plant species were noted. Additionally, total above-ground biomass was measured with four replicates in mid June 2002 in the arable field and the meadow grassland, respectively. In the meadow a second cut was performed in mid August. Dry matter per m² was determined after drying the clippings derived from 4 randomly placed quadrants of 1000 cm² at 60 °C.

Data analysis

The frequencies of individuals of each sown species per plot during each count were log (x+1) transformed prior to further statistical analyses. To test for differences and interactions between treatments and species over time, a repeated-measures ANOVA was performed with species and the treatments gap and litter as fixed factors, block as the random factor and time as the repeated-measures (within subject) factor. Interaction terms with block were used as error terms. Repeated measures ANOVAs were performed separately for the arable field fallow and the meadow site. Differences between both sites in total seedling number and for species were tested with a t-test for paired samples in which spatially corresponding blocks were seen as (paired) replicates. It should be noted that these tests only indicate that there are significant differences between both analysed sites. They cannot be used to generalise about differences between arable field fallows and grasslands, since the blocks are not independent replicates for these categories! Differences in vegetation cover of plots between the treatment categories gap and litter were checked by a t-test for independent samples. Correlations between total vegetation cover and seedling number per plot were analysed by the Spearman rank correlation coefficient. All statistical analyses were carried out with the software package STATISTICA 5.1.

Results

General effects of gaps and litter on seedling recruitment

Repeated-measures ANOVA revealed a highly significant species, time and species*time effect on seedling establishment at both sites (Table 2). The latter confirms significant interspecific differences in germination phenology and seedling survival. Surprisingly, there were no significant treatment effects (i.e. a response in seedling recruitment to the application of gaps and litter) at the arable field site. In contrast, a significant gap*species and litter*species interaction could be found for the grassland site, indicating that the effects of treatments differed among species. Equally, there was a highly significant gap*time interaction, confirming that the response towards gaps changed with time. The same was true for litter whose impact over time was additionally affected by species identity (litter*species*time interaction).

The divergent response towards gaps in the arable field and in the meadow was in line with the measurement of total plant cover (Table 3): Within the meadow, gap treatments had significantly lower total plant cover than the control plots during midsummer 2001 and 2002, which means that the gap effect was still measurable in the second year after sod stripping. In contrast, there was no significant 'gap effect' with respect to total plant cover in the young arable field fallow.

Table 2. Results of the repeated-measures ANOVA model comparing seedling recruitment of six species (S) in gap (G) and litter (L) treatments at the arable field fallow and the grassland site. Time (T) is the repeated-measures factor. Interaction terms with block are used as error terms. Significant effects are given in bold type.

Factor	Effect		Error			
	df	MS	df	MS	*F*	*P*
a) Arable field						
G	1	0.94	3	0.86	1.09	0.3732
L	1	0.45	3	0.75	0.60	0.4964
S	5	11.39	15	0.29	39.93	**0.0000**
T	8	1.99	24	0.08	24.23	**0.0000**
G*L	1	0.09	3	0.19	0.47	0.5408
G*S	5	2.07	15	1.09	1.91	0.1524
L*S	5	0.18	15	0.36	0.50	0.7742
G*T	8	0.06	24	0.06	0.92	0.5207
L*T	8	0.01	24	0.02	0.48	0.8606
S*T	40	0.72	120	0.03	21.64	**0.0000**
G*L*S	5	0.24	15	0.27	0.89	0.5116
G*L*T	8	0.02	24	0.03	0.63	0.7457
G*S*T	40	0.03	120	0.04	0.94	0.5819
L*S*T	40	0.02	120	0.03	0.76	0.8415
G*L*S*T	40	0.02	120	0.04	0.45	0.9978
b) Meadow						
G	1	11.86	3	1.92	6.17	0.0890
L	1	0.43	3	0.28	1.51	0.3069
S	5	5.51	15	0.83	6.61	**0.0019**
T	8	0.29	24	0.12	2.45	**0.0429**
G*L	1	0.20	3	1.26	0.16	0.7169
G*S	5	3.73	15	0.48	7.85	**0.0008**
L*S	5	1.40	15	0.29	4.77	**0.0083**
G*T	8	0.13	24	0.02	7.32	**0.0001**
L*T	8	0.05	24	0.03	1.59	0.1816
S*T	40	0.33	120	0.06	5.42	**0.0000**
G*L*S	5	0.13	15	0.33	0.39	0.8477
G*L*T	8	0.01	24	0.03	0.36	0.9319
G*S*T	40	0.05	120	0.05	1.02	0.4535
L*S*T	40	0.06	120	0.03	1.92	**0.0037**
G*L*S*T	40	0.02	120	0.05	0.43	0.9984

The standing crop in mid June 2002 was more than three times higher in the meadow than in the arable field fallow (Table 3), while differences in total plant cover of undisturbed controls were less pronounced. In line with the considerable difference in productivity the total number of seedlings was higher in the arable field at the end of the second season and the beginning of the third season. The difference was however statistically not significant (results of paired t-test: t = 2.45, P = 0.092 and t = 1.85, P = 0.162, respectively).

Table 3. Vegetation characteristics of the study sites. Different letters in front of the slash indicate significant differences in columns, letters behind the slash those in lines of the same measurement categories. M_2 = Second growth in the meadow grassland cut in mid August 2002.

Year	Community type /site	Biomass [g/m²]	Cover control [%]	Cover gap [%]
2001	A	-	65.4 ± 16.8 a/a	65.6 ± 22.7 a/a
	M		79.0 ± 14.2 b/a	45.4 ± 20.9 b/b
2002	A	134.1 ± 18.3 a	74.0 ± 17.3 a/a	76.0 ± 17.2 a/a
	M	461.6 ± 10.3 b	85.4 ± 6.2 b/a	76.7 ± 18.1 a/b
	M_2	316.3 ± 79.9 c		

Response of individual species

Species differed strongly in total germination rate. While germination rates were extremely low in *Cnidium dubium* (< 2%) they reached up to 20 % of all sown seeds in the best variants of *Iris spuria, Galium wirtgenii* and *Arabis nemorensis* (Fig. 1). Generally, field germination rates reached only 15 to 25 % of those obtained in the control experiment on regularly watered sterile garden soil under outdoor conditions (Table 1, Fig. 1).

With the exception of *Allium angulosum* at both sites and *Galium wirtgenii* at the grassland site all species exhibited a significant effect with time (Table 4). Most species reached a single pronounced peak during midsummer of the first season, followed in some cases by a marked decline towards autumn (e.g. *Galium wirtgenii*). In contrast, the large-seeded *Iris spuria* (Table 1) showed a strongly delayed onset of germination starting as late as July and reaching a first peak only in late September (Fig. 1b). *Iris spuria* was also the only species exhibiting a considerable rate of additional germination during the second year after sowing. After a moderate degree of seedling mortality during the first mid summer (drought) and winter (flooding, frost) almost all species had a surprisingly high survival rate during the

following years and became successfully established at least as vital vegetative (sub)-adult plants. In *Arabis nemorensi*s and in *Galium wirtgenii* flowering started as early as May 2002 whereas in *Viola pumila* the first seed-bearing capsules (cleistogamous flowers) appeared in September 2002 and the first chasmogamous flowers in May 2003. The other three species did not reach a generative state until the end of the observation period. The heavy decline of the short-lived, mostly biennial *Arabis nemorensis* in the third year (Fig. 1a) was partly due to the harsh environmental conditions (long-lasting flooding followed by heavy frost) in winter 2002/2003. The considerable fluctuations in *Allium angulosum* were partly due to herbivory and subsequent resprouting.
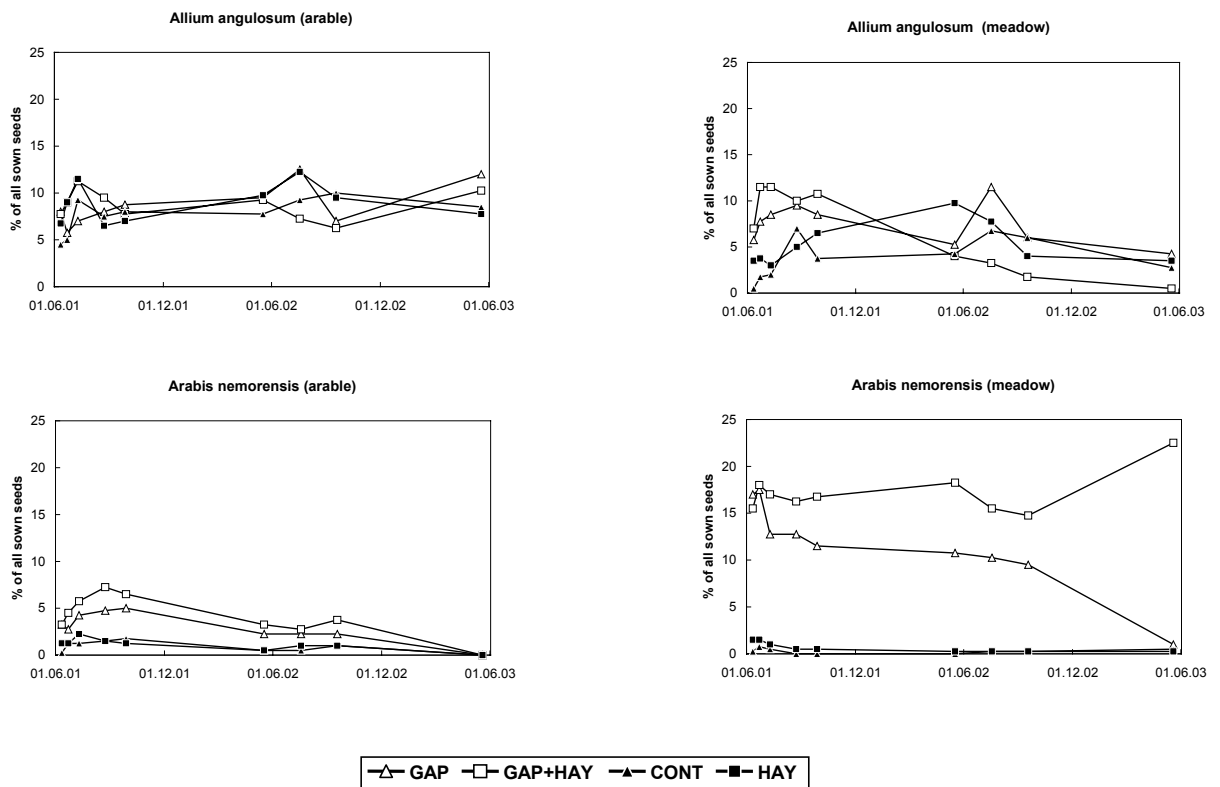
Fig. 1a. Effects of treatments on seedling establishment. GAP = plots with artificial gaps, HAY = plots with litter addition, CONTrol = plots without treatment.
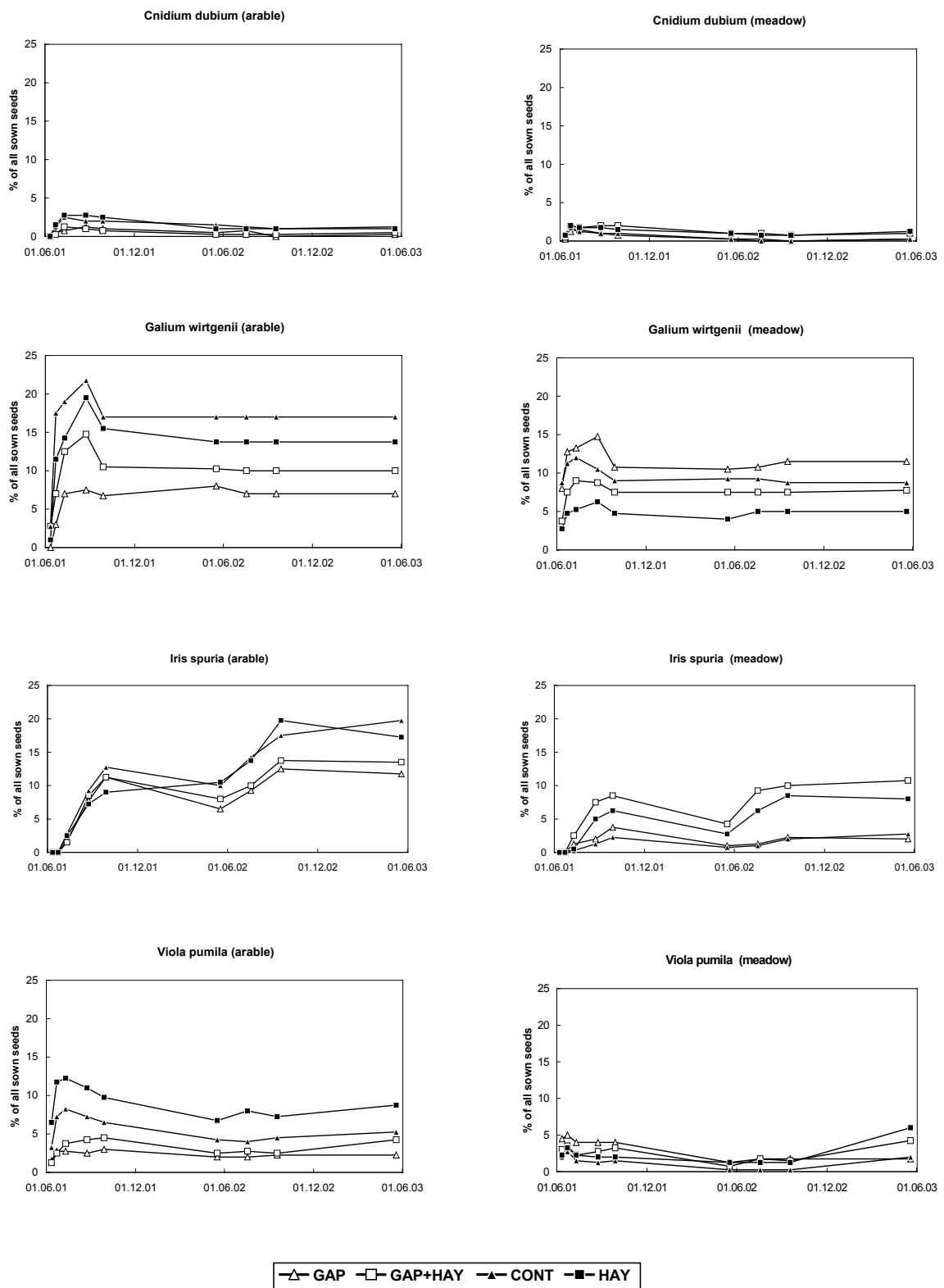
Fig. 1b. Effects of treatments on seedling establishment. GAP = plots with artificial gaps, HAY = plots with litter addition, CONTrol = plots without treatment.

Table 4. Results (*P* as significance of F Values) of repeated measures ANOVA models comparing the effects gaps and litter on seedling recruitment over 3 years. For each site and species a separate repeated-measures ANOVA model was calculated in which gap (G) and litter (L) are the fixed factors, block is the random factor (not shown) and time (T) the repeated-measures factor. Interaction terms with block were used as error terms. For full species names see Table 1; Sites: A = Arable field fallow, M = Meadow grassland. Significant effects are given in bold type.

Factor	df	*Arabis* A	*Arabis* M	Cnidium A	Cnidium M	*Galium* A	*Galium* M	*Iris* A	*Iris* M	*Allium* A	*Allium* M	*Viola* A	*Viola* M
G	1	0.170	**0.012**	0.145	0.949	**0.013**	0.446	0.478	0.876	0.634	0.263	0.292	0.207
L	1	0.496	0.576	0.909	0.179	0.963	**0.006**	0.857	**0.005**	0.430	0.710	**0.035**	0.201
T	8	**0.000**	**0.000**	**0.000**	**0.005**	**0.000**	0.062	**0.000**	**0.000**	0.485	0.352	**0.000**	**0.003**
G*L	1	0.608	0.801	0.619	0.837	0.137	0.980	0.962	0.804	0.847	0.233	0.560	0.397
G*T	8	0.587	0.068	0.896	0.919	**0.038**	0.535	0.823	0.827	0.374	0.082	0.166	0.517
L*T	8	0.937	0.872	0.899	0.764	**0.025**	0.997	0.767	**0.000**	0.538	**0.018**	0.673	0.168
G*L*T	8	0.414	0.823	0.905	0.955	0.861	0.874	0.967	0.931	0.893	0.923	0.809	0.954

The small-seeded *Arabis nemorensis* (Table 1) was the only species that was completely dependent on gap regeneration at the meadow site (Fig. 1a) whereas there was no such effect in the arable field. Accordingly, *Arabis nemorensis* was the only species that showed a highly significant negative correlation (Spearman r = 0.832 *P* < 0.001) between recruitment success and total plant cover in 2001.

In *Galium wirtgenii* there was a negative impact of gaps on recruitment success in the arable field site (Table 4, Fig. 1b). The same species was significantly negatively affected by litter within the meadow. Conversely, litter had a positive impact on recruitment of *Iris spuria* in the meadow and of *Viola pumila* in the arable field site. Only *Arabis nemorensis* reached significantly higher total numbers of seedlings in the meadow, whereas the same was true for *Iris spuria* and *Allium angulosum* in the arable field.

Discussion

After three years all sown species had established successfully at both sites. Thus, the common failure of re-establishment of these flood-meadow target species in habitat restoration (Donath et al. 2003) is obviously due to seed limitation, whereas the lack of regeneration niches seems to be of minor importance. Only in the strongly gap-dependent *Arabis nemorensis* could a significant microsite limitation be confirmed for the meadow. Similar results were obtained in many other seed addition experiments (Tilman 1997, Turnbull et al. 2000, Zobel et al. 2000). In accordance with other studies (Kotorová & Lepš 1999, Isselstein et al. 2002) an apparent decrease in germination rate became evident under

field conditions, presumably an effect of seed predation (e.g. Hulme 1994) and/or physical hazards (e.g. Hutchings & Booth 1996b).

Seedling survivorship and final establishment rates as fully developed vegetative or regenerative adults were higher than in other studies, particularly than those from dry calcareous grasslands (Silvertown & Dickie 1980, Kupferschmid et al. 2000). With regard to the low germination rate of seeds in the control experiment (Table 1), even in the least successful *Cnidium dubium* establishment rates were within the range of the other studied species. Remarkably, the best overall establishment rates were found both in the most common (*Galium wirtgenii*) and in the rarest and most threatened species (*Iris spuria*). Besides the generally low germination rate in *Cnidium dubium* there was no indication that the rarity of most of the studied species may be predominantly caused by detrimental germination requirements or a drawback in microsite availability under the prevailing habitat conditions.

The surprisingly high recruitment success that was achieved must be seen in conjunction with the favourable moisture conditions and the relatively open canopy structure during the successive retreat of flooding water in early summer 2001 when germination started. At this time of the year the studied sites usually exhibit poor conditions for recruitment due to low precipitation and high temperatures that lead to moisture deficits in topsoils and a rapid superficial hardening in the clay-rich substrate. In many studies topsoil desiccation was found to be the major cause of high seedling mortality (e.g. Ryser 1993, Stampfli & Zeiter 1999). In contrast, constant favourable water supply proved to have a strong positive impact on germination and seedling establishment (e.g. Oomes & Elberse 1976, De Jong & Klinkhammer 1988). In a restoration experiment in the same region massive recruitment from transferred plant material could be observed after an unusually long-lasting early summer flood in 1999, whereas under the dry conditions prevailing one year earlier germination and establishment largely failed (Hölzel & Otte 2003). In summer-dry subcontinental flood-meadows regeneration by seeds appears to be strongly facilitated by favourable moisture supply and disturbances of the established vegetation in the course of flooding events (Hölzel & Otte accepted a). Consequently, we have to keep in mind that a replication of the same experiment in a year with different flooding patterns or weather conditions could lead to strongly deviating results.

Contrary to predictions made by plant ecological theory (Bertness & Callaway 1994) responses of species towards gaps and litter and their behaviour along productivity gradients were partly equivocal and more complicated than expected. Although productivity was

considerably lower in the arable field fallow, this did not result in a statistically significant higher overall recruitment success. Presumably, the inhibiting effect of plant biomass in the meadow was partly compensated by early mowing in late June, which reduced the amount of standing crop significantly for the rest of the vegetation period (Table 3). Mowing can be seen as seasonal competitive release (Huston 1994, Grace 2001), increasing the amount of light penetration to the soil surface (e.g. Jutila & Grace 2002). Strong positive effects of above-ground biomass removal by mowing on seedling recruitment in wet meadows have also been described by other authors (Kotorová & Lepš 1999, Jensen & Meyer 2001, Isselstein et al. 2002).

Surprisingly, there was no overall effect of gap and litter treatments in the arable field site. No species showed a positive response towards gaps and one species was even negatively affected. The insignificance of gaps may indicate that seedling recruitment was not hampered by the established vegetation. Actually, as early as mid summer of the first season gaps and controls were no longer distinguishable in the vegetation cover (Table 3). This situation was largely a result of the dominance of annual arable weeds that emerged from the soil seed bank irrespective of gap treatments. In contrast to the meadow site, the sown species, which are preferably perennials of late successional stages, grew in the neighbourhood of simultaneously emerging annual arable weeds. Thus they co-occurred with plants showing completely different functional characteristics, which may result in a reduced amount of inter-specific competition (Holmgren et al. 1997). Remarkably, *Arabis nemorensis*, the species whose functional characteristics are most similar to ruderal arable weeds, showed a much lower establishment success in the arable field than in more open gaps of the meadow site where arable weeds rarely emerged form the soil seed bank after sod stripping.

In the arable field site there was no negative - and in one case even a positive response - towards litter addition on recruitment, indicating that, as in the case of established vegetation, positive (protection against desiccation) and negative (shading) impacts obviously outweighed each other (Holmgren et al. 1997).

In the meadow site there were more treatment effects that met the expectations one could have from plant ecological theory. However, responses strongly depended on species identity. As predicted by theory (Grime 2001) the species with the smallest seeds (*Arabis nemorensis*) proved to be completely gap-dependent for successful recruitment in closed swards. This concurs with results for other rare wet grassland species with small seeds such as *Gentiana pneumonanthe* (Křenová & Lepš 1996). For the very closely related *Arabis hirsuta*, typical of low productive calcareous grasslands, Ryser (1993) found an almost complete failure of

regeneration within gaps due to uprooting by frost heave and following desiccation during dry spring weather, whereas recruitment was much more successful under the shelter of neighbouring plants. Thus, even within the same supra-species (*Arbais hirusta* agg. according to Wisskirchen & Haeupler 1998) protective and competitive effects of the surrounding vegetation may strongly depend on the prevailing environmental conditions. The higher biomass production levels of flood-meadows in conjunction with lower environmental harshness obviously result in a shift towards a strict gap-dependence of seedling establishment, which gives credence to the 'gradient-hypothesis' of Bertness & Callaway (1994). Surprisingly, none of the other species showed a significant response towards gaps in the meadow site. Again, one can presume that positive effects (lower resource competition) were countered by negative effects (no protection against desiccation after mowing) of gaps. Kotorová and Lepš (1999) also reported few differences in recruitment success in a wet meadow between gap treatments and solely mown plots.

Only in one species (*Galium wirtgenii*) did litter addition have a negative impact on recruitment success. In contrast, the large-seeded *Iris spuria* showed a highly significant positive response towards litter addition. The facilitative effect of litter was probably re-enforced by the delayed onset of germination, which is typical of this species due to physical dormancy induced by a particularly thick and compact seed coat (Hölzel & Otte accepted c). Litter treatments presumably provided a better protection against desiccation, caused by high temperatures and relative open vegetation structure prevailing after the first cut of the meadow, when germination of *Iris spuria* started. Equally, litter may act as a shelter against predation by rodents (Hulme 1994). For large-seeded species neutral or even positive effects of litter on recruitment success have been reported from a number of field studies (e.g. Gross 1984, Kotorová & Lepš 1999). Generally, relatively large-seeded species appear to be less susceptible to litter layers and competition by established plants than smaller ones, which increases the likeliness of successful recruitment in seed addition experiments (Jakobsson & Eriksson 2000, Moles & Westoby 2002). Summarizing, one can conclude that even in the meadow site significant responses to treatments were largely confined to the extremes of the seed size spectrum. At both sites the lack of a more general response towards treatments remains at least partly inexplicable.

The results of this study suggest that the interactions between variable site conditions such as flooding, drought and management and differences in biomass and functional characteristics of the established vegetation result in a fragile balance between facilitation and inhibition that may vary considerably among sites and species. Thus the facilitating or inhibiting effects of

neighbouring plants, litter and disturbance regimes on seedling recruitment success are strongly context-dependent and it appears to be difficult to define common rules, particularly on the basis of single relatively short-termed surveys (e.g. Tielborger & Kadmon 2000, Turnbull et al 2000). The findings largely concur with the theoretical considerations on the interplay of facilitation and competition in plant communities made by Holmgren et al. (1997). These authors point out the general co-occurrence and dynamical nature of both effects, which are usually in a non-equilibrium state even on a small temporal and spatial scale. Another aspect that must be considered for the explanation of the obtained results is small-scale environmental heterogenity and stochasticity, which may at least partly outweigh the effects of treatments.

A high variability in the response towards treatments seems to be a common feature of recruitment experiments conducted under field conditions (e.g. Ryser 1993, Suding & Goldberg 1999, Zobel et al. 2000, Coulson et al. 2001). Consequently, the spatial and temporal replication of such experiments appears to be of crucial importance to find more universal rules and to assess the impact of variable meteorological, edaphic and biological marginal conditions.

Generally, the findings made in this study underpin the high significance of local seed availability and species-specific demands to mircrosite quality during recruitment for the structuring and maintenance of species diversity in plant communities (Grubb 1977, Eriksson & Ehrlén 1992, Grace 2001).

Kapitel 8

Ausführliche Zusammenfassung und Synthese

Samenbankpersistenz in Auenwiesen und deren Bedeutung für die Renaturierung
(Kapitel 2)

Zur Charakterisierung der Langlebigkeit von Diasporen fanden bislang aus praktischen Erwägungen überwiegend relativ grobe Kategorisierungen Anwendung (Thompson et al. 1997). Im Gegensatz dazu wird in der vorliegenden Arbeit versucht, die Tendenz einer Art keimfähige Diasporen im Boden zu akkumulieren, mit Hilfe eines kontinuierlichen Indexes zum Ausdruck zu bringen. Dieser sogenannte „seed accumulation index" setzt für ein Kollektiv von Untersuchungsflächen die Frequenz und Abundanz einer Art in der Samenbank des Bodens in Beziehung zu deren Frequenz und Abundanz in der oberirdischen Vegetation. Der Index rangiert zwischen 0 für Arten, die nur in der oberirdischen Vegetation angetroffen werden, und 100 für solche, die nur in der Samenbank vorhanden sind.

Ein Vergleich mit dem sogenannten „seed longevity index", dem derzeit wohl besten verfügbaren Referenzwert für Samenbankpersistenz in der Nordwesteuropäischen Flora (Bekker et al. 1998), ergab eine sehr hohe Übereinstimmung ($R^2 = 0.64$) für einen Satz von 115 Arten, die in beiden Datensätzen vorkamen. Weitere häufig verwendete „einfache" Prädiktoren für Samenbankpersistenz wie Tiefenverteilung der Samen, Samengewicht, -größe und -form (Thompson et al. 1993) erwiesen sich als weitaus weniger geeignet. Relativ am besten schnitt das neu eingeführte Merkmal der maximalen Samendichte in der tieferen beprobten Bodenschicht (5-10 cm) ab ($R^2 = 0.39$).

Im Vergleich zu anderen gefährdeten Grünlandtypen wie z. B. Kalkmagerrasen (Poschlod & Jackel 1993, Hutchings & Booth 1996a) zeichnen sich die untersuchten Auenwiesen durch einen relativ hohen Anteil an Arten mit einer deutlichen Tendenz zur Akkumulation einer langlebigen Diasporenbank im Boden aus. Unter den Zielarten der Stromtalwiesen sind rund 40 % dieser Gruppe zuzurechnen. Der relativ hohe Anteil an ausgesprochenen Samenbankstrategen in der Flora von Auenwiesen spiegelt den dynamischen Charakter dieses Lebensraumtyps wider. Viele Arten mit starker Tendenz zu Samenakkumulation wie *Arabis nemorensis*, *Cerastium dubium* und *Viola persicifolia* spielen in der oberirdischen Vegetation eine völlig untergeordnete Rolle oder fehlen phasenweise sogar vollständig und gelangen erst

nach überflutungsbedingter Störung zu stärkerer Entfaltung. Die Ausbildung einer persistenten Diasporenbank dient hierbei vornehmlich dazu, ungünstige Umweltbedingungen zu überbrücken bzw. unregelmäßig auftretende, kurze Gunstphasen rasch auszunutzen (Grime 2001).

Nur bei einer begrenzten Anzahl von Zielarten kann potenziell mit einer Reetablierung aus der Samenbank im Zuge von Renaturierungsmaßnahmen gerechnet werden. Entsprechendes gilt aber im Wesentlichen nur für Situationen, die ein Überdauern der Diasporenbank begünstigen, wie dies insbesondere bei Brachen der Fall ist. So konnte in der Untersuchungsregion nach Entbuschungsmaßnahmen und/oder der Wiederaufnahme der Mahd in Brachen örtlich eine spontane und teils spektakuläre Reetablierung von Zielarten wie *Arabis nemorensis*, *Viola elatior* und *Viola pumila* aus der persistenten Diasporenbank festgestellt werden (Hölzel et al. 2002). Dagegen führt eine zwischenzeitliche ackerbauliche Nutzung im Regelfall zu einer raschen Aufzehrung der persistenten Diasporenbank von Zielarten (z. B. Vécrin et al. 2002). Hierfür sprechen auch eigene Untersuchungen zum Renaturierungserfolg auf ehemaligen Ackerflächen (Donath et al. 2003, Bissels et al. accepted).

Bedeutung des fluviatilen Eintrags von Diasporen in Auenwiesen
(Kapitel 3)

Anhand eines Vergleichs der Samenbanken von Auenwiesen in verschiedenen hydrologischen Auenkompartimenten mit unterschiedlichen Eintragsbedingungen konnten keine Indizien für einen erhöhten Diasporeneintrag in der frei überfluteten Rezentaue am nördlichen Oberrhein gefunden werden. Die Samenbanken der funktionalen Rezentaue zeichneten sich im Vergleich zur ausgedeichten Altaue und der nur unregelmäßig direkt überfluteten Hybridaue weder durch größere Samendichten noch durch eine höhere Anzahl an allochthonen Arten aus, die der etablierten Vegetation der Probeflächen fehlten. Die in der Samenbank auftretenden allochthonen Arten konnten in der Regel dem lokalen Artenpool in der näheren Umgebung der Probeflächen zugerechnet werden. Artvorkommen, die einen Transport über größere Distanzen zwingend nahe legten, waren extrem seltene Ausnahmen. Entlang eines Gradienten zunehmender Überflutungshäufigkeit konnte in der Rezentaue zwar eine Zunahme der Gesamtsamendichte im Boden festgestellt werden, jedoch keine gleichzeitige Zunahme der Anzahl und Dichte allochthoner Arten. Die Zunahme der Samendichten mit der

Überflutungsdauer ist im wesentlichen auf eine analoge Zunahme ruderaler Störungszeiger in der oberirdischen Vegetation zurückzuführen. Unterschiede in der Zusammensetzung der Samenbank der drei Auenkompartimente reflektierten weitgehend Unterschiede in der oberirdischen Vegetation, dem aktuellen Mahdregime und der Nutzungsgeschichte.

Neben der relativ gerinnefernen Lage der untersuchten Flächen dürfte vor allem der Mangel an potenziellen Samenquellen durch die Zerstörung oder Ausdeichung naturnaher Auenlebensräume entlang des Oberrheins ausschlaggebend für die geringe Bedeutung des aktuellen Diasporeneintrags in der Rezentaue sein.

Da selbst häufige Ackerwildkräuter mit persistenter Samenbank wie *Chenopodium album* und *Capsella bursa-pastoris* kaum in der Samenbank der Rezentaue nachgewiesen wurden, dürfte die Wahrscheinlichkeit des Eintrags von weitaus selteneren Zielarten der Stromtalwiesen nahezu gegen Null tendieren. Von einer Wiederherstellung naturnäherer Überflutungsverhältnisse durch die Öffnung von Deichen und die direkte Wiederanbindung an das Überflutungsregime des Rheins ist dementsprechend kein nennenswerter Beitrag zur Anreicherung von Zielarten auf Renaturierungsflächen zu erwarten. Zu vergleichbaren Schlussfolgerungen führte eine Evaluierung des Renaturierungserfolgs auf ehemaligen Ackerflächen, die vor ca. 20 Jahren in Auengrünland umgewandelt wurden (Bissels et al. accepted). Auch hierbei fanden sich für die Rezentaue keinerlei Anzeichen einer vermehrten oder rascheren Etablierung von Zielarten. Überraschenderweise war die Zielartenanreicherung in der Altaue aufgrund der günstigeren Umfeldsituation (Reliktpopulationen entlang von Grabenrändern) sogar tendenziell besser (Donath et al. 2003).

Interannuelle Dynamik der Bodendiasporenbank in Auenwiesen
(Kapitel 4)

Bei einem Vergleich der Diasporenbanken von 46 Auenwiesen, die nach zwei Perioden mit sehr unterschiedlichem Überflutungsgeschehen (1996-1997: hochwasserarm; 1998-1999 extrem hochwasserreich) beprobt wurden, zeigten sich sehr starke qualitative und quantitative Veränderungen. Binnen zweier Jahre verringerte sich die Samendichte in der Diasporenbank im Mittel um nicht weniger als 50 % und der mittlere Artenreichtum um nicht weniger als 30 %. Dieser Rückgang betraf unterschiedliche funktionale Gruppen in ähnlicher Weise. Die Veränderungen in der Diasporenbank zwischen beiden Beprobungsterminen waren deutlich stärker als jene in der oberirdischen Vegetation. Zugleich verringerte sich die

Übereinstimmung in der Ähnlichkeitsstruktur von Samenbank und oberirdischer Vegetation. Bei einer Analyse der Muster des Rückgangs von Samendichte und Artenreichtum in der Samenbank ergaben sich kaum Beziehungen zur Überflutungsdauer, der Samenbankgesellschaft oder dem hydrologischen Auentyp. Unter den 21 signifikant zurückgegangenen Arten befanden sich auffällig viele Ruderale mit hohen Keimtemperaturansprüchen, während vorzugsweise im Herbst keimende Winterannuelle bezeichnenderweise keine Abnahme aufwiesen. Generell lieferten individuelle Keimtemperaturansprüche das beste Erklärungsmuster für den Rückgang oder Nichtrückgang von Arten in der Samenbank. Der drastische Rückgang der Samen- und Artendichte wird als Folge besonders günstiger Keimungsbedingungen während des schrittweisen Rückgangs eines außergewöhnlich lange anhaltenden Hochwassers im Frühsommer 1999 interpretiert. Eine Keimung aus der Samenbank wurde während dieser Zeit durch optimale Feuchteverhältnisse in Kombination mit hohen Temperaturen stark begünstigt. Zugleich entstanden durch das teilweise oder vollständige Absterben der oberirdischen Vegetation sehr offene Bodenverhältnisse. Dies begünstigt relativ große Temperaturamplituden im Oberboden, wodurch bei vielen Arten die Dunkeldormanz gebrochen wird (Thompson et al. 1977). Bei der Stimulation der Dunkelkeimung können ferner auch erhöhte Nitratgehalte in der Bodenlösung oder temporär anaerobe Bedingungen eine bedeutende Rolle spielen (Pons 1989, Baskin & Baskin 2001).

Starke Keimungsstimulation nach Überflutung und sukzessivem Trockenfallen wurde in der Literatur bereits als „post-flood germination flush" für überflutungsgeprägtes Küstengrasland (Jutila 2001) aber auch für Auwälder beschrieben (Schneider & Sharitz 1986). Bislang liegen hierzu aber nur relativ wenige empirische Untersuchungen vor.

Die gemachten Befunde legen den Schluss nahe, dass die persistente Samenbank sowohl zur Überbrückung als auch zur raschen Ausnutzung überflutungsbedingter Störungen eine herausragende Rolle spielt (z. B. Grime 2001). So konnten etwa an eher trockene Bedingungen adaptierte Arten (z. B. *Arenaria serpyllifolia*) das Hochwasser in der Samenbank schadlos überstehen, während andere Arten (z. B. *Potentilla reptans*) die Gunst der Stunde zur Aktivierung ruhender Samenreservoirs im Boden nutzten. Für die Aufrechterhaltung der spezifischen Phytodiversität der Auenwiesen ist das Überleben ökologisch und funktional sehr unterschiedlicher Arten von entscheidender Bedeutung (Grubb 1977), wozu beide Prozesse einen wesentlichen Beitrag leisten.

Keimungsökologie von Stromtalarten und ihre Bedeutung für die Renaturierung
(Kapitel 5)

Eine Metaanalyse wichtiger, aus Labor- und Freilandexperimenten abgeleiteter keimungsökologischer Einzelmerkmale von 42 Arten mittels Hauptkomponentenanalyse ergab entlang der ersten Achse einen Gradienten zunehmender primärer Dormanz. Hierbei werden Arten mit einer hohen Kapazität für eine rasche und fast vollständige Keimung über ein breites Spektrum von Temperaturstufen von solchen getrennt, die hohe oder enge Keimungstemperaturansprüche und ein stark verzögertes und/oder asynchrones Auflaufverhalten aufweisen. Viele typische Arten der Stromtalwiesen keimen unmittelbar nach der Schüttung fast ausschließlich bei relativ hohen Temperaturen (> 20 °C). Erst nach einer mehrwöchigen Kältestratifikation erfolgte eine Keimung auch bei niedrigeren Temperaturen. Hohe Keimungstemperaturansprüche und ein obligatorisches Kältestratifikationsbedürfnis erweisen sich auch in Stromtalwiesen als bedeutende Mechanismen zur Vermeidung einer für den Sämling im Regelfall nachteiligen Herbstkeimung (Grime 2001). Die Mehrzahl der untersuchten Arten nutzt die hinsichtlich Feuchtigkeit und Lückigkeit des Bestandes für die Keimlingsetablierung besonders günstige Zeit des Vorfrühlings aus. Viele Arten, die in der Lage sind, große langlebige Samenbanken im Boden zu akkumulieren (siehe Kapitel 2), zeigten eine nur sehr geringe Dormanz und keimten sehr rasch und fast vollständig unter Lichteinfluss. Hierbei handelt es sich in erster Linie um besonderes kleinsamige Sippen, welche sich in der Regel durch eine strikte Dunkeldormanz auszeichnen (Grime 2001) und zugleich besonders rasch in die Samenbank des Bodens inkorporiert werden können (Thompson et al. 1993, Bekker et al. 1997). Generell konnten keine signifikanten Beziehungen zwischen Keimungscharakteristika einerseits sowie Stromtalbindung und mitteleuropäischer Arealgröße andererseits nachgewiesen werden.
Lediglich für gefährdete Arten ergab sich ein Trend in Richtung höherer Keimtemperaturansprüche und zeitlich verzögertem, asynchronem Auflaufverhalten. Entsprechende Eigenschaften sind im Falle der durch häufige Sommertrockenheit gekennzeichneten Stromtalwiesenstandorte eher als nachteilig einzuschätzen.

Renaturierung von Auenwiesen durch Oberbodenabtrag und Diasporentransfer mit Mahdgut

(Kapitel 6)

Der auf einer vormals intensiv ackerbaulich genutzten Renaturierungsfläche durchgeführte Oberbodenabtrag führte zur einer raschen und nachhaltigen Degradation der Bodenfruchtbarkeit. Die Ausstattung des Standorts mit N, P und K konnte hierdurch schlagartig auf das Niveau der Zielartengemeinschaften (*Cnidion* und *Molinion*) oder sogar darunter abgesenkt werden. Gleichzeitig führte der Oberbodenabtrag zu einer partiellen (Abtragstiefe 30 cm) oder sogar fast vollständigen (Abtragstiefe 50 cm) Vernichtung der Samenbank des ehemaligen Ackers, die sich vornehmlich aus kurzlebigen Acker- und Ruderalarten, aber auch einigen mesophilen Grünlandarten zusammensetzte.

Im streifenweise aufgebrachten Mahdgut aus nahegelegenen artenreichen Altbeständen von *Cnidion*- und *Molinion*-Wiesen konnten durch Auskeimungsanalysen Samen von über 66 Arten nachgewiesen werden, die sich bis auf wenige Ausnahmen auch erfolgreich auf der Renaturierungsfläche etablierten. Samen- und Artendichten im analysierten Mahdgut schwankten sehr stark zwischen, aber auch innerhalb der einzelnen Mahdgutherkünfte, wobei die Dichten bei der Mehrzahl der gefundenen Arten weniger als 10 Samen / m² betrugen. Die Korrelation zwischen Samendichte im Mahdgut und Etablierungserfolg war insgesamt relativ gering, was auf deutliche artspezifische Unterschiede im Etablierungsvermögen hindeutet.

Die Vegetationsentwicklung auf der Abtragungsfläche war charakterisiert durch einen raschen Rückgang der zunächst dominanten Ackerwildkräuter und Ruderalarten. Im Gegenzug erfolgte ab dem dritten Jahr eine rapide Zunahme und Ausbreitung von mesophilen Grünlandarten, die auf der Fläche bereits vorhanden waren, sowie von Arten, die mit dem aufgebrachten Mahdgut übertragen wurden. Innerhalb von vier Jahren konnten sich 102 Arten etablieren, die eindeutig und ausschließlich aus dem aufgebrachten Mahdgut stammten, darunter mehr als 30 sehr seltene und gefährdete Arten. Insgesamt wurden rund 82 % des Artenpools der Spenderflächen übertragen!

Der Etablierungserfolg von Mahdgutarten war auf regelmäßig und länger anhaltend überschwemmten Teilflächen besonders groß. Neben einer Schwächung der Konkurrenzvegetation sind hierfür aufgrund der warm-trockenen Klimabedingungen der Untersuchungsregion offenbar die günstigen Feuchtebedingungen nach Überflutungen von maßgeblicher Bedeutung. Gleichzeitig konnte in regelmäßig überschwemmten Bereichen eine wesentlich raschere Ausbreitung von Mahdgutarten auf benachbarte Nullflächen beobachtet

werden. Letzteres verdeutlicht bei Vorhandensein ergiebiger Samenquellen die potenzielle Bedeutung von Überflutungen für eine Ausbreitung von Zielarten im Nahbereich.

Die Methode des Diasporentransfers mittels Mahdgut erwies sich als sehr erfolgreiches Mittel zur raschen Entwicklung von artenreichem Grünland. Selbst extrem seltenen Arten wie *Arabis nemorensis* und *Iris spuria* gelang es sehr rasch, große und vitale Populationen zu etablieren. Die Resultate dieses Experiments belegen auf eindrucksvolle Weise, dass der bislang mangelnde Erfolg von Renaturierungsprojekten in Auenwiesen am nördlichen Oberrhein in hohem Maße auf eine Samenlimitierung zurückzuführen ist. Gleichwohl muss der besondere Erfolg der hier dargestellten Maßnahme im Zusammenhang mit dem gleichzeitig durchgeführten Oberbodenabtrag gesehen werden, wodurch sehr günstige Bedingungen für auflaufende Keimlinge geschaffen wurden. Dies gilt natürlich in besonderem Maße für Arten, die obligatorisch, insbesondere in der Keimungs- und Etablierungsphase, auf konkurrenzarme Standortbedingungen angewiesen sind wie z. B. *Succisa pratensis* und *Gentiana pneumonanthe* (Křenová & Lepš 1996, Špačková et al. 1998). Aber auch bei konkurrenzkräftigeren mesophytischen Grünlandarten muss bei geschlossener Narbe und höherer Biomasseproduktion mit einem deutlich geringeren Etablierungserfolg gerechnet werden (Kotorová & Lepš 1999, Jakobsson & Eriksson 2000). Selbst auf der Oberbodenabtragsfläche wurde dies bereits anhand der hochsignifikant negativen Beziehung zwischen dem Deckungsgrad autochthoner mesophiler Grünlandarten und dem Etablierungserfolg von Mahdgutarten deutlich.

Einfluss der Umgebungsvegetation auf die Etablierung von Stromtalwiesenarten (Kapitel 7)

Anhand der faktoriellen Aussaatexperimente, die in einer jungen Ackerbrache und einem benachbarten, artenarmen Grünlandbestand durchgeführt wurden, ergab sich für fünf der sechs getesteten Stromtalarten eine vorherrschende Samenlimitierung. Lediglich bei der besonders kleinsamigen *Arabis nemorensis*, die sich innerhalb des Grünlandbestandes nur in künstlichen Lücken erfolgreich etablieren konnte, liegt offensichtlich zusätzlich ein Mangel an Regenerationsnischen vor. Innerhalb der jungen Ackerbrache hatte die Schaffung von Lücken bei keiner der getesteten Arten eine positive Auswirkung auf den Etablierungserfolg, was den Schluss nahe legt, dass von der im ersten Jahr recht schütteren Ackerwildkrautvegetation keine messbare Beeinträchtigung des Auflaufens ausging. Aber

selbst innerhalb des Grünlandbestandes mit einer im Vergleich zur Ackerbrache dreifach höheren Biomasseproduktion zeigte nur eine Art eine signifikant positive Reaktion gegenüber der Schaffung von Bestandeslücken. Dieser zunächst überraschende Befund ist vermutlich darauf zurückzuführen, dass eine relativ frühe Mahd Ende Juni zu einer deutlichen Verminderung der Lichtkonkurrenz innerhalb des Grünlandbestandes führte. Im Fall von *Iris spuria* zeigten die künstlich applizierten Streuauflagen überraschenderweise sogar eine positive Wirkung auf den Etablierungserfolg. Bei dieser besonders großsamigen Art, die infolge physikalischer Dormanz erst im Hochsommer zur Keimung gelangt (siehe Kapitel 5), überwog offensichtlich die positive Wirkung der Streuauflage als Schutz vor Austrocknung die negative Verdämmungswirkung. Die Eingangshypothese, dass künstliche Lücken als Befreiung vom Konkurrenzdruck benachbarter Pflanzen wirken und Streudecken jenen verschärfen, konnte in dieser kategorischen Form nicht belegt werden. Vielmehr ergaben sich in Abhängigkeit von Artenidentität und umgebender Vegetationsmatrix sowohl positive als auch negative Interaktionen, wobei sich die Mehrzahl der Arten überraschenderweise neutral verhielt. Der gemessen an vergleichbaren Studien fast durchweg relativ hohe Etablierungserfolg, welcher weitgehend unabhängig von Umgebungsvegetation und Behandlungsvarianten erreicht wurde, muss aber vor dem Hintergrund der besonders günstigen Keimungs- und Etablierungsbedingungen gesehen werden, die infolge eines lange anhaltenden Frühjahrhochwassers im ersten Jahr nach der Aussaat herrschten.

Für die Renaturierungspraxis belegen die Ergebnisse dieses Ansaatexperiments, dass eine Etablierung von seltenen Zielarten der Stromtalwiesen auch ohne Oberbodenabtrag und bei weniger offenen und zugleich produktiveren Bodenverhältnissen prinzipiell möglich ist, wenngleich die hier gemachten Befunde nur mit Vorbehalt auf andere Standorte und Jahre mit abweichendem Überflutungs- und Witterungsgeschehen übertragen werden können.

Synthese

Die der Arbeit zugrunde liegende Ausgangshypothese, dass der geringe Erfolg bei der Wiederherstellung artenreicher Auenwiesen am nördlichen Oberrhein überwiegend auf eine Samenlimitierung zurückzuführen ist, konnte weitgehend bestätigt werden. Weder persistente Samenbanken noch der in Auenökosystemen oft als besonders bedeutungsvoll und effektiv angesehene fluviatile Ausbreitungspfad vermögen im vorliegenden Fall einen entscheidenden Beitrag zur Renaturierung zu leisten.

Erwartungsgemäß bilden im durch Überflutungsstörung geprägten Auengrünland persistente Diasporenbanken bei vielen charakteristischen Pflanzenarten einen wichtigen Teil der Lebensstrategie. Dabei handelt es sich überwiegend um relativ konkurrenzschwache und teils nur ephemer auftretende Ruderalstrategen, darunter auch viele besonders charakteristische Zielarten wie *Arabis nemorensis, Cerastium dubium* und alle drei Stromtalveilchen (*Viola elatior, V. persicifolia, V. pumila*). Persistente Samenbanken dienen diesen Arten sowohl zur Überbrückung als auch zur raschen Ausnutzung von singulären Störereignissen und Perioden mit ungünstigen Bedingungen wie sie für die variable Umwelt der untersuchten Flussauen typisch sind.

Gleichwohl erweist sich das von Samenbanken ausgehende Renaturierungspotential insgesamt als äußerst eingeschränkt (Kapitel 2). Lediglich bei günstigen Rahmenbedingungen wie etwa der Wiederaufnahme der Nutzung in Brachen - nicht aber bei ackerbaulicher Vornutzung - kann mit einem wesentlichen Beitrag der persistenten Diasporenbank zur Artenanreicherung gerechnet werden. Dieser umfasst bestenfalls 40 % des Spektrums an Zielarten. Alle übrigen Arten müssen obligatorisch von außen zuwandern.

Der Diasporeneintrag durch Überflutung, mit dem sich vielfach große Renaturierungserwartungen verbinden, erwies sich in vorliegendem Fall als weitgehend ineffektiv um eine Anreicherung mit Zielarten zu gewährleisten. Weder anhand der Zusammensetzung der Bodendiasporenbank (Kapitel 3) noch anhand des Renaturierungserfolgs (Bissels et al. accepted) in verschiedenen hydrologischen Auenkompartimenten ließen sich Indizien finden, die eine Signifikanz des fluviatilen Eintrags belegen könnten. Ob diese Befunde nur am besonders stark regulierten und weitgehend seiner natürlichen Auen beraubten Oberrhein Gültigkeit besitzen, oder ob sie auch für naturnähere Stromauen zutreffen, bedarf zukünftig weiterer Klärung. Allerdings bestätigen auch die Ergebnisse anderer Autoren (Bischoff 2002, Vécrin et al. 2002) eher eine geringe Bedeutung von Überflutungen für die Zielartenanreicherung in Auenwiesen.

Nur bei wenigen Arten wie etwa *Cnidium dubium* und den meisten *Carex*-Sippen ergaben sich Hinweise, dass deren schwaches Etablierungsvermögen auf eine geringe Keimungsfähigkeit der Samen oder nachteilige Keimungseigenschaften (z. B. hohe Temperaturansprüche) zurückzuführen ist (Kapitel 4). Da die meisten der untersuchten Zielarten in der Lage sind, die für eine Keimung und Etablierung besonders günstige Zeit des Vorfrühlings auszunutzen, können Managementmaßnahmen, die zu dieser Zeit offene Boden- und Vegetationsstrukturen schaffen (z. B. Nachbeweidung mit Schafen), eine erfolgreiche Ansiedlung aktiv unterstützen.

In mehreren der hier dargestellten Studien (Kapitel 3, 6 und 7) ergaben sich deutliche Hinweise, dass Hochwasserereignisse, vor allem wenn sie sich bis in die Vegetationsperiode hinein erstrecken, für eine erfolgreiche Keimung und Etablierung sehr förderlich sind. Dies gilt wiederum in besonderem Maße für Arten mit jahreszeitlich stark verzögerter Keimung und/oder hohen Keimtemperaturansprüchen wie z. B. *Scutellaria hastifolia* (Kapitel 5). Neben einer Schwächung konkurrierender Matrixarten bei länger anhaltenden Überflutungen sind hierfür die verbesserten Bodenfeuchteverhältnisse offensichtlich von großer Bedeutung.

Der überragende Erfolg des Mahdgutübertragungsexperiments (Kapitel 6) belegt auf eindrucksvolle Weise die Hypothese einer Samenlimitierung als Hauptursache für den bislang geringen Renaturierungserfolg und stimmt hierin auch mit einer Vielzahl experimenteller Studien überein (Burke & Grime 1996, Tilman 1997, Turnbull et al. 2000). Ähnlich wie bereits für Streu- und Futterwiesen auf Niedermoorstandorten (Patzelt 1998, Biewer 1997), Kalkmagerrasen (Tränkle 1997, Pfadenhauer & Miller 2000) und Sandrasen (Kirmer & Mahn 2001, Stroh et al. 2002) erwies sich auch für Stromtalwiesen die Methode des Diasporentransfers mit Mahdgut als ein überaus probates Mittel zur Überwindung der Ausbreitungslimitierung zahlreicher Zielarten. Die erzielten Übertragungsraten waren insgesamt sogar noch größer als bei den zuvor genannten Experimenten. Der Erfolg der Maßnahme muss allerdings im Zusammenhang mit dem zuvor durchgeführten Oberbodenabtrag gesehen werden, wodurch optimale Bedingungen für die Keimlingsetablierung geschaffen wurden. Der Oberbodenabtrag selbst erwies sich als extrem effektive Methode zur Schaffung relativ nährstoffarmer, unproduktiver Standortverhältnisse. Gleichzeitig kommt es hierbei zu einer starken Ausdünnung oder sogar fast vollständigen Eliminierung der Diasporenbank des Oberbodens. Als besonders bedeutsamer Effekt zeigte sich hierbei insbesondere die starke Schwächung der Dominanz ausdauernder Grünlandarten, während von annuellen Ackerwildkräutern und relativ kurzlebigen Ruderalarten offenbar ein weitaus geringerer Konkurrenzdruck auf etablierende Keimlinge ausgeht. Die negative

Korrelation zwischen dem Deckungsgrad autochthoner mesophiler Grünlandarten und dem Etablierungserfolg von Arten aus dem aufgebrachten Mahdgut belegt, dass es mit zunehmendem Narbenschluss zu einer deutlichen Verknappung an Regenerationsnischen kommt. Es ist daher davon auszugehen, dass ein Mahdgutauftrag bei geschlossenen Narben und/oder höherer Produktivität des Standorts weitaus weniger erfolgreich verläuft.

Gleichwohl konnte anhand des Aussaatexperiments in Kapitel 7 deutlich gezeigt werden, dass auch ohne Oberbodenabtrag für die meisten Zielarten eine erfolgreiche Etablierung prinzipiell möglich ist. Dies gilt sowohl für junge Ackerbrachen mit relativ schütterer Ackerwildkraut- und Ruderalvegetation als auch für vergleichsweise wüchsiges, artenarmes Saatgrünland auf ehemaligen Ackerflächen.

Durch ein sehr lange anhaltendes Frühjahrshochwasser herrschten bei diesem Experiment allerdings besonders günstige Voraussetzungen für eine erfolgreiche Keimlingsetablierung, so dass die hierbei erzielten Ergebnisse sich nur bedingt verallgemeinern lassen. Grundsätzlich besteht weiterer Klärungsbedarf, ob und bis zu welchem Grad ein Mahdgutauftrag auch bei geschlossenen Narben und/oder höheren Trophieniveaus erfolgreich verläuft, bzw. welche Behandlungsvarianten und vorgeschalteten Störungsregimes einer Etablierung von Zielarten förderlich sind. Entsprechende Fragestellungen sind gegenwärtig Hauptgegenstand umfangreicher experimenteller Untersuchungen im Rahmen des E&E-Vorhabens „Stromtalwiesen" (Hölzel & Harnisch 2002). Hierbei werden Verfahren des Diasporentransfers mittels Mahdgutauftrag großflächig und unter praxisnahen Bedingungen erprobt. Bereits heute lässt sich aber feststellen, dass die Mahdgutübertragung in besonderem Maße dazu geeignet ist, die Ausbreitungslimitierung von Pflanzenarten in fragmentierten Kulturlandschaften zu überwinden. Da diese auch in Zukunft ein Hauptproblem bei der Wiederherstellung und Neuschaffung gefährdeter Lebensgemeinschaften darstellen wird, sollten entsprechende Verfahren nicht nur im Rahmen qualitativ besonders hochwertiger Ersatz- und Ausgleichsmaßnahmen zur Anwendung kommen, sondern darüber hinaus als Standard Eingang in die landschaftspflegerische Praxis finden.

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