

Restoration and creation of freshwater wetlands using seed banks*

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Abstract

The minimum information about a seed bank needed for a wetland restoration or creation project is a species list. There are two basic techniques for determining the composition of seed banks: (1) mechanical separation of seeds from a volume of soil and (2) germination of seeds from a volume of soil under appropriate environmental conditions. The latter method always gives biased results. It is best to collect as many random samples as possible when sampling a wetland seed bank. These can be combined as needed for processing. Field studies in India have demonstrated that vestigial seed banks can be used to re-establish a former vegetation type in a monsoonal wetland that had become overgrown by a species of grass. In less than a year, 9 of 11 species in the vestigial seed bank were found growing in areas cleared of the grass. Vestigial seed banks of drained prairie wetlands in the northcentral United States contained a few wetland species after 70 years, although species diversity and seed density declined significantly after 20 to 30 years of drainage and cultivation. In Florida, U.S.A., wetlands have been established in strip-mined areas using donor soils from existing wetlands. Newly established wetlands quickly developed a dense cover of vegetation, although this vegetation often lacked many desirable wetland species. Experimental studies of soil moisture conditions using a seed bank from the Delta Marsh, Canada, demonstrated that soil moisture affected both the total number of seeds, and the relative proportion of seeds of each species that germinated from a seed bank. The density of seedlings of emergent wetland species in the treatments was directly proportional to soil moisture, while that of terrestrial annuals was inversely proportional. Emergent species made up nearly 90% of the seedlings in the wettest treatment and 0% in the driest.

Sommaire

Un projet de restauration ou création exige quelque information concernant le stock grainier, au moins une liste d'espèces. Il y a deux techniques fondamentales pour la détermination de la composition d'un stock grainier: la séparation des graines d'un volume du sol et la germination des graines d'un volume du sol sous conditions du milieu appropriées. La dernière technique donne toujours des résultats partiels. En échantillonnant un stock grainier d'un marécage, il est bon de prendre autant d'échantillons pris au hasard que possible. Ces échantillons peuvent être combinés de façon nécessaire pour le traitement. Les études faites sur le terrain dans l'Inde ont démontré que les stocks grainiers qui ont persisté peuvent être utilisés dans le rétablissement d'une type préexistant

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de végétation dans un marécage de mousson qui a été recouvert par une espèce d'herbe. Les stocks grainiers qui ont persisté dans les marécages de prairie drainés au nord-centre des États-Unis indiquent que quelques espèces des marécages étaient toujours présentes après 70 ans, mais que la diversité des espèces et la densité des graines avaient baissé d'une manière significative après 20 à 30 ans de culture et drainage. En Floride, aux États-Unis, des marécages ont été établis en quelques régions minières en utilisant des sols "donateurs" de marécages. Les marécages ainsi établis développèrent rapidement un tapis végétal dense, mais cette végétation manquait souvent plusieurs espèces désirables. Les études expérimentales des conditions de l'humidité du sol en utilisant un stock grainier de Delta Marsh (Canada) démontra que l'humidité du sol affecta le nombre total des graines, et aussi affecta la proportion relative des graines de chaque espèce qui germinent du stock grainier. L'abondance de jeunes plantes émergentes dans le traitement était directement proportionnelle à l'humidité du sol, tandis que celle des plantes annuelles était inversement proportionnelle. Les espèces émergentes formèrent presque 90% des jeunes plantes dans le traitement le plus humide et 0% dans le plus sec.

Introduction

The seed bank is a living record of the recent vegetation of an area as well as a predictor of its future composition. As environmental conditions change and established species are eliminated, guilds of species that are adapted to the new conditions and whose seeds are present in the seed bank are rapidly recruited (Van der Valk and Davis 1978; Van der Valk 1981; Leck *et al.* 1989). Wetland managers have taken advantage of seed banks for many years to re-establish species that have been lost due to water-level changes or overgrazing (Weller 1981; Van der Valk 1989). More recently the potential for using seed banks for wetland restoration and creation has been recognized and has begun to be exploited (Van der Valk and Pederson 1989). If, in a former wetland, seeds of wetland species are still present in significant numbers, one of the fastest, simplest and cheapest ways to restore wetland vegetation is to recruit species from its vestigial seed bank. The creation of a wetland can also be expedited by establishing a seed bank using soil from an existing wetland. Whether it is ecologically feasible to restore a former wetland or create a new one by exploiting seed banks will depend largely on the composition of the seed banks and the extent to which water levels and other environmental conditions can be controlled or manipulated. To exploit seed banks successfully, however, data on the composition of the seed bank are needed in order to select suitable restoration sites and donor wetlands.

This paper is divided into three sections. First, we

review techniques for determining the composition of wetland seed banks. Second, we review work on wetland restoration and creation using seed banks. Third, we examine the influence of environmental conditions on recruitment from the seed bank and the potential effects of these conditions on the outcome of restoration and creation projects.

Seed Bank Sampling

A seed bank is defined as the number, store, or density of viable seeds in the soil at a given time. Generally, not all species growing at a site are represented in its seed bank, but seeds of species not currently growing at the site may be present. In addition to seeds, small vegetative propagules such as turions (overwintering dwarf shoots) of flowering plants and spores of mosses, liverworts and ferns may be present. Since these vegetative propagules and spores are functionally equivalent to seeds, they are often included in the seed bank. Although it is not essential (Van der Valk and Verhoeven 1988), seed bank samples are usually sieved or cleaned manually to remove bulbs, tubers, rhizomes, and other large vegetative propagules. Under undisturbed conditions, only the seeds present in the upper few centimeters of soil will germinate (Galinato and Van der Valk 1986). However, if soil from a wetland is used to establish a wetland in another area, viable seeds buried at greater depths can be utilized. Viable seeds may be found at considerable depths in the soil (Van der Valk and Davis 1979), but not all wetlands contain subsurface seedbanks.

There are two approaches to estimating the composition of a seed bank: mechanical separation of seeds and seedling emergence. Mechanical separation involves passing a soil sample through a series of sieves. Seedling emergence involves placing the soil sample under conditions suitable for seed germination and counting the number of seedlings that emerge. Mechanical separation is tedious, requires more labor, and may require additional work to determine if extracted seeds are viable. Its major advantage is that data can be obtained quickly after a sample is collected. Seedling emergence techniques require usually 2 or more months to complete. They also require a greenhouse or similar shelter. Biased data are produced because samples can be exposed to only a limited number of environmental conditions during a seedling emergence study, and this will favor the germination of seeds of some species over others. Often seeds of some species may not germinate at all because the seeds remain dormant (Van der Valk and Davis 1978). This may be due to innate dormancy (the embryo is still immature) or enforced dormancy (the proper environmental conditions to break dormancy have not been supplied; Fenner 1985). Differential germination can be an advantage if field conditions, such as soil moisture present during restoration or wetland creation, can be simulated during the seedling emergence trial. By simulating field conditions, a more accurate prediction of field recruitment patterns can be obtained than is possible from mechanical separation data. Practical details for both techniques are found in Roberts (1981) and in the references cited therein.

One of the most troublesome aspects of seed bank sampling is the design of a sampling scheme. Seeds in the soil typically have a clustered distribution. Since most wetland seeds float, their distribution is affected by water-level fluctuations and currents. In wetlands with more stable water levels, seeds often become windrowed along the shoreline (Pederson and Van der Valk 1984). In wetlands with seasonal and interannual water-level fluctuations, seeds may be more evenly dispersed over the entire wetland than the distributions of their parent populations would indicate (Van der Valk and Davis 1976). To improve the precision of seed density estimates, it is best to (1) take randomly a large number of small samples, or to (2)

subdivide a site and take many small subsamples that are then combined into one sample for each area (Bigwood and Inouye 1988). The latter is more practical since it reduces the number of samples to be processed to a minimum. A study by Pederson (1983) estimated that in a 3 m x 3 m area, 38 to 199 samples of 400 cm² (17 to 88% of the surface area) would need to be sampled to estimate seed density per unit area for the four most abundant species to within 10% of the mean. Seed bank studies inevitably have too few samples. Usually the upper limit on the number of seed bank samples is set by either labor available to process samples if mechanical separation techniques are used or available greenhouse space if seedling emergence techniques are used.

For most restoration and creation projects, a precise estimate of seed density for a particular species in the seed bank is not needed. An estimate of the relative abundance of species is usually sufficient. Even a list of species present in the seed bank is enough to establish which desirable and undesirable species are present or absent. A species-area curve can be used to determine the completeness of a species list (Forcella 1984). With the data provided by a seed bank study, environmental conditions can be manipulated during a restoration to ensure the establishment of desirable species and to suppress undesirable ones. Such data also allow selection of suitable wetlands as sources of donor soils for creation projects.

Wetland Restoration and Creation

Vestigial seed banks have been used to restore former wetlands. The best candidates for this approach are freshwater wetlands that had significant daily, seasonal or interannual water-level fluctuations and that have been recently drained or overgrown by undesirable species. We are aware of only four seed-bank studies that have been done in conjunction with completed or proposed restoration projects.

In the Netherlands, an investigation of seed banks of floating forests revealed that they still contained seeds of many fen species and that recruitment from the seed bank could play a significant role in re-establishing fens in cleared forested areas (Van der Valk and Verhoeven 1988). Likewise, montane wet mea-

dows in Germany that have been converted to forage meadows still contain seeds of meadow species that could be used to restore them to wet meadows (Pfadenhauer and Maas 1987). The seed bank alone, however, will not be sufficient to re-establish all the species formerly present.

Only in India has the actual effectiveness of a vestigial seed bank in restoring the previous vegetation been examined. The wetlands of the Keoladeo National Park were overgrown by *Paspalum distichum* after all grazers were removed from the park in 1981. In 1984, the seed bank of a section of the park (L-block) dominated by *P. distichum* was examined using a seedling emergence technique (Table 1). During the summer of 1985 when there was no standing water, an area in L-block was bulldozed to a depth of only a few centimeters to remove the *Paspalum*. Re-vegetation in this cleared area was monitored from December 1985 to September 1986 (Table 1). The seed bank contained species that were characteristic of both the flooded (*Lemna perpusilla*, *Najas* spp., *Nymphaea* spp., *Nymphoides cristata*, *Hydrilla verticillata*) and drawdown (*Sporobolus helvolus*, *Hemiodelphus polyspermus*) phases of the pre-1981 vegetation. Of the 11 species that had seeds in the seed bank with a mean density of 1 seed m⁻² or

higher, 8 species were detected in the vegetation in March and/or July 1986. One of the remaining three species, *Nymphaea*, was found later in the fall of 1986. The vegetation of the cleared area was recruited primarily from the vestigial seed bank, and the composition of the restored vegetation was similar to the composition of the pre-1981 vegetation of this area (Davis and Van der Valk 1988).

The seed banks of drained prairie potholes in the north-central United States have been examined to determine how long seeds remain viable after drainage (Wienhold and Van der Valk 1989). Seed banks of potholes drained and cultivated for less than 20 years generally contained sufficient numbers of species and adequate seed densities of wetland species that their seed banks could be utilized for restoring wetland vegetation (Fig. 1). Seed banks of wetlands drained 70 years previously still contained viable seeds of a few wetland species. How long seeds of wetland species remain viable in vestigial seed banks ultimately determines the extent to which this restoration technique can be used for different types of former wetlands. Unfortunately, vestigial seed banks of most wetland types have never been examined.

Creation of wetlands using donor seed banks has only recently been attempted. It is done by covering the area where a wetland is to be created with a layer of topsoil from an existing wetland. A wetland can be established quickly if the area has been appropriately contoured and is hydrologically suitable. The new vegetation has a greater diversity of species, and usually more uniform and dense populations of these species, than if other techniques (planting, natural revegetation) had been used (Dunn and Best 1984). In experimental studies of wetland creation, there is consistently, a significant difference in the total cover of vegetation between areas with and without donor soils. For example, in a Florida restoration project, Dunn and Best (1984) reported that areas with donor soils had 100% cover while other areas had only 30%. This rapid revegetation is comparable to what happens in wetlands after a disturbance has eliminated the previous vegetation (Van der Valk and Davis 1978; Welling *et al.* 1988a, b). Stockpiling soils before they are used in a restoration can negatively influence recruitments in two ways. Short-lived viable seeds may be lost if the soil is held too long, and en-

Table 1. Seed densities of major species in the seed bank of areas dominated by *Paspalum distichum* in 1984 and mean cover (%) of these species in March and July 1986 in areas cleared of *P. distichum* in 1985 in L-block of the Keoladeo National Park, India. Data taken from Davis and Van der Valk (1988).

Species	Seed bank (seeds m ⁻²)	Vegetation (% cover)	
		March	July
<i>Lemna perpusilla</i>	431.0	0.3	<0.5
<i>Najas graminea/indica</i> ¹	357.0	7.7	0.4
<i>Paspalum distichum</i>	278.7	<0.5	4.1
<i>Nymphaea stellata/nouchali</i> ¹	79.9	–	–
<i>Cyperus alopecuroides</i>	38.7	0.1	0.1
<i>Sporobolus helvolus</i>	25.9	–	1.3
<i>Paspalidium punctatum</i>	13.9	<0.5	0.8
<i>Nymphoides cristata</i>	4.5	28.6	1.8
<i>Vallisneria spiralis</i>	4.5	–	–
<i>Hydrilla verticillata</i>	2.8	3.3	3.9
<i>Hemiodelphus polyspermus</i>	1.2	–	–

¹ Both taxa present, but seedlings could not always be assigned unambiguously to a taxon.

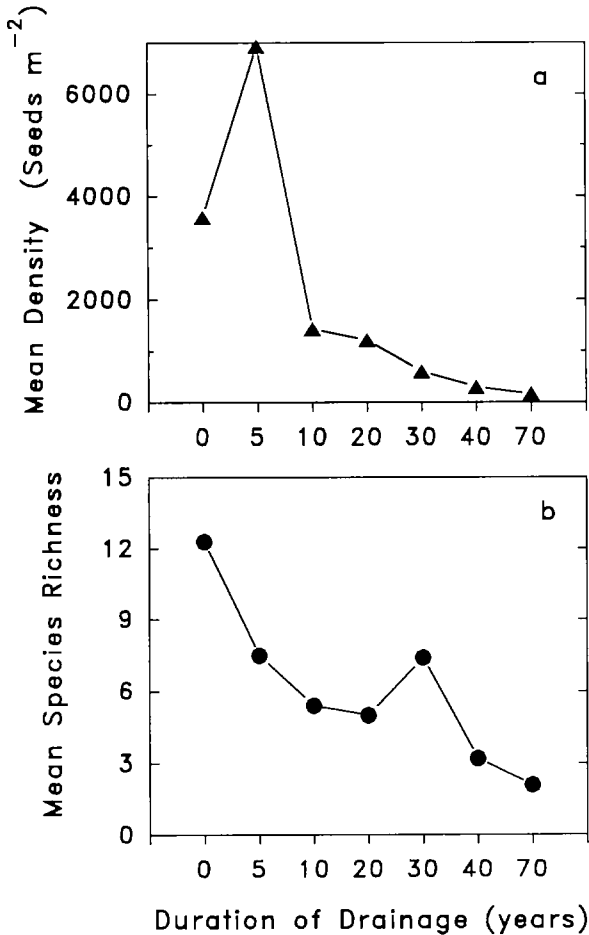


Figure 1. Mean seed density (seeds m⁻²) and mean species richness in surface soil samples from existing (0 yr) and drained prairie pot-holes in Iowa, Minnesota, and North Dakota. Adapted from Wienhold and Van der Valk (1989).

environmental conditions, particularly temperatures, in the stockpiled soil may be so unfavorable that seeds are killed.

One major problem with the use of donor seed banks is the absence of seeds of desirable species. Studies by Dunn and Best (1984) and Brown and Odum (1985) using donor soil to create wetlands in mined areas in Florida found that vegetation recruited from donor seed banks contained annuals and perennials associated with mudflats, but few desirable species (aquatic trees, shrubs, emergents, submersed or floating-leaved species). Seed bank studies from other parts of the world indicate that this is not a universal problem (Leck 1989). Nevertheless, it is

unlikely that all species of a wetland will have long-lived seed. It is unclear from the Florida studies, however, whether the lack of establishment of desirable species was due solely to the absence of seed in donor soils or due to unsuitable conditions for germination.

Another potential problem with using donor seed banks is the presence of seeds of unwanted species. Examination of the seed banks of four potential donor wetlands for a wetland creation project in Lake County, Illinois, indicated that seeds of undesirable species such as *Lythrum salicaria*, *Phalaris arundinacea*, and *Typha* spp. were much more widespread in the seed banks of these wetlands than vegetation sampling had indicated. For example, seeds of *L. salicaria* were found in seed bank samples from areas where there were no extant populations of this species (Nugteren and Van der Valk, pers. comm.).

Environmental Conditions and Recruitment

Even wetland species with the same growth form often do not have the same, or even similar, seed germination requirements (Galinato and Van der Valk 1986). How much conditions during periods of seedling recruitment can influence a restoration or creation project is largely unknown, but available evidence suggests that it may be considerable.

The effects of soil moisture regime on recruitment of species from the seed bank during a drawdown were studied using a composite seed bank from the Delta Marsh, Manitoba, Canada (Pederson, pers. comm.). The composite seed bank was made from soil samples collected in several vegetation types. All roots, rhizomes, and tubers were removed manually from the sample and it was thoroughly mixed. Samples from this homogenized, composite seed bank were exposed to five different soil moisture regimes in a greenhouse: shallowly flooded (FL); saturated (SA); watered every day (W1); watered every other day (W2); and watered every third day (W3) over the growing season.

Eight species were found consistently in this seed bank (Table 2): three annuals, *Aster laurentianus*, *Atriplex patula*, and *Chenopodium rubrum*; three wet-meadow species, *Carex atherodes*, *Scirpus mari-*

Table 2. Mean number of seedlings (per tray) of the most abundant species recruited from a composite seed bank from the Delta Marsh, Manitoba, Canada, under five soil moisture regimes. The soil moisture regimes were shallowly flooded (FL), saturated soil (SA), watered every day (W1), watered every other day (W2), and watered every third day (W3). Data from an unpublished study of R.L. Pederson.

Species	Soil moisture regime				
	FL	SA	W1	W2	W3
<i>Aster laurentianus</i>	24	82	115	91	16
<i>Atriplex patula</i>	0	7	8	5	5
<i>Chenopodium rubrum</i>	0	123	95	68	52
<i>Carex atherodes</i>	0	2	7	4	3
<i>Hordeum jubatum</i>	0	1	3	4	2
<i>Scirpus maritimus</i>	1	6	2	1	0.3
<i>Typha glauca</i>	153	189	102	20	0
<i>Scirpus lacustris</i>	20	20	14	8	0.2
Total	198	430	346	201	78.5

timus, and *Hordeum jubatum*; and two emergents, *Typha glauca* and *Scirpus lacustris*. Both the total number of seeds (Table 2) that germinated and the percent germination (Fig. 2) of each species varied with moisture regime. When the seed bank samples were shallowly flooded, seedlings of emergents predominated (87% of all seedlings). In seed bank samples watered every third day, emergent seedlings represented only 0.3% of the total (Fig. 2). These results were consistent with field studies of drawdowns in the Delta Marsh. Seedling density of emergents was highest where soil moisture was highest, whereas seedling density of annuals was highest where soil moisture was lower (Welling *et al.* 1988 a, b).

A study of seed germination and field emergence of four annuals that dominate mudflats in the Mingo National Wildlife Refuge in southern Missouri, U.S.A., also demonstrated that soil moisture regimes can affect seedling recruitment (Naim 1987; Van der Valk and Pederson 1989). The results of this study indicate that there are enough differences in the optimal soil moisture level required for seed germination among species that it is possible to manipulate soil moisture in the field to favor the germination of desirable species (*Polygonum hydropiperoides*, *Eleocharis ovata*, and *Echinochloa crusgalli*) and to suppress that of an undesirable one (*Xanthium strumarium*).

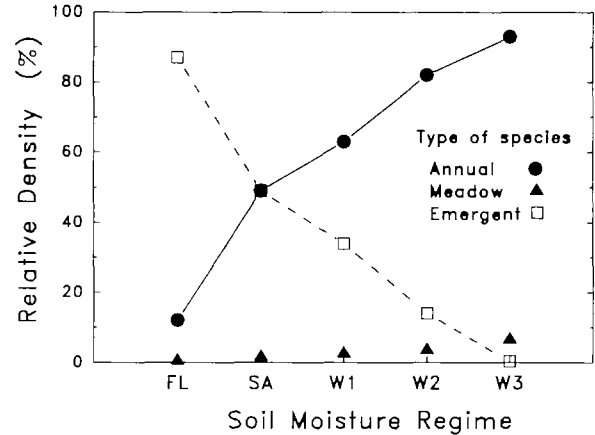


Figure 2. Relative density (%) of annual, meadow, and emergent species in vegetation recruited from a composite seed bank from the Delta Marsh, Canada, under 5 different moisture regimes: FL - shallowly flooded; SA - saturated soil; W1 - watered every day; W2 - water every other day; and W3 - watered every third day. Data from an unpublished study of R.L. Pederson.

Conclusions

Since seed banks are a feature of many types of wetlands, it is sometimes feasible to exploit vestigial seed banks to restore former wetlands, particularly drained wetlands or wetlands overgrown with an undesirable species. New wetlands can also be established rapidly in areas with the appropriate hydrology by covering them with a layer of soil from a nearby wetland with a suitable seed bank. The feasibility of exploiting a seed bank in a given situation should be determined prior to initiating a project. Examination of the composition of the seed bank to be used is important, because seed banks may contain seeds of unwanted species or lack seeds of desirable species. Environmental conditions (soil moisture, temperature and salinity in particular) can greatly influence recruitment from the seed bank, and the success or failure of a project can depend as much on environmental conditions as on the composition of the seed bank. The exploitation of seed banks for wetland restoration and creation has much potential, but it has just begun. A great deal of work is still needed to establish when this is an appropriate approach and how to do it successfully.

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